Biodiversity Research in the Horn of Africa Region

Proceedings of the Third International Symposium on the Flora of Ethiopia and Eritrea at the Carlsberg Academy, Copenhagen, August 25-27, 1999

Edited by IB FRIIS *and* OLOF RYDING

Biologiske Skrifter **54**

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Synopsis

This is the published proceedings of *The Third International Symposium on the Flora of Ethiopia and Eritrea and its relationship to adjacent Floras* held at the Carlsberg Academy on August 25-27, 1999. It contains 26 contributions by 35 scientists from Africa, Arabia, Europe and USA. The papers address a range of questions relevant to the Ethiopian and Eritrean flora, as well as a number of related subjects. Volume 2(2) of this Flora, covering the families Canellaceae to Euphorbiaceae, had been published in 1995. Volume 7 on Poaceae was also published in 1995. Volume 6 on the Monocotyledons (except Poaceae) was published in 1997. Volume 2(1) on the families Annonaceae to Flacourtiaceae appeared in 2000. Currently, two volumes on sympetalous Dicotyledones are in progress. These proceedings present taxonomic case studies on Callitrichaceae, Portulacaceae, Asteraceae and Pedaliaceae, a review of the orchid flora of the Flora area, and identification of an ignored scientific name for a plant described from Ethiopia. Historical reviews analyse the progress of the Flora project and the study of the plants of Ethiopia and Eritrea since the 18th Century. The nomenclatural consequences of the correct identity of Lamiaceae proposed by R. Muschler are surveyed; they are relevant to volume 5 of the Flora. New contributions to the flora of Southern Yemen emphasise the relationship between the floras of both sides of the Red Sea and the Gulf of Aden. Analyses of data from the hitherto published volumes of the Flora of Ethiopia and Eritrea point out centres of diversity and endemism of the region. More detailed papers deal with the phytogeography of recently treated families, *e.g.* Cyperaceae, Commelinaceae, lilioid geophytes ("Liliiflorae"), and the genus *Aloë* (Aloaceae). Analyses of diversity and endemism in the birds of the region show interesting parallels with patterns found in plants. A study of Ethiopian homegardens points out the importance of these for conservation of traditionally grown species and cultivars; there are close relations between the cultivated flora and the indigenous species, especially in the forest region of southwestern Ethiopia. This relationship is studied in detail in enset (*Ensete ventricosum*; Musaceae), an important food plant in southern Ethiopia. A review of plant materials used in traditional Ethiopian handicrafts shows a wide variety of species used, but many traditional materials are now being replaced with synthetic materials. Three papers deal with vegetation, one with degraded bushland of the Adwa region in northern Ethiopia, another with the vegetation of the high Semien Mountains in north-central Ethiopia, and one with the Sudanian dry forests, woodlands and wooded grasslands of the lowlands in western Ethiopia. A study deals with the seeds of grasses in the soil seed banks of the same area. A review paper points out that many features on the vegetation maps hitherto published for Ethiopia and Eritrea do not agree, particularly with regard to the vegetation on the Ethiopian Highlands.

Ib Friis
Botanical Museum and Library
University of Copenhagen
Gothersgade 130
DK-1123 Copenhagen K
Denmark

Olof Ryding
Botanical Museum and Library
University of Copenhagen
Gothersgade 130
DK-1123 Copenhagen K
Denmark

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Three symposia on the Flora of Ethiopia and Eritrea

Ib Friis

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Three symposia on the flora, plant geography, vegetation and other botanical aspects of north-eastern tropical Africa have been arranged since the Ethiopian Flora Project was initiated in 1980. The first, entitled *The First Ethiopian Flora Symposium*, was held at Uppsala University in 1984. The second, entitled *The Second International Symposium on the Flora of Ethiopia and Plants of Eastern and North-Eastern Africa and Southern Arabia*, was held at Addis Ababa University in 1986. These two universities are the places where the Flora of Ethiopia and Eritrea is edited and published. The third, entitled *The Third International Symposium on the Flora of Ethiopia and Eritrea and its relationship to adjacent Floras*, was held at the Carlsberg Academy in Copenhagen in 1999. This institution belongs to the Carlsberg Foundation, which has had traditional links with botany since its foundation in 1876 by J.C. Jacobsen. The Foundation has supported Danish botanical field work in Ethiopia since 1970. The main aim of the symposia has been to put in perspective new research that is related to work with the Ethiopian Flora Project, but can not be published within the rigid format of a modern scientific flora. The major features of the three symposia are described. Some events of importance to the Flora since the second symposium and some special features in association with the third symposium are also outlined.

Ib Friis, Botanical Museum and Library, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark. E-mail: ibf@bot.ku.dk

Introduction

The "Third International Symposium on the Flora of Ethiopia and Eritrea and its relationship to adjacent Floras" was held at the Carlsberg Academy in Copenhagen, 25-27 August 1999. It was with great pleasure that the organisers, Olof Ryding and myself, on behalf of the Editorial Committee of the Flora of Ethiopia and Eritrea, could welcome the participants to Copenhagen where we live and have our daily work. Nearly all the *c.* 35 scientists or students, coming from Ethiopia, Eritrea, Norway, Sweden, Germany, Denmark, United Kingdom and the U.S.A., have previously visited the Botanical Museum and Library in connection with their studies. Nevertheless, it was an exciting opportunity for all to meet for three days with the chance to discuss scientific and practical problems of joint interest in the secluded Carlsberg Academy.

The first Flora symposium in Uppsala

The tradition of organising Ethiopian Flora Symposia started with a symposium held in May 1984 at Uppsala University, Sweden, a few

years after the initiation of the Ethiopian Flora Project. Uppsala University was one of the two places where the Flora was to be edited and published. Dr. Inga Hedberg was, and still is, in charge of the Swedish editorial office. At the first Flora symposium there were papers on Ethiopian vegetation, physical geography and plant geography, in short, subjects which would benefit the forthcoming work with the Flora of Ethiopia. There were also a number of taxonomic papers, especially papers dealing with families relevant to Volume 3 of the *Flora of Ethiopia*, the first volume of the Flora to be published. These families were Fabaceae, Rosaceae, Umbelliferae, and Burseraceae. Other taxonomic papers dealt with families to be written up in future volumes, including Dioscoreaceae, Rubiaceae and Compositae. There were also studies of cultivated plants and their wild relatives, for example the natural populations of *Coffea arabica* in Ethiopian evergreen forests. The symposium lasted for 4 days, and about a year later 21 papers appeared in the Proceeding volume which was published in Uppsala in the series *Symbolae Botanicae Upsaliensis* and had the title "Research on the Ethiopian Flora. Proceedings of the First Ethiopian Flora Symposium held in Uppsala May 22-26, 1984" (Hedberg 1986).

The second Flora symposium in Addis Ababa

The second symposium took place two and a half years later in Addis Ababa, Ethiopia, in October 1986. It was held in the new building complex of the Faculty of Science at Addis Ababa University, a very appropriate place, as this complex is closely connected with the growing biological research in Ethiopia. Also, at Addis Ababa University the Flora was being edited and published, and the printed Flora volumes are in fact produced and bound by printers in that town. Ms. Sue Edwards was, and still is, in charge of the editorial office in Addis Ababa (although for some time in the 1980s the office moved to Asmara University).

The themes of the symposium in Addis Ababa resembled those of the Uppsala meeting. There were papers on Ethiopian vegetation studies, pollen analyses, a phytogeographical study of the family Brassicaceae, and a number of taxonomic papers about families in the Flora volumes that were in progress, such as Poaceae, Euphorbiaceae, and Tiliaceae. There were also papers on utilisation of forest products, medicinal plants, and plant conservation. This symposium lasted for three days, and 20 papers appeared in the volume of proceedings, which was published in Addis Ababa as a supplementary volume to *SINET – an Ethiopian Journal of Science*. The volume appeared more than three years after the symposium with the title "Proceedings of the Second International Symposium on the Flora of Ethiopia and Plants of Eastern and North-Eastern Africa and Southern Arabia." Although the proceedings of the second Flora symposium appeared approximately at the same time as the first published volume of the Flora of Ethiopia (Hedberg & Edwards 1989), they carried the year of the symposium on the title page (Mesfin Tadesse *et al.* 1986).

Ethiopia and Eritrea become independent states

The deterioration of the political situation in Ethiopia was undoubtedly one of the main reasons for delay in publication of the Addis proceedings. The increasingly untenable situation of the Ethiopian government also caused great difficulties for progress with editing and publication of the Flora. War between the Marxist Mengistu Wolde Mariam-regime and the guerrilla forces that were eventually to form the new governments of Ethiopia and Eritrea was extremely serious, and affected life for every-

one. I will just mention a few personal recollections, as I kept visiting Ethiopia during these years of conflict, and went with Ethiopian colleagues on field trips to the ever-diminishing parts of the country where one could safely move. Throughout the period of conflict, the southern and south-western part of the country remained reasonably accessible, but I vividly recollect some of the difficulties of travelling in those days. Travel permits, which took a long time to obtain, had to be presented everywhere to the often suspicious security officers.

Ethiopia suffered a severe shortage of everything during this period, including, of course, fuel and spare parts for cars, as the country's resources were being strained in order to fight the guerrillas. There was also a general fear that new armed confrontations might break out in parts that had hitherto been peaceful. But my memories from visits are of course nothing in comparison with how it must have been to live permanently under these conditions. It should not surprise anybody that we did not think of organising more Flora symposia during this period, but instead endeavoured to proceed with basic tasks in order to keep the Flora Project running.

My colleague Olof Ryding also has vivid memories of this period, when he was employed as a teacher at the University of Asmara (now in Eritrea). He left this post in 1990, and the whole Ethiopian staff at the university was evacuated to Addis Ababa, when the fighting around Asmara made the situation for the Mengistu regime untenable.

After these terrible years it was positive that there was no fighting in Addis Ababa during the ultimate phase of the fall of the Mengistu regime and the transition to the new government in May 1991. From 1992 onwards one could travel to parts of the country which had for many years been inaccessible, even to the border area with the newly established state of Eritrea. The first years after the change of government in Addis Ababa, and the Eritrean independence were full of activities during which we tried to cover previously inaccessible ground, and to recover lost time. A consequence of the political changes was also that the Flora from volume 7 and onwards changed its name to *The Flora of Ethiopia and Eritrea* (Edwards *et al.* 1995; Hedberg & Edwards 1995; Edwards *et al.* 1997).

The third Flora symposium in Copenhagen

The thought of a new Flora symposium did not seem such a luxury in the second half of the 90s as it did towards the end of the 1980s and in the early 1990s. A considerable amount of research had been carried out since the last symposium. New people had come into the group working with the Flora, and new plant families were being studied. One of the ideas behind the two first Ethiopian Flora symposia had been to compile data and review new research that could not be published within the rigid format of a modern scientific flora. There would be no lack of papers for a third symposium.

The notion of a third Flora symposium matured when the Carlsberg Foundation in October 1997 celebrated the inauguration of its new Carlsberg Academy as a place for small scientific meetings and symposia (Matthiessen 1998). This institution had been established in the large private home of the founder of the Carlsberg Foundation, J.C. Jacobsen, in the grounds of the Carlsberg Breweries. Jacobsen had built his home in the style of an Italian villa, and lived there from 1854 to his death in 1887. According to his wishes, the building was to be a place where prominent scientists, artists or politicians could meet. Jacobsen's will specified these ideas further. A prominent scientist or artist should have a residence of honour in

the building. After Jacobsen's death, the Foundation therefore made the fine building the home of a succession of outstanding Danish scientists, of which the best known is the prominent 20th Century physicist Niels Bohr, who received the Nobel Prize in physics in 1922 (Pedersen 1992). However, at the end of the 20th Century it was no longer possible for a scientist to employ the domestic staff necessary for living in such style. In 1997 the Foundation therefore decided that Jacobsen's intentions should be respected by establishing a place where scientific meetings and symposia in the sciences or humanities could be held.

The opportunity to have a Flora of Ethiopia and Eritrea-symposium in the new Carlsberg Academy was irresistible. We had never had an Ethiopian Flora symposium in Copenhagen, in spite of nearly 30 years Danish association with the flora of Ethiopia. Such a symposium would involve somewhere between 20 and 40 people, which would be the right number for the capacity of the Academy. Moreover, the Carlsberg Foundation had steadily supported field work of Danish botanists in Ethiopia since the contacts began in 1970. In December 1997 Sebsebe Demissew and I wrote a letter from Addis Ababa to the Board of Directors, and soon afterwards we received a positive reply, which resulted in us all being able to meet in Copenhagen in August 1999.

The sources of funds we solicited fortunately all reacted positively. The Council for Development Research under the Danish Ministry of Foreign Affairs granted the travel expensed for the Ethiopian and Eritrean participants. The Danish National Science Research Council, and the Niels Bohr-endowment under the Royal Danish Academy of Science and Letters supported the European and American participants. Finally the Carlsberg Foundation supported the arrangements at the Academy.

It has been a tradition that nearly all participants in these symposia gave presentations; we were very happy that this was also the case at the third symposium in Copenhagen. There were almost 30 presentations and posters, and 26 are represented in this volume of proceedings.

The scientific programme of this meeting was put together in the style of the two previous Flora symposia. The choice of subjects reflected the fact that the situation in 1999 was rather different from that of 1984 and 1986, and that it was now possible to produce review papers on the history of exploration, broader studies in phytogeography, vegetation, etc. The programme was approved at a meeting of the Editorial Committee of the Flora of Ethiopia and Eritrea in Addis Ababa in 1998. There were general papers, studies of vegetation, useful plants, phytogeography, especially two papers on the phytogeography of monocotyledons (a group which appeared in the two recently published volumes no. 6 and 7), history of the study of the flora, and a number of taxonomic studies of families in the pipeline for the coming Flora volumes, *e.g.* Pedaliaceae, Scrophulariaceae and Compositae.

As on previous occasions, we publish a volume of proceedings, this time with 26 papers by 35 authors and co-authors (some of which not present in Copenhagen). We have decided to name this volume *Biodiversity Research in the Horn of Africa Region. Proceedings of the Third International Symposium on the Flora of Ethiopia and Eritrea at Carlsberg Academy August 25-27, 1999.* We have chosen to shorten the formal part of the title by leaving out the words "and its relationship to adjacent Floras." The geographical scope of the papers is slightly wider than at the two previous symposia, reflecting that it is now possible to see the Ethiopian and Eritrean flora in a wider context. There is for example a paper on the flora of Yemen, and many papers touch on conditions in neighbouring countries, such as Sudan, Somalia and countries in East Africa (Fig. 1). We have

Fig. 1. The neighbouring countries of Ethiopia and Eritrea. In this symposium various combinations of these countries, or parts of them, are referred to as the Horn of Africa, and the whole area as the Horn of Africa region.

stressed the wider geographical scope in the first part of the title, as well as the presence of one paper on the geography of the birds of the region.

The Royal Danish Academy of Sciences and Letters, which is closely associated with the Carlsberg Foundation (the Academy elects the Board of Directors of among its own members), has kindly published the symposium volume in its series *Biologiske Skrifter* [Danish for "Biological monographs"].

Proceedings of symposia are published to make the papers known to colleagues world wide. However, the particular importance of publishing the proceedings of the Flora symposia was made obvious when I spoke to students and scientists at Addis Ababa University and elsewhere. For these students and scientists, working without the facilities of scientific libraries of Europe or America, it had been very useful to have so many papers dedicated to scientific study of Ethiopian and Eritrean plants in one easily accessible place as in the two previous volumes of proceedings from the Flora symposia. This will encourage research in the Horn of Africa region, and increase our

knowledge of the flora. We hope that this third volume of proceedings may supplement the two previous volumes well, also in this respect.

The Carlsberg Academy and botany

Because this symposium was held in the Carlsberg Academy, previously the home of J.C. Jacobsen, I will conclude by explaining the connection between Jacobsen, his home and garden, and an important event in the history of Danish botany. Jacobsen was interested in rare plants, and had in the 1860s, after his home had been built, developed beside it a large and beautiful garden planted with rare trees; now this is the garden of the Academy.

In 1870 Jacobsen was appointed member of a government committee for the planning of a new botanical garden at the University of Copenhagen, then the only university in Denmark. Jacobsen was a Member of Parliament, and in this capacity he was selected for the unusual post. He became chairman of the committee in 1871, and soon also chairman of the subcommittee for planning the buildings in the garden. Apart from Jacobsen, the committee consisted of the professors of botany, zoology, and geology, university administrators, and the head gardener of the old botanical garden. Jacobsen added to the committee two professional garden designers, not surprisingly those who had created his own garden at Carlsberg. He took part in the planning of most details in the new garden, drafted the first design for the new, large greenhouses, and later took a particular interest in their technical facilities. The new botanical garden of Copenhagen University was inaugurated in 1874 and still serves us well today. Jacobsen was awarded an honorary doctorate by the University at its 400 years jubilee in 1879. To receive the degree with justification, Jacobsen decided to write a thesis on his work connected with the new botanical garden, and produced an impressive folio volume on the design and technology of the greenhouses in the Copenhagen botanical garden (Christensen 1924-1926; Glamann 1991; Jacobsen & Rothe 1879; Ostenfeld 1924; Wagner 1990).

There is no doubt that the botanical establishments in Copenhagen would not have such good facilities today without Jacobsen's enthusiasm and influence. Lange (1876), director of the botanical garden, has summed up Jacobsen's achievements very well: "That the plan, except for the building of the Botanical Museum, could be carried out ... is more than anything else due to the energy, knowledge and burning interest in the matter which was shown by captain, brewer Jacobsen, who was elected chairman of the building committee, and for a period of three years directed the whole establishment ..."

Jacobsen's indirect significance for Danish botany, through the research grant from the Carlsberg Foundation, is too complex to trace here. Jacobsen established this foundation in 1876 as the future owner of his brewery. The foundation should secure a scientifically based administration of the production, and support basic research in the sciences and in the humanities, especially the study of history and languages (Glamann 1976, 1991).

As mentioned above, a large proportion of the Danish field work abroad, including nearly all our field work in Ethiopia through 30 years, has been supported by the Foundation. We hope and trust that our work on botany in Ethiopia would have met with Jacobsen's approval.

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Thirty years with the Ethiopian Flora project

INGA HEDBERG

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The Flora of Ethiopia project was launched in 1980 in collaboration between the National Herbarium, Addis Ababa University and the Department of Systematic Botany, Uppsala University. Requests for collaboration had, however, been made already in 1967, when also searching for funds was started from the Swedish side. This period is reviewed and the development of the project from its start on July 1st 1980 up to now is surveyed. Apart from producing a Flora the project also has included the training of Ethiopian students to a Ph.D. in Systematic Botany and strengthening of the infrastructure at the National Herbarium. The training component has been very successful. A number of collecting expeditions organised mainly from the University of Copenhagen and the National Herbarium have brought new and interesting material from various parts of Ethiopia, and the number of specimens at the National Herbarium has grown to over 70000. Botanists from many countries have contributed to the Flora, of which 4 volumes have been published and another two are in the pipeline. The remaining volumes are planned to appear before the end of 2001.

Inga Hedberg, Uppsala University, Evolutionary Biology Centre, Department of Systematic Botany, Norbyvägen 18D, SE-752 36 Uppsala, Sweden. E-mail: inga.hedberg@ebc.uu.se

Introduction

The first Ethiopian Flora symposium was held in Uppsala in 1984, the second one in Addis Ababa two and a half year later. It is therefore very timely to arrange the third symposium – this time with a slightly wider scope and – in view of the very important contributions made by Professor Ib Friis – to hold it in Copenhagen. As now almost 20 years have passed since the start of the Ethiopian Flora Project, I find it an excellent opportunity to survey the work from the Uppsala side during these years, as well as the years before the start. It is a rather informal presentation of the project as seen from my horizon, dealing with history and experiences, not with scientific results.

1967-1980

As already mentioned it is almost 20 years since the project was launched. To those years should, however, be added another 13 years, because Ethiopian requests for assistance with fundraising and manpower were made already in 1967. I will therefore first touch upon the pioneering phase between 1968 and 1980 and then briefly review the development of the project up to the present days.

A proper setting for the project is, I think, excellently given in the AETFAT bulletin 41 by Dr. J.J.F.E. de Wilde (1993) in his review of the first Flora volume published: "Contemplating in this DNA-era the enterprise of a conventional Flora certainly needs thinking twice. To

start a Flora for a country of the size and complexity of Ethiopia certainly requires a lot of courage …"

The need for courage was, however, nothing I anticipated when, in mid-December 1967, Olov Hedberg returned from a three and a half months stay in Ethiopia and East Africa, carrying *inter alia* a request by the Parks and Landscape Development and the Faculty of Science in Addis Ababa for assistance in finding the funds and manpower needed to produce a Flora of Ethiopia. Supported by hard arguments from various sources, *e.g.*, Brenan's "The value of Floras to underdeveloped countries" (Brenan 1963), and knowing that SAREC (Swedish Agency for Research Co-operation with Developing Countries) had a special interest in Africa, I felt that obtaining funds for such a laudable enterprise would be a fairly easy matter. – Little did I know!

To-day any application for a project closely inter-linked with biodiversity and conservation in a developing country would stand a fair chance of being positively received and evaluated. But 30 years ago the understanding for the need of a Flora was almost completely lacking, not only in SAREC, but also in a number of other organisations approached. Even if the DNA-era had only started its triumphal advance, it was quite obvious that the kind of work needed for a Flora was considered more or less out of date. What we managed to do was to obtain a small grant from a private foundation, which, however, didn't take us far.

At that stage the need of the fund hunters obviously became a question of optimism and tenacity rather than of courage, and in that spirit, parallel to the continuous fund hunting, more concrete planning for a Flora project was started. The most important discussions were held between Tewolde B.G. Egziabher, Professor and Dean of the Faculty of Science at Addis Ababa University, and Olov Hedberg, Associate Professor at the Botany Department, Uppsala University. The ongoing publication of the *Adumbratio Florae Aethiopicae*, by Professor Pichi Sermolli in Florence, and the fact that Professor H.C.D. de Wit in Wageningen was contemplating a more elaborate Flora of Ethiopia, called for some kind of agreement.

Therefore, an informal meeting was arranged in Florence in April 1968 between Professor Pichi Sermolli, Professor de Wit, Olov Hedberg and myself. Because of the urgent need to produce a complete (as far as possible) Flora of Ethiopia in the shortest possible time both Professor Pichi Sermolli and Professor de Wit gave their blessing to the enterprise. The AETFAT meeting in Munich in 1970 gave its moral support to the project, and a working committee as well as an advisory committee were formed. For reasons not known to me the question of fundraising was, however, entirely left with us in Uppsala.

As a preparation for the work on the Flora, and in order to secure an up to date checklist, requests were sent to a large number of specialists, working on various families occurring in the Flora area, asking if they would be willing to contribute to an updating of Richard's *Tentamen Florae Abyssinicae* (1847-1851). At that time, and for many years to come Roger Polhill at Kew gave us invaluable assistance – we could not have managed without him! Our request was very positively received and a number of our colleagues had already started their work when suddenly, in December 1979 Olov Hedberg was asked by SAREC to stop over in Addis Ababa to assist our Ethiopian colleagues with an application for funding of a Flora project. Such a project had been given high priority by ESTC (Ethiopian Science and Technology Commission), which obviously made SAREC reconsider the matter.

From then on things moved quickly. The formal proposal for a Flora of Ethiopia Project was submitted in early 1980 and SAREC decided in May that year to allocate funds from

July 1st. The application concerned an overall strengthening of taxonomic botany in Ethiopia and therefore included not only the production of a Flora but also training of Ethiopian students to a Ph.D. in Systematic Botany and the strengthening of the National Herbarium and its library. A Flora office should be created at the National Herbarium and a small "satellite" office at the Department of Systematic Botany in Uppsala. At the National Herbarium Sue Edwards, with a small staff, would handle incoming manuscripts and see to all the other new activities induced at the Herbarium by the project, whereas I, with a part-time assistant, would serve as co-editor as well as see about purchase of equipment for the National Herbarium and matters related to activities outside Ethiopia. Because of the shortage of Ethiopian expertise two European botanists with considerable experience of African botany, Mike Gilbert and Kaj Vollesen, were employed by the project as full time botanists based at Kew. The overall responsibility was given to the two initiators of the Project, Professors Tewolde and Hedberg.

It was at this stage that the need for courage became very obvious, because to "modern" scientists Flora work was considered less scientific, my own research demanded more time, and 13 years of fund hunting had taken its toll.

Furthermore Olov Hedberg had become Professor and Head of our department, which would give him much less time for the project and thus leave me with a responsibility much greater than I had anticipated. Hence my simple reaction to the message about funds was "I don't want to commit myself to a project, which will probably put an end to my own ongoing research and leave me with problems of a dimension that I can't foresee". However, I almost immediately realised that having been talking for so many years about the urgency and importance of a Flora of Ethiopia, I couldn't possibly withdraw when money at long last became available, and the fact that so many of my colleagues round the world had shown a great interest in the project was fundamental for my decision to accept.

1980-1999

Already from the start the time schedule for the entire Flora work caused some worry, since whereas the project leaders, aware of the dimension of our task, wanted to settle the frame for the project to 20 years, ESTC, on the contrary, did not want to give it more than 10 years, which, needless to say, would be far too short. To solve the problem 15 years was agreed upon, with a possibility of extension, should need be. Of course we all knew that this possibility would become a necessity – to produce a Flora of the size envisaged within less than 20 years would be quite impossible.

The launching of the project went like a dream, at least from the Uppsala side. Since, awaiting funding of the project, so many botanists had offered to contribute, those colleagues and others were asked if they would be willing to write up their respective family. As far as I can remember, hardly any one refused, which meant that already in the autumn of 1980 we had a fairly complete list of contributors for all families, and even manuscripts for a few small ones. But naturally the building up of a Flora office at the National Herbarium, planning for, finding and buying suitable equipment for the work both for the staff in Addis and for our work in Uppsala, took its time, as did also learning enough about the computer handling of manuscripts, and creating satisfactory routines for the co-operation between the two offices, and between them and the contributors.

Since no Ethiopian taxonomists were available, a training programme leading to a Ph.D. in Systematic Botany was elaborated. In October, 1980, Mesfin Tadesse came to Uppsala,

soon followed by Sebsebe Demissew, Ensermu Kelbessa and Zemede Asfaw. This part of the project was for us in Uppsala one of the most stimulating and uncomplicated parts of the project, but I certainly realise that living in a foreign country in an entirely different culture, spending long periods far from home, now and then must have caused our Ethiopian students considerable difficulties, though none of them complained. My own shortcomings in taking care of them in their leisure hours was a constant worry to me, but since I was working more or less round the clock I had practically no time for a social life, let alone for my own family. However, they were all very successful in their studies and it is good to know that through the project Ethiopia, as time went by, has been able to replace the two full time European botanists, employed from the start of the project, with its own taxonomists.

During the project period the number of specimens at the National Herbarium has grown considerably, from about 16000 to more than 70000. The credit for this should go to the National Herbarium and to a considerable extent to Professor Ib Friis, who, with funding from the Carlsberg Foundation and DANIDA, has organised a large number of collecting expeditions to various parts of Ethiopia.

The most time-consuming and expensive part of the project, the elaboration of a Flora, certainly would be worth a paper of its own. The choice of which volume to start on was easy: the importance of the legumes and the fact that they had already been dealt with by Mats Thulin (Thulin 1983) made Vol. 3, in which the family would appear, the most suitable to start on. Manuscripts for this and other volumes accumulated very fast. Hence the main problem was not, as a rule, late incoming manuscripts but rather the available time for checking and editing at the National Herbarium.

It would not be fair to state that the Flora work has been without complications, and there have been moments when I have regretted my decision to leave my own research to work mainly on that of others, which has also meant that I sometimes feel more of an administrator than a scientist. Some of the more difficult problems arose in early 1984 when the project leader and my co-editor had to move to Asmara. This meant that equipment, etc., had to be bought for a second office, causing expenses which were not budgeted for.

It was about the same time that SAREC for the first time hoisted a flag of warning. The Director General of SAREC paid a visit to us in Uppsala because he was worried about the future of the project. It had been going on for *more than three and a half years and nothing had yet been published!* He asked if he at least could have some proofs, since it was quite clear that not all SAREC Board members were convinced that an Ethiopian Flora project was a good project, on which SAREC should spend a considerable amount of money. However, we had at that stage not enough formatted material. Another six years were to pass before we saw the first volume published, but a very interesting fact is that, as far as I can remember, we had no serious trouble during that period in getting the funds required. However, in the early 1990's, when only one volume had been published, SAREC complained again. But then we had received an impressive amount of manuscripts, vols. 6 and 2(2) were well under way and a grass specialist, Sylvia Phillips, had been contracted to write Vol. 7, which would cover the grasses. By assigning the editing of that volume to us in Uppsala, the project was able to show satisfactory results in the form of three more volumes from 1995 to 1997. From the first of those volumes published, vol. 7, the title of the Flora, because of the independence of Eritrea in 1993, was altered to *Flora of Ethiopia and Eritrea.*

The need to finish the project within a time

span of fairly close to 20 years has made it desirable to assign the editing of another volume, vol. 4, to Uppsala, while Addis finishes the work on vol. 2(1). More detailed information on the project has been given in symposium proceedings and a number of reports from 1983 and onwards (*e.g.* I. Hedberg 1986, 1990, 1996; O. Hedberg 1983; Mesfin Tadesse 1988; Tewolde B.G. Egziabher 1991). In those papers accounts of the progress of the project are given, but most of them are far too optimistic about the time needed to complete each volume.

June 30th, the year 2000, marks the end of the period for the project as outlined by the project leaders in December 1979. With only one year to go we have four volumes published, two volumes more or less in the pipeline (vols. 2(1) and 4) and only two "real" Flora volumes left (vols. 5 and 1). It is quite clear that we will not see the complete Flora within the period envisaged at the start of the project. Being optimistic, I would say that an additional two years will be needed, and if we are able to present a complete Flora before the end of 2001 I think SAREC ought to be satisfied. After all, 22 years is not a long time for producing a Flora of a tropical area of the size of Ethiopia and Eritrea.

Looking back at the 19 years I have been working with the Ethiopian Flora Project I find that the only real problem, as we see it from the Swedish side, has been the time schedule. The co-operation between the National Herbarium and us in Uppsala, and between Uppsala and the large number of contributors, has been remarkably free from serious conflicts.

I would like to end this presentation by expressing my deep-felt thanks to Olov Hedberg for his everlasting support, and to all those colleagues, who not only have contributed to the Flora, but also demonstrated a considerable understanding and patience, and in difficult situations shown me a kindness far greater than I ever expected.

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Tropical African Callitriche – a neglected and taxonomically difficult part of an evolutionary extremely interesting family

Olov Hedberg & Inga Hedberg

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Adaptation to life in water has implied so drastic reductions in flower morphology that it has been difficult to revise the genus *Callitriche* and to trace the taxonomic affinity of the monogeneric family Callitrichaceae. Morphological differences between the six species of *Callitriche* from tropical Africa are few and sometimes difficult to discern. The most useful ones are found in fruit and leaf shape, and in petiole venation. Additional evidence is provided by chromosome numbers, but so far counts from three species only are available. Pollen data support the distinctions between the species and provide a clue to the taxonomic affinites of the genus. Keys for the species based on gross morphology and on pollen morphology, respectively, are given. Information from studies in European and North American material reveals interesting similarities in chromosome number and in pollen characteristics. Phylogenetic studies on North American species are briefly touched upon and the need for a worldwide revision of the small but difficult family is pointed out.

Olov Hedberg & Inga Hedberg, Evolutionary Biology Centre, Department of Systematic Botany, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden. E-mails: olov.hedberg@ebc.uu.se; inga.hedberg@ebc.uu.se

Introduction

The family Callitrichaceae with the single genus *Callitriche* comprises monoecious herbs with opposite, entire leaves and axillary flowers. Adaptation to shoreline or submerged conditions has implied so widegoing reductions in flower morphology that few taxonomically useful characters remain – it is even difficult to find its closest relatives in the angiosperm system. The flowers are very inconspicuous with no perianth, and consist of only one stamen in the male ones and one pistil with a two-lobed style in the female ones. They are either solitary or sometimes one male and one female together in the same leaf axil (Fig. 1). The stamens are usually very short but may elongate at maturation. The style-lobes are filiform, 1 to 4 mm long, and the fruit is a schizocarp, separating on maturity into two or four mericarps, which are winged, keeled or rounded.

The genus has an almost cosmopolitan distribution and is claimed to comprise from 17 species (Mabberley 1997) up to 50 (Philbrick 1994). It occurs in three different growth habits: terrestrial, amphibious and submerged, and is evolutionary interesting because of the

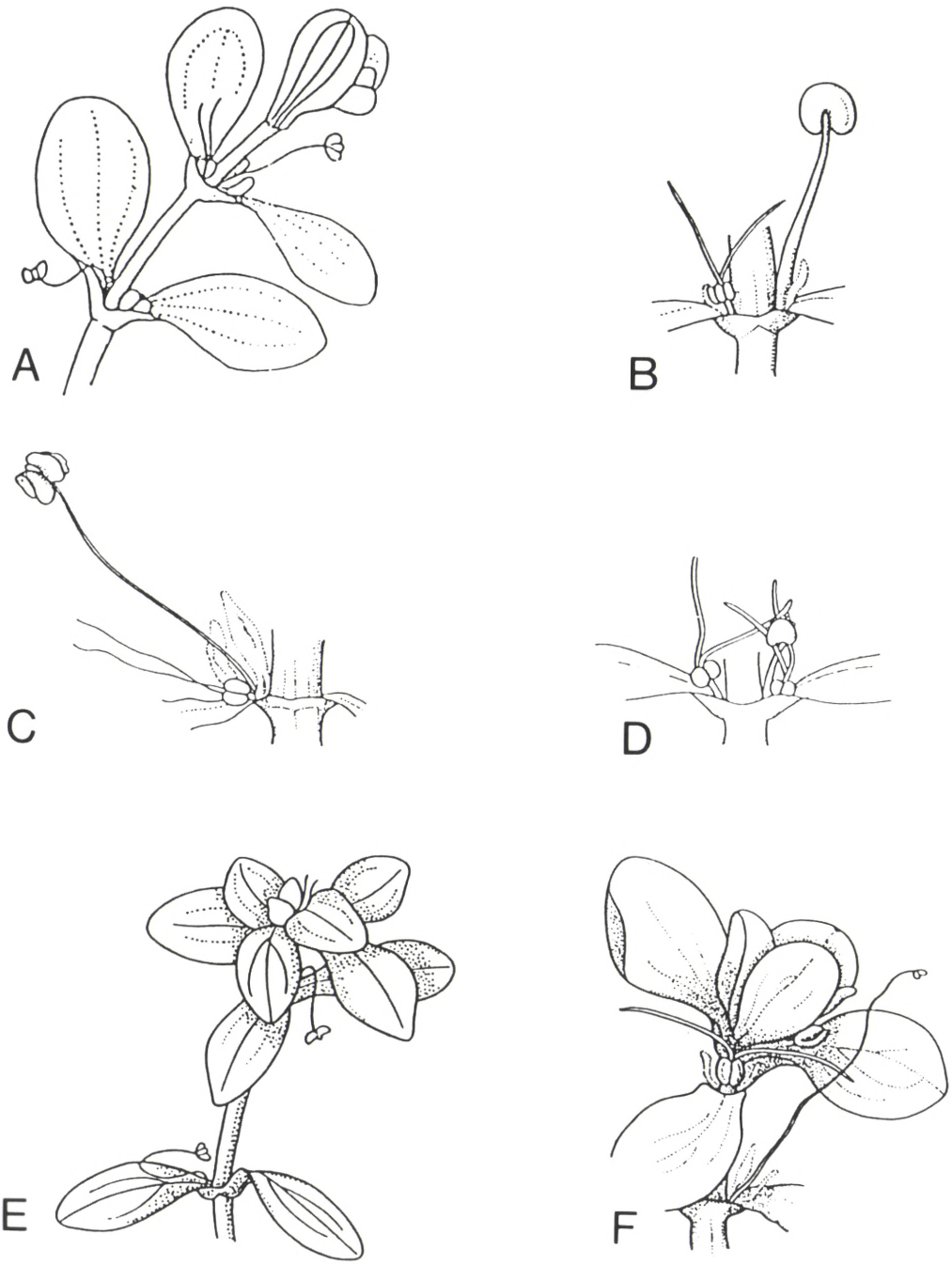

Fig. 1. Flower arrangements in Tropical East African *Callitriche*. **A**: *C. oreophila* (x 6). **B**: *C. anisoptera* (x 9). **C**: *C. keniensis* (x 8). **D**: *C. favargeri* (x 13). **E**: *C. vulcanicola* (x 4). **F**: *C. hedbergiorum* (x 7). A and E from Schotsman 1985 (Courtesy Bull. Jard. Bot. Nat. Belg.); B, C and F from Schotsman 1988 (Courtesy Birkhäuser Verlag AG); D from Schotsman 1984 (Courtesy Bull. Mus. Natl. Hist. Nat.)

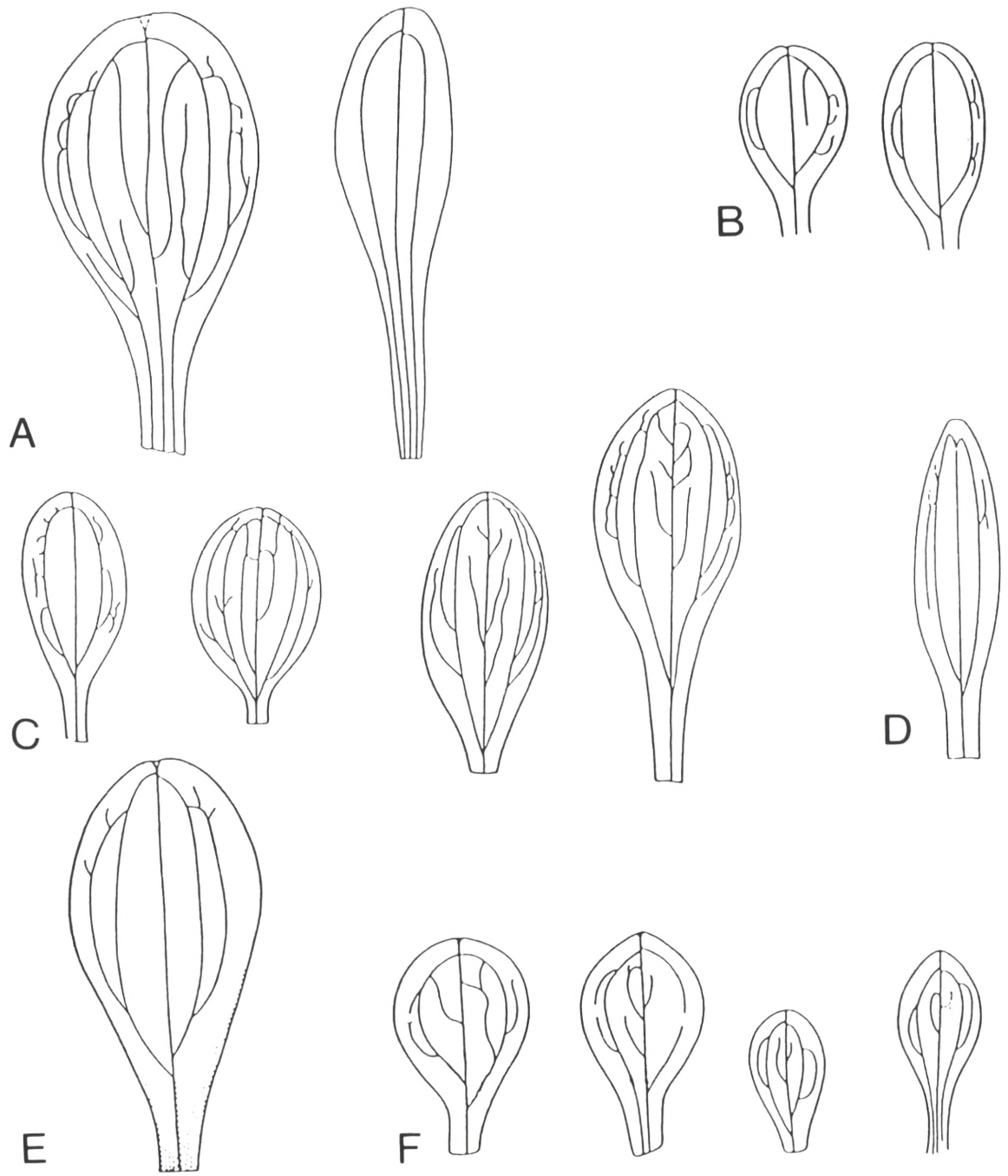

Fig. 2. Variation in leaf shape and venation in Tropical East African *Callitriche*. **A**: *C. oreophila* (x 7). **B**: *C. anisoptera* (x 6). **C**: *C. keniensis* (x 4). **D**: *C. favargeri* (x 10). **E**: *C. vulcanicola* (x 7). **F**: *C. hedbergiorum* (x 6). A and E from Schotsman 1985 (Courtesy Bull. Jard. Bot. Nat. Belg.); B, C and F from Schotsman 1988 (Courtesy Birkhäuser Verlag AG); D from Schotsman 1984 (Courtesy Bull. Mus. Natl. Hist. Nat.)

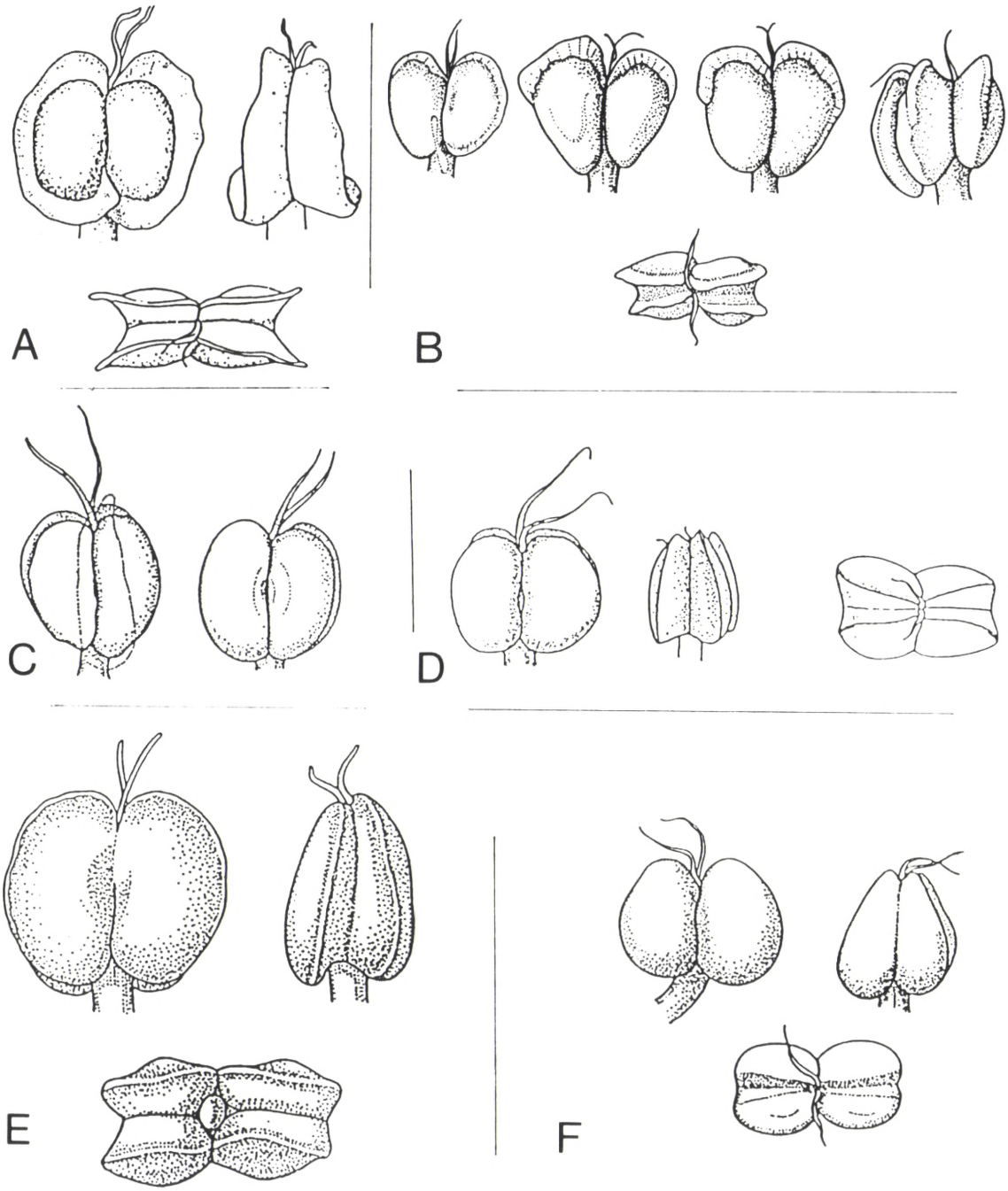

Fig. 3. Fruit shape (front view, side view and top view) in Tropical East African *Callitriche*. **A**: *C. oreophila* (x 15). **B**: *C. anisoptera* (x 15). **C**: *C. keniensis* (x 15). **D**: *C. favargeri* (x 20). **E**: *C. vulcanicola* (x 20). **F**: *C. hedbergiorum* (x 15). A and E from Schotsman 1985 (Courtesy Bull. Jard. Bot. Nat. Belg.); B, C and F from Schotsman 1988 (Courtesy Birkhäuser Verlag AG); D from Schotsman 1984 (Courtesy Bull. Mus. Natl. Hist. Nat.).

variation in pollination systems. It is, however, obvious that "taxonomic and logistic difficulties have dissuaded people from working in the Callitrichaceae" (Philbrick & Anderson 1992: 282).

Those difficulties have resulted in a rather meagre amount of herbarium material of African *Callitriche* available, a fact that became strikingly obvious to the senior author at an early stage in his work. Realizing the need for more material of the genus from tropical Africa he consequently put particular attention to it during his field-work, also collecting root tips for chromosome studies. This resulted in what appears to be the first chromosome studies in African *Callitriche* (Hedberg & Hedberg 1977) and yielded very interesting results: no less than three different somatic chromosome numbers were found in the collections.

Differences in ploidy between different populations have long been considered taxonomically important, and differences in basic chromosome number are usually deemed even more significant. Originally all indigenous Tropical East African material was classified as *Callitriche stagnalis* (*cp. e.g.* Hedberg 1957: 127), but Schotsman's studies of morphological differences, supported by our chromosome counts, made her describe six new species from Tropical Africa, viz. *Callitriche favargeri, C. oreophila, C. vulcanicola, C. anisoptera, C. hedbergiorum* and *C. keniensis* (Schotsman 1984, 1985, 1988). The distinctions between these species were not entirely apparent, however, and in order to prepare accounts for the Flora of Ethiopia and Eritrea and Flora of Tropical East Africa, we found it necessary to revise the material in greater detail. For this revision the following features were used: leaf and fruit morphology, chromosome numbers, and pollen morphology. The latter character was shown by Martinsson (1993) to provide useful distinctions in Scandinavian material of *Callitriche.*

Gross morphology

As to leaf morphology the shape of the lamina varies from lanceolate to spathulate, and the size is very variable. Shape and size are therefore difficult to use for taxonomic distinction, also because the infraspecific variation is considerable (Fig. 2), but the total length and the width of the leaves may sometimes be useful. Thus in *C. keniensis* the larger leaves are considerably longer than in all the other species, and in *C. favargeri* the leaves are narrower than in its closest relatives. The number of veins in the petiole, which is normally 1 or 3, seems to be the most reliable leaf feature.

A more rewarding set of characters is found in the fruits, separating at maturity into four mericarps (Fig. 3). In two of the species the mericarps are distinctly winged, symmetrically so in *Callitriche oreophila* (Fig. 3A) and asymmetrically in *C. anisoptera* (Fig. 3B). In three other species (*C. keniensis* (Fig. 3C), *C. favargeri* (Fig. 3D), and *C. vulcanicola* (Fig. 3E)) the mericarps are edged, and in the sixth one, *C. hedbergiorum* (Fig. 3F) they are evenly rounded.

Chromosome numbers

Counts in material from Europe (Schotsman 1967; Schotsman & Andreas 1980) and North America (Philbrick 1994) revealed considerable variation in chromosome numbers within *Callitriche,* with somatic numbers between 6 and 40 (*cp.* Table 1). The numbers obtained by the authors for three tropical African species fall well within the same range of variation. Thus 2n=10 was found in *C. favargeri*, 2n= 18 in *C. vulcanicola* and 2n=10 or 20 in *C. hedbergiorum.* In this connection it is interesting to note that the African *C. hedbergiorum* displays the same type of infraspecific polyploidy as *C. heterophylla* in North America.

Table 1. Somatic chromosome numbers in *Callitriche* L.

Taxon	2n	Origin	References
C. brutia	28	Europe	Schotsman 1967
C. cophocarpa	10	Europe	Schotsman 1967
C. favargeri	10	E. trop. Africa	Schotsman 1984
C. hamulata	38	Europe	Schotsman 1967
C. hedbergiorum	10, 20	E. trop. Africa	Schotsman 1988
C. hermafroditica	6	U.S.A.	Philbrick 1994
C. heterophylla var. *heterophylla*	20, 40	U.S.A.	Philbrick 1994
C. heterophylla var. *bolanderi*	20	Canada	Philbrick 1994
C. lusitanica	8	Europe	Schotsman 1967
C. marginata	20	Canada	Philbrick 1994
C. nuttallii	20	U.S.A.	Philbrick 1994
C. obtusangulata	10	Europe	Schotsman 1967
C. peploides	10	U.S.A.	Philbrick 1994
C. platycarpa	20	Europe	Schotsman 1967
C. pulchra	8	Europe	Martinsson 1991
C. stagnalis	10	Europe U.S.A.	Schotsman 1967 Philbrick 1994
C. terrestris	10	U.S.A.	Philbrick 1994
C. trochlearis	40	U.S.A.	Philbrick 1994
C. truncata subsp. *truncata*	6	Europe	Martinsson 1991
C. truncata subsp. *occidentalis*	6	Europe	Schotsman 1967
C. verna	20	Canada	Philbrick 1994
C. vulcanicola	18	Kenya	Unpublished, counted in *Hedberg* 5485

Pollen morphology

One of the most useful taxonomic characters is provided by the pollen. Studies of pollen morphology in *Callitriche* have earlier been published by Erdtman (1952), Martinsson (1993) and Osborn & Philbrick (1994). The exine surface displays a structure for which Erdtman (1952: 169, 173) coined the term *Croton* pattern: a reticulate pattern with processes (clavae) at the intersections of the walls (muri). This pattern was reported by Martinsson (1993) from three Swedish species and occurs in all the six species described from Tropical Africa. In the latter the differences between the species are large enough to be used for species discrimination (Fig. 4). The shape of the clava tops forms a series from *Callitriche anisoptera* over *C. favargeri* and *C. vulcanicola* to *C. oreophila*, *C. keniensis* and *C. hedbergiorum*. In *C. anisoptera* (Fig. 4B) the top of the clava is regularly rounded. In *C. favargeri* (Fig. 4D) the top has distinct angles but a more or less flat and smooth surface. In *C. vulcanicola* (Fig. 4E) the top has distinct angles and a flat

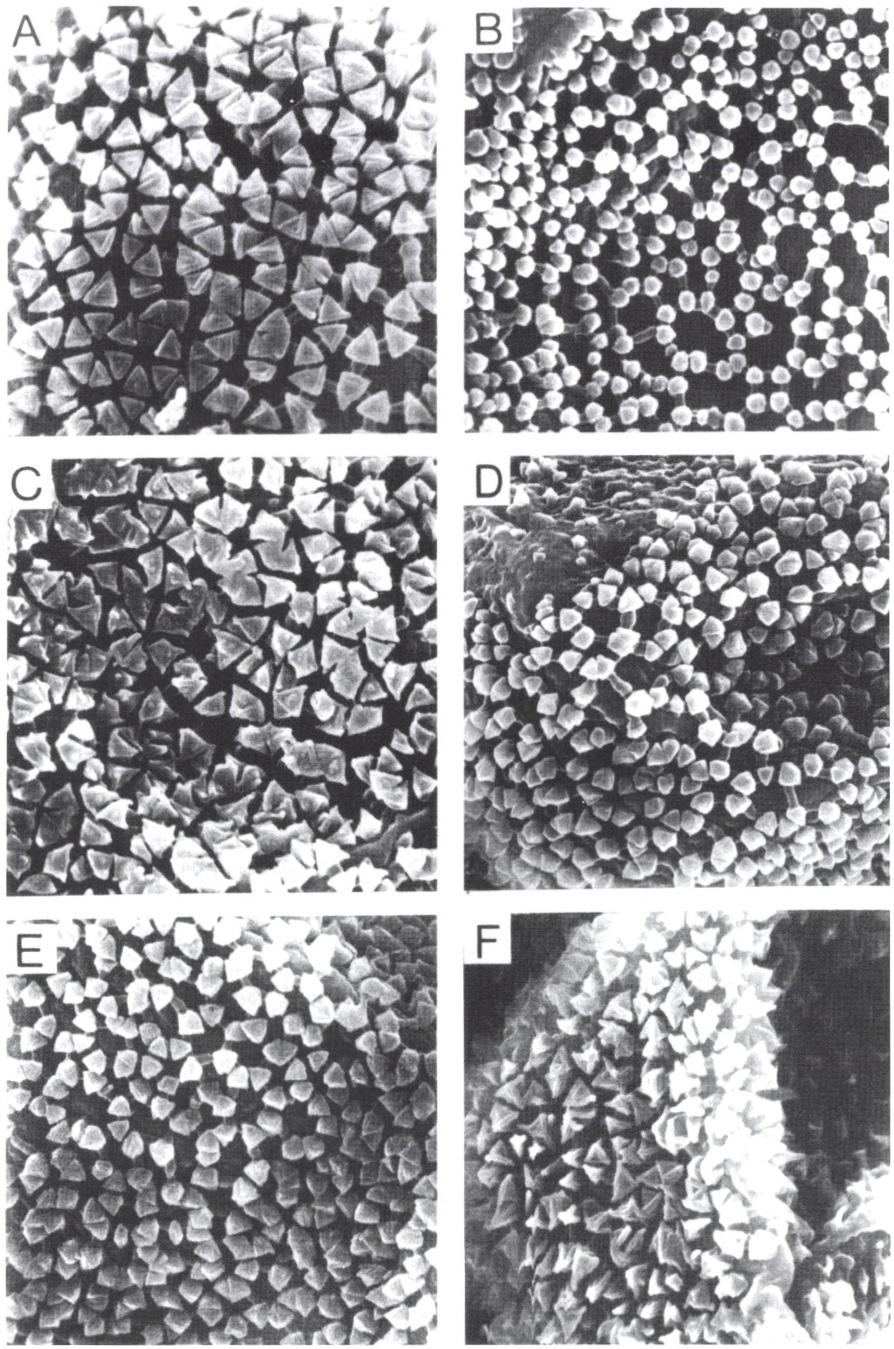

Fig. 4. Exine surface of pollen grains in Tropical East African *Callitriche*. **A**: *C. oreophila*. **B**: *C. anisoptera*. **C**: *C. keniensis*. **D**: *C. favargeri*. **E**: *C. vulcanicola*. **F**: *C. hedbergiorum*. Scale in A-E x 10,000; in F x 13,000. Voucher specimens for A: *Eriksson* 623 (UPS), for B: *Hedberg* 398 (type, UPS), for C: *Paolo* 997 (isotype K), for D: *Friis et al.* 5631 (C), for E: *Hedberg* 4403 (UPS), for F: *Hedberg & Aweke* 5485 (UPS).

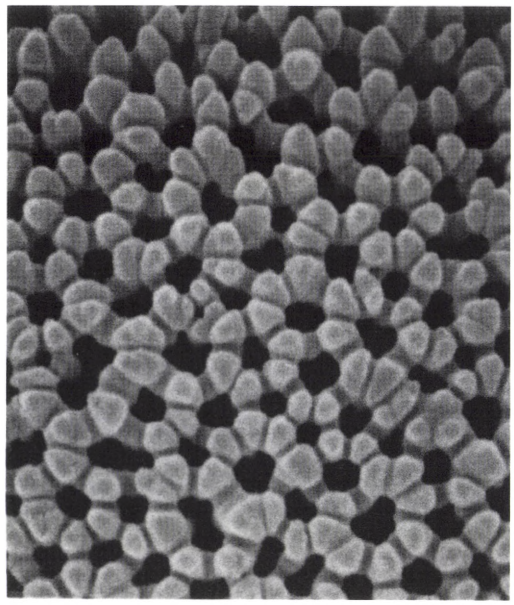

Fig. 5. *Croton* pattern in exine surface of pollen in *Bartsia longiflora* subsp. *macrophylla*. SEM photo x 10,000. (From O. Hedberg *et al.* 1979).

and scabrid surface. In *C. oreophila* (Fig. 4A) most tops are regularly triangular with broken surface. In *C. keniensis* (Fig. 4C) the top is irregularly triangular with a central papilla. In *C. hedbergiorum* finally (Fig. 4F), most tops are irregularly triangular without a central papilla.

A *Croton* pattern, resembling that in *Callitriche favargeri*, was described for *C. marginata* and *C. stagnalis* in Osborn & Philbrick (1994: 262) as well as in Philbrick & Osborn (1994: Figs. 4 and 10). The virtual absence of an exine in the perennial form of the hypohydrophilous *C. hermaphroditica* was also described in both papers.

The width of the reticulum meshes furnishes an additional character for species delimitation. In *C. anisoptera* they are much wider than the clavae, in *C. favargeri* equal, and in the other species narrower than the clavae.

Systematics and evolution

Because of its strongly reduced flowers Callitrichaceae has not been easy to connect to other taxonomic groups. In earlier taxonomic literature the family has, for instance, been placed either near Haloragaceae or Euphorbiaceae and Verbenaceae (*cp. e.g.* Melchior 1964), or Plantaginaceae (Cronquist 1981).

According to a cladistic study performed by Olmstead & Reeves (1995) *Callitriche* and *Hippuris* form a strongly supported clade. These two together with *Antirrhinum, Digitalis, Veronica* and *Plantago* form a larger, equally well-supported, clade. On the base of these results the APG (1998) tentatively included *Callitriche* and *Hippuris* in the Plantaginaceae. However, the possibility to delimit an extended Plantaginaceae by morphological criteria remains to be tested. And the same *Croton* pattern, which is found in the pollen of Callitrichaceae occurs not only in *Bartsia* of the Scrophulariaceae (Fig. 5, *cp.* Hedberg *et al.* 1979, Fig. 3) but also in Euphorbiaceae.

Philbrick & Jansen (1991) conducted a detailed phylogenetic study of North American *Callitriche*, utilizing chloroplast DNA restriction fragment analysis, combined with several morphological characters. Their task was mared by

difficulties to find a functional outgroup and they finally selected species from the families Verbenaceae and Lamiaceae. They found *Callitriche hermaphroditica* basal to all other North American taxa, which formed two opposing clades. One Wagner parsimony analysis resulted in 5 equally parsimonius trees (of 78), and Doko analysis generated 8 trees. From these was derived a strict consensus tree which the authors suggest reflects the evolution within the group. Their result may obviously be useful for further studies, the results of which, however, may not necessarily confirm the clade structure presented.

Also because of the various types of pollination found within the family, Callitrichaceae offers very interesting evolutionary aspects. According to Philbrick & Andersson (1992: 282) *Callitriche* is outstanding in this respect, since it is the only genus in which aerial, water surface, and subsurface pollination systems have been recorded. They therefore consider that the Callitrichaceae could serve as a model system for understanding the nature of changes that occur during the evolution from aerial pollination systems to hydrophily. They made a good start by investigating in detail taxa occurring in North America north of Mexico. Of particular interest was the unique mode of self-fertilization developed in *C. palustris*, where the pollen germinates already within the anthers, with the pollen tubes growing through vegetative tissue and entering the ovary (internal geitonogamy, Philbrick 1984). The occurrence of underwater cross-pollination (hypohydrophily) in *C. hermaphroditica* has been assumed by several authors, but evidence for this has been rather circumstantial. Strong supporting evidence was, however, supplied by Philbrick (1993) through paternity exclusion analysis using random amplified polymorphic DNA markers.

For the African species little is known about the pollination, but according to Schotsman (1984) "pollination in *C. favargeri* is accomplished by contact between stigma and anther and seems to be mainly aerial". Further detailed pollination studies in African material would obviously be highly desirable.

Additional understanding of the breeding system in *Callitriche* might be obtained through studies of the pattern of intra- and interpopulational allozyme variation. Such analyses were, according to Philbrick & Anderson (1992) currently under way in 1992. We have, however, not been able to find a reference to any results from those studies.

Distribution

The *Callitriche* species of Tropical Africa are mainly concentrated to mountain areas. Two of them, *C. oreophila* and *C. vulcanicola* are rather widespread, whereas the four others have a very restricted distribution. For details, see below (Taxonomic synopsis).

Conclusion

From this short survey it is obvious that *Callitriche* offers some difficulties in species delimitation because of its very reduced flowers and the considerable variation in the vegetative parts. At the same time it offers extremely interesting problems from an evolutionary point of view, and should therefore be subjected to in-dept studies, preferably comprising the whole genus.

Taxonomic synopsis

Callitriche L. (1753). Type: *C. palustris* L.

Key to Tropical African species based on gross morphology

1. Fruits distinctly winged 2
– Fruits not winged 3
2. Wings symmetrical around the mericarp; petiole mostly 3-veined 1. *C. oreophila*

– Wings assymmetric; petioles at base 1-veined 2. *C. anisoptera*
3. Larger leaves at least 10 mm long, 5(-8)-veined 3. *C. keniensis*
– Larger leaves less than 10 mm long; usually 3-veined 4
4. Mericarps evenly rounded 4. *C. hedbergiorum*
– Mericarps edged 5
5. Leaves lanceolate, up to 2 mm wide 5. *C. favargeri*
– Leaves spathulate, at least 2.5 mm wide 6. *C. vulcanicola*

Key to species based on pollen morphology

1. Clavae tops regularly rounded, without angles 2. *C. anisoptera*
– Clavae tops with distinct angles 2
2. Clavae tops with more or less flat surface 3
– Clavae tops with uneven surface 4
3. Clavae tops with smooth surface 5. *C. favargeri*
– Clavae tops with scabrid surface 6. *C. vulcanicola*
4. Most clavae tops regularly triangular 1. *C. oreophila*
– Most clavae tops irregularly triangular 5
5. Clavae tops often with central papilla 3. C. *keniensis*
– Clavae tops without central papilla 4. *C. hedbergiorum*

1. ***C. oreophila*** Schotsman (1985).
Type: Rwanda, Gitovu, *Becquet* 780 (BR holotype).
C. stagnalis auct. non Scop. 1772

Stems 10-35 cm in water, or 3-20 cm on mud. All leaves with elliptic to spathulate, 3-7-veined blade and 3-veined petiole, up to 11 x 5 mm, but often much smaller. Flowers solitary, in the axiles of both submerged and floating or aerial leaves, bracteoles 2, falcate. Stamen at dehiscence 1-2 mm long, after dehiscence up to 7 mm; anther 0.5-0.6 mm. Style-lobes up to 2 mm long, erect or spreading. Fruit suborbicular, *c.* 1.6-1.8 x 1.6-2 mm, with distinctly winged mericarps. Reticulum meshes of the pollen surface not as wide as the clavae; the latter irregularly triangular with broken top surface. Chromosome number unknown. Evidently anemophilous. – Figs 1A, 2A, 3A, 4A.

On moist ground along streams and ponds, sometimes submerged, and in forest; 1150-3200 m. Ethiopia, Uganda, Kenya, Tanzania, Burundi and Cameroon.

2. ***C. anisoptera*** Schotsman (1988).
Type: Uganda, Ruwenzori, Bujuki valley near Bigo camp, *Hedberg 398* (BR holotype; BM, EA, K, UPS isotypes).
C. stagnalis auct. non Scop. 1772

Stem prostrate, mat-forming. Leaves spathulate with elliptic, 3-5-veined blade *c.* 4-6 x 2-2.5 mm and 1-veined petiole. Flowers solitary, the male ones with 2 narrow bracteoles, the female without or with 2 bracteoles. Stamen 2-6 mm long; anther *c.* 0.5 mm long. Style-lobes 1.5-3.5 mm. Fruit *c.* 1.3-1.5 x 1.6-1.8 mm, unequally and variously winged with better developed wing in the terminal part. Some reticulum meshes of the pollen grain surface more than twice as wide as the clavae; the latter with globular top. Chromosome number unknown. – Figs 1B, 2B, 3B, 4B.

On moist ground along streams or in bogs; 3450-4000 m. Uganda and Zaire: Ruwenzori.

3. ***C. keniensis*** Schotsman (1988).
Type: Kenya, Murua Nysigar, *Paulo* 977 (BR holotype; EA, K, PRE isotypes).
C. stagnalis auct. non Scop. 1772: Hedberg 1957: 127, p.p.

Robust aquatic plant; stems 30-40 cm long, 0.8-0.9 mm in diam., with sparse hairs. Leaf rosettes with 6-8(-10) leaves; rosette leaves

spathulate, with elliptic, 3-7-veined blade, 15-20 x 4-6 mm; petiole of the same length as blade or shorter, with a single vein. Flowers solitary, or staminate and pistillate forming an axillary pair, usually the opposite axils with a solitary flower and a pair of flowers; bracteoles 2, 1.5-2 x 0.6 mm. Staminate flower with erect stamen, at dehiscense *c.* 4 mm long; extending to 6.5 mm after dehiscence, occasionally recurving; anther 0.7-0.9 mm long. Pistillate flower subsessile, with erect or patent style-lobes, 2-3 mm long, persistent. Fruit subsessile, ellipsoid or rarely subglobose, 1.6-1.8 x 1.3-1.5 x 0.8-1 mm, with style remnants to 1 mm long, splits between mericarps shallow, mericarps obtuse, edged but not winged. Reticulum meshes of pollen surface not as wide as the clavae, the latter irregularly triangular with sharp angles and often carrying a central papilla. Chromosome number unknown. – Figs 1C, 2C, 3C, 4C.

In streams, ponds and bogs; 2150-4300 m. Endemic to Kenya (Elgon, Mt Kenya, Murua Nysigar Peak) and known from 6 collections only.

4. ***C. hedbergiorum*** Schotsman (1988).
Type: Ethiopia, Gonder, Simien, *O. Hedberg & Getachew Aweke* 5485 (UPS holotype).

C. stagnalis auct. non Scop. 1772; I. & O. Hedberg 1977: 5,6, 16, p.p.

Stems 5-25 cm. All leaves with elliptic, 3-5 veined blade, 4-6 x 2-3 mm, and 1-2(rarely 3)-veined petiole. Flowers solitary, bracteoles absent or 1-2, falcate. Stamen at dehiscence *c.* 1 mm long, after dehiscence up to 10 mm; anther 0.5-0.8 mm. Style-lobes up to 3 mm, first erect, later spreading. Fruit suborbicular, *c.* 1.3 x 1.6 mm, with rounded mericarps. Reticulum meshes of pollen not as wide as the clavae; the latter with triangular irregularly pyramidal top with broken surface. Chromosome number 2n=10 (*Hedberg* 5485); 2n=20 (*Hedberg* 5574). Probably anemophilous.
– Figs 1F, 2F, 3F, 4F.

More or less submerged in small streams; 3650-3950 m. Endemic to Ethiopia (Gonder and Bale regions) and known only from 2 collections.

5. ***C. favargeri*** Schotsman (1984).
Type: Ethiopia, Arsi, *Hedberg* 4234 (UPS holotype; ETH, K isotypes).

C. stagnalis auct. non Scop. 1772; I. & O. Hedberg, 1977: 5, 6, 16, p.p.

Stems to 35 cm long, submerged or terrestrial. Submerged leaves linear, up to 9 x 0.5-1 mm, 1-3-veined; aerial leaves lanceolate, up to 6.5 x 2 mm, 1-3-veined; petioles always 1-veined. Flowers on both submerged and aerial shoots, without bracteoles; most often one male flower in one leaf axil and one female – or one male and one female – in the opposite axil. Stamen short, *c.* 0.5 mm long before, and up to 1.3 mm after dehiscence; anther 0.3-0.4 mm. Style-lobes 1-1.5 mm. Fruit *c.* 1 mm long and 1.3 mm wide, with slightly edged mericarps. Reticulum meshes of pollen surface rarely as wide as the clavae; the latter with triangular, irregularly pyramidal top with smooth surface. Chromosome number 2n=10 (type collection). The species appears to be persistently autogamous. – Figs 1D, 2D, 3D, 4D.

In small streams and ponds in the afroalpine belt, 3800-4050 m. Ethiopia, Arsi and Bale Regions. Known only from 6 collections.

6. ***C. vulcanicola*** Schotsman (1985).
Type: Kenya, Mt Kenya, Burguret track, *Hedberg* 4403 (UPS holotype; BR, EA, K isotypes).

C. stagnalis auct. non Scop.1772: Hedberg 1957: 127, p.p.; I. & O. Hedberg 1977: 5, 6, 16, p.p.; Robyns 1958: 350.

Amphibious. Rosette leaves spathulate, 5-12 x 2-5 mm, blade elliptic-rhomboid, with 3-5 main veins; petiole 1-veined, shorter than the blade. Flowers solitary, the male ones with 1 or 2 bracteoles, 1-1.3 x 0.1-0.2 mm. Ripe stamen

erect, 2-3 mm long, after flowering increasing up to 8 mm; anther 0.7-1 mm long. Female flowers usually without bracteoles; style-lobes at first erect, 1.5-2 mm long. Fruit wider than long, 1.2-1.5 x 1.6-2.2 mm. Mericarps keeled. Some reticulum meshes of the pollen surface as wide as the clavae, which are obtusely triangular, almost flat, with scabrid surface. Chromosome number 2n=18. – Figs 1E, 2E, 3E, 4E.

In pools, on moist ground along streams, and in flushed grassland; 3000-4000 m. Uganda, Kenya, Rwanda and Zaire.

Note

One collection from East Africa of a seventh species, *C. deflexa* A. Br. ex Hegelm., was found in the Kew Herbarium (Tanzania, Kilimanjaro Coffee Research Station, Lyamungu, 22.7. 1967, *Bigger* 1236). This is, however, an introduction of a South African species occurring as a weed also in Portugal, Morocco and the Azores, and it has no close relation to the Tropical African species treated here.

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Species delimitation in Portulaca sect. Portulaca (Portulacaceae) in East and Northeast Tropical Africa

Sylvia M. Phillips

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Twenty three species are recognised in *Portulaca* sect. *Portulaca* from East and Northeast Tropical Africa. The reliability of the characters used to distinguish them is assessed, especially with reference to the works of Peter and von Poellnitz, and with the use of examples from the area. Distribution patterns and habitat preferences are discussed. The morphology of the seed testa is described for each species, and most are illustrated by means of SEM photographs. A key to the species is provided.

Sylvia M. Phillips, The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, U.K. E-mail: s.phillips@rbgkew.org.uk

Introduction

The genus *Portulaca* was divided by Geesink (1969) into two subgenera: subgen. *Portulacella* (F. Muell.) Legrand with glabrous nodes and flowers in dichasia, and subgen. *Portulaca* with nodal scales or hairs and flowers aggregated into terminal heads. Subgenus *Portulaca* was further subdivided into two sections: sect. *Neossia* Legrand with opposite leaves and sect. *Portulaca* with alternate leaves. Sect. *Neossia* has been addressed elsewhere (Gilbert & Phillips 2000). Sect. *Portulaca* occurs throughout the world in tropical and warm temperate areas, and includes a number of species complexes and a few widespread and variable weedy species. Species delimitation in this section in east and northeast tropical Africa is discussed in this paper.

The number of species in sect. *Portulaca* is much disputed owing to problems in drawing specific boundaries, and collections are notoriously difficult to name. The dehisced stamens are always to be found adhering to the stigma-branches within the collapsed perianth of the calyptra, and indeed have often dehisced whilst the flower is still in bud. Hence it appears that self-pollination is the norm, explaining the multiplicity of local variants. Danin *et al.* (1978) have shown the pantropical weedy annual *P. oleracea* L. to be a polyploid complex. It is highly likely that polyploidy also plays a part in the variability of some other species. This paper arises out of the necessity to sort out the African species for the *Flora of Tropical East Africa* account. It attempts to evaluate characters that have been used in keys in the past, and set out those which have been found to be most useful.

Portulaca collections make very poor herbarium specimens, due to shrinkage of the succulent stems and leaves and the fugacious nature of the delicate flowers, which open only for a few hours. Unless great care is taken, all the leaves tend to fall off on drying and details of the flowers are lost. Characters, which should be recorded in the field and areas where further field work would be beneficial, are noted.

History of Portulaca sect. Portulaca in eastern tropical Africa

The account of the family by Oliver (1868) in *Flora of Tropical Africa* included only two species from this section: the pantropical weed *P. oleracea* L. and *P. foliosa* Ker-Gawl. which is confined to Africa. The name *P. foliosa* has been widely misapplied in Africa since that time. Six more species were described by various authors over the next 60 years, but it was not until the 1930s that the number of species was suddenly increased, mainly through the publications of two German botanists, Peter and von Poellnitz.

Peter published seven more species in his *Flora von Deutsch Ost-Afrika* (1932-1938), all from Tanzania. These were based on his knowledge of the plants in the field, and are described and illustrated in detail. Poellnitz, working in Berlin on Peter's herbarium specimens, added another four species and three varieties (Poellnitz 1933, 1940a, 1940b). His descriptions, alphabetically arranged, are essentially translations into German of Peter's Latin, with the addition of seed morphology that was omitted by Peter. Thus within a decade the number of taxa in this section was almost tripled.

Poellnitz's account of *Portulacaceae* in East Africa (Poellnitz 1940a), published two years after the completion of Peter's Flora, has remained the standard work of reference for the region up to the present time. The difficulty of using this work, and doubts about the validity of some of his new taxa, have meant that until very recently it has not been possible to determine collections of *Portulaca* from eastern Africa with any degree of confidence. This situation is now being remedied by the publication of modern Flora accounts for the *Flora of Somalia* (Gilbert 1993), and the *Flora of Ethiopia and Eritrea* (Gilbert 2000), and the account for the *Flora of Tropical East Africa* is completed and awaiting publication.

Assessment of characters

The keys in both Peter's and Poellnitz's accounts of East African *Portulaca* are very difficult to use. Peter's key relies heavily on characters of the flower which are best suited to fresh material. His first couplet asks whether the petals are free or connate below which, whilst important, is often impossible to determine from dried material. His supporting characters of stamen number and leaf shape are not contrasting, and do not distinguish the species in the two halves of his key. He also frequently uses flower or petal length, likewise not usually determinable in herbarium material. Poellnitz's use of variable characters, and occasional faulty observation, has necessitated keying out several species more than once, *P. oleracea* and *P. somalica* no less than three times! The search for reliable characters to delimit the species, suitable for use both in the field and herbarium, has therefore been the primary concern in the preparation of recent African Flora accounts. Characters found to be useful are discussed below, using examples from eastern tropical Africa.

Habit

Providing basal parts are present, the species are quite easily distinguishable into short-lived annuals or ephemerals, and those with a more persistent perennial habit. *P. decorticans* Gilbert, from north Kenya and Somalia, forms

a definite shrublet eventually broader than high, with much-branched stems and a base 1 cm or more thick. *P. massaica* is a common perennial herb from dry stony soils in southern Kenya and northern Tanzania. It has a wide-spreading, branching root system sometimes more extensive than the aerial parts. *P. centrali-africana* is the only species in eastern Africa to possess fleshy creeping stolons, whilst *P. somalica* has a thickened subtuberous tap root. Annual species, such as the widespread *P. kermesina* N.E. Br., arise from a single slender root.

Whether the habit is erect, ascending or decumbent appears to be fairly constant. For example, *P. fischeri*, locally common in the area around Lake Victoria, has decumbent stems radiating from a central root which, together with the close-set leaves, imparts a recognisable facies to this species. In contrast, in typical *P. kermesina* the branches are rather stiffly ascending above an erect base, and the more widely spaced leaves contribute to a more open appearance.

Stems

The stems are always more or less succulent, and frequently flushed red or purple. A few species exhibit distinctive stem characteristics. In *P. decorticans* the old stems are clothed in an exfoliating papery brown bark, whilst the young shoots are densely papillose. Papillose young shoots also occur in *P. conoidea* from northeast Kenya and flaking bark in *P. stuhlmannii* from north Tanzania. Both these species are known only from the type collections. *P. grandis*, a close relative of *P. massaica* and occupying the same area, has a typically smooth, light grey bark.

Axillary hairs

The hair-tufts in the leaf-axils may have slightly broadened bases, and are almost certainly derived by the subdivision of scales, a derivation more clearly evident in sect. *Neossia*. They are variously interpreted as either trichomes or stipules (Carolin 1993: 545).

These hair-tufts are a most useful identification aid, as their form is constant within species and they are easily visible, even in the most poorly preserved herbarium material. In a few species the hairs are very short and inconspicuous. *P. oleracea* is the commonest example of this, and in *P. foliosa* the hairs are also short and inconspicuous. *P. humilis*, known only from the type from northern Tanzania, has distinctive dense tufts of stiff white hairs only 1 mm long. The majority of species divide into those with loosely shaggy long hairs (*e.g. P. kermesina*) and those with compact woolly tufts (*e.g. P. decorticans*). In *P. massaica* and *P. grandis* the outermost hairs of each shaggy tuft are connate at the base into two conspicuous crescentic white scales. This is seen to a lesser degree in other species and reinforces the derivation of the hairs from scales. In *P. somalica* the tufts are composed of a mixture of conspicuous long slender brown scales and much shorter hairs at their base. The hairs are often brown in herbarium material, but this may be at least partly an artefact of drying. *P. olosirwa* is said to have golden hairs.

Leaves

Leaves are important for identification, but unfortunately shrivel badly and often drop on drying. Nevertheless, approximate leaf-shape can be seen and was used extensively by Peter in his key. The commonest leaf-shape is linear-terete. *P. oleracea* is usually immediately recognisable by its obovate to spathulate leaves. *P. ramosa*, a species of local distribution in Tanzania, is also easily recognisable by its large, flat, oblanceolate-oblong leaves up to 3 cm long and 5 mm wide. The form of the leaf-tip, whether acute-apiculate or obtuse, has proved useful in distinguishing species with linear or narrowly oblong leaves. In *P. kermesina* it is always apiculate but

obtuse in *P. foliosa*, two species which are frequently confused. Characters lost in pressing include leaf colour, cross-section shape, and whether the nerve is impressed.

Although leaf-size and shape are usually reasonably constant, there are indications that they can vary widely in some species, especially *P. kermesina* where some forms have shorter, broader leaves than usual. An extreme variant from the Kenya/Uganda border area near Kacheliba has rather short elliptic leaves (*e.g. Thomas* 3400; *Tweedie* 3338).

Flowers

Flowers open in succession within the head. The total number is not easy to count in the herbarium, but seems to vary within narrow limits. *P. ramosa* and *P. conoidea* are unusual in usually having solitary flowers. In contrast, *P. oleracea* and *P. kermesina* may have up to six or more flowers in each head, and *P. fischeri* has bulky clusters of up to ten.

Peter gives very precise measurements for flower size in his key, but only rarely can flowers be measured accurately from herbarium material. Clearly some species have larger flowers than others, notably *P. centrali-africana* from the type locality in the Ruzizi valley, which has showy magenta flowers almost as large as some cultivated *Portulaca*, and also *P. somalica* with large yellow flowers. However, flower size seems to be very variable in some species, and the basis for this variation requires further investigation. It may be that the first central flowers to open in the head are larger than subsequent ones. Another possibility is that polyploidy is involved. *P. kermesina* is particularly variable, some specimens from Kenya having flowers twice as large as others (*e.g. Polhill & Paulo* 581, petals 7 mm long; *Gillett* 20997, petals 3 mm long). The same phenomenon has been seen in *P. kermesina* in Zimbabwe, where two collections from the same population varied widely in size (*Garley* 316, flowers 1/4 in. (= 6.4 mm) wide; *Garley* 317, flowers 3/4 in. (= 19 mm) wide). Flowers in *P. fischeri* are always small, but petal length varies from 2.5-4.5 mm long. Danin *et al.* (1978: 182) reported that in *P. oleracea* flowers may sometimes be cleistogamous, varying between chasmogamy and cleistogamy even within the life cycle of an individual plant, and the cleistogamous flowers are smaller with fewer stamens. This may explain variation in flower size in other species. Geesink (1969: 280) reports that flower size and stamen number in *P. pilosa* vary according to growing conditions.

The time of day that the fugacious flowers open is likely to be significant, but is very seldom recorded. The sparse information available indicates that flowers open as follows: *P. oleracea*, *P. kermesina* and *P. centrali-africana* in the morning; *P. massaica* and *P. grandis* in late morning; *P. decorticans* at midday. This contrasts with the genus *Talinum* in Africa, where the few records note flowers opening in late afternoon and early evening. More field observations are needed for this character.

Sepals

The two sepals are always more or less ovate-triangular, basally connate and concave, with broad thin margins and a crested tip. They present few useful characters, although the size of the apical crest varies slightly between species. In *P. oleracea* and *P. oblonga* the crest is extended down the midline as a narrow wing, whilst in *P. conoidea* it is narrowed into a rostrate extension 1.5 mm long.

Petals

Details of the petals are mostly lost on drying, especially as open flowers are only rarely present in herbarium specimens. Full details of petal morphology should therefore be included in field notes.

Flowers normally have five petals in sect. *Portulaca*, in contrast to sect. *Neossia* where the flowers are 4-petalled. There are a few excep-

tions; *P. ramosa* and *P. grandis* are occasionally 6-petalled. The petals appear to be usually connate or at least adherent below, but this is very difficult to make out in collapsed dried flowers. Peter describes the petals as free in *P. ramosa*, and this does seem to be correct. Petal shape is important, but likewise very difficult to determine in the herbarium. The petals are usually ovate or ovate-oblong, with a rounded or subtruncate tip with a small central apiculum as illustrated by Peter for most of his new species. The presence of retuse petals, as in *P. foliosa*, is a significant difference.

Variation in petal colour requires more field observations, and is sometimes not even mentioned in older collections. It seems that whilst some species are stable in this character others are more variable, and even in species where flower colour is normally stable exceptions can occur. Species known only with yellow flowers include *P. foliosa*, *P. massaica*, *P. grandis* and *P. oblonga*. Species with magenta-pink flowers include *P. centrali-africana*, *P. fischeri* and *P. pilosa*. *P. kermesina* usually has red or pink flowers, but orange- and yellow-flowered variants occur occasionally. There are even pink-flowered variants of the yellow-flowered weed *P. oleracea*. Thus whilst petal colour is useful and obvious, it must always be used with caution as a character for identification, and should not be given a high priority in keys.

Stamens

Stamen number is indeterminate, but varies within a limited range for each species. The number can vary in different flowers from the same plant. *P. fischeri* is described as having five stamens only, but may have from five to twelve. The range in *P. kermesina* is 8-13, with a few exceptional specimens having up to 20. *P. foliosa* has 10-25 stamens, whilst *P. somalica*, P. *ramosa*, *P. grandis* and *P. humilis* all have more than 30. Thus stamen number is useful in broad terms, but precise numbers cannot be given.

Capsule

Capsules and seeds are usually present, and provide some of the most easily observed and useful characters for species delimitation. Strangely, these characters were almost entirely ignored by Peter in his key and he does not even mention the seeds or their distinctive surface sculpture in his descriptions. In contrast, Poellnitz recognised the importance of seed surface morphology and made frequent use of it in his key.

The most striking distinction in capsule structure is between *P. oleracea* and *P. oblonga* on the one hand and the rest of the species on the other. In these two species the capsule lid is papery in texture, with a constriction about two-thirds up. The nipple-like apical portion is thinner walled with obvious veins, and retains one or more seeds within it when the capsule lid falls. The capsule in *P. nogalensis* is also thin with obvious veins, but without an apical constriction. In all the other species the capsule is coriaceous without a constriction, and glossy yellow or infrequently whitish in colour.

The capsule in all *Portulaca* species is circumscissile, opening by a circular split into base and lid. Poellnitz placed great emphasis on the position of this split, whether at the midpoint or above or below it. This probably has some validity, but is not easily observed in complete capsules before dehiscence as they are usually immersed in dense hairs. Capsule lids and bases fall separately, but their relative shape will give some guide. In *P. conoidea* dehiscence is very low, and the capsule base is almost disc-like. The most usual situation is a dehiscence line between 1/3-1/2 up the capsule, as in *P. foliosa*, *P. kermesina*, *P. massaica* and *P. decorticans*. Dehiscence is at the midpoint in *P. centrali-africana* and *P. fischeri*. In *P. ramosa* dehiscence is above the middle, resulting in a deeply infundibular capsule base and a shallowly domed lid. Capsule size is variable, even within individual plants, most likely mirroring variation in flower size.

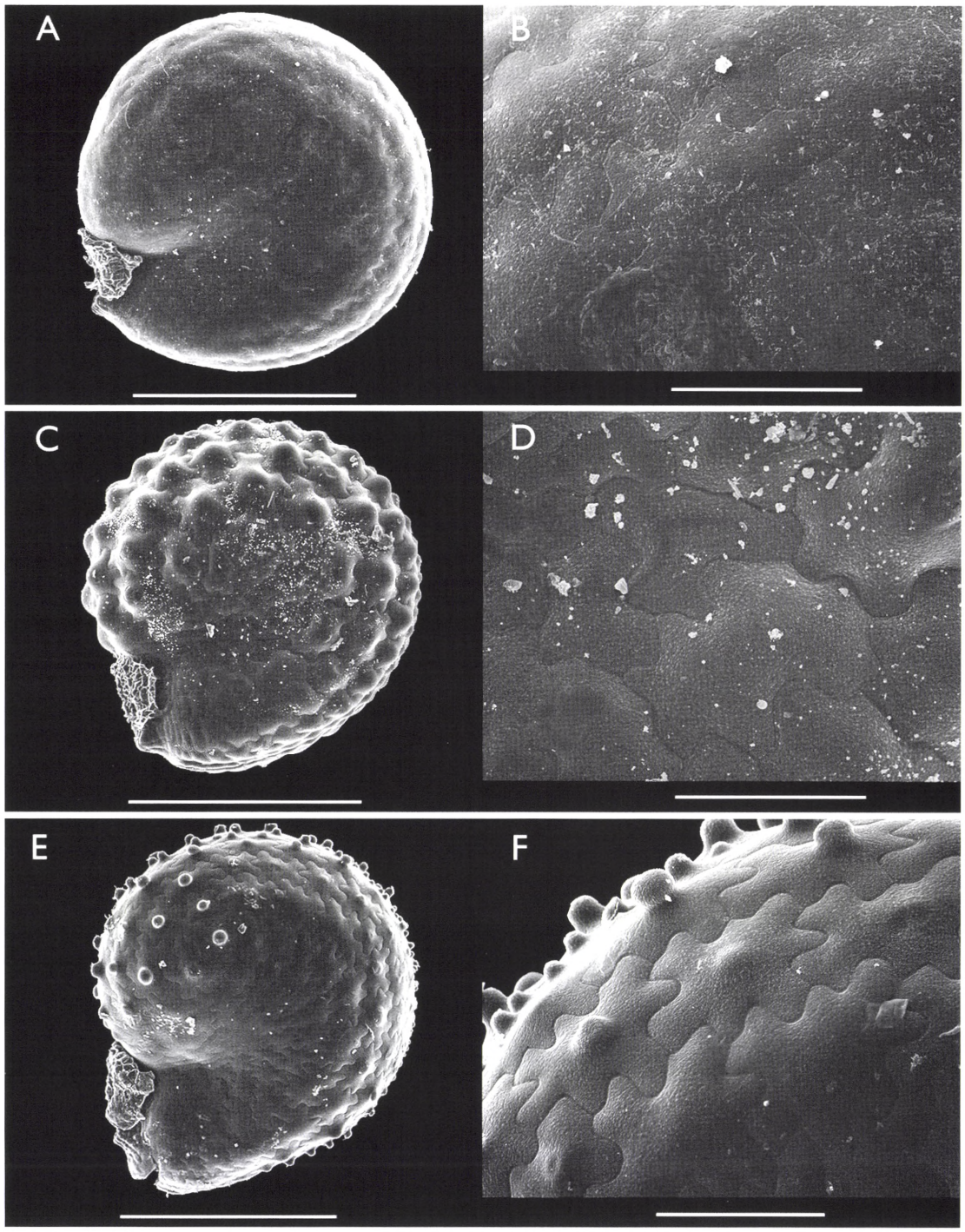

Fig. 1. Seeds and details of testa morphology (SEM). *Portulaca grandiflora*. **A-B:** *Miers* 408 (Argentina). **C-D:** *Reed* s.n. (Argentina); **E-F:** *Matthew* RHT 53107 (cult. India). A, C, E: scale bar equals 500 μm; B, D, F: scale bar equals 100 μm.

The style disarticulates from the capsule lid at maturity, but remains inside the marcescent flower with the anthers adhering to the recurved stigma-branches. The number of stigma-branches varies within the range 3-5 in most species (sometimes increasing to 8 in *P. grandis*), and may vary between flowers on the same plant. The most common number of stigma-branches is four.

Seeds

Seeds in *Portulaca* are reniform, sometimes broadly so and almost circular in outline, with a small aril. The testa-cells are arranged more or less concentrically on the flanks, and usually in regular rows on the peripheral rim. Seeds are always plentifully produced, and are often iridescent and ornamented. It is curious that Peter completely ignored seeds both in his keys and descriptions, as they are both useful and obvious. Poellnitz recognised the importance of seed characters, but unfortunately some faulty observations have led to mistakes in his key. Descriptions of testa cell shape refer to the cells on the flanks.

The testa cells are usually sinuous in outline, and the anticlinal walls interlock irregularly in jigsaw-fashion. The cells are thus slightly to conspicuously jigsaw- to stellate-shaped depending on the degree of interlocking. *P. olosirwa* (Fig. 4C-F), *P. conoidea* (Fig. 5E, 5F) and *P. cifferii* (Fig. 7E, 7F) have only slightly sinuous walls. Seeds vary in size between species from about 0.5 mm up to 1 mm long, but size is usually fairly constant within a species. Particularly small seeds occur in *P. coralloides* (Fig. 6A, 6B) and *P. humilis* (0.45 mm). Most species have seeds 0.6-0.8 mm long, whilst large seeds over 0.8 mm long are found in *P. massaica* (Fig. 5A, 5B), P. *grandis*, *P. ramosa* (Fig. 2E, 2F) and *P. conoidea* (Fig. 5E, 5F). Danin *et al.* (1978: 180) found seed size to be related to ploidy level in *P. oleracea*.

Immature seeds are always brown, but as they mature the colour usually changes either to a glossy black, or shades of metallic grey or silver. The iridescent metallic sheen appears quite late, and it is not unusual for the tips of tubercles of otherwise silvery seeds to remain black. Most seeds of *P. coralloides* are still brown when shed, but a silvery sheen may eventually develop. The seeds of *P. foliosa* are normally black, but may rarely be metallic-grey *e.g. Hepper* 3781 from Mali. *P. kermesina* seeds are mostly metallic-grey, but may occasionally be silvery as in *P. fischeri*. Hence whilst seed colour is usually diagnostic for a species, it cannot be relied on absolutely as exceptions sometimes occur.

The thickness of the anticlinal (usually sinuous) cell walls varies between species. For example, they are thin and rather obscure in *P. grandiflora* (Fig. 1A-F), sunken in *P. kermesina* (Fig. 6C-F), raised in *P. ramosa* (Fig. 2E, 2F), and thick and obvious in *P. olosirwa* (Fig. 4C-F). Thus seed size and colour, and the outline and wall thickness of the testa cells are all reasonably constant within species, and appear to be good characters for use in species delimitation.

The surface of the testa cells may be flat or convex to domed, and is often raised into a conical tubercle or a central peg. When present, this is a very striking feature of the seed surface morphology, but unfortunately is sometimes variable and can only be used with caution for the delimitation of species. In most species the surface relief is stable, for example *P. ramosa* (Fig.2E, 2F) has flat cells, *P. fischeri* (Fig. 3E, 3F) tuberculate cells, and *P. massaica* (Fig. 5A, 5B) flat cells with a central peg. However, infraspecific variability in this character can be demonstrated in *P. grandiflora*, a native of Argentina now widely cultivated and known from gardens in Africa. Seeds may be completely smooth with flat cells (Fig. 1A, 1B), raised into conical tubercles (Fig. 1C, 1D), or with central pegs (Fig. 1E, 1F). Pegs may be present in some cells and not in others of the

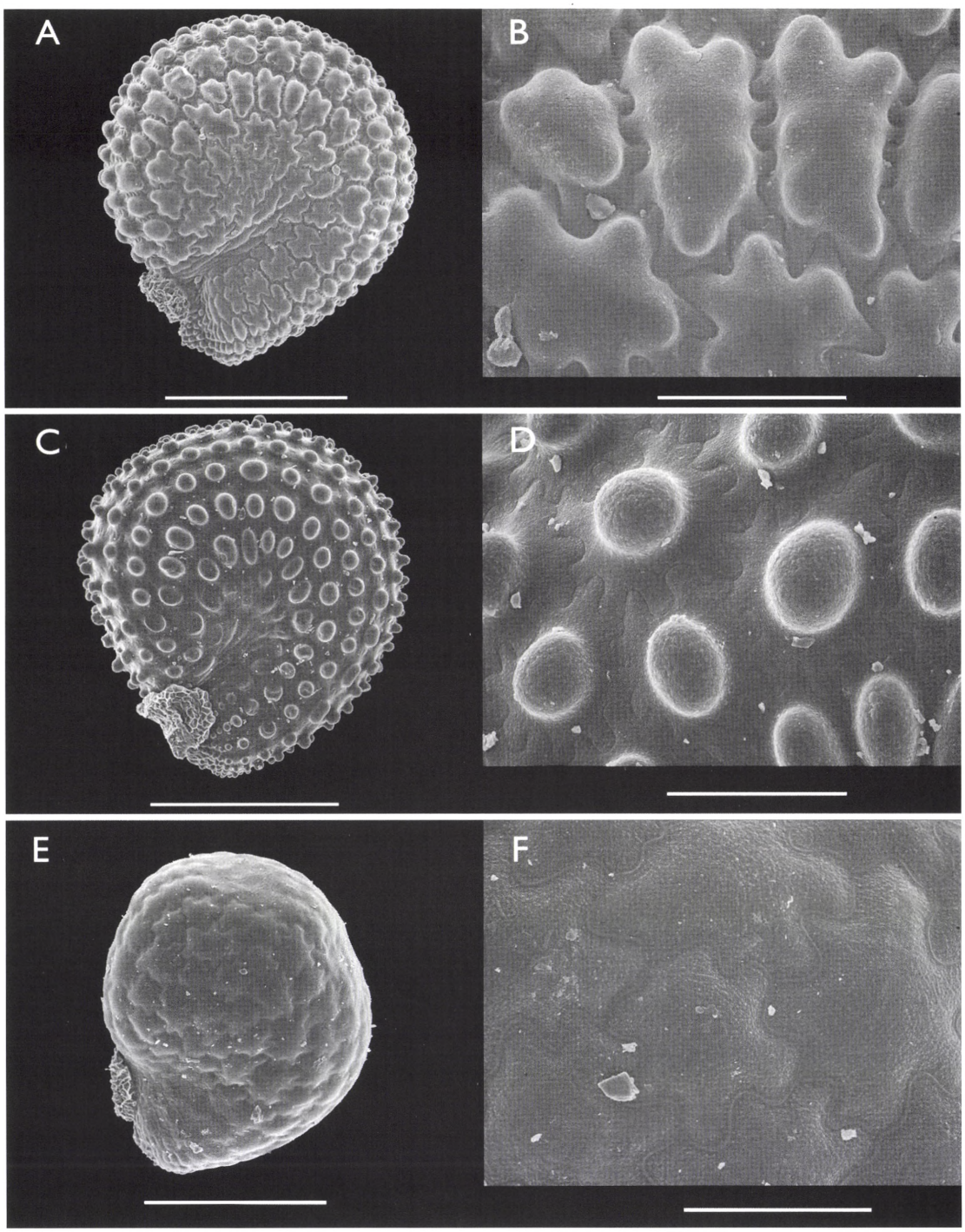

Fig. 2. Seeds and details of testa morphology (SEM). **A-B:** *Portulaca oblonga; Greenway* 2154 (Tanzania). **C-D:** *P. oblonga; Polhill & Paulo* 640 (Kenya). **E-F**: *P. ramosa; Williams* 27 (Tanzania). A, C, E: scale bar equals 500 µm; B, D, F: scale bar equals 100 µm.

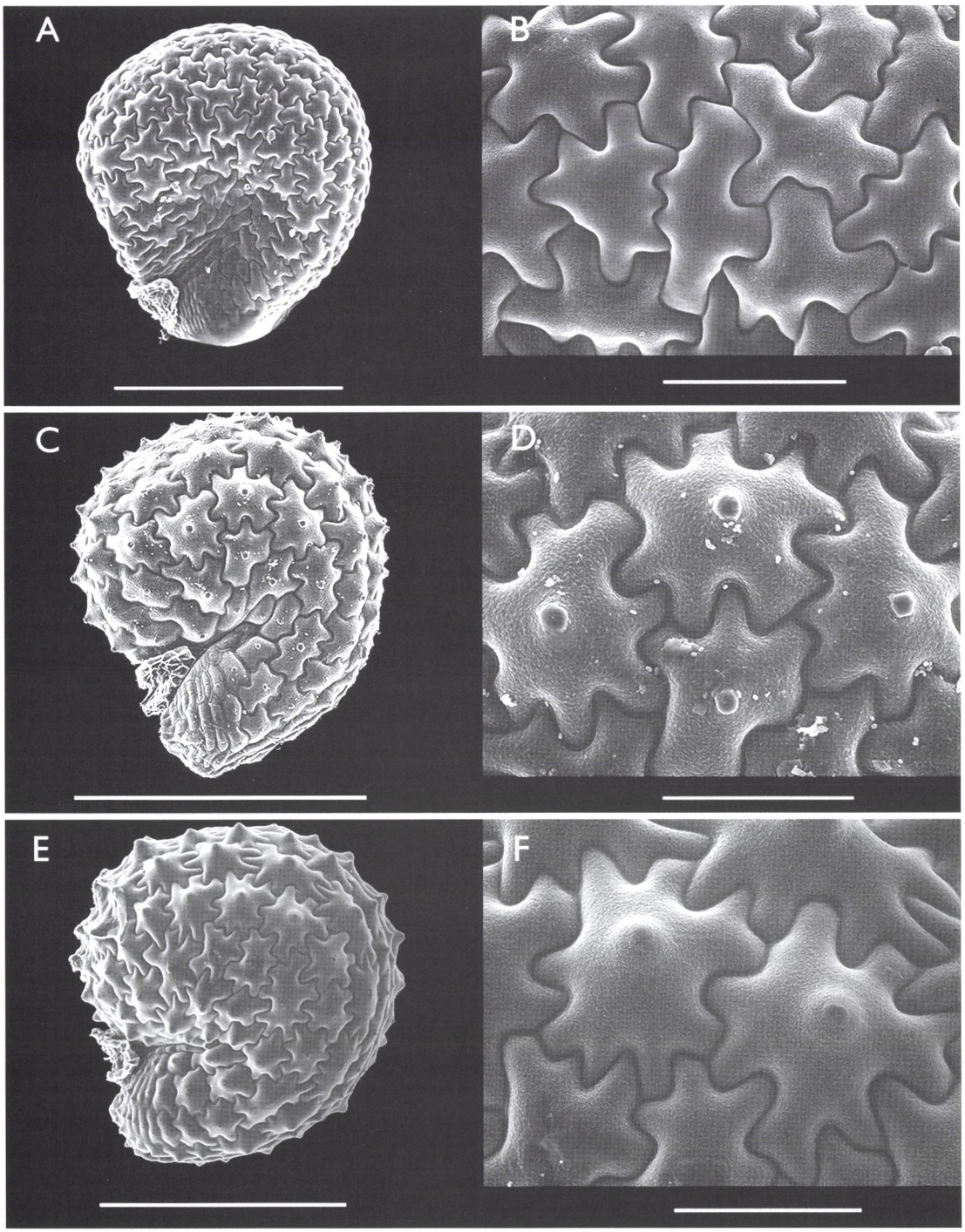

Fig. 3. Seeds and details of testa morphology (SEM). **A-B:** *Portulaca foliosa; McClintock* 71 (Nigeria). **C-D:** *P. centrali-africana; Reekmans* 5791 (Burundi). **E-F**: *P. fischeri; Tanner* 4164 (Tanzania). A, C, E: scale bar equals 500 µm; B, D, F: scale bar equals 100 µm.

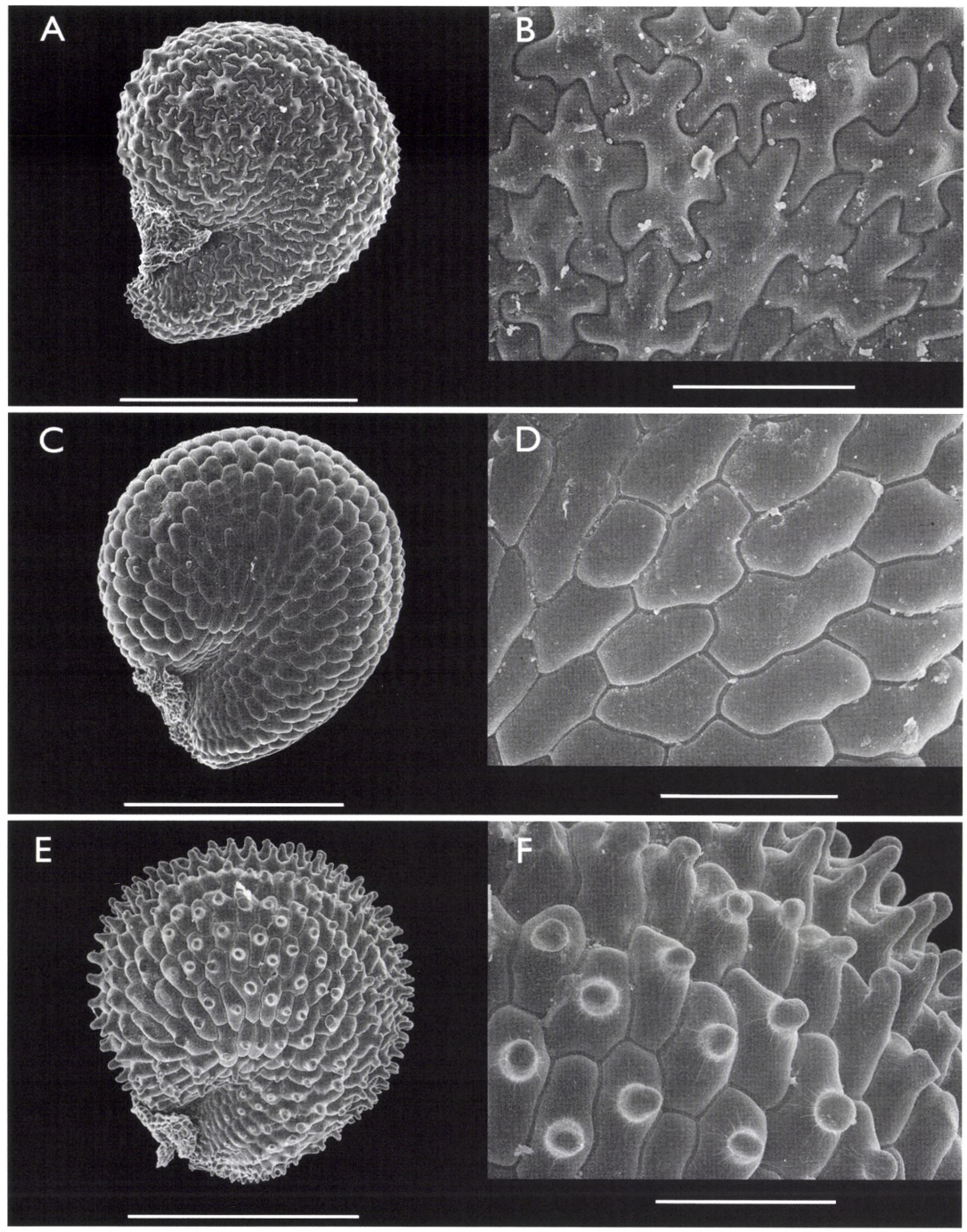

Fig. 4. Seeds and details of testa morphology (SEM). **A-B:** *Portulaca decorticans; Bally & Smith* 14454 (Kenya). **C-D:** *P. olosirwa; Harger* 35 (Kenya). **E-F**: *P. olosirwa*; *Glover et al.* 2234 (Kenya). A, C, E: scale bar equals 500 µm; B, D, F: scale bar equals 100 µm.

same seed. *P. olosirwa* has distinctive black seeds with non-sinuate cells, but likewise may be smooth (Fig. 4C, 4D) or tuberculate (Fig. 4E, 4F). In *P. kermesina* the cells are usually lightly convex, but occasionally some cells may develop a tubercle (Fig. 6E, 6F). Thus the ability to develop a tubercle or peg seems to be latent in perhaps most species, but is only sometimes expressed.

A review of seed morphology

P. anceps: Seed unknown.

P. centrali-africana: Seeds 0.6-0.7 mm long, metallic-grey or silvery; cells stellate-conical with short arms and black tips, the walls fairly thick (Fig. 3C, 3D).

P. ciferrii: Seeds 0.65-0.7 mm long, iridescent grey-black; cells slightly domed, only slightly jigsaw-shaped, the walls shallowly sinuous (Fig. 7E, 7F).

P. conoidea: Seeds 1 mm long, dull grey; cells slightly domed, not jigsaw-shaped or stellate, the walls only slightly interlocking (Fig. 5E, 5F).

P. coralloides: Seeds 0.45 mm long, brown, finally with a silvery-grey iridescent sheen; cells jigsaw-shaped, almost flat (Fig. 6A, 6B).

P. decorticans: Seeds 0.6 mm long, dark brown; cells with jigsaw-shaped to stellate, domed to conical, sometimes with a central tubercle (Fig. 4A, 4B).

P. erythraeae: Seeds 1 mm long, glossy black; cells stellate, gently domed.

P. fischeri: Seeds 0.6-0.7 mm long, iridescent silvery-grey; cells stellate, conical-tuberculate with black tips (Fig. 3E, 3F).

P. foliosa: Seeds 0.7-0.8 mm long, black (rarely metallic-grey); cells slightly convex to domed (Fig. 3A, 3B).

P. grandiflora: Seeds 0.8 mm long, iridescent grey; cells stellate with narrow obscure walls, flat to conical, often tipped with a peg especially round the periphery (Fig. 1A-F).

P. grandis: Seeds 0.85-0.95 mm long, light grey with a dull lustre; cells small, flat, jigsaw-shaped with broad cell walls, usually with a black central peg (identical with seeds of *P. massaica*).

P. heterophylla: Seeds 0.5-0.6 mm long, iridescent grey; cells stellate, domed to conical-tuberculate.

P. humilis: Seeds 0.45 mm long, iridescent silvery-grey; cells stellate, domed, tuberculate round the periphery.

P. kermesina: Seeds 0.5-0.75 mm long, metallic-grey or occasionally silvery; cells jigsaw-shaped to stellate, usually convex to slightly conical, rarely with a few tubercles (Fig. 6C-F).

P. massaica: Seeds 0.8-0.9 mm long, light grey with a dull lustre; cells small, flat, jigsaw-shaped with broad cell walls, usually with a black central peg (Fig. 5A, 5B).

P. nogalensis: Seeds 0.75 mm long, dark brown; cells small, jigsaw-shaped to stellate with a central peg (Fig. 7C, 7D).

P. oblonga: Seeds 0.85-1 mm long, black; cells stellate with short arms, the body raised as a broad irregular tubercle with low papillae on its surface (Fig. 2A, 2B), or sometimes peg-like (Fig. 2C, 2D). This same variation is found in subspecies of *P. oleracea*, illustrated by Danin *et al.* (1978).

P. oleracea: Seeds 0.65-1 mm long, black; cells stellate, often also tuberculate and/or papillose (Danin *et al.* 1978).

P. olosirwa: Seeds 0.75 mm long, black, glossy; cells small, elliptic, convex to domed, with thick almost straight walls, sometimes with a central tubercle (Fig. 4C-F).

P. pilosa: Seeds 0.6-0.7 mm long, black or dark metallic-grey; cells jigsaw-shaped to stellate, conical, tuberculate round the periphery (Fig. 5C, 5D).

P. ramosa: Seeds 0.8 mm long, metallic-grey, smooth in outline; cells stellate with short arms, almost flat, the walls prominent (Fig. 2E, 2F).

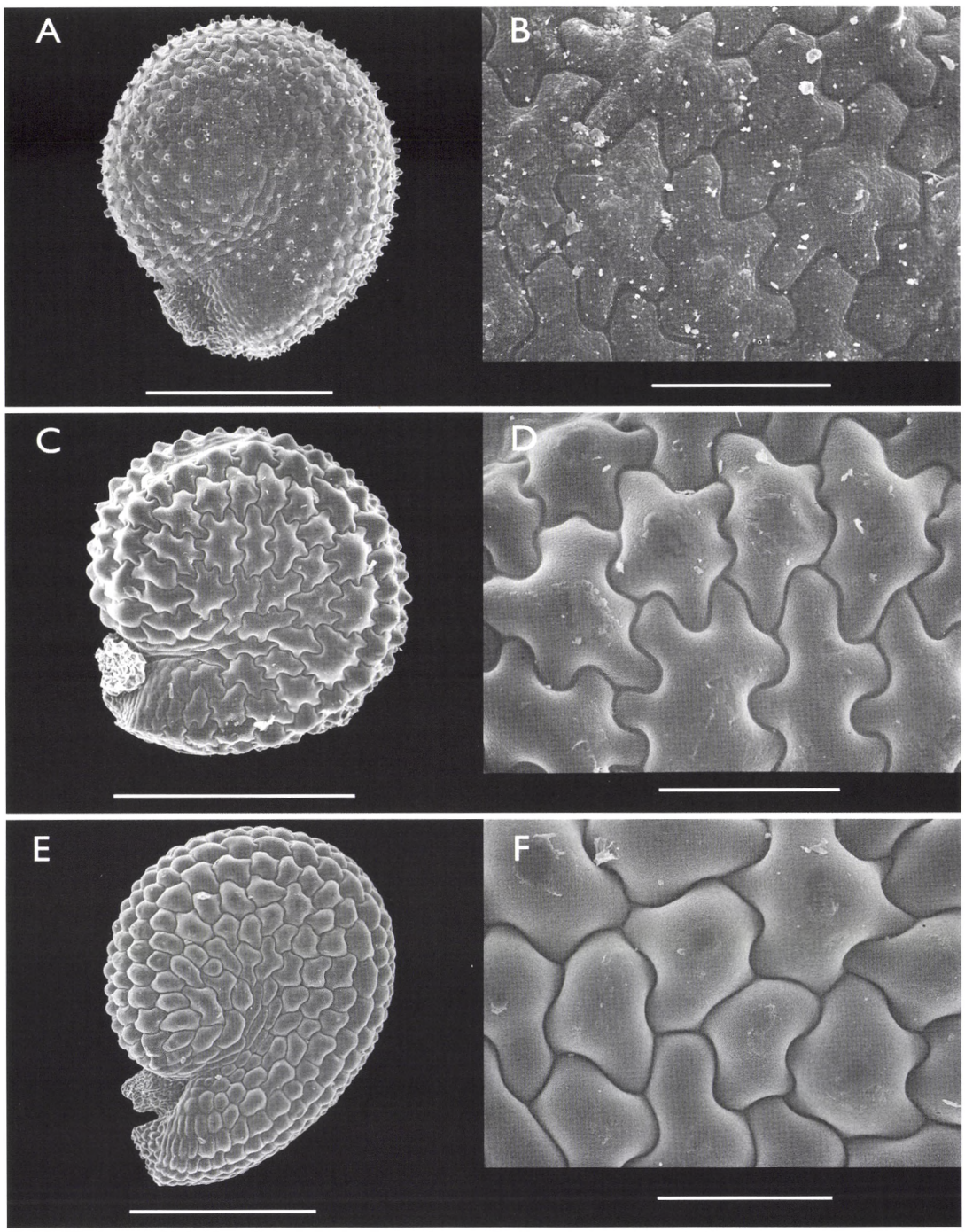

Fig. 5. Seeds and details of testa morphology (SEM). **A-B:** *Portulaca massaica; Faden & Evans* 74/595 (Kenya). **C-D:** *P. pilosa; Bidgood & Vollesen* 3092 (Tanzania). **E-F**: *P. conoidea; Gillett & Gachathi* 20624 (Kenya). A, C, E: scale bar equals 500 µm; B, D, F: scale bar equals 100 µm.

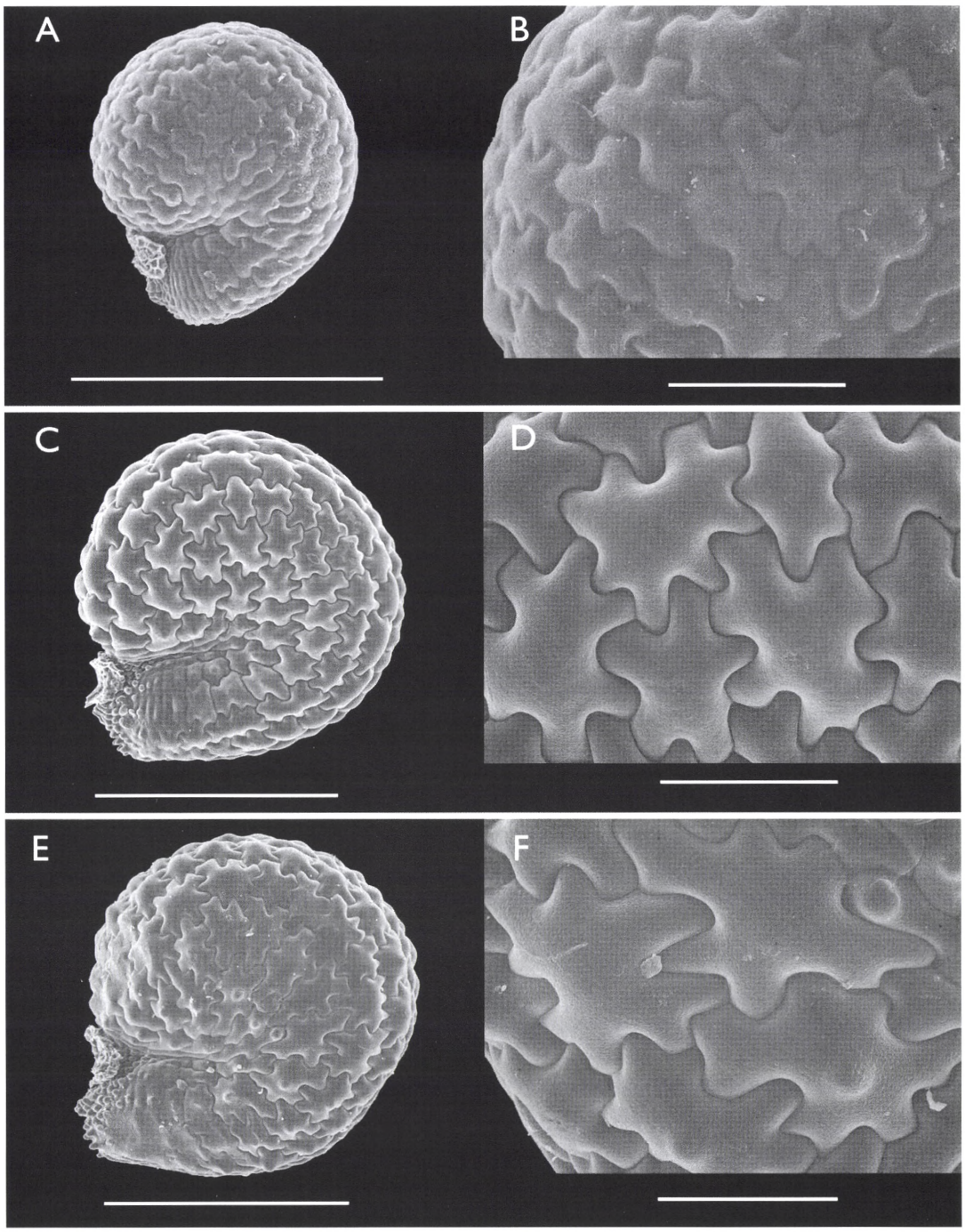

Fig. 6. Seeds and details of testa morphology (SEM). **A-B:** *Portulaca coralloides; Greenway & Rawlins* 9423 (Kenya). **C-D:** *P.kermesina; Richards* 14617 (Botswana). **E-F**: *P. kermesina; Smith* 2158 (Botswana). A, C, E: scale bar equals 500 µm; B, D, F: scale bar equals 100 µm.

P. somalica: Seeds 0.85-1 mm long, iridescent dark grey or silvery; cells elongate-stellate with short arms, flat (Fig. 7A, 7B).

P. stuhlmannii: Seeds 0.9 mm long, grey with a dull lustre; cells stellate, slightly convex.

Distribution and habitat

All *Portulaca* species in Africa occur in dry, often semi-arid places. Whilst a few species are widespread, more are of local distribution and often restricted to particular habitats. For example, *P. massaica* and the closely related *P. grandis* occur on dry stony hillsides, rock crevices and volcanic ash in the area of southern Kenya and northern Tanzania formerly known as Masailand. *P. ramosa* is known only from inselbergs in northeastern Tanzania, whilst *P. decorticans* grows in rocky places in the *Acacia-Commiphora* bushland of northeastern Kenya and neighbouring Somalia. *P. somalica* and *P. nogalensis* are endemic in N Somalia. *P. cifferii* and *P. coralloides* are both restricted to coastal sand.

P. foliosa and *P. kermesina* are both more widespread and have been very much confused, although they are actually quite different. They can be distinguished as follows:

1. Leaves obtuse; axillary hairs inconspicuous; petals yellow, retuse; seeds black. *P. foliosa*
– Leaves acute; axillary hairs long and shaggy; petals red, acute; seeds metallic-grey. *P. kermesina*

These two names have also been widely misapplied to other species in the area. *P. kermesina* occurs from South Africa northwards to Eritrea on dry sandy soils, but is absent from W Africa. In contrast, *P. foliosa* is commonest in W Africa, and occurs only sporadically elsewhere in Africa. It is particularly associated with seasonally dry sandy river beds and sandbanks in rivers. In eastern Africa it is known from the Baro river in Ethiopia, the Ruaha in Tanzania, and also from the Zambezi valley. It is to be expected in other river valleys in East Africa.

Key to sect. Portulaca in East and Northeast tropical Africa

1. Petals up to 15 mm long; flowers with 5(-6) petals. 2
– Petals 15-30 mm long; flowers often with more than 5 petals, sometimes double (garden escape). *P. grandiflora*
2. Axillary hairs 1 mm long or less; capsule lid usually with an apical nipple-like constriction of different texture containing a few seeds. 3
– Axillary hairs almost always over 1 mm long; capsule lid without an apical constriction. 5
3. Leaves up to 20 mm wide; capsule lid uniformly textured with obvious veins, lacking a constriction and not retaining any seeds. *P. erythraeae*
– Leaves up to 10 mm wide; capsule lid with a prominent constriction, smooth and opaque below, thinner with obvious veins above. 4
4. Flowers up to 1.5 cm diam.; stamens 7-12; leaves obovate or spathulate. *P. oleracea*
– Flowers 2-3 cm diam.; stamens over 20; leaves narrowly oblong. *P. oblonga*
5. Shrublets; basal stems up to 1 cm thick, sometimes with exfoliating papery bark; young shoots often papillose. 6
– Annual or perennial herbs; basal stems less than 0.5 cm thick, toughened but usually without flaking bark; young shoots not papillose (except *P. conoidea*). 8
6. Leaves narrowly oblong-spathulate, up to 8 mm long, obtuse; axillary hairs brown, accompanied by longer scales; petals purple. *P. nogalensis*
– Leaves linear, up to 25 mm long, acute; axil-

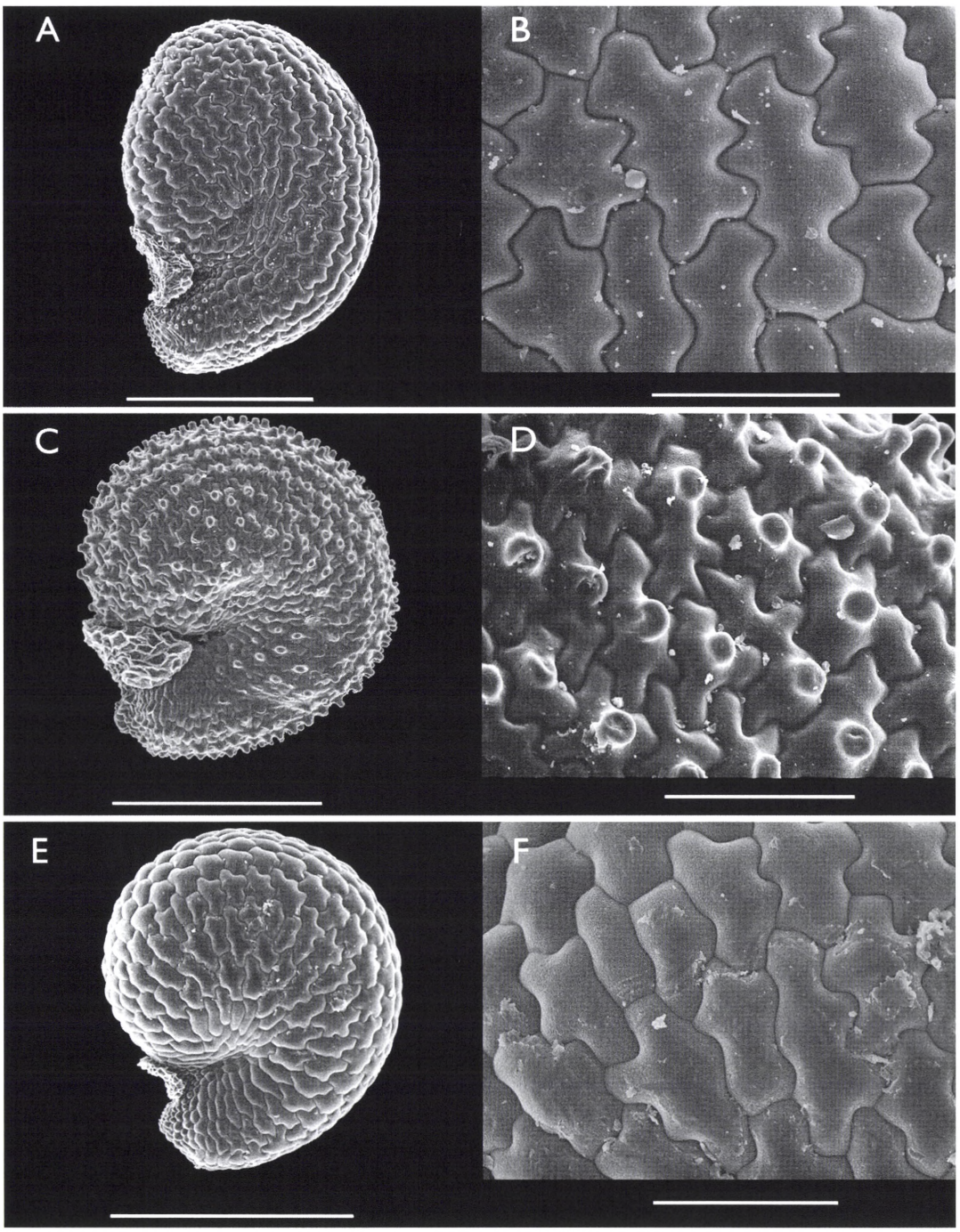

Fig. 7. Seeds and details of testa morphology (SEM). **A-B:** *Portulaca somalica; Godding* 169 (Somalia); **C-D** *P. nogalensis* (Somalia, *McKinnon* 5/157); **E-F**: *P. cifferii; Friis et al.* 5036 (Somalia). A, C, E: scale bar equals 500 µm; B, D, F: scale bar equals 100 µm.

lary hairs in dense white woolly tufts lacking scales; petals pink, orange or yellow. 7
7. Young stems minutely papillose; petals pink and orange. *P. decorticans*
– Young stems smooth; petals yellow. aff. *P. grandis*
8. Leaves obtuse. 9
– Leaves acute to apiculate. 13
9. Axillary hairs shorter than the internodes; seeds black; petals retuse, yellow. *P. foliosa*
– Axillary hairs conspicuous, often longer than the internodes; seeds silvery-grey or brown; petals acute to obtuse, pink, red or purple. 10
10. Stamens 25 or more; petals 7-12 mm long; perennial with fleshy spreading stolons. *P. centrali-africana*
– Stamens up to 20; petals 2.5-4.5 mm long; annuals or perennials from a central root, lacking stolons. 11
11. Stamens 17-19; leaves 2.5-5 mm long; seed brown, 0.45 mm long, testa cells almost flat. *P. coralloides*
– Stamens 4-12; leaves 5-15 mm long; seed metallic-grey, 0.6-0.9 mm long, testa cells raised to conical. 12
12. Stems decumbent, 1.5-2 mm thick near base; leaves elliptic to oblong, 5-8.5 mm long; seed 0.6-0.7 mm long, testa cells conical-tuberculate. *P. fischeri*
– Stems ascending, 3 mm thick near base; leaves linear-terete, up to 15 mm long; seed 0.9 mm long, testa cells slightly raised. *P. stuhlmannii*
13. Stamens 30-50. 14
– Stamens less than 30. 18
14. Seeds 0.45 mm long, silvery, the testa-cells stellate-conical; axillary hairs c. 1 mm long, straight, in stiff dense tufts. *P. humilis*
– Seeds 0.65-1 mm long, metallic-grey (rarely silvery), the testa-cells ± flat, sometimes with a central peg; axillary hairs and scales mostly > 1 mm long (if short not straight and stiff). 15
15. Leaves 3-5 mm wide; petals purple-pink; seeds smooth. *P. ramosa*
– Leaves 1.5-3 mm wide; petals yellow. 16
16. Cells of seed testa not stellate, scarcely interlocking, the walls shallowly sinuous; tufts of axillary hairs compact, densely woolly, white. *P. cifferii*
– Cells of seed testa stellate with interlocking walls; tufts of axillary hairs loose and shaggy, sometimes with scales (if woolly-white, plant a robust shrublet). 17
17. Root subtuberous; seeds with flat smooth testa cells; axillary tufts of slender curved scales and much shorter hairs. *P. somalica*
– Roots fibrous; seeds with papillate or conical testa cells; axillary tufts of hairs only, scales absent. *P. grandis*
18. Perennials with woody base and extensive branching roots; petals yellow. 19
– Short-lived herbs with slender base and a single main root; petals usually in shades of pink or red (infrequently yellow). 20
19. Seeds dull grey, the testa cells jigsaw-shaped to stellate, flat, mostly with a central papilla; petals 5-8 mm long. *P. massaica*
– Seeds black, glossy, the testa cells with straight walls; petals 3.5 mm long. *P. olosirwa*
20. Seeds black; axillary hairs densely woolly, thickly clothing the stems; stems decumbent with crowded flattened leaves; petals pink. *P. pilosa*
– Seeds grey, often iridescent; axillary hairs in loose shaggy tufts; stems usually erect or ascending with spaced terete leaves (if stems decumbent with flattened leaves, then petals yellow). 21
21. Sepals 8 mm long, rostrate; capsule lid conical, twice as high as wide; seeds with only slightly interlocking testa cells. *P. conoidea*
– Sepals 4-5 mm long, slightly crested; capsule lid domed, about as high as

wide; seeds with interlocking jigsaw-shaped testa cells. 22

22. Leaves all linear-terete, 1-2 mm wide; petals red, pink or orange (rarely yellow). *P. kermesina*

– Leaves variable, some lanceolate or oblong-spathulate, up to 3 mm wide. 23

23. Petals purple; flowers surrounded by 4-5 involucral leaves. *P. anceps*

– Petals yellow; flowers surrounded by *c.* 8 involucral leaves. *P. heterophylla*

Conclusion

East Africa is the centre of diversity for *Portulaca* sect. *Portulaca* in Africa, with only a few species extending beyond this area into the rest of the continent. One third of the species are endemic to southern Kenya and northern Tanzania. Most of the others are of very local distribution, often being confined to particular ecological niches. The following six species are known only from the type collections: *P. anceps*, *P. conoidea*, *P. erythraeae*, *P. heterophylla*, *P. humilis* and *P. stuhlmannii*. Some of these may prove to be extreme examples of other species. Variation in general is still very incompletely understood, and the stability of a number of characters used in keys needs further investigation.

Among the more widespread species local variants are commonplace. This is particularly true of *P. kermesina* in eastern Africa. The Kenyan coastal lowlands and the Tana River area are particularly rich in small annual forms, some of which may merit separate status when they are better known. Another outstanding problem is the separate specific status of *P. massaica* and *P. grandis*. They have an identical and distinctive seed, occupy the same habitat, and intermediates occur between them although they are readily distinguishable separately in their typical form. A chromosome survey of this complex is desirable. Plants named as *P. grandis* from northern Kenya and Ethiopia (aff. *grandis* in the key) differ from typical *P. grandis* by their white-woolly persistent axillary hairs, tuberculate seeds and much-branched habit, all characters found in *P. decorticans* from northern Kenya.

Seed colour and ornamentation are found to be very useful for species delimitation, but are not absolutely stable. In particular, the basis for the development of tubercles and pegs on the testa-cells, and the appearance of a silvery metallic layer on the mature seed require investigation. More collecting is desirable throughout the area, and new collections should always be accompanied by full field notes. Further work is required, both in the field and experimentally, to complement the present study, which is based entirely on herbarium material. Only then will a stable classification for this group of *Portulaca* in Africa be achieved.

Conspectus of species

P. anceps A. Rich. (1848)
P. centrali-africana R.E. Fr. (1914)
P. ciferrii Chiov. (1936)
P. conoidea S.M. Phillips (2000)
P. coralloides S.M. Phillips (2000)
P. decorticans M.G. Gilbert (1992)
P. erythraeae Schweinf. (1896)
P. fischeri *Pax* (1893)
P. foliosa Ker-Gawl. (1824); *P. fischeri* Pax var. *robusta* Poelln. (1940)
P. grandiflora Hook. (1829)
P. grandis Peter (1938)
P. heterophylla Peter (1938); *P. mkatensis* Poelln. (1940)
P. humilis Peter (1938)
P. kermesina N.E. Br. (1909); *P. holosericea* Peter (1938); *P. tenera* Peter (1938); *P. rubriflora* Poelln. (1941)
P. kermesina var. ***lutea*** (Poelln.) S.M. Phillips; *P. fischeri* Pax var. *lutea* Poelln.
P. massaica S.M. Phillips (2000)

P. nogalensis Chiov. (1929); *P. nogalensis* var. *atricha* Chiov. (1929); *P. nogalensis* var. *homotricha* Chiov. (1929)
P. nogalensis var. ***heterotricha*** Chiov. (1929)
P. oblonga Peter (1932); *P. neumannii* Poelln. (1933); *P. neumannii* Poelln. var. *robusta* Poelln. (1940)
P. oleracea L. (1753)
P. olosirwa S.M. Phillips (2000)
P. pilosa L. (1753)
P. ramosa Peter (1938); *P. schliebenii* Poelln. (1940)
P. somalica N. E. Br. (1886)
P. stuhlmannii Poelln. (1933).

Acknowledgements

I am much indebted to M.G. Gilbert for many helpful discussions, his readiness to make his unpublished data available to me, and for giving me the benefit of his wide experience of *Portulaca* in the field. I am also grateful to the director of the Berlin herbarium (B) for sending Peter and Poellnitz type specimens on loan.

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The identity of Polyscias lepidota Chiov. (1940). A name missing in Vol. 3 of the Flora of Ethiopia

Ib Friis

Friis, I. 2001. The identity of Polyscias lepidota Chiov. (1940). A name missing in Vol. 3 of the Flora of Ethiopia. *Biol. Skr.* **54**: 49-54. ISSN 0366-3612. ISBN 87-7876-246-4.

The type material of *Polyscias lepidota* Chiov. (1940) has been found to consist of a rachis and nine detached terminal and lateral leaflets. It was collected in the mosaic of farmland and secondary evergreen bushland near Jimma in the Kefa Region, and said by Chiovenda to be closely related to the endemic Ethiopian species *Polyscias farinosa* (Del.) Harms (Araliaceae), which is restricted to rocky outcrops in regularly burnt deciduous woodland and wooded grassland. *Polyscias lepidota* was placed in synonymy of *P. farinosa* (Araliaceae) by Bamps in 1974, but he did not examine the type material. In 1979 the present author identified the type material as *Ekebergia capensis* Sparrm. (Meliaceae), but did not publish the identification. The name *Polyscias lepidota* is mentioned neither in the account of the Araliaceae, nor in that of the Meliaceae in the Flora of Ethiopia, Vol. 3, published 10 years later. The author's identification is confirmed here, and the name *Polyscias lepidota* Chiov. is formally placed in synonymy of *Ekebergia capensis* Sparrm. (Meliaceae).

I. Friis, Botanical Museum and Library, Gothersgade 130, DK-1123 Copenhagen K, Denmark. E-mail: ibf@bot.ku.dk

Introduction

In August 1939 Emilio Chiovenda (born 1871, died 1940) submitted a paper on new Ethiopian plants to the Reale Accademia d'Italia in Rome, of which he was an associate ("Aggregato"). The paper (Chiovenda 1940) contained the protologues of 66 new species and infraspecific taxa from Ethiopia, Eritrea and Italian Somaliland. The work, which was one of Chiovenda's last publications, is of very mixed quality. It contains a number of striking new species that have stood the test of time well, such as the beautiful red-flowered endemic species *Acanthus sennii* Chiov. (Acanthaceae), first observed around 1770 by James Bruce and Luigi Balugani (Hulton, Hepper & Friis 1991); *Manilkara botugii* Chiov. (Sapotaceae), which is still the correct name for an important forest tree which is narrowly distributed in south-western Ethiopia, the Imatong Mountains, and adjacent parts of Uganda; *Arisaema addis-ababense* Chiov. (Araceae), which is still the correct name for a species restricted to the surrounding of Addis Ababa; and *Erythrina burana* Chiov. (Fabaceae), which is still the correct name for a tall tree with orange red flowers known only from Harar and adjacent parts of Bale. However, not all the new taxa from 1940 have fared so well. The names for four more species of Sapotaceae (Chiovenda

1940: 42-45 & 47) are all now reduced to synonymy (Friis 1985a), just to mention a few. There is also a number of astounding misidentifications, which resulted in Chiovenda (1940) describing already well established taxa as new ones in completely wrong families, usually based on poor or inadequate material. De Wilde (1968) pointed out that the type material of *Trichilia siderotricha* Chiov. consisted of two detached leaflets of the small tree *Brucea antidysenterica* Mill. (Simaroubaceae), and nine unidentified reniform seeds with a red testa. Vollesen (1985) demonstrated that the poor type material of *Commiphora reghinii* Chiov. belonged to a species of *Euphorbia* (Euphorbiaceae) later identified by Gilbert (1995) as *Euphorbia jatrophoides* Pax. Equally far off the mark was the description of a small, immature twig of *Buxus hildebrandtii* Pax (Buxaceae) as a new species of *Garcinia* (Clusiaceae), *G. buxifolia* Chiov. The true identity of this name was demonstrated by Friis (1985b) after dissection of the very immature flower buds of the type material.

Most of the taxa described in Chiovenda (1940) are dealt with in the volumes of *Flora of Ethiopia and Eritrea* where they belong. The completely misplaced ones, such as *Trichilia siderotricha*, *Commiphora reghinii* and *Garcinia buxifolia*, have been mentioned both in the family where Chiovenda suggested they belonged, and where it has subsequently been found that they truly pertain. This, however, is not the case with *Polyscias lepidota* Chiov. (Chiovenda 1940: 32), which at least should have been mentioned as a species of uncertain position under Araliaceae on pp. 537-542 of *Flora of Ethiopia*, Vol. 3 (Bamps 1989).

This half-forgotten case was again brought to my attention when Sr. Marcello Tardelli of the Erbario Tropicale, Florence, in July, 1999, wrote to me. For curatorial purposes he wanted to know if I still stood with an identification I had written in November 1979 on a label attached to the type material at FT of *Polyscias lepidota*, and if I had published anything about my observations. I therefore had to re-examine the whole reasoning, and bring it to a conclusion by publishing the findings.

The identity of Polyscias lepidota Chiov.

Very little has been written about *Polyscias lepidota.* since it was first published. Cufodontis (1959: 636) listed the name in his check-list of Ethiopian plant species. Bamps (1974a: 121) later placed it in the synonymy of *Polyscias farinosa* (Del.) Harms in his revision of African Araliaceae. However, he pointed out that he had not seen the cited type specimen, and the accompanying distribution map (Bamps 1974b) does not show a record of *Polyscias farinosa* from the type locality of *P. lepidota* near Jimma.

In correspondence with Paul Bamps while Vol. 3 of the *Flora of Ethiopia* was in the course of publication I described him my impression of the ecological preferences of *Polyscias farinosa.* The species could be found in deciduous woodland and wooded grassland with regular burning, for example in the river gorges of Kefa, but not in the evergreen bushland and montane forests in the near surroundings of Jimma. In November 1979 I examined the type material of *Polyscias lepidota* (Fig. 1) in the Erbario Tropicale (FT) in connection with my study of the forest trees of the Horn of Africa for a book on that subject (Friis 1992). The type, which is annotated "*Polyscias* aff. *P. farinosa* ..." in Chiovenda's hand, consists of one sheet of paper, on which is mounted a rachis with opposite scars from leaflets and nine detached leaflets. The three detached terminal leaflets have more or less drawn-out, up to *c.* 1.4 cm long acuminate apex, and still attached to the leaflets are 1.3-2.5 cm long petiolules. The six detached lateral leaflets have more or less

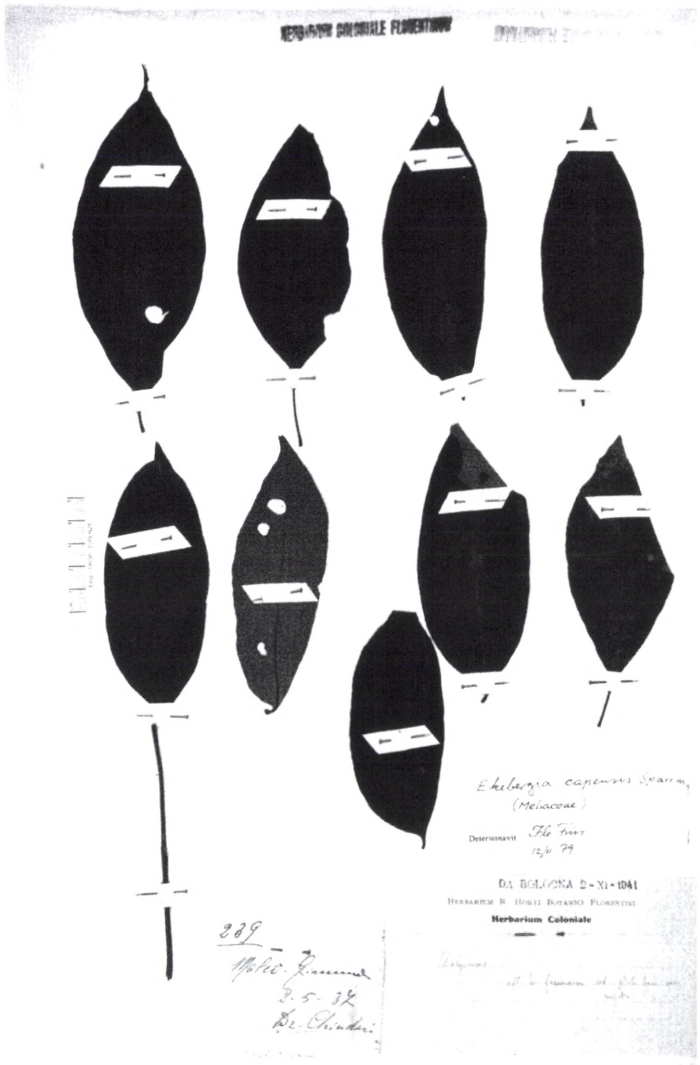

Fig. 1. Photograph of the holotype of *Polyscias lepidota* Chiov., *Chiuderi* 239 (FT), collected between the town of Jimma and Malcó (on the way to Bonga), Kefa Region, southwestern Ethiopia. Photo kindly provided by FT.

curved, acuminate apex, more or less oblique base, and very short, often bent petiolules. Other dimensions and overall morphology are as described by Chiovenda.

Chiuderi, a little known collector, had collected the type material of *P. lepidota* as his no. 239. The type locality, "Malcó-Gimma", is somewhere between the town of Jimma, capital of the old Kefa Region (KF), and Malcó. Guida d'Italia (1938) described the latter place as a site of colonial agricultural development, reached by driving *c.* 3 km out of Jimma along the road to Bonga, past the airport, and a few km to the right, up into the hilly country which overlooks Jimma. The altitude of the type locality is therefore probably 1700-2000 m, and, like today, the area must have supported a mosaic of farmland and secondary evergreen bushland with scattered trees, and must have had good rainfall well distributed through the year.

Polyscias farinosa is, as mentioned, a species of deciduous woodland and wooded grassland associated with rocky outcrops in the deep river valleys of the Ethiopian Plateau, where regular burning of the extensive and tall grasslands occur. *P. farinosa* can be found in the upper reaches of the Ghibe Gorge, for example on some rocky outcrops between Abelti and Assendabo, *c.* 100 km from Jimma towards Addis Ababa, and in the Omo Valley between Waka and Soddu; I have collected it in both places. Most likely, it also occurs in the Gojeb Valley, but I have never seen *Polyscias farinosa* in the near surroundings of Jimma.

When studying the type material of *P. lepidota* in 1979, I decided that this scanty and fragmented leaf-material should all be referred to *Ekebergia capensis* Sparrm. (Meliaceae). This is a very common tree in the mosaic of farmland and secondary evergreen bushland with scattered trees which covers most of the hills around Jimma. I noted this identification on a *determinavit* slip. The type material is a fairly good match for leaf-material of *Ekebergia capensis,* especially poorly preserved material that has gone black on drying, except for the pale grey lower surface of some of the lateral leaflets. Moreover, most of Chiovenda's description in the protologue of *Polyscias lepidota* fits leaves of *Ekebergia capensis* very well. The dimensions of the leaflets, their papery texture and overall morphology, the acuminate apex which may be slightly curved or falcate, the characteristically unequal base which is wider in the apical than in the basal half, and the pale or grey-glaucescent undersides.

Chiovenda points to the unequal base of the lateral leaflets of the type material as an optimal diagnostic character separating *Polyscias lepidota* from the subcordate bases of the leaflets of *P. farinosa.* In fact, the leaflets of the Ethiopian species of *Polyscias, e.g. P. fulva* (Hiern) Harms and *P. farinosa,* have rounded, subcordate or cordate bases, whereas most Ethiopian species of Meliaceae have characteristic unequal base on the leaflets. The leaves of *Ekebergia capensis* offer the best match with the type material, and *Ekebergia capensis* is, as mentioned above, very common around the type locality. The leaves of other Ethiopian species of Meliaceae, including the two species of *Trichilia, T. emetica* Vahl and *T. dregeana* Sonder, do not really mach the type specimen in detail, and the distribution and ecology do not agree. The two species of *Trichilia* are not very likely to be encountered in disturbed evergreen bushland at 1700-2000 m around Jimma, as *T. emetica* is almost entirely a riverine species of lower altitudes, and *T. dregeana* occurs in lowland and transitional evergreen forest below 1500 m.

However, the following set of characters mentioned in the protologue of *Polyscias lepidota* does not fit with characters known from normal material of *Ekebergia capensis*: Chiovenda described the lower side of the leaflets as being provided with large, sparse and scattered scales mixed with plentiful, short and mealy hairs. When studying the type material in 1979 I found it difficult to observe features which fitted at all well with that part of Chiovenda's description, and to me the leaflets generally appeared to be glabrous beneath. However, a partial infection of mould fungi on some leaflets could perhaps have been interpreted as a mixture of scales and mealy hairs. The infection would have occurred during the unsuccessful conservation process, which also accounted for the blackening of the leaf-material.

I have also considered the possibility that poorly preserved leaflets of *Lepidotrichilia volkensii* (Gürke) Leroy could have been mixed into the type material or been used by Chiovenda when he prepared the description, because *L. volkensii* has scattered scale-like hairs on the lower surface of the leaflets. However, a mixture of the type material with leaflets

of *Lepidotrichilia volkensii* is not at all likely. The extant type material appears homogenous, the leaflets of *L. volkensii* are generally smaller and more narrowly lanceolate than the leaflets of the type material, and they almost always dry green, even in poorly preserved material. In Ethiopia I have almost exclusively seen *Lepidotrichilia volkensii* in closed evergreen or riverine forest, for example in Beletta Forest, *c.* 60 km south-west of Jimma, and in forests near Bonga, but hardly in secondary vegetation around Jimma. A theory that Chiovenda saw scales on leaflets that are not preserved among the current type material seems therefore farfetched.

In conclusion, I find it most probable that all the material seen by Chiovenda was of one species, and that his observation of scales was due to a misinterpretation of the material. More information about the ecological range and distribution of *Ekebergia capensis*, *Lepidotrichilia volkensii*, *Trichilia emetica* and *T. dregeana* on the Horn of Africa can be found in Friis (1992: 196-200 & Map 95-98). I will therefore stand with my tentative identification in 1979 of *Polyscias lepidota* with *Ekebergia capensis*. I still find it fully convincing. However, because of the criteria used for the inclusion of synonyms in Friis (1992: 84), the name *Polyscias lepidota* was not then included as a synonym of *Ekebergia capensis*, and a separate paper with the new synonymy was not published.

The ecological arguments I advanced in 1979 against an identification of *Polyscias lepidota* with *P. farinosa* is most likely the reason why Bamps (1989: 537) did not mention the former name under *Polyscias* in Vol. 3 of *Flora of Ethiopia*. However, Styles & White (1989: 489) did not include *Polyscias lepidota* Chiov. in synonymy of *Ekebergia capensis* Sparrm. either. The name is not mentioned in their account of the Meliaceae on p. 479-489 in the same Flora-volume. On principle, all synonyms from the Flora area should be dealt with in the *Flora of Ethiopia and Eritrea*, and I therefore find it correct formally here to place the name *P. lepidota* in synonymy of *E. capensis*.

Ekebergia capensis Sparrm. in Sv. Vet. Akad. Handl. 40: 282, tab. 9 (1779).
Type: South Africa, *Sparrmann* s.n. (S holotype).

Polyscias lepidota Chiov. (Chiovenda 1940: 32); Cufodontis (1959: 636), ***synon. nov.*** Type: Ethiopia, KF, between Malcó and Gimma [Jimma], 2.5.1937, *Chiuderi* 239 (FT, holotype; C, ETH, K, photo of holo.).

Acknowledgement

I wish to thank Sr. Marcello Tardelli of the Erbario Tropicale, Florence, for reminding me of the case, and for promptly sending me adequate photographic documentation of the type material when I asked to reconsider the case.

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Gomphocarpus (Apocynaceae: Asclepiadeae) in an African and a global context – an outline of the problem

DAVID GOYDER

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Aids to distinguish the species of *Gomphocarpus* found in Ethiopia and Eritrea are presented, together with a discussion on the wider relationships and systematic position of the genus, firstly in an African context, and secondly when New World taxa are taken into consideration.

David Goyder, The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK. E-mail: d.goyder@rbgkew.org.uk

Introduction

Gomphocarpus is a familiar genus of somewhat weedy subshrubs in the derived, asclepiad, end of the Apocynaceae. The group has presented systematists with serious difficulties for decades, with no taxonomic consensus at either the species or the generic level. In the course of a study of the group over its entire geographic range, the author was able to delimit the taxa found in the Ethiopia and Eritrea Flora region. Results are presented in the form of a key to species and a stylised diagram of corona lobes, to illustrate that apparently intractable patterns of variation can be resolved by careful observation.

Controversy remains, however, in the delimitation of the genus, with North American authors including *Gomphocarpus* within a broadly defined *Asclepias*, and Old-World specialists retaining a narrower generic concept. The context for these differing views is discussed, and areas requiring further investigation are identified.

The account of *Gomphocarpus* for the Flora of Ethiopia and Eritrea is now in press, and a revision of the entire genus (as currently understood), treating African and Arabian taxa, is nearing completion.

Gomphocarpus in the Flora of Ethiopia and Eritrea region

The Flora region contains seven species of *Gomphocarpus*. Some of these were known in the mid-19th century, but the majority of taxa were described under *Asclepias* by N.E. Brown, in the *Flora of Tropical Africa* (Brown 1902-1903). Bullock (1952, 1953a, 1953b), disagreeing with Brown's broad generic concept, restricted *Asclepias* to the New World, and placed the Old World species in *Gomphocarpus*. He neither articulated his reasons for this view,

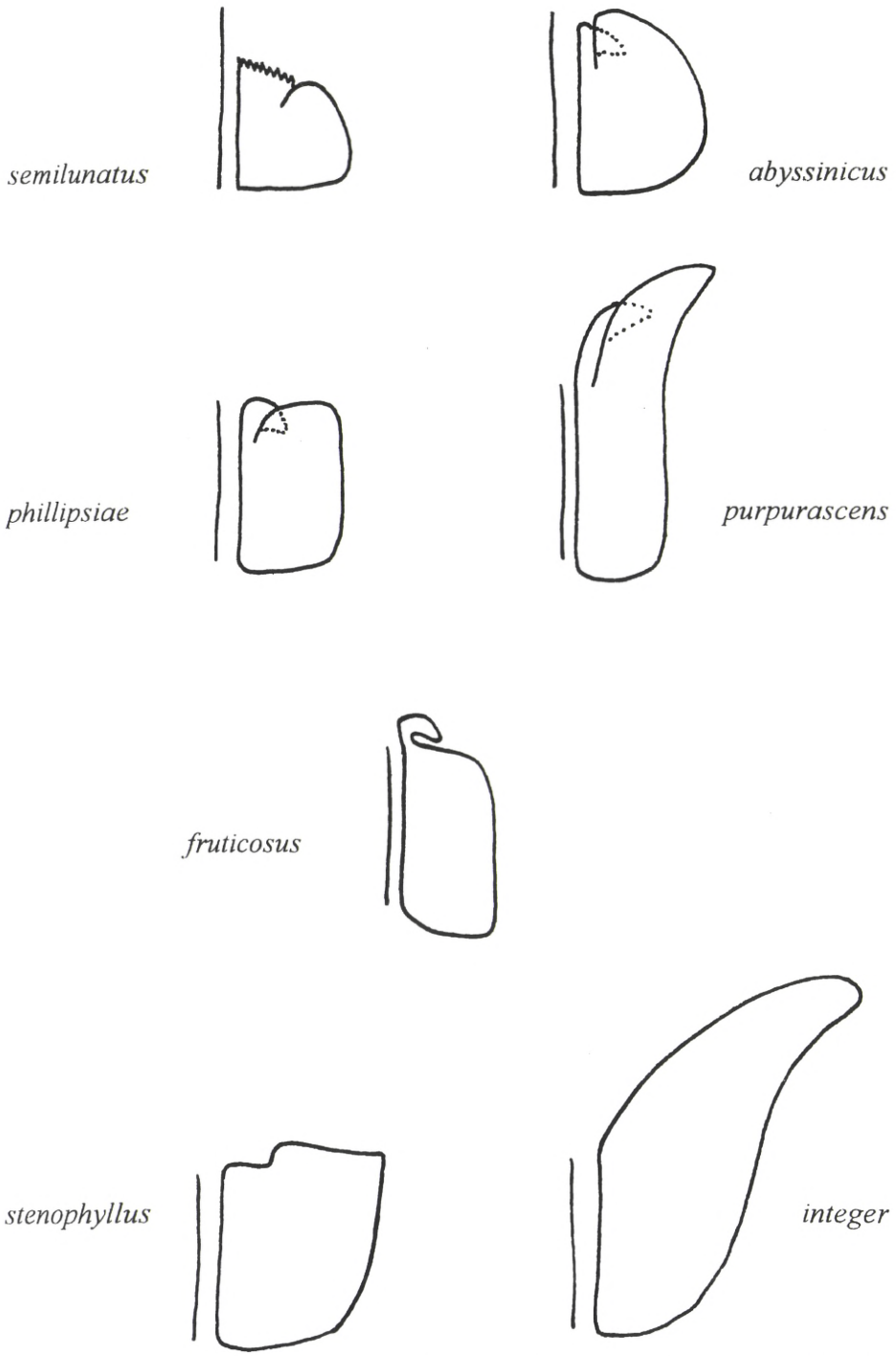

Fig. 1. Stylised corona lobes of *Gomphocarpus* species in Ethiopia and Eritrea, relative to the height of the staminal column (vertical line).

nor presented characters to support the treatment, but the two groups can generally be separated on the presence (*Asclepias*) or absence (*Gomphocarpus*) of a prominent tooth within the cavity of the corona lobe. Bullock's review of *Gomphocarpus* in tropical Africa identified some broad patterns of variation, but ultimately his treatment served only to confuse through an uneven mix of accurate nomenclature and inadequate observation of corona morphologies. Many critical but well-defined taxa were lumped into an extremely variable *G. fruticosus*, and his specific concept was never widely adopted. In the treatment presented here, many of Brown's taxa are reinstated. In a forthcoming revision (Goyder, in prep.); these will be placed in a pan-African context to reflect the wider patterns of variation.

The taxa are readily identifiable from corona morphology. A series of stylised corona lobes is presented in Fig. 1 to illustrate this point. These corona forms are correlated with features observable in nature, but which are frequently absent from herbarium sheets (growth form, branching patterns *etc.*). Collectors are encouraged to make accurate notes of such features or, even better, link photographs to herbarium specimens.

Key to species in Flora region:

1. Corolla rotate; corona lobes shorter than the column; follicles subglobose, not beaked 1. *G. semilunatus*
– Corolla reflexed; corona lobes as long as or longer than the column; follicles never subglobose, narrowing gradually or abruptly into a beak 2
2. Softly branched shrubby herbs; corona lobes ± entire; sepals ovate 3
– Stiffly branched shrubby herbs; corona lobes with a pair of proximal teeth pointing along or between upper margins; sepals lanceolate or triangular 4
3. Corona lobes oblong, taller than the column; follicles generally subglobose at the base, narrowing abruptly into an attenuate beak; corolla mostly white or cream 6. *G. integer*
– Corona lobes quadrate, ± as tall as the column; follicles more slender, narrowing gradually into the attenuate beak; corolla yellow 7. *G. stenophyllus*
4. Corona lobes brown or purple, without a distinct notch on upper margins at base of proximal teeth; corolla yellow or greenish yellow 2. *G. fruticosus*
– Corona lobes cream or green, upper margins with a distinct notch at base of proximal teeth; corolla white or cream, rarely green 5
5. Corona lobes 4.5-6 mm long, taller than the column; upper parts of the plant frequently tomentose 4. *G. purpurascens*
– Corona lobes 2-4 mm long, ± as tall as the column; upper parts of the plant pubescent but never tomentose 6
6. Corona lobes quadrate, upper margins rising gently from notch at base of proximal teeth; leaves mostly less than 5 cm long, with strongly revolute margins 3. *G. phillipsiae*
– Corona lobes D-shaped, upper margins forming an acute angle by the proximal teeth then falling away distally: leaves 7-14 cm long, margins weakly to strongly revolute 5. *G. abyssinicus*

The wider African picture

Gomphocarpus comprises a series of critical complexes containing 25 taxa in Africa and the Arabian Peninsula. There is a core group of 15 shrubby species, with a satellite group of 5 species with one or more annual stems arising from a woody rootstock. A revision of the genus is nearing completion (Goyder, in prep.). More distant, but clearly related, are genera such as *Pachycarpus* (revised by Goyder

(1998a) for tropical Africa and Smith (1988) for South Africa), *Stathmostelma* (Goyder 1998b), *Trachycalymma* (Goyder 2001) and *Xysmalobium*, each with their own distinctive suites of morphological characters. Further groups of species occur in southern Africa, although many of these have not yet been given generic rank. See Appendix 1 for a summary of the Old World genera that form a natural group around *Gomphocarpus*.

Asclepias in the Americas

Asclepias in the New World comprises *c.* 120 species, mostly in Mexico and the southern United States (Woodson 1954), but with a dozen species in drier parts of South America (Bollwinkel 1969). Vegetative diversity parallels or even exceeds that in African genera, but the floral morphology is relatively conservative, with far fewer species diverging markedly from the basic coronal plan. There are, nevertheless, some species groups with highly derived coronas analogous to Old World forms – for example, subgenus *Asclepiodora* has parallels with some of the more extreme *Trachycalymma* species from Africa. The New World treatment of *Asclepias* in outlined in Appendix 1.

How do the two systems relate?

Can the two systems be integrated and what are the factors that limit our understanding of the group as a whole? Huge morphological diversity in *Gomphocarpus* and related groups in Africa has resulted in their recognition at generic rank, while a lower, but still substantial, degree of diversity in the Americas is recognised taxonomically within a single variable genus *Asclepias*. Morphologically, the African genera that appear most closely allied to American *Asclepias* are *Gomphocarpus* and *Stathmostelma*, with the other African groups showing progressively less affinity.

Little attempt has been made to unify the classification globally and, as most potentially useful morphological characters are inextricably linked to functional pollination syndromes, it is not at all clear whether the morphological similarities displayed by a number of Old and New World species pairs are a result of close phylogenetic relation or are due to convergence. The latter is thought to be more likely in the case of *Asclepias lynchiana* (NW) and *Pachycarpus lineolatus* (OW), which show both vegetative and floral similarities; *Asclepias subulata* (NW) and *Gomphocarpus filiformis* (OW), both adapted vegetatively to extreme desert conditions; and *Asclepias tuberosa* or *A. barjoniaefolia* (NW) and *Stathmostelma pauciflorum* (OW) which share the same brightly coloured visual attraction mechanisms.

Traditional floral characters are invaluable for delimiting species, but have severe limitations at higher rank when they are so closely linked to, and are probably driven by, pollinator pressures. There is a serious danger that a global classification of the *Asclepias* group based purely on morphology would in effect be a classification of pollination syndromes rather than reflecting the evolutionary history of the group. Disparities of basic data and understanding of the mechanisms on the two continents are striking. Pollination data is all but unknown for African taxa in their native environment, whereas the American literature is replete with studies on pollinators and population studies of North American species. See Appendix 2 and 3 for a comparison.

Fishbein (1996) analysed the morphology of many of the relevant taxa cladistically, but the results are still arguably skewed by heavy reliance on pollination-related organs. His results place the four African *Gomphocarpus* taxa sampled in widely separate parts of American *Asclepias*, a situation not easy to explain convincingly, and with the remaining African genera more basal. Fishbein, Goyder, Liede and

Nicholas are now sampling across the spectrum to investigate the molecular systematics of the group in the expectation that a more independent source of data will shed some light on evolutionary relationships in the group.

Acknowledgements

I am most grateful to the compilers of ASCLEPOL for access to their database on putative pollinators of the Asclepiadeae and the associated literature. My attendance at the meeting was made possible by a generous grant from the Danish Natural Science Research Council and the Royal Danish Academy of Sciences and Letters.

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Appendix 1. A survey of *Asclepias* sensu latissimo.

<table>
<tr><th colspan="4">Asclepias sensu latissimo – c. 380 spp.</th></tr>
<tr><th colspan="2">a. Old World</th><th colspan="2">b. New World</th></tr>
<tr><td>Gomphocarpus</td><td>25 spp. in 2 informal grups (Goyder in prep.)</td><td>Asclepias</td><td>c. 120 spp. in 9 subgenera (Woodson 1954); Bollwinkel 1969)</td></tr>
<tr><td>Stathmostelma</td><td>13 spp. (Goyder 1998)</td><td>subgen. Asclepias</td><td>in 9 series – includes Gomphocarpus fruticosus</td></tr>
<tr><td rowspan="2">Asclepias
Xysmalobium</td><td rowspan="2">A polyphyletic assemblage of c. 80 spp. In 7 major groups (Nicholas & Goyder unpubl.) remaining in these two genera from Brown (1902-1903 & 1907-1909)</td><td>subgen. Podostemma</td><td></td></tr>
<tr><td>subgen. Anantherix</td><td></td></tr>
<tr><td>Trachycalymma</td><td>10 spp. (Goyder 2001)</td><td>subgen. Asclepiodella</td><td></td></tr>
<tr><td>Glossostelma</td><td>12 spp. (Goyder 1995)</td><td>subgen. Acerates</td><td></td></tr>
<tr><td rowspan="2">Pachycarpus</td><td rowspan="2">37 spp. (Smith 1988; Goyder 1998)</td><td>subgen. Solanoa</td><td></td></tr>
<tr><td>subgen. Polyotus</td><td></td></tr>
<tr><td>Kanahia</td><td>2 spp. (Field et al. 1986)</td><td>subgen. Asclepiodora</td><td></td></tr>
<tr><td>Aspidonepsis</td><td>5 spp. (Nicholas & Goyder 1992)</td><td>subgen. Podostigma</td><td></td></tr>
<tr><td>Aspidoglossum
Schizoglossum
Miraglossum</td><td>34 spp.
12 spp. (Kupicha 1984)
7 spp.</td><td colspan="2" rowspan="4"></td></tr>
<tr><td>Stenostelma</td><td>3 spp. (Bullock 1952; 1957)</td></tr>
<tr><td>Parapodium
Woodia
Periglossum
Cordylogyne
Fanninia</td><td>3 spp.
3 spp.
4 spp. (Brown 1908)
1 sp.
1 sp.</td></tr>
<tr><td colspan="2">Undescribed or unplaced c. 15 spp.</td></tr>
</table>

Appendix 2. Inferred pollination of the New World species. A list of insects observed with pollinia attached under natural conditions.

Asclepias cornuti **Coleoptera:** Scarabaeidae. **Diptera:** Midasidae. **Hymenoptera:** Apidae; Scoliidae; Sphecidae; Vespidae. **Lepidoptera:** Danaidae; Hesperiidae; Nymphalidae; Papilionidae; Pieridae	Robertson (1891)
A. cryptoceras **Hymenoptera:** Apidae	Payson (1916)
A. curassavica **Hymenoptera:** Formicidae; Vespidae. **Lepidoptera:** Danaidae; Heliconiidae; Nymphalidae; Papilionidae; Pieridae	Atsatt (1969); Bierzychudek (1981); Chaturvedi & Pant (1986); Ule (1897)
A. exaltata **Hymenoptera:** Apidae. **Coleoptera:** Cantharidae	Queller (1985)
A. incarnata **Coleoptera:** Cantharidae; Scarabaeidae. **Diptera:** Conopidae; Midasidae; Stratiomyidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Colletidae; Eumenidae; Halictidae; Nyssonidae; Pompilidae; Scolidae; Sphecidae; Tiphiidae; Vespidae. **Lepidoptera:** Arctiidae; Danaidae Hesperiidae; Libytheidae; Nymphalidae; Papilionidae; Pieridae	Kephart (1979); Macior (1965); Robertson (1887, 1891 & 1928)
A. longifolia **Coleoptera:** Scarabaeidae. **Hymenoptera:** Apidae; Megachilidae; Pompilidae; Sphecidae	Robertson (1887, 1891 & 1928)
A. purpurascens **Diptera:** Conopidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Megachilidae. **Lepidoptera:** Hesperiidae; Nymphalidae	Robertson (1887, 1891 & 1928)
A. solanoana **Hymenoptera:** Apidae	Lynch (1977)
A. sullivantii **Diptera:** Conopidae; Stratiomyidae. **Hymenoptera:** Apidae; Ichneumonidae; Megachilidae; Sphecidae. **Lepidoptera:** Danaidae Hesperiidae; Lycaenidae; Nymphalidae; Papilionidae; Pieridae	Robertson (1887, 1891 & 1928)
A. syriaca **Coleoptera:** Lampyridae. **Diptera:** Anthomyidae; Calliphoridae; Conopidae; Midasidae; Syrphidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Colletidae; Eumenidae; Formicidae; Halictidae; Megachilidae; Scolidae; Sphecidae; Vespidae. **Lepidoptera:** Arctiidae; Ctenuchidae; Danaidae; Geometridae; Hesperiidae; Lycaenidae; Noctuidae; Nymphalidae; Pentatomidae; Pieridae; Satyridae; Sphingidae. **Neuroptera:** Chrysopidae	Jennersten & Morse (1991); Kephart (1979); Macior (1965); Morse (1981 & 1982); Robertson (1928); Willson & Bertin (1979); Willson & Rathcke (1974)
A. tomentosa **Hymenoptera:** Apidae	Krombein et al. (1979)
A. tuberosa **Diptera:** Conopidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Halictidae; Megachilidae; Scolidae; Sphecidae; Vespidae. **Lepidoptera:** Ctenuchidae; Danaidae; Hesperiidae; Lycaenidae; Noctuidae; Papilionidae; Pieridae	Fishbein & Venable (1996); Robertson (1887, 1891 & 1928)
A. verticillata **Coleoptera:** Cantharidae. **Diptera:** Conopidae; Midasidae; Muscidae; Sarcophagidae; Syrphidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Argidae Colletidae; Eumenidae; Halictidae; Megachilidae Pompilidae; Scolidae; Sphecidae; Tiphiidae; Vespidae. **Lepidoptera:** Arctiidae; Danaidae Hesperiidae; Noctuidae; Nymphalidae; Pieridae	Kephart (1979); Macior (1965); Robertson (1887, 1891 & 1928); Willson & Bertin (1979)
A. viridiflora **Hymenoptera:** Apidae; Sphecidae	Robertson (1887 & 1928)
A. viridis **Hymenoptera:** Apidae	Bernhardt (1990)

Data from ASCLEPOL (http:\\www.uni-bayreuth.de) compiled by Jeff Ollerton (Nene-University College, Northampton, UK) & Sigrid Liede (University of Bayreuth, Germany).

Appendix 3. Inferred pollination of Old World species. A list of insects observed with pollinia attached under natural conditions

Gomphocarpus physocarpus (Australia – introduced) **Hymenoptera:** Apidae; Formicidae; Ichneumonidae; Pompilidae; Vespidae **Lepidoptera:** Danaidae	Forster (1994)
Gomphocarpus sp. (Europe – introduced) **Hymenoptera:** Apidae; Vespidae	Ollerton (unpublished, 1995)
Gomphocarpus 2 spp. (South Africa) **Coleoptera:** Lycidae **Hymenoptera:** "several species of winged Hymenoptera" **Lepidoptera:** Nymphalidae	Weale (1873)

Data from ASCLEPOL (http:\\www.uni-bayreuth.de) compiled by Jeff Ollerton (Nene-University College, Northampton, UK) & Sigrid Liede (University of Bayreuth, Germany). See database for Ollerton reference cited above.

Fitting pieces together – Pterodiscus Hooker (Pedaliaceae) in tropical NE Africa. A case study

HANS-DIETER IHLENFELDT

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The genus *Pterodiscus* presents difficult taxonomic problems, especially in tropical NE Africa, which are mainly due to: (1) high variability in nearly all characters, albeit the fruit morphology being the most stable character complex; (2) clines and character introgression, where distribution areas are in contact or overlap; (3) very inadequate type specimens, often not exhibiting the taxonomically important characters, and subsequent incomplete, sometimes even erroneous descriptions. Due to intensified collecting during the two last decades and the availability of living material and photographs taken in the natural habitat, it has now been possible to clarify the taxonomy of the tropical NE African species and to provide more complete descriptions. The presence of three fruit types that do not agree with the original generic description, necessitates a reconsideration of the concept of *Pterodiscus*. *Pterodiscus* in its present circumscription cannot be considered a natural group from a strictly phylogenetic point of view. The genus is a good example of the often irreconcilable conflict between practical (Linnaean) and phylogenetic (monophyletic or cladistic) taxonomy, currently a topic of discussion in the literature.

Prof. Dr. Hans-Dieter Ihlenfeldt, Institut für Allgemeine Botanik, Universität Hamburg; Private address: Ostseestr. 40, D-24369 Waabs, Germany. Email: hd.ihlenfeldt@t-online.de

Introduction

The family Pedaliaceae, comprising 13 genera (see Table 1) with approximately 70 species, is a comparatively small family, nevertheless a very interesting one in many respects.

It is an exclusively Old World family. Eight genera are confined to the African continent and one genus (*Uncarina*) is endemic to Madagascar. Four genera (*Sesamum*, *Josephinia*, *Pedalium*, *Dicerocaryum*) are mainly African, but have outliers to the east (Madagascar, India, Sri Lanka, Malayan Islands, N Australia).

The family belongs to what, in former times, has been called the Personatae; currently it is grouped either under Bignoniales (Thorne 1983) or Scrophulariales (Dahlgren 1983; Takhtajan 1980) or, quite recently, Lamiales (APG 1998).

The vast majority of the species are adapted to an arid climate, many of them preferring unstable, degraded or disturbed habitats. The African species occur in a large arc from the southern edge of the Sahara through East Africa to South Africa, Namibia and Angola (for details see Ihlenfeldt 1994).

It is well known that in the clade of Bignon-

iales/Scrophulariales the boundaries of many families are debatable. The family Pedaliaceae, however, is an exception: it is clearly delimited by an unspectacular anatomical feature, which, however, is *unique* within the Angiosperms: a remarkable type of hair. These hairs are composed of a generally short stalk of 1-3 cells and a head of invariably 4 cells (for details see Abels 1975: 28-50); after contact with water, the outer cell walls of the four cells forming the head completely dissolve, producing an enormous amount of mucilage, which is used as a lubricant in traditional medicine and for body care. The biological function of this unique structure is not yet understood.

This anatomical feature clearly separates the family from its closest relatives, the New World Martyniaceae with a similar ecology, the Old World Trapellaceae, water plants from East Asia, and the pantropical Bignoniaceae. In fact, the family Pedaliaceae has been interpreted as an ancient, highly specialised Old World branch of the Bignoniaceae (Ihlenfeldt 1967).

The family is well known for its highly specialised fruits adapted to quite diverse dispersal strategies: animal dispersal by the aid of burrs, which are either distributed by the feet (*Dicerocaryum, Harpagophytum, Josephinia)* or in the fur of passing animals (*Uncarina*); wind dispersal by the aid of winged fruits (*Holubia, Pterodiscus*), or by winged seeds (*Sesamothamnus, Sesamum* p.p.*)* or as so-called wind-ballists (*Ceratotheca, Rogeria)*. In wind-ballists the fruits only open in the upper part and stay on the plant, and the seeds are gradually expelled when the stems perform strong movements. In several cases the morphology of the fruit, adapted to a special mode of dispersal, is reflected in the generic name (see Table 1), and this implies that in this family the most important character for delimiting genera is the morphology of the fruits.

However, fruit morphology does not only serve to define the genera, but more subtle traits of the fruit types in question have also been used as important markers to delimit species within genera, *e.g.* in *Ceratotheca* and *Dicerocaryum* (Abels 1975), and in *Harpagophytum* (Ihlenfeldt & Hartmann 1970).

The 13 genera have been grouped in three tribes, which are well separated by a number of characters (Table 1).

Sesamothamneae with the sole genus *Sesamothamnus*. The species of this genus are large shrubs or even trees. The fruits are woody flattened capsules, which release seeds with broad wings. The most striking feature of this genus, however, is the succulence of the main stems.

Without any doubt, *Sesamothamnus* is the most primitive extant representative of the family. It combines certain features that are characteristic of the two remaining tribes, and could, therefore, well be the ancestor of these generally more advanced tribes. Moreover, this genus is very close to the family Bignoniaceae, and, in fact, inclusion in Bignoniaceae has been discussed in detail *e.g.* by Bruce (1953), but, in the end, rejected by the same author, mainly due to the occurrence of the mucilage hairs already described. Moreover, pollen morphology (Straka 1964; Straka & Ihlenfeldt 1965) clearly points to Pedaliaceae.

The author wishes to stress three features, which will play an important role in the further discussion:

(1) that the main stems are succulent,
(2) that the fruits are strongly sclerified (woody),
(3) and that the fruits are dehiscent.

Pedalieae: seven genera, including the genus *Pterodiscus*, which is part of a cluster of closely related genera and which will be discussed in some detail.

Sesameae: five genera including the important crop plant *Sesamum orientale* L.

Table 1. Classification and other data on Pedaliaceae.

1. The tribes and genera of Pedaliaceae R. Br.

Tribe Sesamothamneae Ihlenf.
Sesamothamnus Welw.

Tribe Pedalieae Meisn.
Uncarina (Baill.) Stapf
Rogeria J.Gay ex Del.
Pterodiscus Hooker
Pedalium Royen ex L.
Pedaliodiscus Ihlenf.
Harpagophytum DC. ex Meisn.
Holubia Oliv.

Tribe Sesameae (Endl.) Meisn.
Sesamum L.
Ceratotheca Endl.
Dicerocarum Bojer
Linariopsis Welw.
Josephinia Vent.

2. The closest relatives of Pedaliaceae and their geographical distribution and habitat:
Bignoniaceae Juss. – pantropic.
Trapellaceae Honda & Sakis – East Asian water plants.
Martyniaceae Stapf – New World, ecology similar to Pedaliaceae

3. The meaning of genus names with allusion to fruit structure:
Ceratotheca – *keras* = horn, *theke* = capsule.
Dicerocarum – *di* = 2, *keras* = horn, *karyon* = nut.
Harpagophytum – *harpago* = hook, *phyton* = plant.
Pedaliodiscus – *pedalion* = rudder, *discus* = disc.
Pedalium – *pedalion* = rudder of a ship.
Pterodiscus – *pteron* = wing, *discus* = disc.
Uncarina – *unca* = hook.

The genus Pterodiscus

The genus was established by Hooker (1844) based on a single species from South Africa, *P. speciosus* Hooker. Hooker, too, chose a name that alludes to the structure of the fruit (and, indirectly, to the mode of dispersal). He derived the generic name (in a latinised form) from the Greek *pteron* = wing, and *discos* = disk, thus characterising a fruit that is flattened and bears wings (Fig. 3).

Pterodiscus is restricted to the African continent and exhibits a distinctive NE (Somalia, Ethiopia, N Kenya, 5 species) – S (Zimbabwe, Zambia, Botswana. S Angola, Namibia, South Africa, 7 species) disjunction which, within the family, it shares with the genera *Sesamothamnus* and *Dicerocaryum* (Ihlenfeldt 1994). The two distribution centres are linked by a single, only sporadically occurring species (*P. angustifolius* Engl., Tanzania, N Mozambique).

Hooker defined his new genus by a combination of two remarkable features. These two features also occur individually (in different combinations) in related genera, *i.e.* they are not restricted to this genus.

Growth form. The plants possess as the perennating organ a thickened and ± succulent structure, termed a "caudex" (already used by Hooker in the generic description), which is partly aerial and partly subterranean. This succulent caudex ensures the survival of the plants during the dry season. Morphologically the caudex of *Pterodiscus* originates from the lower portion of the primary stem and the upper part of the taproot (Ihlenfeldt, unpublished data). The lower subterranean part of the caudex is always succulent and may form a large tuber, often bearing some lateral roots that are also swollen (Fig. 1); the upper part (at least partly aerial) also may be swollen and succulent (Fig. 2).

Every rainy season the top of the caudex produces one to several erect annual shoots, which bear single axillary flowers, from which the characteristic fruits develop. Occasionally the upper part of the caudex may be branched. The usually unbranched annual shoots are mostly unliginified, only rarely slightly lignified, and usually disintegrate at the end of the season and decay. To spot a *Pterodiscus* during the dry season, therefore, may be difficult.

It is apparent that this remarkable structure evolved from the succulent main stem found in *Sesamothamnus* by miniaturising the succulent stem and extending succulence to the upper part of the taproot. The succulent stem of *Sesamothamnus* has a characteristic translucent papery bark, and the same type of bark is found in aerial parts of the caudex in *Pterodiscus*.

As has already been mentioned, the caudex structure is not restricted to the genus *Pterodiscus*, but also occurs *e.g.* in *Harpagophytum*, where it may reach an enormous size.

Fruit. According to the original generic description, the fruit consists of a coriaceous, laterally compressed, indehiscent oblong body (which is the fruit proper), which bears 4 pergamentaceous wings, longitudinally arranged in pairs in the median plane of the fruit (Fig. 3). The fruit has two locules, each of which (in the type species, see below) contains a single (very rarely 2) oblong seed with a smooth testa. The ripe fruits become detached and are blown around by the wind, rolling on the ground like wheels.

The author wishes to stress the following features: body coriaceous, wings pergamentaceous, fruit indehiscent, single oblong seed per locule.

Again, this highly adapted fruit type is not restricted to the genus, it is also found in the genus *Holubia*. *Holubia*, however, lacks a caudex, it is a strict annual, and the fruits contain numerous seeds.

Taxonomic problems in Pterodiscus, with special emphasis on the tropical NE African species

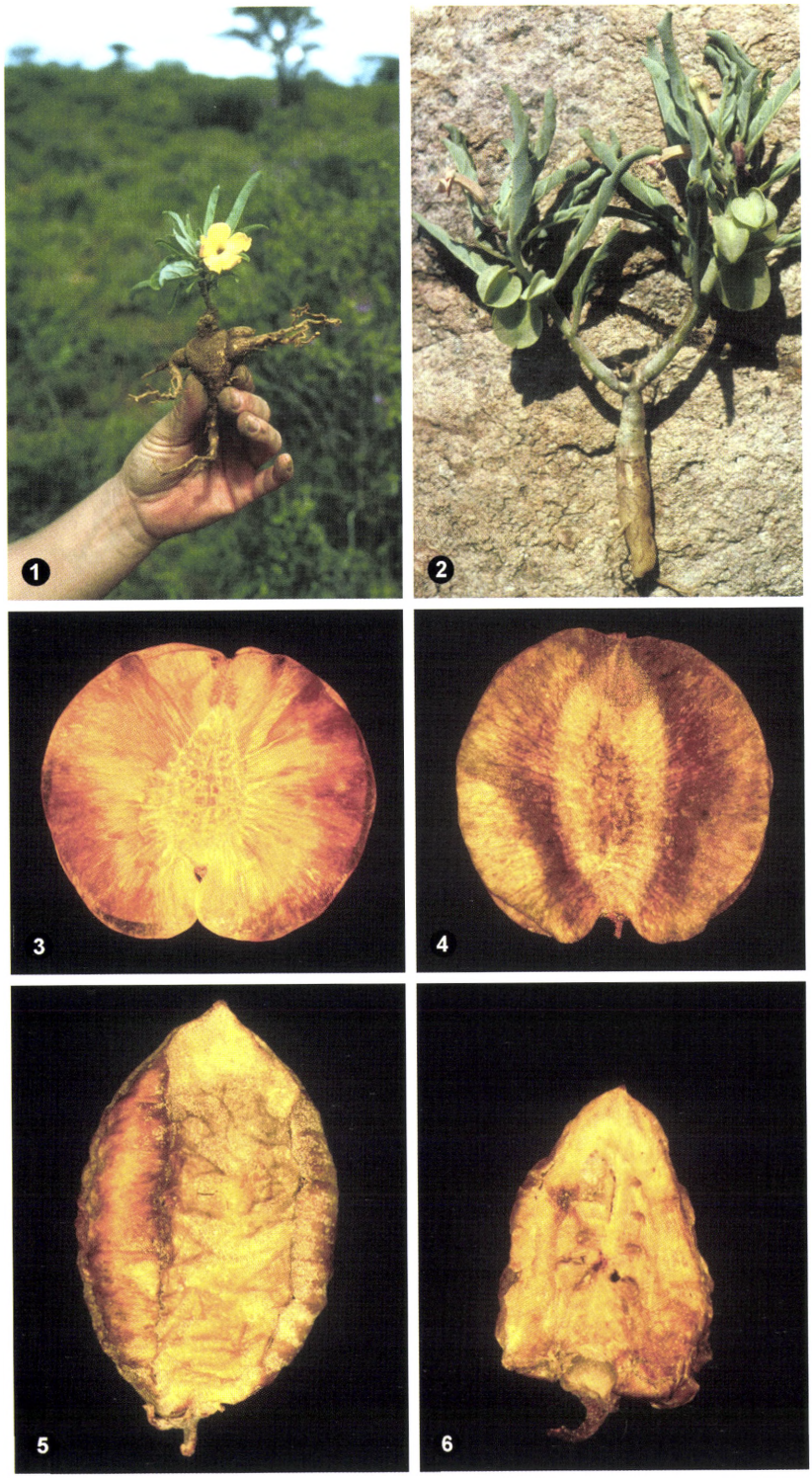
Of a total of 19 species (17 described in *Pterodiscus*, plus 2 species, originally described in related genera, but now considered as belonging to *Pterodiscus*), 10 species have been described from tropical NE Africa (Table 2).

Generally, the delimitation of the species, the interpretation of the descriptions and subsequently the correct naming of the species in *Pterodiscus* is difficult. This is mainly due to three reasons:

1. All species, especially those with a larger distribution area, exhibit a high variability in nearly all characters. In several cases single characters or complexes of characters may form topoclines (see example described below).

Fig 1-2: Habit and the two basic types of caudex in *Pterodiscus*. **Fig. 1**: *P. kellerianus* (*Specks* 804, Ethiopia, Sidamo). The lower part of the caudex forms a large succulent tuber with some lateral roots that are also swollen (succulent). The diameter of the upper part, which is partly aerial, is much less swollen and rather short; it bears a single annual shoot with a large flower. The plant has unusual oblong leaves with entire margins, apparently due to character introgression from *P. ruspolii* (see text). (Photo courtesy of E. Specks). **Fig. 2**: *P. aurantiacus* Welw. (*Wilke & Thiede* 104927, N Namiba). Subterranean and aerial parts of the caudex are of approximately the same diameter and length. The plant bears two annual shoots with flowers and several immature fruits. (Photo courtesy of J. Thiede). →

Fig. 3-6: Fruit types in *Pterodiscus* (see Table 3 and text). **Fig. 3**: *P. aurantiacus* (*Dinter* 7092, Namibia). The coriaceous body of the fruit (the fruit proper) is ovate and the upper part is much narrowed, forming a needle-like structure (compare with Fig. 4). The four pergamentaceous wings are very broad and overlap at the base of the fruit. Each locule contains a single oblong seed, and the fruit is indehiscent. Natural size: 33 x 39 mm. **Fig. 4**: *P. kellerianus* (*Friis et al.* 3260, Ethiopia, Sidamo). The coriaceous body is oblong and not narrowed in the upper part, the broad wings are pergamentaceous. Each locule contains *c.* 2-6 obovate seeds, and the fruit is tardily dehiscent. Natural size: 28 x 27 mm. **Fig. 5**: *P. coeruleus* (*Senni* 545, S Somalia). The body of the fruit is woody like the narrow wings (except their extreme margins). Each locule contains a single oblong seed, and the fruit is indehiscent. Natural size: 10 x 8 mm. **Fig. 6**: *P. saccatus* (*Bally* 9960, CN Somalia). The body of the fruit is woody, the *c.* 3 mm broad wings are pergamentaceous, but very indistinct as they are curled and pressed to the body. Each locule contains *c.* 6 obovate seeds, and the fruit is tardily deshiscent. Natural size: 20 x 13 mm.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Shape and size of the leaves are greatly influenced by the position of a given leaf within the leaf sequence of a season (the first leaves generally are much smaller and less divided, so that the plants have occasionally been described as "heterophyllous", *e.g. P. heterophyllus* from tropical NE Africa). The shape is also influenced by environmental conditions, especially by the amount of available water.

In many species size and coloration of the flower is also very variable, even within a single population.

The morphology of the taxonomically important caudex (Ihlenfeldt 1988) depends on the age of the plant. Only fully grown plants exhibit a caudex that is typical of the species in question.

Occurrence of intermediate forms (apparently due to character introgressions) in contact zones of allopatric species, or where partly sympatric species overlap (see example described below).

However, the morphology of the fruit represents the most stable and thus the taxonomically most reliable character complex (as in many other genera of the family), though the first fruits of the season may look different.

In many cases unambiguous identification is only possible if the following parts are available (an "ideal" herbarium specimen): caudex of an adult plant (plant collectors usually refrain from providing the caudex as preserving this succulent structure is troublesome); annual shoots with a full leaf sequence, at least leaves from the middle of the season; flowers; mature fruits (except the first ones). It is nearly impossible to match all these requirements in a collection made in the wild. Incomplete material, therefore, is one of the main reasons for the taxonomic problems in the genus, and this applies unfortunately also to the type specimens (see below).

A good example of problems caused by clines and character introgression, which is now fairly well documented, is the *P. kellerianus*-*P. ruspolii* complex from Somalia and Ethiopia. For the most part the two species are allopatric. *P. kellerianus* inhabits a comparatively narrow strip from NE Somalia (Bari) to C Somalia (Bakool and Gedo), then extending westward into Ethiopia (Sidamo). According to the type specimen, it is a medium-sized plant (about 15 cm high) with yellow flowers and pinnatifid leaves with a dense cover of mucilage hairs on the lower surface. *P. ruspolii* occurs in a parallel strip from N Somalia (Sanaag) through Ethiopia (Harerge, Bale, Sidamo), then extending into the whole of northern Kenya; that means, in Sidamo the areas of the two species overlap. *P. ruspolii* is a much more robust plant, with large elliptic leaves with entire margins, mucilage hairs are sparse, the long annual shoots (up to 50 cm) are often prostrate, and the fruits are larger. The flowers are yellow as in *P. kellerianus*.

Plants of *P. kellerianus* from NE Somalia are very tiny (only a few cm tall). The leaves are extremely pinnatifid, the cover of mucilage hairs extremely dense, so that the leaves appear grey, and in contrast to the type specimen, the flowers are red. Proceeding southwards, the plants become larger, the leaves less deeply pinnatifid, the cover of mucilage hairs less dense, and the colour of the flower gradually changes via pink to yellow, often tinged with orange. In the SE corner of Ethiopia the specimens nicely match the type. However, proceeding westwards into Sidamo, where the distribution area of the two species in question overlap, specimens are found with lanceolate, only slightly toothed leaves and even specimens with oblong leaves and completely entire margins (Fig. 1). In this area many specimens can no longer be identified unambiguously, as even the fruits, usually very distinctive in this genus and therefore taxonomically reliable, are very similar in these two species (and represent an aberrant type, see below).

Table 2: Availability of information on taxonomically important characters from the type specimens of the tropical NE African species of *Pterodiscus*. ex descr. = information available from the description. * = description apparently taken from another specimen.

Species	Caudex	annual shoot with flower	Fruit
P. coeruleus Chiov.	– ("annual" ex descr.)	+	+
P. kellerianus Schinz (2 syntypes)	± (seedling)	+	± (immature)
P. ruspolii Engl. (2 syntypes)	± (young plant)	+	–
P. somaliensis Baker ex Stapf	–	+	–
P. wellbyi Stapf	± (young plant)	+	–
P. saccatus S.Moore	–	+	–
P. heterophyllus Stapf	–	+	–
P. intermedius Engl. (type lost)	± (ex descr.)	+ (ex descr.)	–
P. undulatus Baker f.	± (incomplete)	+	+
P. purpureus Chiov.	+	± (no flower*)	–

2. Very incomplete or even lost type specimens. Many type specimens only consist of an annual shoot with poorly preserved flowers (Table 2), in one case even flowers are lacking, and especially mature fruits are missing. Subsequently the descriptions of the species are generally very incomplete, especially with respect to the taxonomically important characters.

Moreover, the type localities are often very vague and tracing of obsolete place-names is often difficult.

3. In some cases the descriptions are erroneous or even misleading by claiming certain characters as diagnostic ones which in reality are shared by all species of the genus. One example has already been cited, the succession of leaves in *P. heterophyllus*; another example is *P. saccatus* from NW Somalia. The epithet alludes to a sac-like protrusion at the base of the corolla tube, which can easily be identified as a reduced spur, found in several genera of the Pedaliaceae. This structure is found in all species of *Pterodiscus*, *i.e.* it is a generic character.

All these three factors are especially true for the tropical NE African species, and thus the taxonomy the tropical NE African species presents particularly difficult problems.

Due to intensified collecting during the last two decades and especially due the availability of living material and photographs taken in the natural habitat, it has been possible to present more complete descriptions and to clarify the taxonomy of these tropical NE African species. A detailed description of the fruits of all species has been published elsewhere (Ihlenfeldt 2001), and detailed specific descriptions will be included in the *Flora of Ethiopia and Eritrea* and in the forthcoming new *Illustrated Handbook of Succulent Plants* (Editor: U. Eggli, Zürich).

For the flora of Ethiopia and Somalia 4 species, now sufficiently well known, can be accepted: *P. kellerianus*, *P. ruspolii* (syn. *P. somaliensis* and *P. wellbyi*), *P. saccatus* (syn. *P. heterophyllus* and *P. intermedius*), *P. undulatus* (syn. *P. purpureus*). Only a single species, *P. coeruleus*, which is only known from the type collection from the extreme south of Somalia, remains

doubtful. This species has a strange woody fruit with equally sclerified wings (see below). The fruit is very similar to the that of *P. angustifolius* from Tanzania and N. Mozambique, and *P. coeruleus* might therefore be a purplish-flowered variety of this yellow-flowered species; however, this would extend the known area of this ecologically deviating species considerably.

Aberrant fruit types in Pterodiscus

The study of the fruits of *Pterodiscus* in tropical NE Africa revealed interesting novel facts, which shed completely new light on the relationships, the evolution and especially the genus concept of *Pterodiscus*.

There are three fruit types that do not agree with the original generic description (Table 3), two of them already known:

Stapf (1906) pointed out that at least some of the tropical NE African species contain several seeds per locule. This is true for *P. kellerianus, P. ruspolii* (and *P. saccatus*, see below) whose fruits contain 2-6 seeds per locule. In these fruits the upper part of the body is much broader (compare Fig. 3 with Fig. 4). Most of the species, including the type species, have only one seed per locule; in these species the seeds are invariably oblong and exhibit a smooth testa. In the polyspermous fruits, however, the seeds are obovate and have a sculptured testa. Moreover, what is much more interesting, these polyspermous fruits are not at all indehiscent (as claimed in the generic description), in fact they are dehiscent, though tardily so, a fact that has been overlooked until now. Against the background of the dispersal mode, it makes sense that these polyspermous fruits open some time after their detachment from the plant and gradually release their seeds while being dispersed, in contrast to those with only two seeds, which remain closed.

Another aberrant fruit type, already mentioned, has been described for *P. angustifolius* Engl. from Tanzania. This species has strongly sclerified, woody fruits with narrow wings which are also sclerified (except their extreme margins), not pergamentaceous. The locules contain a single oblong seed, and the fruit is indehiscent, which agrees with the generic description. Engler described this species twice: in 1894 as *P. angustifolius*, based on a specimen without fruits, and again in 1902, based on a specimen that possessed mature fruits, in a separate new monotypic genus as *Pedaliophyton busseanum* Engl. By choice of the generic name *Pedaliophyton* he apparently intended to indicate the similarity of the fruit of his new genus with the equally woody fruit of

Table 3: The four fruit types in *Pterodiscus*. Note the reticulate distribution of characters and character states. The fruits of the following species agree with the generic description: *P. aurantiacus* Welw., *P. brasiliensis* (DC.) Asch., *P. elliottii* Stapf, *P. luridus* Hooker f., *P. ngamicus* Stapf, *P. speciosus* Hooker, *P. undulatus* E.G. Baker; all except *P. undulatus* native af Southern Africa.

taxon & plant	fruit body	wings	dehiscent?	seeds per locule	shape of seeds
generic description (type species)	coriaceous	broad pergamentaceous	no	1	oblong
P. ruspolii *P. kellerianus*	coriaceous	broad pergamentaceous	yes	2-6	obovate
P. coeruleus *P. angustifolius*	woody	narrow woody	no	1	oblong
P. saccatus	woody	narrow pergamentaceous	yes	4-6	obovate

Pedalium, where the four (woody) wings are reduced to four spines at the base of the fruit. Bruce (1953) detected that *P. angustifolius* and *Pedaliophyton busseanum* are synonyms, and transferred *Pedaliophyton busseanum* in spite of the aberrant fruit to the genus *Pterodiscus*. As has already been mentioned, the structure of this fruit agrees with that of *P. coeruleus* (Fig. 5).

The third, still undescribed aberrant fruit type was first collected by Bally in 1954 (*Bally* 9960, K) in N Somalia. Unfortunately the collection in question only consisted of fruits and some leaves. The body of this fruit is also strongly sclerified (as in *P. angustifolius* and *P. coeruleus*), but has four narrow pergamentaceous wings, which in the mature fruit are curled and pressed to the body of the fruit and are therefore very indistinct (Fig. 6). Each locule contains several obovate seeds with a sculptured testa, and the fruit is tardily dehiscent (as in the *P. kellerianus-P. ruspolii* complex). Only recent collections revealed that this aberrant fruit type belongs to *P. saccatus* (with the two synonyms *P. heterophyllus* and *P. intermedius*, see above), already described by Moore in 1899.

Comments on the circumscription of Pterodiscus

The existence of four different fruit types within the genus, three of them basically differing from the fruit of the type species, led the present author to re-evaluate the genus concept of *Pterodiscus*.

Attempts to produce a computer-generated cladogram of the "core genera" of the tribe *Pedalieae* (*i.e.* excluding the genera *Uncarina* and *Rogeria* which apparently represent early side branches, see Ihlenfeldt 1967) failed due to the impossibility of setting up a usable matrix which would at least meet the minimum requirements. The main reasons are:

1) Nearly all characters and character states that could be used, form parts of the highly evolved dispersal systems, that means that they are functionally interdependent and, therefore, cannot evolve independently (see Ihlenfeldt 1967). These complex character syndromes are even not restricted to the fruits, but they also integrate growth form and life strategy, the latter in turn being connected with ecological constraints. This drastically reduces the number of available characters.
2) There are uncertainties about the homology (in a strict sense) of the morphological fruit structures, *i.e.* they may represent homoplasies.
3) There are uncertainties about the correct coding of the character states.

Diagram 1 ("phylogenetic tree") illustrates the putative phylogeny of the core genera of the Pedalieae. It has been constructed on the basis of a number of plausible assumptions. It is mainly based on life forms and fruit morphology, and the underlying evolutionary steps are indicated in the diagram. The starting point (bottom) is *Sesamothamnus,* with succulent stems and a sclerified dehiscent capsule containing numerous seeds with broad wings. The first step would be the formation of a caudex with annual shoots by miniaturising the whole plant, reduction of the seed wings and especially the formation of four longitudinal emergences ("wings") on the fruit, and the fruit becomes tardily dehiscent. The wings may be sclerified or pergamentaceous, the latter state is considered as derived.

What comes out clearly, even if one tries other versions, is that the species of *Pterodiscus* appear in different lineages; that means *Pterodiscus* in its present circumscription cannot be considered a natural group applying the concept of cladistics, as the species are kept together by a (relatively) primitive (plesiomor-

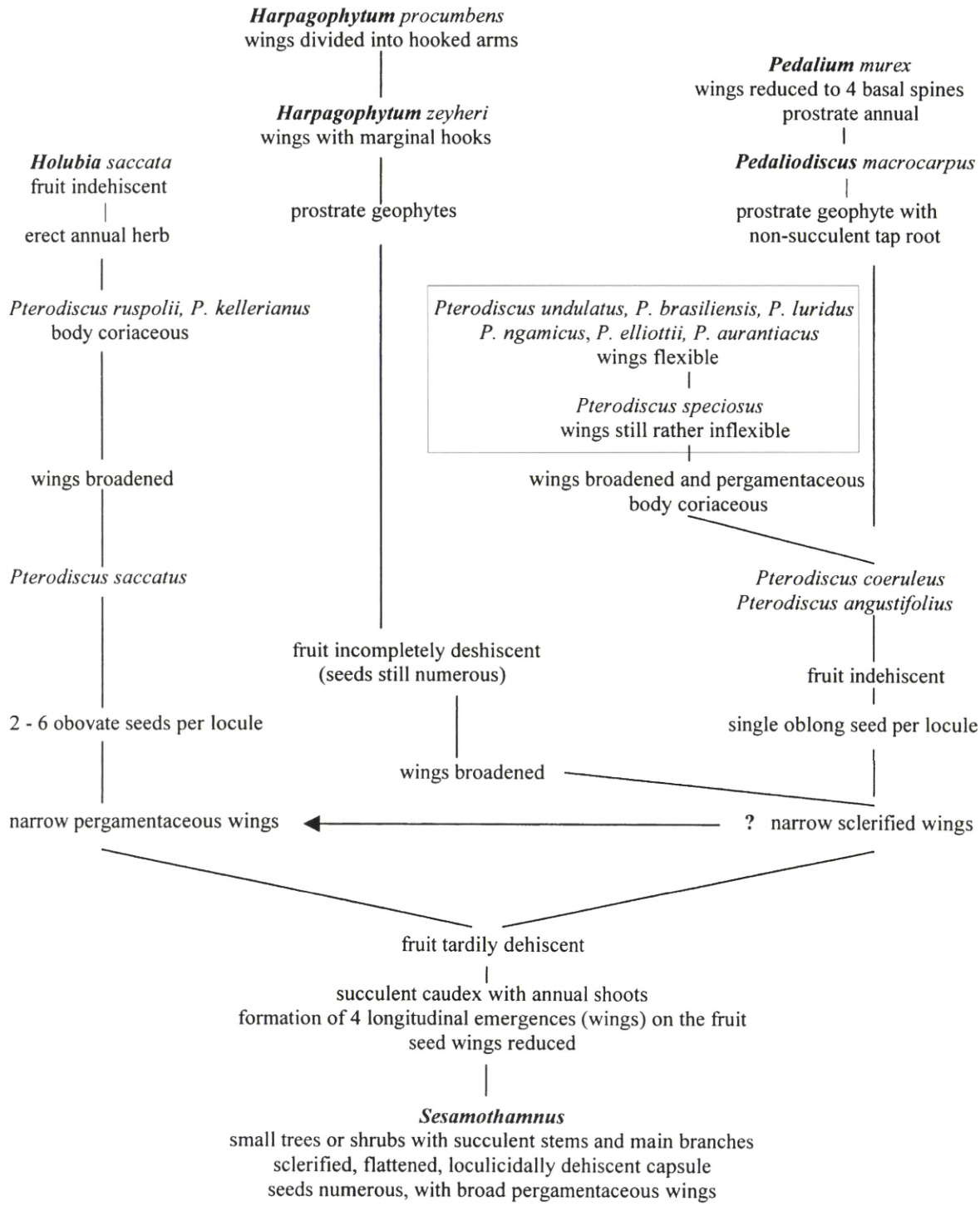

Diagram 1. Possible phylogeny of *Pterodiscus* and related genera. For details compare text.

phic) character only, namely life form based on a caudex. Only a cluster of 7 species (mainly from southern Africa), whose fruits agree with the original generic description and which includes the type species *P. speciosus*, can be considered a natural ("monophyletic") unit.

One can put it this way: *Pterodiscus* in its present circumscription appears to represent a moderately advanced evolutionary layer within the tribe Pedalieae, from which several highly specialised genera (*Holubia*, *Harpagophytum*, *Pedaliodiscus* and *Pedalium*) evolved.

Pterodiscus in the generally accepted present circumscription, is a good example of the conflict between practical (Linnaean) taxonomy and phylogenetic (monophyletic or cladistic) taxonomy. Quite recently Sosef (1997) gave convincing reasons for this irreconcilable conflict. For the case of *Pterodiscus* this means: it is easy to assign a specimen, even if the material is incomplete, if *e.g.* the taxonomically extremely important fruits are lacking, to the genus *Pterodiscus*. Strict application of phylogenetic concepts, however, would require redefinition of most of the genera in the tribe Pedalieae and produce groups difficult to circumscribe and difficult to handle with regard to the easy identification of taxa.

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The orchids of Ethiopia and Eritrea

PHILLIP J. CRIBB, SARAH THOMAS & FINN N. RASMUSSEN

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The orchid flora of Ethiopia and Eritrea comprises 160 species in 37 genera. It is poor in numbers of species and genera in comparison with other parts of tropical Africa. Although 26 endemic species have been recorded, amounting to 16% of the orchid flora, this is considerably less than previous estimates. Most of the orchids are terrestrial and only about a fifth are epiphytic or lithophytic, reflecting the relative aridity of much of the region. Surprisingly, six (23%) of the endemic species are epiphytic. Many Ethiopian and Eritrean orchids are known from one or a few collections in herbaria and, consequently, many are still poorly understood. More targeted collecting will undoubtedly increase the number of species in the flora, and allow a better understanding of their distribution, conservation status and ecology. The *Flora of Ethiopia and Eritrea* account should be considered only as a status report of current rather inadequate understanding of the orchids of the region. A better knowledge of Ethiopian and Eritrean orchids might be a useful conservation tool.

Phillip J. Cribb, The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, England, UK. E-mail: p.cribb@rbgkew.org.uk

Sarah Thomas, c/o The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, England, UK.

Finn N. Rasmussen, Botanical Institute, University of Copenhagen, Gothersgade 140, DK-1123 Copenhagen K, Denmark. E-mail: finnr@bot.ku.dk

Introduction

Orchidaceae are probably the fifth largest family in the *Flora of Ethiopia and Eritrea*, with an estimated 160 species in 37 genera (Table 1, after Friis *et al.* 1982; Cribb & Thomas 1997; Bidgood & Cribb 1999), representing four of the five subfamilies recognised in Pridgeon *et al.* (1999). This estimate represents an increase from the 123 species in 24 genera reported by Tournay (1972).

Compared with other parts of tropical and South Africa, Ethiopia and Eritrea have a rather depauperate orchid flora. Orchid numbers compare poorly with those of the much richer floras of tropical East Africa (679 spp.), West Africa (413 spp.), Central Africa (517 spp.) and South Africa (425 spp.), as appears in Diagram 1 where the numbers of epiphytes and terrestrials are also shown. Moreover, the orchid flora of the Ethiopian and Eritrean region shows a distinct cline of decreasing richness from the south-west to the north-east (Diagram 2), mirroring the similarly decreasing rainfall patterns; elevation is also a factor (Friis *et al.* 1982). The majority of Ethiopian orchids are terrestrials of the grasslands and woodlands. Only 20%

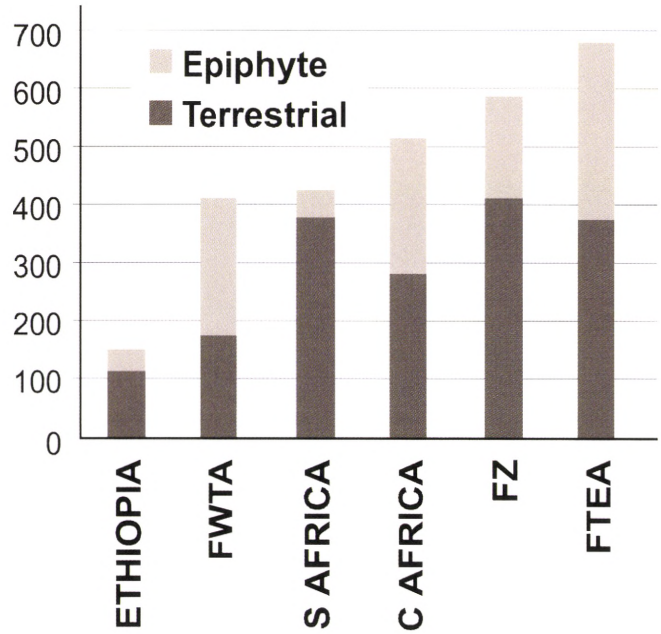

Diagram 1. Number of orchid species in major African floras. ETHIOPIA: Flora of Ethiopia and Eritrea. FWTA: Flora of West Tropical Africa. S AFRICA: Flora of Southern Africa. C AFRICA: Flore d'Afrique centrale. FZ: Flora Zambesiaca. FTEA: Flora of Tropical East Africa.

are epiphytes, and these are mostly confined to the wetter and more forested areas of the west and south-west of the country. Notable amongst the epiphytes are the white-flowered *Aerangis*, such as *A. kotschyana*, *A. brachycarpa* (Fig. 13) and *A. luteo-alba* var. *rhodosticta* (Fig. 14), three of the few Ethiopian species likely to be seen in living orchid collections.

Collectors such as R. Quartin-Dillon, W.G. Schimper and H. Steudner made some of the earliest collections of tropical African orchids in the Ethiopian and Eritrean region. Thus we have *Bonatea steudneri*, *Habenaria schimperiana*, *Diaphananthe schimperi* and *Eulophia quartiniana* (now considered conspecific with *E. guineensis*). Despite this, the diversity of the orchid family, and the popularity it has with collectors, the orchids of the region are still poorly represented in herbaria: 25 (16%) have been collected once and a further 29 have been collected only twice (c. 18%). The majority of the remaining species are known from ten or less collections. Some orchids admittedly are difficult to collect *e.g. Nervilia* which flower after the leaf has withered, and the fleshy and leathery leafed species which make poor herbarium specimens. Others flower at times when collecting is difficult such as during the rainy season. However, from these figures we can state that the orchids of the region are generally poorly collected and little understood. The forests, particularly of south-west Ethiopia are underexplored and the orchids of the Gamo-Gofa and Ilubabor regions are very poorly represented in herbaria. New records are likely as the remoter regions become better explored. No orchids have yet been recorded from the low, arid lands of the Afar region.

The larger genera

Only three orchid genera are represented by more than ten species in the region: the terrestrial genera *Habenaria* (45 species) and *Eulophia* (19 species), and the predominantly epiphytic *Polystachya* (11 species).

Table 1. Numbers of Ethiopian orchids by genus.

GENUS	TOURNAY (1972)	CURRENT NO. OF SPECIES	TERRESTRIAL (T) OR EPIPHYTIC (E)	ENDEMICS
Cheirostylis	–	1	T	
Corymborkis	–	1	T	
Holothrix	11	7	T	1
Brachycorythis	1	3	T	
Cynorkis	2	2	T	
Habenaria	36	45	T	10
Bonatea	2	2	T	
Platycoryne	1	1	T	
Roeperocharis	4	3	T	2
Disa	5	4	T	
Satyrium	7	7	T	1
Disperis	5	6	T	3
Epipactis	3	2	T	
Nervilia	2	3	T	
Vanilla	–	1	T	
Platylepis	–	1	T	
Malaxis	–	1	T	
Oberonia	–	1	E	
Liparis	1	3	T	1
Polystachya	8	12	T	3
Stolzia	–	2	E	1
Bulbophyllum	2	4	E	
Oeceoclades	–	2	E	
Pteroglossaspis	1	1	T	
Eulophia	18	19	T	2
Graphorkis	–	1	E	
Calyptrochilum	1	1	E	
Angraecum	1	3	E	
Microcoelia	1	1	E	
Diaphananthe	4	6	E	1
Bolusiella	–	1	E	
Aerangis	5	5	E	
Rangaeris	1	1	E	
Cyrtorchis	1	2	E	1
Ancistrorhynchus	–	1	E	
Angraecopsis	–	3	E	
Tridactyle	–	1	E	
Total	123	160		26

A cosmopolitan genus, *Habenaria* is particularly well-represented in tropical Africa with possibly 300 species. With twice as many species as *Eulophia,* the next largest genus in the region, it boasts over one-third of the Ethiopian orchid flora. Several sections are represented by one or two species in Ethiopia, for example, *Habenaria cornuta,* of section *Ceratopetalae,* is a terrestrial found in *Combretum-Terminalia* woodland and *Habenaria macrura,* of

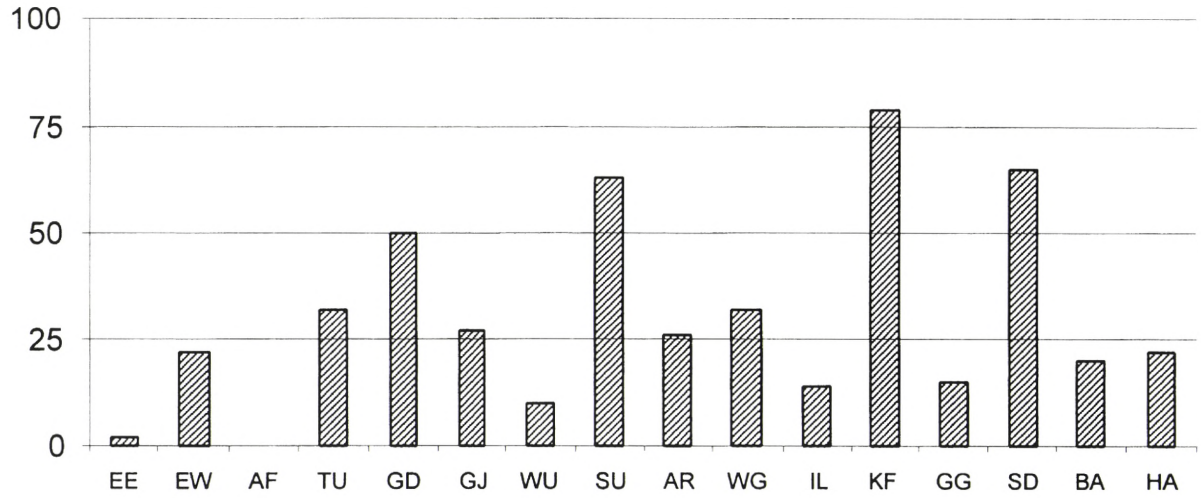

Diagram 2. Number of orchid species in the regions used to indicate distribution in the *Flora of Ethiopia and Eritrea*. For abbreviations, see Edwards, Mesfin Tadesse & Hedberg (1997). The southern, especially Sidamo, southwestern, especially Kefa, and central flora regions, especially the uplands of Shewa, have the highest number of species, the eastern and northern flora regions the lowest numbers.

sect. *Macrurae*, is a species of seasonally wet grassland. For these and many others, Ethiopia represents the northern extent of the range of the species. In contrast, Ethiopia appears to be a centre of diversity for section *Multipartitae* with 11 species. Some of the most impressive members of the genus belong in this section such as the appropriately named *H. excelsa*, *H. praestans*, and *H. decorata*.

Eulophia is represented by 19 species (almost 12%). Most of these are widespread species in tropical Africa such as *E. cucullata* and *E. odontoglossa*, while a few, such as *E. streptopetala* and *E. speciosa*, are found throughout East Africa south to South Africa. The remarkable *E. petersii*, also widespread in East and South Africa, grows in some of the most arid conditions tolerated by orchids. It somewhat resembles a *Sansevieria* when not in flower and is equally tolerant of drought because of its stout pseudobulb and succulent leaves.

Polystachya, another pantropical genus with its centre of diversity in tropical Africa, is mainly epiphytic but some species can also be found growing as lithophytes. Eleven species are found in Ethiopia. Most are plants of moist woodland or forest such as *P. lindblomii* (Fig. 7-8), *P. paniculata* (Fig. 10) and *P. golungensis* (Figs. 5-6), but some such as *P. eurychila* (Fig 9) and *P. steudneri* can survive relative aridity by losing their leaves in the dry season. Several of the Ethiopian species are widespread in tropical Africa, such as *P. cultriformis* and *P. bennettiana* (Fig. 3), but most are more restricted in their distribution, a frequent feature of *Polystachya* in Africa.

Many of the other genera, whilst common in tropical Africa, are only represented by one to a few species in Ethiopia, *e.g. Platycoryne*, *Brachycorythis*, *Disa*, *Satyrium*, *Microcoelia*, *Tridactyle* and *Cyrtorchis* (Fig. 12). The large genus *Angraecum* is represented by a few very different species: the miniature orchids *A. humile* and *A. minus*, and at the other end of the scale *A. infundibulare* (Fig. 18), one of the largest flowered orchids on the African continent.

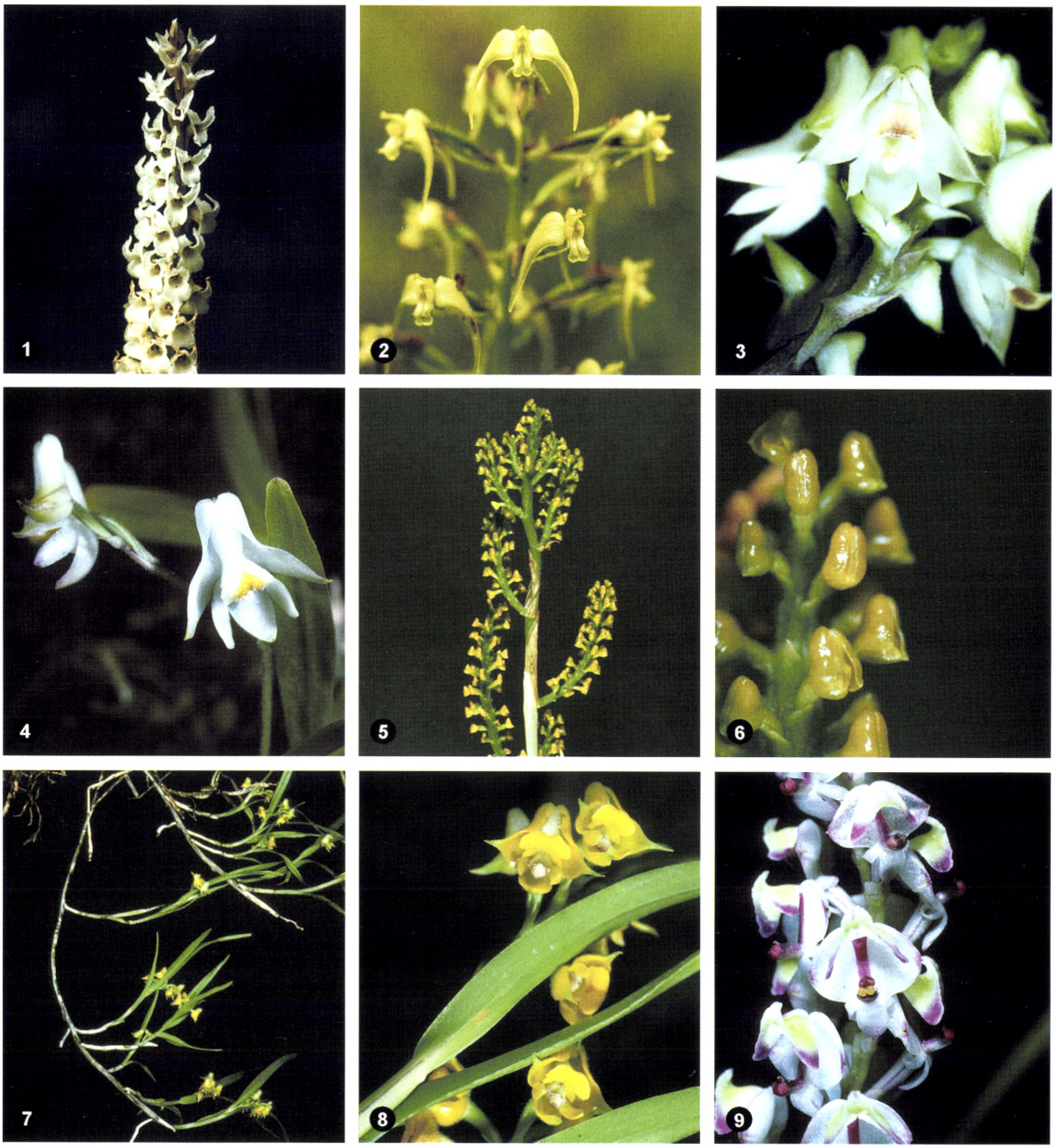

Fig. 1. *Holothrix unifolia* (Rchb. f.) Rchb. f. (Shewa, Entoto Hills, DEBL 73-13). **Fig 2**. *Habenaria cultriformis* Kraenzl. (Sidamo, SE of Neghelle, *Friis et al.* 72-917). **Fig. 3**. *Polystachya bennettiana* Rchb. f. (Bale, N of Masslo, FV 84038). **Fig. 4.** *Polystachya caduca* Rchb.f. (Bale, N of Masslo, FV 84053). **Figs. 5-6.** *Polystachya golungensis* Reichb. f. (Kefa, E of Bonga, DEBL 73-57 = *Friis et al.* 73-2321). **Figs. 7-8**. *Polystachya lindblomii* Schltr. (Kefa, Bebeka Forest, FV 84094). **Fig. 9.** *Polystachya eurychila* Summerh. (Bale, 20 km N of Masslo, FV 84030). Vouchers at C; collectors: DEBL and *Friis & al.* year 1972: *I. Friis, F. N. Rasmussen, K. Vollesen* & *G. Aweke.* FV: *I. Friis, K. Vollesen* & *M. Gilbert* year 1984. Photos by Finn N. Rasmussen.

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Biogeographical affinities

Three-quarters of Ethiopian species also occur in the *Flora of Tropical East Africa* (FTEA) region *i.e.* Kenya, Uganda and Tanzania. A comparison of the two regions shows that whilst the FTEA orchid flora has a much higher proportion of epiphytes, the Ethiopian flora is dominated by terrestrials (Diagram 1).

65 species (c. 41%) are common to both Ethiopia and West Africa. Excluding the pan-African species, the West African connection is less marked with 17 species (c. 11%) being found in West Africa and Ethiopia.

Twenty of the 23 orchid species recorded from the Arabian Peninsular also occur in Ethiopia (Cribb 1979; Thomas 1992), the majority of them being confined to the highlands of the Yemen. Amongst these is the remarkable *Epipactis veratrifolia*, often found growing in seepages in near desert-like conditions. It is an orchid of the Middle East and eastern Mediterranean, the only species from the region that also occurs in Africa. It is also found in Somalia, in an orchid flora of eleven species of which ten species are also found in Ethiopia (Pettersson 1995).

Of particular interest has been the recent discovery of *Vanilla roscheri* by Sally Bidgood and Ib Friis collected from Gamo-Gofa region of south-western Ethiopia at 1050 m a.s.l. It was growing in sandy soil in *Acacia* bushland with scattered evergreen shrubs with an annual rainfall of c. 900 mm, similar to its habitats in Kenya and coastal Tanzania (Bidgood & Cribb 1999). In this area it was apparently locally common. Apart from suggesting that a thorough survey of the orchid flora would reveal much that is currently unrecorded, the disjunct distribution of this species between the East African coast and southern Ethiopia is noteworthy and reminiscent of the distribution of some other flowering plants such as *Portulaca petersii* (Portulacaceae), *Ruellia amabilis* (Acanthaceae) and *Abelmoschus ficulneus* (Malvaceae).

Endemism

Tournay (1972) reported 50 endemic orchids in a flora of 123 species, *i.e.* about 40% endemism. The current study indicates that this is an overestimate: 26 species, just under 17% of the region's orchids, are endemic (see Diagram 3). Of these, 20 are terrestrial and only 6 are epiphytic (Table 2). If those orchids shared by Ethiopia and the Yemen are included another five species can be added. A further 10 Ethiopian species are endemic if adjacent Kenya, Uganda and Sudan are included.

Nine species of *Habenaria* are endemic, including *Habenaria cultriformis* (Fig. 2), *H. vollesenii*, *H. gilbertii*, *H. montolivaea*, *H. taeniodema* and *H. excelsa*, all montane grassland species. Amongst the other endemic terrestrial species are three of *Disperis*, two species each of *Roeperocharis* and *Eulophia*, *Satyrium aethiopicum*, which is found at between 2000 and 2500 m elevation in the highlands of Ethiopia, *Holothrix unifolia* (Fig. 1), and *Liparis abyssinica* (known only from the type collection).

← **Fig. 10.** *Polystachya paniculata* Lindl. (Kefa, at Bako river, FV 84102). **Fig. 11.** *Diaphananthe tenuicalcar* Summerh. (Bale, N of Masslo, FV 84065). **Fig 12.** *Cyrtorchis arcuata* (Lindl.) Schltr. (Kefa, Bebeka Forest, FV 84086). **Fig. 13.** *Aerangis brachycarpa* (A. Rich.) Dur. & Schinz (Illubabor, S of Gore, DEBL 72-29). **Fig. 14.** *Aerangis luteo-alba* (Kraenzl.) Schltr. var. *rhodosticta* (Kraenzl.) J. Stewart (Kefa, Bonga, DEBL 73-53). **Fig. 15.** *Diaphananthe adoxa* F. Rasm. (Kefa, Bonga, DEBL 73-52 (type)). **Fig. 16.** *Angraecopsis holochila* Summerh. (Sidamo, N of Kebre Mengest, DEBL 72-04). **Fig. 17.** *Angraecopsis cf. trifurca* (Rchb. f.) Schltr. (Illubabor, 15 km E of Tepi, FV 84109). **Fig. 18.** *Angraecum infundibulare* Lindl. (Illubabor, 15 km E of Tepi, FV 84108). Vouchers at C; collectors: DEBL and *Friis et al.* year 1972: *I. Friis, F. N. Rasmussen, K. Vollesen & G. Aweke.* FV: *I. Friis, K. Vollesen & M. Gilbert* year 1984. Photos by Finn N. Rasmussen.

Table 2. Endemic and near endemic orchids in the Ethiopian Flora. For abbreviations used to indicate distribution, see Edwards *et al.* (1997).

Species	Distribution	Altitudinal range (m)
Holothrix squammata (A.Rich.) Rchb.f.	GD, GJ, SU, AR, SD, Uganda, Sudan	2400-2800
Holothrix unifolia (Rchb.f.) Rchb.f.	GD, SU	2500-2900
Habenaria montolivaea Kraenzl. ex Engl.	AR, GD, SU, WU	1000-2600
Habenaria platyanthera Rchb.f.	GD	Unknown
Habenaria cavatibrachia Summerh.	BA, Kenya, Uganda	2100-2700
Habenaria tricruris (A.Rich.) Rchb.f.	AR, EW, GJ, SD, SU, TU	2000-3000
Habenaria aethiopica S.Thomas & P.J. Cribb	GJ, KF, SU, WG	2250-2450
Habenaria decorata A.Rich.	AR, GD, GJ, SU, WU, Uganda, Kenya	2200-3800
Habenaria quartiniana A.Rich.	BA, GD, SU, TU, Uganda, Kenya	2100-2600
Habenaria gilbertii S.Thomas & P.J. Cribb	SU	2100
Habenaria macrantha A.Rich.	AR, BA, EW, GD, GJ, SD, SU, WU, Uganda, Kenya, Somalia, Yemen	1900-3100
Habenaria taeniodema Summerh.	GJ	3150-3500
Habenaria excelsa S.Thomas & P.J. Cribb	GJ	3150-3500
Habenaria vollesenii S.Thomas & P.J. Cribb	SD	1200-1575
Habenaria antennifera A.Rich.	GJ, KF, SU, TU, Yemen	2000-3300
Habenaria cultrata A.Rich.	EW, SU, TU, Yemen, Oman	1700-2100
Habenaria cultriformis Kraenzl.	GG, HA, KF, SD, TU, Yemen	1140-2200
Habenaria rivae Kraenzl.	SD	Unknown
Habenaria perbella Rchb.f.	EW, GD, TU	1200-1500
Habenaria decumbens S.Thomas & Cribb	AR, SD	1900-2600
Roeperocharis alcicornis Kraenzl.	AR, GD, TU	2600
Roeperocharis urbaniana Kraenzl.	GD	2750
Disa pulchella Hochst. ex A.Rich.	AR, BA, GD, GJ, SD, Yemen	1800-3800
Satyrium aethiopicum Summerh.	KF, SD, SU, TU, WG	2000-2500
Satyrium brachypetalum A.Rich.	AR, SD, SU, TU, Yemen	2000-2500
Disperis crassicaulis Rchb.f.	GD, HA, SD, SU, TU	2000-2500
Disperis galerita Rchb.f.	GD, GJ, SD	2000-3800
Disperis meirax Rchb.f.	GD	3500-3800
Liparis abyssinica A.Rich.	TU	Unknown
Polystachya rivae Schweinf.	EW, KF, SU, WG	1770-2490
Polystachya aethiopica P.J. Cribb	AR, SU, SD, KF, IL	1350-2200
Polystachya caduca Rchb.f.	AR, BA, GD, KF, SD, SU, WG	2400-2600
Polystachya eurychila Summerh.	AR, KF, SD, SU, Uganda, Kenya	1700-2000

→

Species	Distribution	Altitudinal range (m)
Stolzia grandiflora P.J. Cribb	BA, SD, SU, WG	1900-2850
Eulophia abyssinica Rchb.f.	EW, GD, GJ, KF, SD, TU	2250-2600
Eulophia albobrunnea Kraenzl.	AR, BA, GJ, KF, HA, SD, SU, WU	1600-2500
Diaphananathe adoxa Rasmussen	BA, IL, KF, SD, WG, Kenya, Uganda	1300-2300
Diaphananthe candida P.J. Cribb	KF, SD, WG	2000-2100
Diaphananthe schimperiana (A.Rich.) Summerh.	AR, BA, GD, HA, KF, SD, SU, Sudan, Uganda	2100-2850
Diaphananthe tenuicalcar Summerh.	GD, GJ, KF, SD, SU, WG, Kenya, Uganda	1350-2400
Cyrtorchis erythraeae (Rolfe) Schltr.	EW, KF, SD	1350-1700
Angraecopsis holochila Summerh.	GD, SD, TU, Uganda	1500-2300

Endemic epiphytes include *Stolzia grandiflora*, a large-flowered member of tiny, creeping, peperomia-like epiphytic genus related to the Asiatic genus *Eria*, three species of *Polystachya*, including the common *P. caduca* (Fig. 4), probably the most frequently collected Ethiopian orchid, and *P. aethiopica*. The Afro-Madagascan group of monopodial orchids known as "angraecoids" has some interesting endemics in this region, including the poorly understood *Cyrtorchis erythraeae*, the charming but rare *Diaphananthe candida* that resembles a

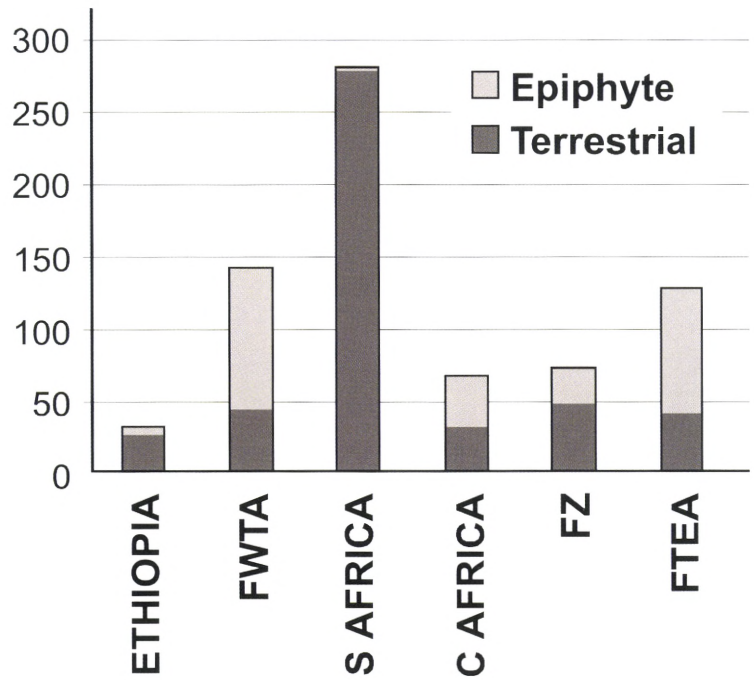

Diagram 3. Number of endemic orchid species in major African floras. ETHIOPIA: Flora of Ethiopia and Eritrea. FWTA: Flora of West Tropical Africa. S AFRICA: Flora of Southern Africa. C AFRICA: Flore d'Afrique centrale. FZ: Flora Zambesiaca. FTEA: Flora of Tropical East Africa.

small *Aerangis*, *D. tenuicalcar* (Fig. 11), and the frequent but tiny *D. adoxa* (Fig. 15), known only from a few collections outside Ethiopia. The vaguely defined genus *Angraecopsis* has a species that is almost exclusively Ethiopian, *A. holochila* (Fig. 16), and two collections of a relatively large-flowered broad-leaved species that have been identified as *A. trifurca* (Fig. 17), otherwise known only from Zambia and Grande Comore (Rasmussen 1978; unpublished observations). More collections of this entity are much needed.

Conclusions

Although Ethiopian orchids have been relatively well documented in the literature over many years compared with other families (Richard 1850; Tournay 1972; Cribb & Thomas 1997), they are still rather poorly understood. For example, little can be said of their biology, ecology and conservation status, although at first sight many would appear to be rare. We suspect that the epiphytes are particularly threatened because of widespread felling of Ethiopia's remaining woodlands and forest. However, the evidence is flimsy and more detailed surveys are urgently needed to assess the status of these species.

Novelties will most likely continue to be added to the Flora and would suggest that specialised field work aimed at the orchids would be particularly productive.

Orchids have been widely used elsewhere to highlight the importance of plant conservation and to protect orchid-rich habitats, thereby protecting other plants and animals in those places. A better understanding of the orchids of the region may be useful in helping protect its biodiversity (Hagsater & Dumont 1996). For example, orchids, particularly if they contain showy, rare or endemic orchids, can be used as an education tool, in raising public support and funding for conservation, in pin-pointing areas worthy of conservation, and for ecotourism.

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A cladistic analysis of morphological features in Bidens L. and Coreopsis L. (Asteraceae-Heliantheae) with notes on generic delimitation and systematics

MESFIN TADESSE, DANIEL J. CRAWFORD & SEUNG-CHUL KIM

MESFIN TADESSE, CRAWFORD, D.J. & SEUNG-CHUL KIM. 2001. A cladistic analysis of morphological features in Bidens L. and Coreopsis L. (Asteraceae-Heliantheae) with notes on generic delimitation and systematics. *Biol. Skr.* **54**: 85-102. ISSN 0366-3612. ISBN 87-7876-246-4.

A cladistic analysis of morphological characters obtained from representative species of *Bidens* from North, Central & South America and Africa, and *Coreopsis* from North and South America indicate that: (a) *Bidens* and *Coreopsis* are not monophyletic; (b) *Bidens* is a paraphyletic genus and is closer to *Cosmos*, *Thelesperma*, *Heterosperma*, *Isostigma*, etc., than it is to *Coreopsis*; (c) the African species that were formerly kept in *Coreopsis* form a paraphyletic grade within *Bidens* that are sister to western hemisphere groups; (d) *Coreopsis* is paraphyletic with two major clades and is restricted to the New World; and (e) the phylogeny based on morphology shows certain similarities to one generated from DNA sequences, but the relationships portrayed differ in several basic respects.

Mesfin Tadesse, Ohio State University, Department of Evolution, Ecology and Organismal Biology, Columbus, Ohio 43210-1293, USA (permanent address Addis Ababa University, Department of biology, National Herbarium, P.O. Box 3434, Addis Ababa, Ethiopia). E-mail: tadesse.1@osu.edu

Daniel J. Crawford, University of Kansas, Department of Ecology and Evolutionary Biology, Lawrence, Kansas 66045-2106, USA. E-mail: djcrawfor@yahoo.com

Seung-Chul Kim, formerly: Indiana University, Department of Biology, Bloomington. Now: University of California at Riverside, Department of Botany and Plant Sciences, Riverside, Califonia 92521-0124, USA. E-mail: sckim@citrus.ucr.edu

Introduction

Bidens L. and *Coreopsis* L. belong to the tribe Heliantheae, subtribe Coreopsidinae of Asteraceae. In a systematic review of the tribe, the Coreopsidinae was subdivided into seven informal groups (Stuessy 1977). *Bidens* L. and *Coreopsis* L., along with other genera, were put in group 1. A number of authors also place *Bidens* near *Coreopsis*, *Cosmos* Cav. and *Coreocarpus* Benth. (Smith 1975, 1989; Melchert & Turner 1990; Karis & Ryding 1994). Recently the systematic position of *Bidens* within the Coreopsidinae has been the focus of studies by Ryding & Bremer (1992) and by Karis & Ryding (1994). The latter stated that *Bidens* and *Coreopsis* offer one of "the most striking examples of difficulties with generic delimitation" in the Asteraceae.

In a cladistic analysis of the Coreopsidinae (given as tribe Coreopsideae), Ryding & Bremer (1992: 653) recognized three large generic groups, although their strict consensus tree does not resolve relationships among the groups. An analysis of 18 of the same genera (four genera have been relegated to synonymy, cf. Bremer 1994; Veldkamp & Kreffer 1991), with fuller data sets than hitherto, also produced an unresolved strict consensus tree. Shannon & Wagner (1997) pointed out that the conclusions of Ryding & Bremer (1992) "... concerning relationships within the Coreopsideae should be viewed with some caution ..." Much data are missing from their matrix (*e.g.* 23 of 37 characters are unknown for *Cyathomone* S.F. Blake, and approximately a third of the characters for *Bidens* and *Coreopsis* are recorded as variable).

One reason given for the unresolved position of *Bidens* in the cladograms generated by Ryding & Bremer (1992) was lack of diagnostic characters between it and *Coreopsis*. The traditional delimitation of these genera, which, as shown elsewhere as inadequate (*e.g.* Wild 1967; Agnew 1974; Mesfin Tadesse 1984, 1986), are adopted in their work. A number of studies, particularly on *Cosmos* (Melchert 1967, 1968, 1990a), *Dahlia* Cav. (Sorensen 1969; Giannasi 1972, 1975a, 1975b), *Coreopsis* (many articles by Crawford & Smith), *Bidens* (Hart 1979; Ballard 1986; Ganders & Nagata 1983, 1984; Mesfin Tadesse 1984, 1986, 1993; Helenurm & Ganders 1985; Mesfin Tadesse *et al.* 1995a, 1995b, 1996; Roseman 1986), *Coreocarpus* (Smith 1989; Melchert & Turner 1990), and *Thelesperma* Less. (Melchert 1963), have indicated that prior circumscriptions of genera are in need of modification in light of newly emerging data. Melchert (1975) reiterated that the main reason that *Bidens* and *Cosmos* "appear to intergrade is due to the *a priori* inclusion of all annuals with beaked or rostrate achenes within *Cosmos*. Similarly, the inclusion of all taxa with winged achenes in *Coreopsis* (Sherff 1936), without considering other features, has blurred the boundary between this genus and *Bidens*. Smith & Parker (1971) showed that the presence or absence of wings on achenes of *Coreopsis tinctoria* L. is under simple genetic control. Similar problems exist with delimiting *Coreocarpus* from *Bidens* and *Coreopsis* (Smith 1983b, 1984b, 1989; Melchert & Turner 1990).

Most North American (excluding Mexico) species of *Bidens* are annual plants and are distinct from *Coreopsis* both in capitular and gross morphology. The Mexican species, however, intergrade particularly with *Cosmos* and *Coreocarpus* (Melchert 1990b). The only true species of *Coreopsis* in the eastern hemisphere are the few cultivated and/or ornamental species: *C. grandiflora* Hogg, *C. verticillata* L. and *C. lanceolata* L.

The paucity of features distinguishing *Bidens* from *Coreopsis*, the instability of the characters traditionally used for segregating the two genera, and the large amount of phenotypic plasticity of particularly *Bidens* as exemplified by studies on amphibious taxa (Wheedon 1974) and those of oceanic islands, have obscured the boundary between *Coreopsis* and *Bidens*.

There are morphological similarities between some species of *Bidens* and *Coreopsis*. However, there are also capitular and foliar resemblances between some species of *Bidens* and other related genera, *i.e. Cosmos*, *Coreocarpus*, *Isostigma* Less., etc. In order to determine the relationships between particularly *Bidens* and *Coreopsis*, a cladistic analysis of genera of the Coreopsidinae incorporating data from previous (Ryding & Bremer 1992; Mesfin Tadesse *et al.* 1995a, 1995b) and current studies is attempted here.

The objectives of the present work are a) to determine the phylogenetic positions of *Bidens* and *Coreopsis* within the Coreopsidinae, b) to test the monophyly of *Bidens* and *Coreopsis*, and also evaluate the characters that have been

used traditionally for generic segregation, c) to provide a cladistic analysis of the relationships between *Bidens* and *Coreopsis*, (including those African species which have previously been kept in *Coreopsis*), and d) to provide an assessment of the utility of certain characters used for sectional classification in *Bidens*.

Materials and methods

Taxa

For the initial cladistic analysis of subtribe Coreopsidinae, sensu Ryding & Bremer (1992), a total of 15 genera and 28 characters were included (Appendix 1 and Table 1). From the twenty-five genera included in the subtribe by Ryding & Bremer (1992), four (*i.e. Eryngiophyllum* Greenm. (= *Chrysanthellum* Rich.), *Glossogyne* Cass., *Guerreroia* Merr., and *Neuractis* Cass. (= *Glossocardia* Cass.; cfr. Veldkamp & Kreffer 1991; Bremer 1994) have since then been relegated to synonymy. Of the remaining 21 genera, *Cyathomone* S.F. Blake, *Dicranocarpus* A. Gray, *Goldmanella* Greenm., *Ericentrodea* S.F. Blake & Sherff and *Petrobium* R.Br. are excluded from the analysis due to lack of complete data or specimens. *Megalodonta* Greene (Roberts 1985; Bremer 1994), which was considered by Sherff (1937) as a monotypic section of *Bidens* and was embedded in *Bidens* in the ITS phylogeny by Kim *et al.* (1999)), was included in the present analysis. *Trioncinia* (F. Muell.) Veldkamp (a monotypic North Australian genus 'distinguished from *Bidens* only by its alternate leaves') was likewise included in the present analysis.

Genera rather than species were used as terminal units for this analysis. It is possible that some of the genera may not be monophyletic. However, since we are not interested in investigating the phylogenetic status of genera other than *Bidens* and *Coreopsis*, it is unnecessary to replace the genera with species. Furthermore, it seems inevitable to allow some terminal units to be paraphyletic (Rieseberg & Brouillet 1994).

The first run on the entire data matrix (18 genera, 28 characters) produced an unresolved consensus tree (tree not shown). Subsequently, a few of the heterogeneous genera (*Chrysanthellum*, *Coreocarpus*, and *Fitchia* Hook.f.) and those, which assumed many different positions (*Chrysanthellum*, *Coreocarpus*, *Moonia* Arn. and *Henricksonia* B.L. Turner) on the cladograms, were excluded from the analysis, except for *Coreocarpus*. This did not adversely affect the topology. The result is presented in Fig. 1.

As shown in Fig. 1, *Bidens* is closely related to several other genera, *i.e. Thelesperma* Less., *Cosmos*, *Megalodonta*, *Heterosperma* Cav., *Narvalina* Cass., *Trioncinia*, and *Coreocarpus*. *Coreopsis* is sister to the clade containing the above mentioned taxa, as well as *Dahlia* Cav. and *Isostigma*. Therefore, in the subsequent cladistic analysis of *Bidens* and *Coreopsis*, a representative from each of the *Dahlia-Isostigma* clade, *Cosmos-Megalodonta-Thelesperma* clade, and *Heterosperma-Narvalina-Trioncinia-Coreocarpus* clade was also included. A total of 32 species and 45 characters (Appendix 2 and Table 2) were used. Several representatives of *Coreopsis* from North America (6 spp.) and Mexico & South America (3 spp.), were included. In the case of *Bidens*, several members from Africa (10 spp.), North America excluding Mexico (5 spp.), and South America & Mexico (5 spp.), were also included in the analysis.

Characters

The characters used in the analysis were obtained from herbarium specimens, plants cultivated in the greenhouse at Ohio State University and from the literature. Specimens were obtained on loan from the following herbaria (abbreviations according to Holmgren *et al.* 1990): BM, F, K, MO, OS and WAG. Details concerning character measurement

and assessment are provided in Mesfin Tadesse *et al.* (1995a). Characters that require additional explanations are provided in Appendix 2.

Character states were polarised based on out-group comparison. The characters were coded as '0' (plesiomorphic character state) and '1' or upwards (apomorphic character state).

Some genera are variable in certain features. Characters shared by all taxa in the 'in-group' and autapomorphies were excluded from the analyses.

Data analyses

MacClade 3.0 (Maddison & Maddison 1992) was used to edit the data set (Tables 1 and 2) for input into PAUP 4.0b4a (Swofford 2000). Phylogenetic analysis was performed with the aid of PAUP using Power Macintosh G3. For initial cladistic analysis of Coreopsidinae, a branch and bound search strategy was employed using maximum parsimony with characters unordered and equally weighted. In a subsequent analysis of *Bidens*, *Coreopsis*, and several other closely related genera, heuristic search option with TBR branch swapping and MULPARS on was used. A search for multiple islands of trees (Maddison 1991) was carried out with 100 replications of "random" taxa addition. Relative support for individual clades was estimated with 100 bootstraps (Felsenstein 1985) using simple addition sequence and TBR branch swapping for each bootstrap (max tree = 20000). Decay analysis (Bremer 1988; Donoghue *et al.* 1992) was also employed to provide an assessment of support for clades with trees that are three or fewer steps longer than the minimal length tree.

Choice of outgroups

Guizotia (currently in subtribe Melampodiinae, one of the subtribes allied to the Coreopsidinae according to Karis 1993) was chosen as an outgroup for the genera of the Coreopsidinae. Formerly *Guizotia* was placed within the Coreopsidinae (Stuessy 1977). *Fitchia speciosa* was chosen as the outgroup for the subsequent analysis of *Bidens* and *Coreopsis* because in the cladistic analysis of morphological features of the Heliantheae by Karis (1993), *Fitchia* is the sister group to *Coreopsis* and the group of genera allied to it. Chloroplast DNA restriction site data by Jansen & Kim (1996) also produced a similar relationship.

Results and discussion

Genera of Coreopsidinae

The analysis of fifteen genera of Coreopsidinae (Table 1, Fig. 1), for which nearly complete morphological data were assembled, resulted in six equally most parsimonious trees with a tree length of 51, consistency index (CI) of 0.58 and retention index (RI) of 0.60. *Coreopsis* is sister to a lineage that includes *Bidens*, *Thelesperma*, *Cosmos*, *Heterosperma*, *Coreocarpus*, and other mainly American genera. Thus, *Coreopsis* appears as a basal element within New World elements of Coreopsidinae.

Bidens and Coreopsis

The subsequent analysis of *Bidens* and *Coreopsis*, including several other closely related genera, produced 3098 most parsimonious trees with a length of 139, consistency index (CI) of 0.43, and retention index (RI) of 0.79 (Table 2; Fig. 2). As can be seen from Fig. 2, the strict consensus tree is not fully resolved. *Cosmos*, *Heterosperma*, *Isostigma* and *Coreocarpus*, representing the various clades in Fig. 1, are clustered with the North and South American/Mexican *Bidens*, indicating their derived position within the Coreopsidinae. There is moderate support for certain clades such as Mexican and South American *Coreopsis*, *Bidens barteri-B. prestinaria* and North American *Bidens* (Fig. 2). One of the 3098 equally parsimonious trees was ran-

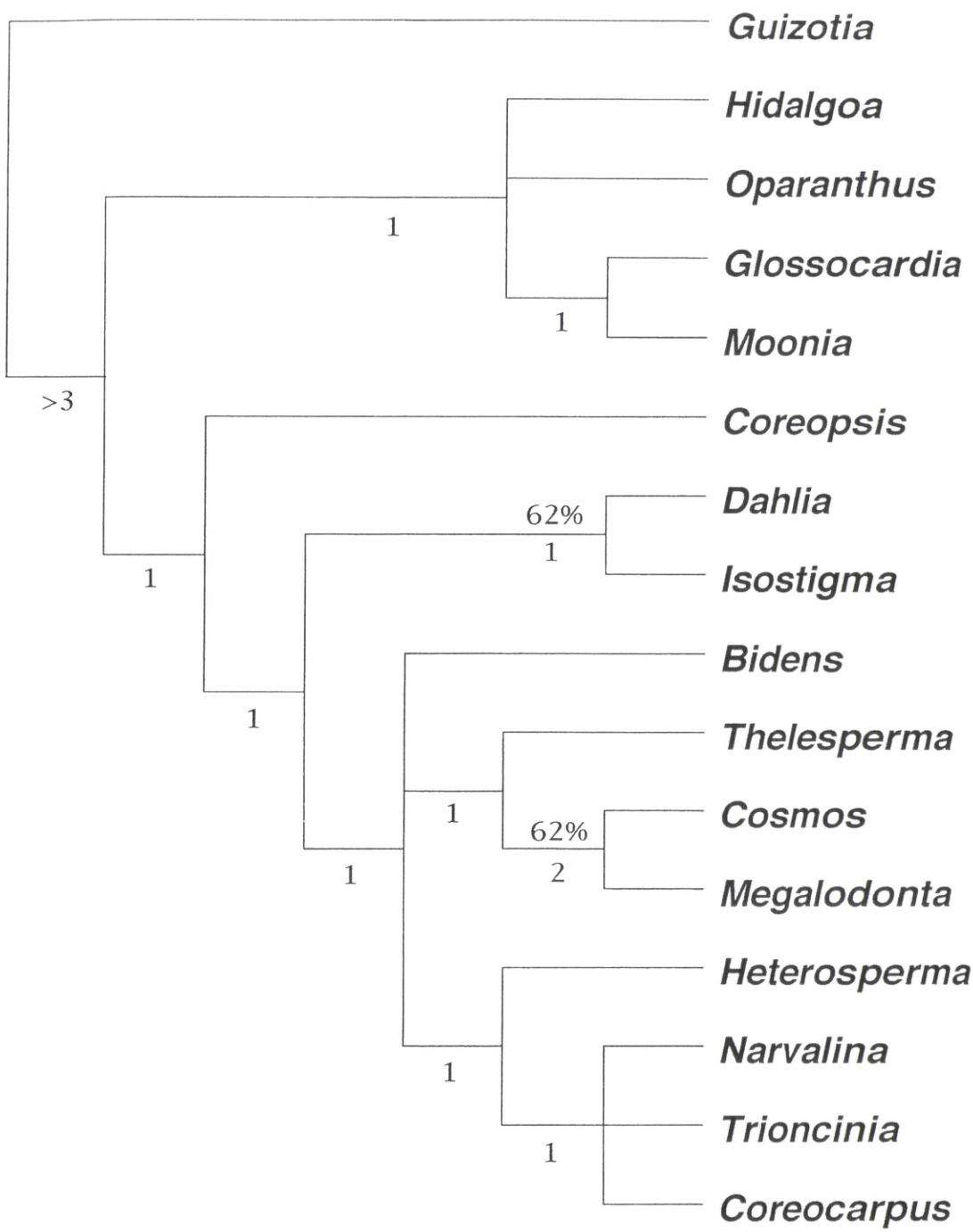

Fig. 1. Strict consensus of 6 equally parsimonious trees of genera of Coreopsidinae depicting the position of *Bidens* in relation to *Coreopsis* obtained using *Guizotia* as an outgroup. Bootstrap (%) and decay values (below horizontal lines) are given. The characters are given in Appendix 1 and the data in Table 1.

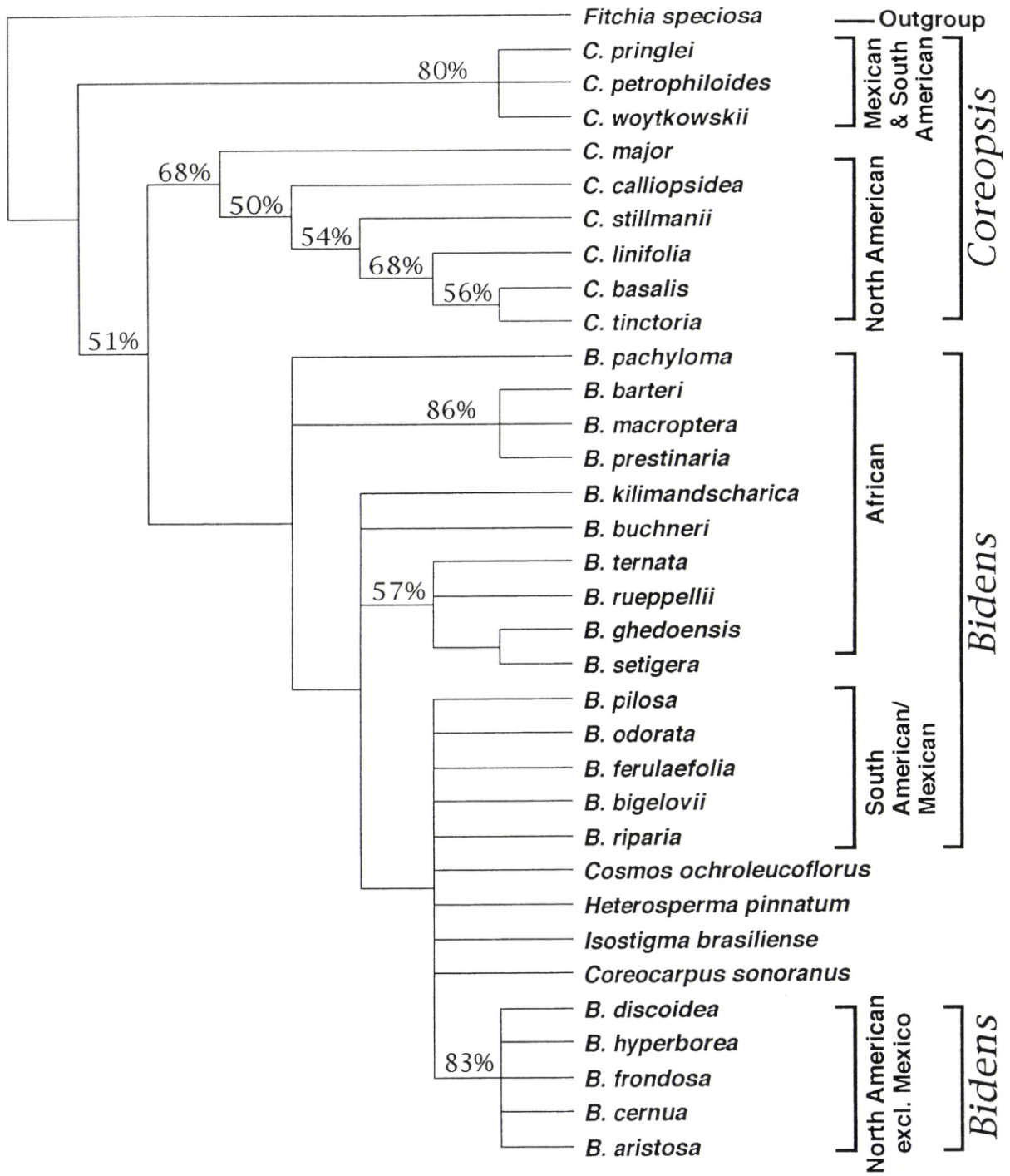

Fig. 2. Strict consensus of 3098 equally parsimonious trees of *Bidens*, *Coreopsis* and allied genera. The characters are given in Appendix 2 and the data in Table 2. Bootstrap (%) values are indicated.

domly chosen to map some of the characters on the cladogram (Fig. 3). Many of the mapped characters have not been previously employed for generic delimitation. Some of the achenial features, however, have been used in both generic delimitation and infra-generic classifications. The consistency index shows that there is considerable homoplasy but this is not unexpected in any analysis of morphological features (cf. Jansen *et al.* 1987; Ryding & Bremer 1992; Karis 1993). However, the clades are constant and they are supported by a number of non-homoplastic characters.

The shrubby or perennial Mexican and South American *Coreopsis* sect. *Pseudoagarista* (Figs. 2 and 3) forms the basal group and it is sister to the rest of *Coreopsis* and *Bidens*. This lineage is characterized by a single non-homoplastic feature (pubescence of paleae, character 16) and two homoplastic characters, one of which is seen only in one other section of *Coreopsis*, *i.e.* *C.* sect. *Pugiopappus* (A. Gray) Blake (*C. calliopsidea* (DC.) A. Gray), wherein the paleae are attached to the achene at the base and are deciduous with it (character 17). *Coreopsis* sect. *Pseudoagarista* is also distinguished from the rest of the species in *Coreopsis* and *Bidens* by an autapomorphic feature, *i.e.* regularly or irregularly 3-cleft paleae. This section of *Coreopsis* is unique in consisting of taxa with invariable achene morphology but diverse foliar features. The group occurs in Mexico, Colombia, Peru, Ecuador, and Chile. Other species within *Coreopsis* and *Bidens* have developed other means of fruit dispersal, such as winged or flat fruits, retrorsely barbed pappi, etc.

The North American species of *Coreopsis* excluding *C.* sect. *Pseudoagarista* form a monophyletic group with weak to moderate support (Fig. 2). It is supported by one non-homoplastic (character 38) and several homoplastic features (Fig. 3). These sections of *Coreopsis* have been the subject of numerous taxonomic, chemosystematic, biosystematic, and molecular systematic studies and the relationships between the sections and the species have been well documented (cf., as examples, Crawford 1969, 1970, 1971, 1976; Crawford & Bayer 1981; Crawford & Smith 1983a, 1983b, 1984, 1985; Crawford & Stuessy 1981; Crawford *et al.* 1980, 1984, 1990a & b, 1991, 1992; Smith 1972, 1973, 1975, 1976, 1982, 1983a, 1983b, 1983c, 1984a, 1984b; Smith & Crawford, 1981; Smith & Parker 1971, etc.).

Bidens and *Coreopsis* share a number of synapomorphies but these are beset with reversals (Fig. 3). Compared to *Coreopsis*, *Bidens* has more non-homoplastic synapomorphies. These include a phytomelanin layer characterized by black, commonly irregular peg-like deposits (character 34/4), and basic chromosome numbers of 12, 16, 17, 18, and 21 (character 44/2). The large germinal pores of the pollen (character 45), although homoplastic, are found only in *Bidens*. The penicellate and attenuate style arm apices with decurrent sweeping hairs (character 21), shown to be homoplastic (reversed in *Cosmos*, Fig. 3), are not found in *Coreopsis*. As shown in an earlier paper (Mesfin Tadesse *et al.* 1995b), the pollen grains of *Bidens* and *Coreopsis* are very similar and only few quantitative and qualitative differences were obtained. Of these, the difference in the size of the germinal pore (os) was quite significant with all the examined species of *Bidens* having much wider and longer ora. There was no overlap in this feature in pollen of the two genera. Although many species of *Bidens* have chromosome numbers based on x = 12, this number is also found in a few sections of *Coreopsis*.

As shown in Fig. 3, those African species with winged achenes, which were formerly placed in *Coreopsis* (Sherff 1936; Ryding & Bremer 1992), form a paraphyletic grade (with *B. pachyloma* being basal) and cluster with the rest of *Bidens*. The strongly supported (86%) *B.*

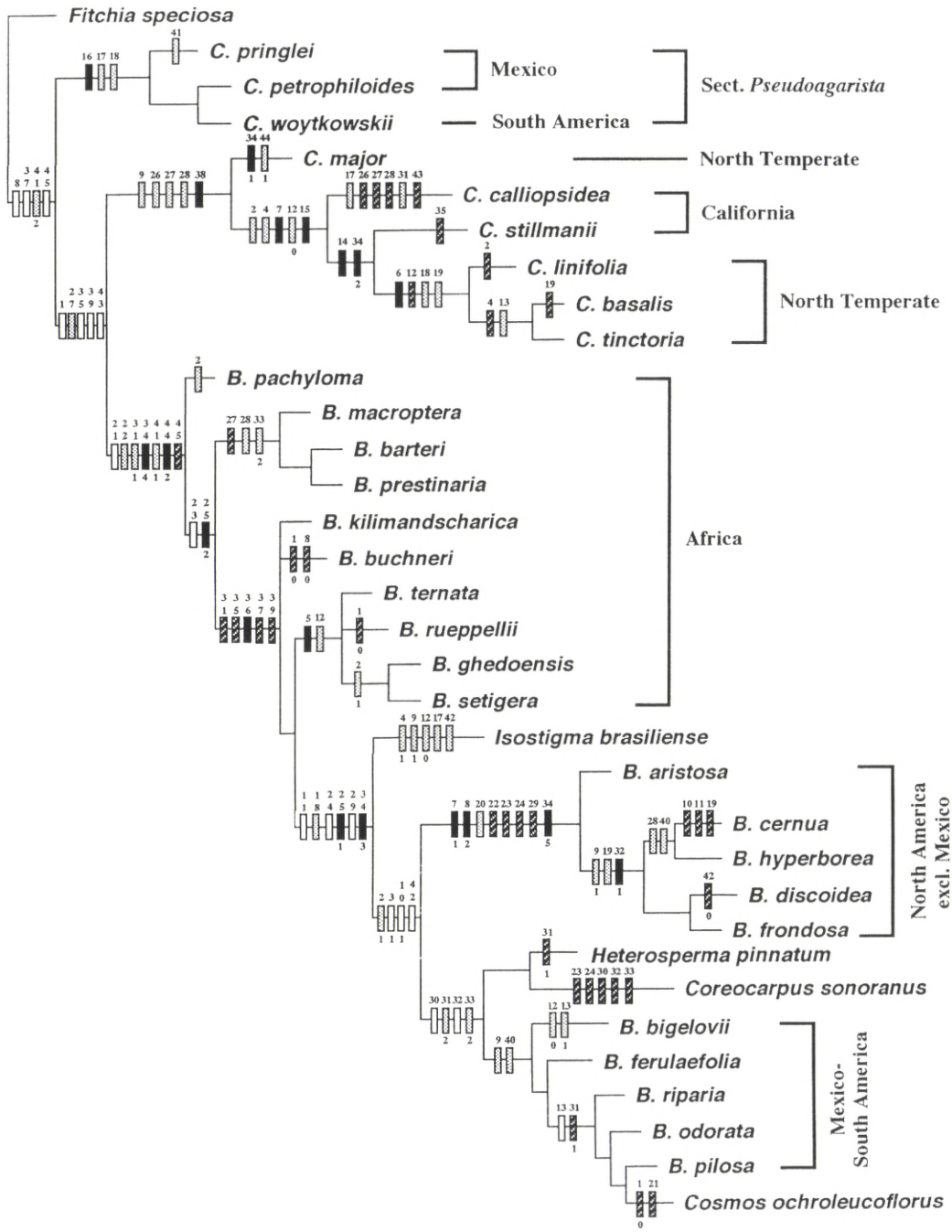

Fig. 3. One of the 3098 equally parsimonious trees of *Bidens*, *Coreopsis* and allied genera illustrating character distributions. *Fitchia speciosa* is the outgroup. Solid bars indicate non-homoplastic synapomorphies; open bars indicate homoplastic synapomorphies with reversal; stippled bars indicate parallelisms; striped bars indicate reversal. Characters and data set are as for Appendix 2 and Table 2.

macroptera-B. prestinaria clade is sister to the rest of *Bidens* and the other genera in the subtribe. The remaining African *Bidens*, *i.e. B. kilimandscharica* to *B. setigera*, form a paraphyletic grade with the *B. ternata-B. setigera* clade sister to all remaining *Bidens* and four other genera. Both the North and South American species of *Bidens* have accumulated a higher number of autapomorphies than the African *Bidens* (characters 7, 8/2, 25/1, 32, 34/3, 34/5). The New World taxa could thus be hypothesized as having a relatively recent origin.

A general comparison of the phylogeny generated from the present study may be made with the phylogeny for *Bidens* and *Coreopsis* produced by Kim *et al.* (1999) from nucleotide sequences of the internal transcribed spacer region of nuclear ribosomal DNA (ITS). More detailed analyses of the morphological and molecular data sets are in progress and will be reported later; here, we consider only basic similarities and differences, and do not attempt to evaluate the causes of nonconcordance. Only North Temperate *Bidens* form the same monophyletic groups in the two phylogenies (cf. Figs. 3, 4). Relationships in *Coreopsis* are quite different in the two phylogenies. In the present study, *C.* sect. *Pseudoagarista* is basal, and a monophyletic assemblage (Fig. 3). By contrast, the ITS phylogeny has Mexican and South American members of the section in different clades with neither being basal (Fig. 4). The phylogeny produced from morphology does not place the California and North Temperate *Coreopsis* in separate clades (68% bootstrap value), as is done in the ITS phylogeny (Figs. 3 & 4). African *Bidens* form a paraphyletic grade in the present study (Fig. 3) whereas they are a strongly supported monophyletic group in the ITS phylogeny (Fig. 4). The Mexican and South American *Bidens* group together in the phylogeny generated from morphological characters, but with several other genera embedded in the clade (Fig. 3). The ITS phylogeny also contains a strongly supported clade of Mexican and South American *Bidens* (Fig. 4), but since other genera such as *Cosmos*, *Heterosperma* and *Coreocarpus*, were not included in the Kim *et al.* (1999) study it is not known whether they would appear in the clade if their sequences were included. However, preliminary results from ITS studies suggest that none of the genera embedded in the North Temperate *Bidens* clade (Fig. 3) occur with *Bidens* in an ITS tree (Crawford *et al.*, unpublished data).

Sectional and geographical distribution of characters.

In *Bidens* the characters display more aggregation within geographically segregated taxa than within previously delimited sections. For instance, the species from Mexico and South America form a group distinct from those from the United States and Canada (Fig. 2). Within the latter group are members of sections *Meduseae* (Nutt.) Sherff and *Platycarpaea* DC. and within the former fall members of the large and heterogeneous section *Psilocarpaea* DC. The African species are dispersed in three major groups; those with winged achenes form the basal group (*B. pachyloma-B. prestinaria*), and those without winged achenes are sisters to the species in the New World. Square stems, characteristic of many annual species of *Bidens* sect. *Psilocarpaea*, also occur in a few of the African species. Two other characters utilized to delimit sections of Old World *Bidens* by Sherff (1937), *i.e.* adnate inner phyllaries and medially thickened corolla, are homoplastic. However, character 5, *i.e.* setigerous foliar teeth, which was utilized by Sherff (1937) in defining a section of African *Bidens*, *i.e. B.* sect. *Steppia* (Sch. Bip. ex Walp.) Sherff, is found to be non-homoplastic.

Sherff (1937) kept the African species of *Bidens* in sections *Psilocarpaea* DC., *Steppia* (Sch. Bip. ex Walp) Sherff, *Lesperthema* Sherff and

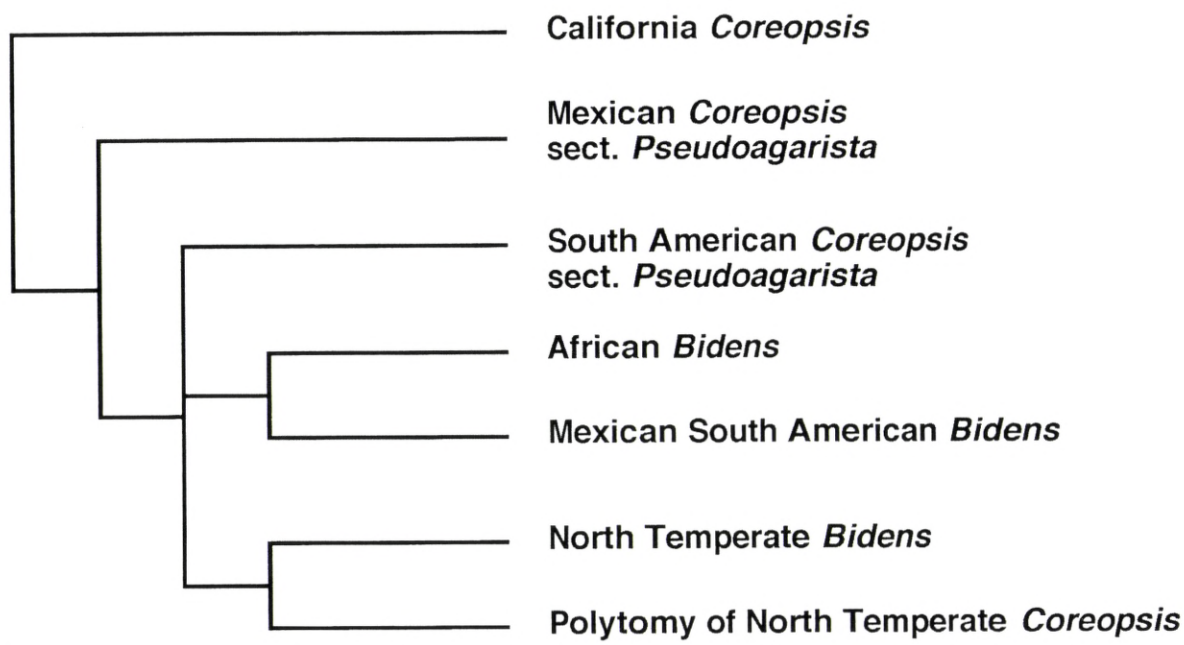

Fig. 4. Strict consensus tree for *Bidens* and *Coreopsis* based on ITS sequence. Condensed and modified from Kim *et al.* (1999). All branches shown have bootstrap support above 80% except for North Temperate *Bidens* with 77%.

Ebussa Sherff and noted that sect. *Psilocarpaea*, which also includes all the Mexican and South American taxa, may need to be split into smaller groups. Currently a more thorough re-examination of species in the sections mentioned above is being carried out.

The delimitation of *Coreopsis* into sections, by contrast, is relatively clear-cut with the exception of section *Pseudoagarista*. Although supported by morphological data (Jansen *et al.* 1987, this study), the molecular data (Kim *et al.* 1999) does not support the monophyly of this section.

Conclusion

Using morphological features, *Bidens* and *Coreopsis*, the two largest and most complex genera of the *Coreopsidinae*, are shown not to be monophyletic. *Bidens* is a paraphyletic genus that is more closely related to six other mainly North American genera than to *Coreopsis*. Morphologically, it can be distinguished from *Coreopsis* by the striate and grooved achenes. These are thin-walled parenchymatous and often translucent areas on the achene wall, which break up easily during seed germination. The seedlings of *B. bipinnata* were observed to emerge by breaking open this thin-walled area of the achene surface (Mesfin Tadesse *et al.*, in prep.). Retrorsely barbed aristae are also features found in many species of *Bidens* and have not been observed in any species of *Coreopsis*. The North American (excl. Mexico) and the South American & Mexican *Bidens* form distinct clades within the genus. The infra-generic relationships, particularly sectional relationships within this large genus, need to be investigated further.

Coreopsis is paraphyletic with two major lineages. *Coreopsis* sect. *Pseudoagarista*, constituting one of these lineages, is basal within the genus.

In spite of some shared features with some of the North American species, this section consists of species with a number of unique features. Taxa from the African continent formerly kept in *Coreopsis* (*B. pachyloma*, *B. macroptera*, *B. barteri* and *B. prestinaria*) are shown to belong to *Bidens*.

The African and North American *Bidens* with flattened (and sometimes also winged) achenes are different from the largely Mexican and South American species with usually tetragonal and unwinged achenes. The latter have also developed traits such as white or purplish ray florets, which set them apart from the species in Africa (except for two species in south-central Africa) and North America. These major trends in the diversification of *Bidens*, observed during this study, deserve further studies.

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Appendix 1. Characters used in the analysis of the genera of Coreopsidinae.

1. (0) Herbs or small shrubs; (1) trees or large shrubs.
2. Duration: (0) perennial; (1) annual.
3. Stem or branches: (0) erect; (1) decumbent or prostrate; (2) climbing.
4. Roots: (0) non-tuberiferous; (1) tuberiferous.
5. Petiole: (0) stiff, not tendril-like; (1) tendril-like.
6. Leaves: (0) herbaceous/foliaceous; (1) coriaceous.
7. Leaves: (0) opposite; (1) alternate.
8. Capitula: (0) heterogamous or homogamous, radiate or discoid; (1) ligulate.
9. Capitula: (0) heterogamous; (1) homogamous.
10. Involucre: (0) campanulate-hemispheric; (1) cylindric-campanulate.
11. Inner phyllaries: (0) free except at base; (1) united at least up to 1/3rd of length.
12. Ray floret apex: (0) 3-5-fid; (1) entire, emarginate or deeply bifid.
13. Ray florets: (0) pistillate, fertile or sterile; (1) neuter.
14. Ray florets: (0) yellow or orange-yellow; (1) white, purple or pink.
15. Paleae and phyllaries: (0) homomorphic; (1) heteromorphic.
16. Disc florets: (0) hermaphrodite and fertile; (1) abortive or functionally male.
17. Disc corolla: (0) 5; (1) 3-4.
18. Disc floret style: (0) bifid; (1) entire or only notched at apex.
19. Filament: (0) glabrous; (1) hairy.
20. Apex of disc floret style branches: (0) short; (1) long and appendaged.
21. Ray and disc achenes: (0) dissimilar; (1) monomorphic or graded monomorphic.
22. Disc achenes: (0) not striated; (1) striated.
23. Disc achenes: (0) smooth; (1) grooved or sulcate.
24. Disc achenes: (0) not winged; (1) winged.
25. Apex of disc achenes: (0) not beaked; (1) beaked.
26. Pappus of disc achenes: (0) scales; (1) 2-4 aristae; (2) 5-16 aristae.
27. Pappus: (0) smooth or coroniform; (1) antrorsely barbed; (2) retrorsely barbed.
28. Length of pappus: (0) less than 1/2 of achene; (1) greater than half to exceeding achene.

Appendix 2. Characters used in the analysis of Bidens and Coreopsis.

Habit and stem The stems and/or branches display a few important features, *e.g.* stature, persistent petiole bases, shape, pubescence, etc. While a large number of the species of *Bidens* have erect stems, a few of the African, Central American and Mexican taxa have prostrate, decumbent, scandent or climbing (vine-like) stems. In

Table 1. Data for the Coreopsidinae Less., using *Guizotia* (Melampodiinae Less.) as outgroup. The characters are provided in Appendix 1. Variable (V), unknown (?) and inapplicable (-) characters are indicated.

Character number	.....	1	11111	11112	22222	222
	12345	67890	12345	67890	12345	678
Guizotia	00000	00000	00000	00000	00000	---
Bidens	0VV00	00000	00001	0V000	111VV	VV0
Coreocarpus	0V000	00001	010V0	00000	10010	120
Coreopsis	0V000	00000	00001	0V000	100V0	VV0
Cosmos	0V010	00000	00111	00010	11101	220
Dahlia	00V10	00000	00011	00001	11100	---
Glossocardia	0V000	01011	00011	11V00	10100	100
Heterosperma	01000	00001	00001	00000	01110	120
Hidalgoa	00201	00000	01001	10100	00000	100
Isostigma	00000	01000	00011	00001	11100	1V0
Megalodonta	00100	00000	00100	00000	1??01	221
Moonia	00000	00110	00001	11100	0----	---
Narvalina	10000	1000?	01000	00000	11100	110
Oparanthus	10000	10000	01001	11100	00010	100
Thelesperma	00000	00000	10101	00000	1??00	120
Trioncinia	00000	01001	11000	01000	11100	120

many of the African species of *Bidens* and the Mexican and South American *Coreopsis* the main stem is terete and the branches are diffusely multi-ribbed to quadrangular. Tetragonal stems are characteristic of specially the annual Mexican and some central African species of *Bidens*.

1. Habit: (0) tree, shrub or subshrub with several stems from a rhizomatous, thickened or tuberous rootstock; (1) herb with solitary, herbaceous or woody stem.
2. Duration: (0) perennial; (1) annual.
3. Main stem: (0) terete or multi-ribbed; (1) tetragonal.

Leaves. Leaves in *Bidens* and *Coreopsis* are quite variable in a number of features including the degree of dissection of the lamina. There is sometimes considerable variation even within one individual plant. Interpretation of leaf margins in compound leaves can be misleading. Variously dissected leaflets could be described as having serrate or lobulate margins. It is only in simple leaves that interpretation of margins becomes consistent. Consequently, only the following among leaf characters were chosen.

4. Leaf arrangement: (0) opposite; (1) alternate.
5. Leaf teeth: (0) short, acute; (1) setigerous.

Receptacle. The receptacle, in longitudinal section, may be flat, convex, conical or globular. Often those species with flat or convex receptacles have erect, basally thickened or indurate inner phyllaries which are never reflexed in fruit thus keeping the achenes firmly enclosed within. Species with globular receptacles have thin to thickish phyllaries that are either totally reflexed at maturity exposing the fruits or bent inwards. The Mexican and South American species of *Bidens* allied to *B. pilosa*, *B. bipinnata*, *B. riparia*, etc., have globular receptacles with totally reflexed phyllaries and radiating fruits at post anthesis. The North American *Coreopsis* sect. *Coreopsis* have globular or conical receptacles but the phyllaries are not reflexed.

6. Receptacle: (0) flat or convex; (1) conic or globular.

Phyllaries. The phyllaries display a number of characters and states such as shape, pubescence, length, etc., which are useful for species recognition. The ratio of the outer phyllary to the inner was found most useful in distinguishing most members of *Bidens* from *Coreopsis*. The colour and number of striae of the inner phyllaries also display these differences.

7. Ratio of length of outer to inner: (0) 0.7-1.5; (1) 1.5-5; (2) 0.1-0.7.
8. Texture: (0) woody to coriaceous; (1) subcoriaceous, bracteaceous; (2) leaf-like.
9. Pubescence of inner phyllaries: (0) one or both surfaces hairy; (1) glabrescent to glabrous.
10. Colour of inner phyllaries: (0) orange yellow or brown; (1) greenish-yellow, yellowish brown, or brownish-green.

Ray Florets. The ray floret number appears to follow the fibonaci series, *i.e.*, 0, 3, 5, 8, 13, and 21. The modal number in *Bidens* appears to be 5 (in Mexican, Central and South American species) and 8 (mostly African species), while in *Coreopsis* it is 8. There is far greater variation in number of florets in individual plants in *Bidens* than in *Coreopsis*. Some species in *Bidens* have fewer florets or these may even totally be absent.

11. Number based on: (0) 8; (1) 3 or 5.
12. Sexual condition: (0) pistillate; (1) neuter.
13. Colour: (0) yellow; (1) yellow with reddish/purple blotch; white; (2) pink, purple.
14. Apex: (0) entire to minutely 1-3-fid or dentate; (1) deeply 3-4-lobed with the central lobe longer than the laterals. Note: Interpretation of this state is problematical. The fused and apically 3-lobed or 3-fid ray floret of the Heliantheae is often considered more primitive than other types involving 3 corolla lobes (Smith 1975; Jeffrey 1977).
15. Shape: (0) oblong, oblong-elliptic; (1) linear, linear-lanceolate, attenuate.

Paleae. The paleae display a number of unique features that are shared by only a few of the species in both genera. In *Bidens* they are generally glabrous with individuals of a few species possessing a few moniliform hairs towards the apex, commonly oblong or oblong-elliptic and free from the achenes. In *Coreopsis* sect. *Pseudoagarista* and *Pugiopappus*, the paleae possess long, flexuose, twin hairs similar to those found on the achenes. They are attached to the achene at the base and are dislodged and dispersed from the receptacle together at maturity. The paleae in *Coreopsis* are more varied in shape.

16. Pubescence: (0) hairy; (1) glabrous or glabrescent.
17. Attachment to achene: (0) attached; (1) free or clasping.
18. Shape: (0) oblong to oblong-elliptic; (1) linear, linear-lanceolate or attenuate.

Disc florets. The corolla lobes are commonly 5 in both *Bidens* and *Coreopsis* but 4 corolla lobes are known in 2 sections of North American *Coreopsis* and 3 corolla lobes in some species of *Bidens* from South America and Mexico (*e.g.* *B. lemonii*). Of the other characters of the corolla displaying

differences between taxa, the ratio of the tube to the limb is found to be useful. The corolla in many species of both *Bidens* and *Coreopsis* is ampliate, *i.e.* the limb is abruptly widened at the apex of the tube. Usually there is little difference in size between the limb and the tube. In some species of *Bidens* of South America, the corolla is nearly tubular with a very small portion of it being constituted by the tube. The ampliate corolla is considered less derived in other Asteraceae (Jeffrey 1977; Zhang & Bremer 1993).

19. Corolla lobes: (0) 5; (1) 3 or 4.
20. Corolla shape: (0) tubular or funnelform, tube and throat not sharply differentiated; (1) tubular, tube and throat sharply differentiated.
21. Style arm apex: (0) conic, cuspidate to truncate with limited sweeping hairs; (1) penicellate or attenuate with decurrent sweeping hairs.

Achenes. In both *Bidens* and *Coreopsis* the achene surface is carbonized (Robinson 1981). In many species of *Bidens* this carbonized layer is interrupted by longitudinal bands of parenchyma which are referred to as striations. They are also sunken areas or grooves along the achene surface. These areas were recently (Mesfin Tadesse & Crawford, in prep.) found to be weak spots along the achene surface through which the cotyledons and the hypocotyl emerge during germination of the seed. In achenes where these parenchymatous areas are absent, the germinating seedlings emerge by breaking through the margins at the lower half of the achene. The presence of thin-walled parenchyma along the achene wall appears to be an adaptation for successful germination and hence it is considered to be a derived feature.

22. Surface: (0) not striated; (1) striated.
23. Texture: (0) smooth; (1) grooved.
24. Compression: (0) 2-sided; (1) 4-sided. Note: Many species of *Bidens* and *Coreopsis* have dorsiventrally flattened achenes. The majority of the Mexican, Central and South American species of *Bidens* have quadrangular achenes. Many species of North American *Bidens* have cuneate achenes with the upper part being conspicuously 3-4-ridged or angled.
25. Number of grooves on each face: (0) no grooves; (1) 2; (2) 4-8(-16). Note: In bifacial or dorsiventrally flattened achenes with grooves the number of grooves on each surface ranges between 6 and 16 while in quadrangular achenes they are predominantly 2, except in *B. lemmonii* and *B. gardneri*, where there are 4 grooves on one or more surfaces.
26. Surface hairs: (0) twin hairs; (1) absent or wart-like processes.
27. Twin hairs: (0) long and flexuous; (1) short and stiff; (2) absent. Note: Twin hairs are characteristic features of the achenes of many Asteraceae (Robinson 1981) occurring in the Astereae, Eupatorieae, Vernonieae, Heliantheae (Small 1919: 72) and Mutisieae. There are both long and flexuous and short and rigid twin hairs associated with the achenes of *Bidens*. The short ridged twin hairs are more or less similar in all species of *Bidens*. These are absent in *Coreopsis* but the long and flexuous types are found in *C.* sect. *Pugiopappus* and *Pseudoagrista*.
28. Hairs on margins: (0) appressed, antrorse; (1) spreading; (2) retrorse; (3) not present.
29. Ratio of length to width: (0) 1-5; (1) 7-20. Note: Differences between taxa in qualitative features such as shape could be expressed quantitatively to portray relationships better. The achenes of many South American and Mexican species of *Bidens* have been described as clavate, linear, linear-tetragonal and club-shaped and those of African species as ovate, oblong, oblong-lanceolate, obovate, oblanceolate, etc. The length/width ratio provides a better grouping of the species within *Bidens* and *Coreopsis* than the descriptive qualitative features. It was also noted that species with narrow but long achenes were, in many instances, associated with the annual habit.
30. Apex: (0) not differentiated; (1) elongated, narrowed above.
31. Size: (0) more or less uniform; (1) graded monomorphic; (2) dimorphic. Note: In most of the species of *Bidens* and *Coreopsis*, the achenes are monomorphic but there are progressive differences in size and sometimes also in shape centrifugally. Dimorphous achenes are more prevalent in Mexican and South American species of *Bidens* than in the African and North American species of the genus and also in *Coreopsis*. In the later group there are differences in size and shape between the disc and ray floret achenes, but often these differences are not strikingly evident. In the former group, several of the achenes towards the periphery of the capitula are club-shaped (clavate), and yellowish or rubrocastaneous while those near and in the centre of the capitula are linear-tetragonal and black. Dimorphism is thus associated more with the disc floret achenes of Mexican and South American *Bidens*.
32. Exsertion: (0) included or barely exceeding the involucre; (1) achenes exserted above the involucre. Note: In many species of *Bidens* the phyllaries are often thickened at base. In a number of species these thickenings often extend medially to the apex. Yet in some species the thickening also extends into the receptacle making the whole lower portion of the

Table 2. Data for the analysis of *Bidens* and *Coreopsis* with *Fitchia speciosa* as the outgroup. The characters are listed in Appendix 2. Unknown (?) and inapplicable (-) characters are indicated.

Character number	. . . . .	1	1111	111112	22222	22223	33333	33334	44444
	12345	67890	12345	67890	12345	67890	12345	67890	12345
Fitchia speciosa	00000	00000	-----	10000	00000	00000	00000	00000	000?0
Bidens aristosa	11100	01211	01000	10101	10000	01000	00050	10000	11110
B. barteri	11000	00110	01000	10000	11102	00100	10241	01010	101?0
B. bigelovii	11100	00111	10100	10100	11111	01011	21230	10000	11110
B. buchneri	00000	00000	01000	10000	11102	01000	00040	10000	101?0
B. cernua	11100	01200	01000	10101	11000	01200	00150	10001	11110
B. discoidea	11100	01211	-----	10111	10000	01000	00150	10000	10110
B. ferulaefolia	11100	00111	11000	10100	11111	01011	21230	10000	11110
B. frondosa	11100	01211	11000	10111	10000	01000	00150	10000	11110
B. ghedoensis	11001	00110	00000	10000	11102	01000	00040	10000	10120
B. hyperborea	11100	01211	11000	10111	11000	01200	00150	10001	11110
B. kilimandscharica	10000	00100	01000	10000	11102	01000	00040	10000	101?0
B. macroptera	10000	00100	01000	10000	11102	00100	10241	01010	10120
B. odorata	11100	00111	11200	10100	11111	01011	11230	10000	11110
B. pachyloma	11000	00110	01000	10000	11000	01000	10041	01010	101?0
B. pilosa	11100	00111	11200	10100	11111	01011	11230	10001	11110
B. prestinaria	11000	00110	01000	10000	11102	00100	10241	01010	10120
B. riparia	11100	00111	11000	10100	11111	01011	21230	10001	11110
B. rueppellii	00001	00110	00000	10000	11102	01000	00040	10000	10120
B. setigera	11001	00110	00000	10000	11102	01000	00040	10000	10120
B. ternata	10001	00100	00000	10000	11102	01000	00040	10000	10120
Coreocarpus sonoranus	00000	00111	00000	11100	0?000	12300	100?1	10000	2111?
Coreopsis basalis	11000	12100	01111	10100	00000	12300	00021	01110	20101
C. calliopsidea	11010	02100	00001	11000	00000	00100	20001	01110	20001
C. linifolia	10010	12100	01011	10110	00000	12300	00021	01110	20101
C. major	10000	00110	01000	10000	00000	12300	00011	01110	20111
C. petrophiloides	00000	00110	01000	01000	00000	00100	00000	01000	20001
C. pringlei	00000	00110	01000	01000	00000	00100	00000	01000	10001
C. stillmanii	11010	02110	00011	10000	00000	12300	00020	-----	2--01
C. tinctoria	11000	12100	01111	10110	00000	12300	00021	01110	20101
C. woytkowskii	00000	00110	01000	01000	00000	00100	00000	01000	20001
Cosmos ochroleucoflorus	00000	00111	11200	11101	01111	01011	112?1	10000	2111?
Heterosperma pinnatum	11100	00111	00000	11100	01111	12301	212?1	10000	2111?
Isostigma brasiliense	00010	00110	10000	11100	11111	01010	000?0	10000	201??

involucre appear swollen. The thickened portion is due to the deposition of layers of sclerotic parenchyma and collenchyma. As a result of this deposition a number of species have phyllaries that are never reflexed at maturity but remain erect keeping the fruits firmly enclosed within. In such cases the dispersal of fruits is apparently ballistic. In a number of particularly annual species, the phyllaries are not thickened at the base. They are thin and flexible and at maturity both the phyllaries and the paleae are reflexed exposing the achenes. The thin phyllaries are probably adaptations to zoochory and anemochory.

33. Shape: (0) linear-oblong, oblong-elliptic, obovate to oblanceolate; (1) cuneate, tapering to the base; (2) linear-fusiform or linear-attenuate, tapering to the apex and/or base.
34. Type of phytomelanin deposition pattern: (0) A; (1) B; (2) C; (3) D; (4) E; (5) F. Note: The outer surface of the pericarp is carbonized in many species of *Bidens* and *Coreopsis*. This carbonized layer, also referred to as phytomelanin, is either black or light to yellowish-brown. The light to yellowish-brown phytomelanin gets deposited along cell walls and cell surfaces leav-

ing small to large circular to slit-like openings. In cross-section, the pericarp appears smooth. In those species with black pericarp, in addition to the deposition along cell walls and cell surfaces, the phytomelanin on adjacent cell surfaces fuse forming circular to elliptical "pegs" with elaborate deposition pattern. The six different types of phytomelanin deposition patterns (A-F) are: A = along the radial and tangential walls in an irregular manner; B = along serveral cell surfaces octagonally; C = either uniformly covered or slit-like openings in the middle; D = black, irregular, globular or rectangular deposits across several cell walls; E = black, narrow bands along the radial axis of hypodermal cells; F = regular deposition along cell walls, not across cell surfaces.

35. Margins: (0) not winged to narrowly hyaline or tuberculate; (1) winged with flat, spongy or corky wings. Note: In both *Bidens* and *Coreopsis* a number of species have flat or corky achene margins. In some species of *Bidens*, the margins are covered with narrow hyaline tissue or the fused bases of the twin hairs may again be joined to each other creating a wing-like structure on the margin. The marginal thickenings and wings are made up of sclerified parenchyma that vary in size from short concentric to long columnar types. Often the sclerified parenchyma forms an easily detachable cover on the pericarp and it may also form globular or peg-like (verrucose) projections from the achene surface.

Pappus. In describing the structure of the Composite achene pappus, Small (1919: 77-80) recognized setose, paleaceous and aristate types. Although a seta is not defined, it appears that he used this term to refer to the individual cells making up the pappus. But he also used it in a different sense. He defined a scabrid seta as 'composed of uniseriate rows of cells fused together'. Small defined an arista as 'a thick, more or less ridged structure'. Both *Bidens* and *Coreopsis* are described by Small (1919: 80) as having 'barbato-aristate' pappus with the 'bristles projecting downwards in *Bidens*, or upwards as in *Coreopsis*'. The acute end of the seta is referred to as a bristle. From these statements and definitions, it appears that the difference between setose and aristate pappi lies in the way the cells fuse to each other, *i.e.* in the aristate pappus, the cells 'fuse in a clump' rather than laterally forming a file of cells.

The structure of the pappus in *Bidens* and *Coreopsis* was discussed in a previous article (Mesfin Tadesse *et al.* 1995a) and it was related therein that the paleaceous type is found in *Coreopsis*. Also the type described by Small (1919: 79) as aristate is found in *Coreopsis* sect. *Eublepharis* (cf. Mesfin Tadesse *et al.* 1995a). These terms (*i.e.*, seta, arista, awn, bristle) have been loosely utilized in the literature in reference to the achene pappus in *Bidens* and *Coreopsis*. As discussed in Mesfin Tadesse *et al.* (1995a), the cells making up the pappi are sclerotic parenchyma with different degrees of cell wall thickness and fusion. Those at the centre of the pappus (the shaft) are cylindrical and those toward the periphery more elliptic, oblong or oblong-lanceolate. Those that project from the sides are linear with sharp pointed apices. The shaft may be composed of few to many rows of cylindrical cells. One difference between *Bidens* and *Coreopsis* appears to lie in the composition of the pappus rather than in its gross morphology. In *Bidens* and *Coreopsis* sect. *Pseudoagarista*, the shaft is composed of many rows of cells and in cross-section it is circular or triquetrous. In *Coreopsis* sect. *Coreopsis*, *Pugiopappus*, etc., the shaft is absent or composed of few rows of cells with flat or star-shaped uniseriate wings.

36. Nature: (0) scale-like or paleaceous; (1) setaceous.
37. Outline in cross-section: (0) cylindrical; (1) triquetrous, flat or star-shaped.
38. Morphology: (0) multi-layered and fibrous; (1) unilayered and parenchymatous.
39. Plane: (0) 3-angled at least at base; (1) flat.
40. Number: (0) 2, rarely 3; (1) 3-5, rarely 2 or 5. Note: In *Bidens*, the number of pappi is related to the shape of the achene. Dorsiventrally flattened achenes commonly have 2 pappus aristae while the quadrangular achenes have 4-5 retrorsely directed pappus aristae. Species with the later type of pappus are predominantly annual herbs.
41. Relative size: (0) one-half to exceeding achenes; (1) up to one-half; (2) absent to up to 1/3.
42. Barb direction on pappus: (0) antrorse or nude; (1) retrorse.
43. Barb size: (0) long & flexuous; (1) short & rigid or absent.
44. Chromosome number based on: (0) 13; (1) 10, 11 or 12; (2) 16, 17, 18 or 21.
45. Width of os of pollen: (0) 8.3-11.8; (1) 1.1-5.8.

By whom and when was the flora of Ethiopia and Eritrea named?

Ib Friis & Sue Edwards

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Over 300 botanists have during the last 218 years named over 2700 taxa of flowering plants based on material from Ethiopia and Eritrea. The record of these in the Index Kewensis on CD-ROM forms an easily analysed sample, which documents the history of scientific study of the Ethiopian and Eritrean flora. This is supported by the available written accounts for the Flora. Characteristic features of that history are an early start and a massive early contribution by A. Richard ("Tentamen Florae Abyssinicae"; 1847-51), based on the collections of the ill-fated Quartin-Dillon and Petit, and on the extensive collections made by G.H.W. Schimper. The widely distributed Schimper material also encouraged studies elsewhere in Europe. Later in the 19th century, and in the first decades of the 20th, British, German and Italian contributions were strong, partly based on new collections. The founding of the National Herbarium for Ethiopia in Addis Ababa in 1958, and the beginning of the Ethiopian Flora Project in 1980 mark the entrance of Ethiopian and Eritrean scientists on the scene, together with other African and Asian botanists. There has been good correlation between collecting activity and naming of new taxa, particularly where the duplicates from collections are well distributed.

Ib Friis, Botanical Museum and Library, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen, K, Denmark. E-mail: ibf@bot.ku.dk

Sue Edwards, Ethiopian Flora Project, National Herbarium of Ethiopia, Addis Ababa University, P.O. Box 3434, Addis Ababa, Ethiopia. E-mail: sustain@telecom.net.et

Introduction

The two co-authors are involved with the editorial process of producing the *Flora of Ethiopia and Eritrea* (FEE). Thus they have frequently discussed matters relating to the naming of plants from the Flora area. Who were the botanists behind the scientific names in the Flora? Sorting out the scientific names based on material from the Flora area is a special responsibility of the Flora project, as such names need to be well documented in the printed volumes. So focussing for a while on the botanists rather than the plants is not really drifting away from the subject of a *Flora of Ethiopia and Eritrea* Symposium.

International scientific knowledge of the plants from the Flora area started with the works of Linné f. (Linné 1781) and James Bruce (1790, 1804). The history up to 1800 has been sorted out by Hulton *et al.* (1991), preliminary reviews of the work of Schimper and Richard were available (Gillett 1972; Stearn

1982), and some observations on the names proposed by Hochstetter and adopted by A. Richard have also been published (Friis 1993). Many older authorities have been dealt with in the second edition of "Taxonomic Literature" (Stafleu & Cowan 1976-1988), and most of the newer ones have been at least mentioned in the index of author abbreviations by Brummitt & Powell (1992). The main source of information is the second edition of Index Kewensis (IK) on CD-ROM, 2. Ed. (Index Kewensis 1997) that could be searched for certain types of data. The result is a sequence of 9 tables with names of more than 300 people who have named over 2700 plants based on material from the Flora area. These people are arranged into groups, which serve to illustrate the activities with the study of the flora of Ethiopia and Eritrea in various geographical areas, and during different historical periods. In connection with that, we have tried to extract information about the available herbarium material from the lists of collectors compiled by Cufodontis (1962) and Friis. Cufodontis attempted to cover the period up to *c.* 1960, while Friis has attempted to complete Cufodontis' list and cover the period after 1960. Friis' list is maintained in electronic form in Copenhagen, but was been given a limited distribution on paper as Friis (1981a). An extract of the information relating to collectors after 1962 in enclosed here as an Appendix entitled *List of Collectors and their Collections since 1960.*

Materials and methods; sources of error

We originally attempted to compile a critical list of names based on material collected from the Flora area found in the published volumes of FEE, supplemented by data from Cufodontis (1953-1972) and the IK on CD-ROM, which contains all records published up to June 1996. The first aim was to produce a searchable database from which various information could be extracted. However, this exercise turned out to be too time-consuming to be finished in time for the Symposium.

Almost all data for this paper have, therefore, been extracted from the IK on CD-ROM. It is easy, but sometimes slightly tricky, to do searches for taxa described from particular parts of the world by specified authorities in this version of the IK. The ease of use is improved by the inclusion of the file used for the production of a standard set of author abbreviations (Brummitt & Powell 1992). However, the IK file and the Brummitt & Powell file often do not correspond with regard to author abbreviations, making exact identification of certain authors difficult. We have used combined searches for truncated names of authorities in the "Author" field and a sequence of truncated place-names in the field marked "Anywhere". Unfortunately, one cannot make a search with Boolean operators in the "Notes" field where the geographical information is placed. After experimentation, we decided to use the following truncated geographical names in the searches: "Abys* or Galla* or Eth* or Aethiop* or Erit* or Eryt*" This combination found most taxa from the Flora area in genera where we knew exactly which taxa should be found. Some of the truncated geographical terms, especially "Aethiop*", "Galla*" and "Eryt*" have been commonly used in generic names, epithets and book-titles. When these key terms were used for searches "Anywhere", we retrieve a large number of unwanted records of plant names or literature references, such as all species names published under *Erythraea*, *Erythrina* and *Erythroxylum*. The output has, therefore, always had to be inspected and sorted manually.

There are also considerable problems with the precise locality of taxa described from the eastern part of the Flora area (BA and HA).

Taxa described from these areas can under Notes in the older volumes of IK be stated to come from "Somaliland", "Afr. Trop.", "Reg. Somal", or some other similar geographical indication. This has meant checking, as far as possible, the exact location of the collection. Cufodontis (1953-1972) is no help until after 1964, as, up to that date, he used the geographical system from the Italian occupation where most of the Ogaden was placed together with southern Italian Somaliland. But even if one consults the original place of publication, there can be difficulties. The names based on types collected by Robecchi-Bricchetti from the region "Merehan" are an example of this; Merehan spans the modern border between Ethiopia and Somalia, and is an area where a nomadic group of that name moves. If there was any doubt, the record has been omitted from this review.

Changing the rules of botanical nomenclature is another complication. The original volumes of the IK and its Supplements 1-3 follow the special "Kew rules" of botanical nomenclature. Therefore searches of the CD-ROM IK produce results that are sometimes incorrect with regard to modern nomenclature. Thus, too many records represent the early authors, because some of these records in fact represent new combinations rather than new taxa. Until 1970, the IK did not record infraspecific taxa; thus these are not represented in this review. Another problem in the early volumes of the IK is that *nomina nuda* are frequently recorded as published names. We have also encountered the complication that cultivated plants described from the Flora area (grasses, Leguminosae, etc.) do not always have an indication of their origin in the original volumes and early supplements of the IK.

These sources of error tend to balance each other; some, especially the Kew rule, increase the number of records for a particular author, while other sources of error tend to decrease the figure. We hope that authors of taxa from the FEE area who see these tables will forgive us if we have not picked up all their taxa. The purpose of this paper is to point out some general trends, not to provide a work of reference where one can look up the production of individual authors. This can only be done when a database, as described earlier, has been made.

A complication in identifying the nationality of the people who named plants from the Flora area is that the concept of nationality in the 18th and 19th centuries was not identical with the present as the states, particularly in Central Europe, were very different from the present ones. So we can say little of nationalities, but the tables show the best national affiliation that the authors of this paper can give. Where authors have not been mentioned by Stafleu & Cowan (1976-1988) or Brummitt & Powell (1992), we have consulted Barnhart (1965), or occasionally, but only where other sources were inadequate, we have gone to obituaries etc., cited in these works.

Names based on Ethiopian and Eritrean material

The latest version of our list of names based on material from the Flora area contains over 2700 entries. These names were proposed by over 300 authors, based on the list extracted from IK on CD-ROM and printed copies of FEE. These figures will almost certainly not agree exactly if compared carefully, but they are in our opinion a reasonable estimate.

The names are found in 129 families, but are unevenly represented among them. The family with most such names is the Poaceae with 357 names, followed by the Asteraceae with 284 names, Fabaceae with 228 names, Lamiaceae with 113, and Cyperaceae and Euphorbiaceae, each with 102 names. Orchidaceae, Asclepiadaceae, Acanthaceae, Rubiaceae, Scrophulariaceae and Convolvulaceae follow closely with

between 40 and 100 names; 15 more families have between 20 and 40 names, 19 families have between 20 and 10 names, 66 families have 2-10 names, and 15 have only one name established on material from the Flora area.

Early contacts between Ethiopia and Europe; the results of James Bruce's and Luigi Balugani's journey

International scientific studies of plants began early in Ethiopia and Eritrea when compared with other parts of tropical Africa. The first names proposed for plants of the Flora area were based on material collected by Bruce and Balugani who arrived in Mitsiwa on 19 September 1769. They reached Gonder on 14 February 1770 where Balugani died in late 1770 or early 1771. Bruce left western Ethiopia for the Sudan in March 1772.

This early start into a scientific study of the plants of the Flora area is not surprising considering the early contacts there had been between this ancient Christian kingdom and Europe. Firstly, there has been a long and strong tradition, including written records, for using a wide variety of cultivated and wild plants for herbal medicine in Ethiopia and Eritrea, as there has been in Europe (see a number of essays in Mercier & Marchal 1992). Secondly, the contact between Eritrea and Ethiopia, and the Mediterranean part of Europe and the Middle East has existed for a very long time. It is interesting to note that there are records of an Ethiopian mission of about 30 people to Western Europe in 1306 (R.A Skelton in Crawford 1958: 212-215). This mission visited the important centres of Avignon, Genoa and Rome, but unfortunately we know very little for certain about this mission, only that it stayed for some months in Genoa. Shortly before 1524 Alessandro Zorzi of Venice compiled a work on the itineraries between Alexandria and Ethiopia, as well as itineraries within Ethiopia (Crawford 1958); the sources of these itineraries were chiefly Ethiopian monks in Italy. The visits of Ethiopian orthodox clergy to Rome continued in the seventeenth century. In 1649 the German scholar Job Ludolf met at the church of Santo Stefano dei Mori in Rome the Ethiopian monk Abba Gregory from the monastery of Mekane Selassie in the Amhara Region of Ethiopia. Until 1652 they worked together in Rome and Germany publishing works on Ethiopian language and history (Ullendorf 1960).

Thus, by the beginning of the 18th century, Ethiopians and Europeans had definitely much better knowledge of each other's countries and religion than was the case with most other parts of Africa. But the systematic knowledge of natural history was limited. In this respect, Bruce's and Balugani's journey in Ethiopia was breaking new ground, providing the first possibilities for applying the new comparative Linnaean methods, and provide the plants with scientific names according to the Linnaean rules for nomenclature. The material which Bruce and Balugani collected in Ethiopia, and which Bruce subsequently brought back to Europe, resulted in a significant number of taxa from the Flora area being described by 18th century Linnaean botanists. Table 1 summarises the results: 19 botanists from Austria, Britain, France, German states, Italian states, Russia, Sweden and Switzerland published 39 species on the rather limited material of seeds and bulbs given to botanical gardens in southern and western Europe and the drawings published in Bruce's "Travels". Altogether Bruce and Balugani had recorded 160 plant species from their journey in drawings and notes, most of those from Eritrea and Ethiopia. However, the largest part of these 160 species did not come to the knowledge of scientists because Bruce did not give access to the original drawings in his possession: Hulton *et al.* (1991) only identified these drawings in the 1980s.

Table 1. Botanists and the number of plants they named based on material from the FEE region brought to Europe by J. Bruce (Hulton *et al.* 1991). Years of birth and death of the botanists have been indicated where known; otherwise the year(s) when the botanist published name(s) for plants from the FEE-region is given between rules.

Botanist (dates)	Number of names
J.F. Gmelin (1748-1804)	12
J.N.J. Jacquin (1727-1817)	4
C.L. L'Héritier (1746-1800)	4
C. Linné filius (1741-1783)	2
A.P. De Candolle (1778-1841)	2
J. Bruce (1730-1794)	2
A. Murray (-1805-)[1]	1
W. Aiton (1731-1793)	1
N.A. Desveaux (1784-1856)	1[2]
G. Picci[v]oli (-1818)[3]	1
G. Schweinfurth (1836-1925)	1[4]
J.F. Miller (1715-1794)	1
J.B Lamarck (1744-1829)	1
J.A. Murray (1740-1791)	1
J.L.M. Poiret (1755-1804)	1
C.L. Willdenow (1765-1812)	1 var. name
A. Zuccagni (1754-1807)	1
G.F. Hoffmann (1761-1826)	1
J.A. Schultes (1773-1831)	1

1. The editor of the 2nd and 3rd editions of James Bruce's Travels; apparently not identical with any of the people named A. Murray by Barnhart (1965).
2. This is *Bauhinia farek*, a name demonstrated by Thulin (1990) to be based on a fake.
3. This is the author of *Panciatica purpurea* Picc. (*Cadia purpurea* (Picc.) Ait); not to be confused with the more well known A. Piccioli, curator of the Florence Botanical Garden and stated by Stafleu & Cowan (1976-1988) to have lived 1741-1842.
4. This is *Erythina brucei*, demonstrated by Gillett (1962a) to have been confused with *Erythrina abyssinica* by Balugani when he drew a plate with flowers and fruits of the two species.

By contrast, the flora of inland East Africa (Uganda, Kenya and Tanzania) was not studied scientifically for another 100 years. Gillett (1962b) characterised the period of botanical exploration in East Africa between 1860 and 1888 as "the Heroic Period". According to Mendonça (1962), very little scientific material was collected in Angola before F. Welwitsch arrived in 1853. White (1962) mentions the collections made by J. Kirk on Livingstone's Zambezi expedition in 1858-1863 as the first substantial botanical collecting in Zambia. Keay (1962) has pointed out that, apart from Michel Adanson's collections from Senegal, very little was known about the rich West African flora before Palisot de Beauvois (1803-1820) and Schumacher (1827), and intensive collecting activities began much later. Thus Bruce's material from the Flora area had a much wider impact that might be expected from the size of the sample.

Botanical work before the Tentamen Florae Abyssinicae

The next botanical collections that left Ethiopia and Eritrea for Europe were those made by Henry Salt in 1804-1806 and 1809-1810. These small collections were given to the British Museum (now in the herbarium of the Natural History Museum, London), and were studied by Robert Brown, who published them as a list of *nomina nuda* (Salt 1814). Other authors later took up some of these names.

The next collector in the Flora area was the German naturalist Eduard Rüppell who travelled in Ethiopia in 1832-1833; his collections were studied by J.B.G.W. Fresenius at the Senckenberg Institution in Frankfurt am Main, Germany, where the small collection can still be found (Fresenius 1836-1839). The study resulted in the description of 50 new taxa from the Flora area (Table 2).

Shortly after, in early 1837, Wilhelm Georg Schimper entered Ethiopia. Schimper came

Table 2. Botanists from various European countries and the number of plants they named from the FEE-area working before or contemporarily with the Tentamen Florae Abyssinicae (period ending 1847-1851). Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
A. Richard (1794-1852)	1018
J.B.G.W. Fresenius (1808-1866)	50
T.F.L. Nees (1776-1858)	32
H.G. Reichenbach (f.) (1824-1889)	25
A.P. De Candolle (1778-1841)	25
W.G. Walpers (1816-1856)	25
C.G. Ehrenberg (1801-1849)	25[5]
A.R Delile (1778-1850)	24
P.E. Boissier (1810-1885)	13
H.F. Jaubert (with Spach) (1798-1874)	12
E. Spach (1801-1879)	12
A. Braun (1805-1877)	10
F.A.W. Miquel (1811-1871)	10
K.S. Kunth (1788-1850)	9
C.B. Trinius (1778-1844)	9
J.D. Choisy (1799-1859)	8
F.J. Ruprecht (1814-1870)	8
P.B. Webb (1793-1854)	7
A.L.P.P. De Candolle (1806-1893)	5
K. Sprengel (1766-1833)	5
A.T. Brongniart (1801-1876)	5
H.A. Weddell (1819-1877)	5
C.H.B.A Moquin-Tandon (1804-1863)	5
T. Kotschy (1813-1866)	4
E. Fournier (1834-1884)	4
J. Müller Argoviensis (1828-1896)	3
P.K.N.S. Turczaninow (1796-1863)	3
C.A. Meyer (1795-1855)	3
F.E.L. Fischer (1782-1854)	3
C.V. Naudin (1815-1899)	3
R. Brown (1773-1858)	2[6]
M.F. Dunal (1789-1856)	2
E.A. Regel (1815-1892)	2
J. Lindley (1799-1865)	2
S.F.L. Endlicher (1804-1849)	2
F.W. Sieber (1789-1844)	2
H.W. Schott (1794-1865)	2
K.L. Blume (1796-1862)	2
O.K. Berg (1815-1866)	2
J.F. Klotzsch (1805-1860)	2
F.G.C. Alefeld (1820-1872)	1
C.A.F. Garcke (1819-1904)	1
H.C. Andrews (1794-1830)	1
A. Courbon (-1862-)[7]	1
E. Fenzl (1808-1879)	1
A.A. Bunge (1803-1890)	1
E.H.F. Meyer (1791-1858)	1
G.H.A. Scheele (1808-1864)	1
O.N. Hammar (1821-1875)	1
J.L. Schönlein (1793-1864)	1
G. Savi (1769-1844)	1
K.F.W. Wallroth (1792-1857)	1
R. Visiani (1800-1878)	1
R.L. Desfontaine (1750-1833)	1

5. Most of C.G. Ehrenberg's names for Eritrean or Ethiopian plants are *nomina nuda*.
6. Nearly all Robert Brown's names for Eritrean or Ethiopian plants, based on the collections by H. Salt 1805-1810, are *nomina nuda*.
7. According to Barnhart (1965) born 1829; year of death not ascertainable according to our sources.

from the small German State of Baden, situated on the east bank of the upper River Rhine and in the valley of the River Neckar. The West Bank of the River Rhine belongs to Alsace in France. Baden is now part of the Baden-Württemberg Land, a constituent state of modern Germany.

The Schimper family produced several famous botanists, and was closely associated with the state of Baden and surroundings (one became a botanist and geologist in Strasbourg in Alsace, a second a botanist in Basle in the nearby part of Switzerland and a third a botanist in Munich and Mannheim). The Ethiopian Schimper seems to have been close to his contemporary cousin, the bryologist and geologist Wilhelm Phillip Schimper, who lived in Alsace and became director of the Strasbourg Natural History Museum and professor at the University of Strasbourg.

After arriving in Ethiopia, Schimper soon settled at Adua, at that time the capital of Tigre, which was ruled by Dejazmach Wube Haile Mariam. Schimper had since 1831 worked as a collector for the Esslinger Reiseverein ("The Esslingen Travel Society"), a botanical society that sent out travellers to collect scientific material for its members and for exchange. Esslingen is a small town on the Neckar River just south-east of Stuttgart. The Esslinger Reiseverein, founded in 1825 and active to 1842, was lead by Christian Ferdinand Hochstetter, vicar and professor at the teachers' training college in Esslingen, and Ernst Gottlieb Steudel, medical doctor in the same town. The main activities of the Esslinger Reiseverein seems to have been to send Schimper to remote places, first to Algeria, Egypt and Arabia, and from 1837 to Ethiopia, where he was in fact going to spend the rest of his life. He made collections with many duplicates, first for the Esslinger Reiseverein, and after its dissolution in 1842 for Rudolf Friedrich Hohenacker in Esslingen, who also organised distribution and exchange of specimens. As a result, the early Schimper collections were widely distributed to scientific institutions and learned amateur botanists throughout Europe. Also seeds from Ethiopia were distributed in that way, and Schimper's original collections, or specimens made from plants grown from seeds he had sent, can now be found in more than 60 different herbaria (Hettie Vegter 1986).

Hochstetter and Steudel published a considerable number of scientific names based on Schimper's collections. Quite a few of these names, but not all, were *nomina nuda* validated by others (Friis 1993). Most of these validations, but again not all, were made by A. Richard in *Tentamen Florae Abyssinicae*. Apart from Richard, who is dealt with in the next section, 54 botanists proposed 479 names. Schimper had collected the type material of most of these new names.

The list in Table 2 shows how widely distributed the duplicates from Schimper's collections were. Among the botanists are people from Austria, Britain, France, a number of German states, the Netherlands, a number of Italian states, Russia, Sweden and Switzerland. The country of residence and nationality can be confusing: P.B. Webb and H.A. Weddell were both born in England but spent most of their working life in Paris. Ruprecht was of German extraction, born in Prague, and spent his working life in St. Petersburg, Russia.

Table 2 includes names based on other collectors' material including that of Rochét d'Hericourt who collected in central Ethiopia in 1842-1844 and 1850. Other collectors were d'Arnaud, Ferret & Galinier, and Roth, who collected in 1841-1842, and Plowden, who collected in 1848. These collections are not very widespread, many of them being unicates in British or French herbaria, chiefly the Museum d'Histoire Naturelle, Paris (P), and the Natural History Museum, London (BM).

Tentamen Florae Abyssinicae

In 1838 the French government sent a group of scientist to Ethiopia. The group consisted of the naval officer Théophile Lefebvre, and the naturalists Richard Quartin-Dillon and Antoine Petit, and had, as many other groups or individuals from big European countries, been given a political as well as a scientific role to play (Rubenson 1976: 84-92). Especially Lefebvre negotiated with Ethiopian authorities on behalf of France. It is notable that there is overlap between the collecting localities of Schimper, Quartin-Dillon and Petit during the following five years, during which they all frequently stayed at Adua. The exact relationship between Schimper and Quartin-Dillon and Petit in Ethiopia is not known to us, but it is hard to avoid thinking like Gillett (pers. comm.) that the French botanists would have been shown round by the pro-French and more experienced traveller Schimper.

Both the two French naturalists met an unfortunate end in Ethiopia. Quartin-Dillon died of illness 1840, and a crocodile in the Tacazze River drowned Petit in 1843. However, their collections of approximately 1500 plants reached the Museum d'Histoire Naturelle (P) in Paris; very few of these collections have duplicates elsewhere. Richard commemorated the work of the French collectors by dedicating the *Tentamen* to their memory. In all he provided descriptions for 1018 taxa, some of which had already appeared as *nomina nuda*. A comparison between the tables 1-9 shows clearly that this was the largest single contribution to names for the plants from Ethiopia and Eritrea, the second highest being Chiovenda's 268 names (Table 6). The result of Richard's work with the *Tentamen* is the well-known combinations of authorities: "Hochst. ex A. Rich." for 369 species; "Steud. ex A. Rich." for 67 species and "Schultz-Bip. ex A. Rich." for 51 species names. Richard described in the introduction to *Tentamen* how he tried to adopt the *nomina nuda* of Hochstetter and Steudel, but he took no notice of names on material distributed later than with the Esslingen Reiseverein's third series of Schimper's *exsiccata*. Undoubtedly, the *Tentamen Florae Abyssinicae* represents the largest single contribution to our stock of scientific names for the *Flora of Ethiopia and Eritrea*.

Although Schimper plays an important part also in the next section, it seems appropriate to continue with the description of his activities in Ethiopia here. Fairly early during his stay in Ethiopia, he became mixed up in Ethiopian and European politics (Rubenson 1976). The travellers from the larger European countries at that time had almost all a side activity in trying to further the interest of their country, while the Ethiopian rulers had interests in securing arms and support against their immediate enemies, chiefly the expanding influence of Egypt along the Red Sea. The Ethiopians were not naive, and did not immediately believe that the Europeans came just because of scientific interests. Rubenson (1976) quotes a story about how Dejazmach Wube Haile Mariam, the ruler of Tigre, wanted to have Quartin-Dillon and Petit questioned in order to check their knowledge of medicinal herbs when they arrived in 1838 under the pretence of being naturalists! Schimper married a daughter of Dejazmach Wube, probably in 1841. During the years 1841-1855 Schimper was given the responsibility by his father-in-law for the administration of the district of Entitcho, northeast of Adua.

In 1845 Schimper was deeply involved in negotiations which Dejazmach Wube had with the French government for an agreement to deliver arms against concessions to the French, and he assisted (and influenced) correspondence which Dejazmach Wube had with France. Although Schimper came from a small German state, he seems to have felt so close to France that he supported links with that coun-

Table 3. Mostly German botanists mainly of the "Engler period" (c. 1875-1925) and the number of plants they named from the FEE-area. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
A. Engler (1844-1930)	91
G. Schweinfurth (1836-1925)	79
G.C.W. Vatke (1849-1889)	43
J.O. Böckeler (1803-1899)	26
F.A. Pax (1858-1942)	21
O. Kuntze (1843-1907)	21
O. Penzig (1856-1929)	21
H.L.F. Solms-Laubach (1842-1915)	18
K.M. Schumann (1851-1904)	15
E.G. Gilg (1867-1933)	13
E. Hackel (1850-1926)	10
R.L.A.M. Gürke (1854-1911)	9
C.L.U. Dammer (1860-1920)	8
O.E. Ulbrich (1879-1952)	8
P.H.W. Taubert (1862-1897)	7
F.W.L. Kränzlin (1847-1934)	6
K. von Pöllnitz (1896-1945)	6
P.F. Ascherson (1834-1913)	5
H.A.T. Harms (1870-1942)	5
C. Gilg-Benedict (-1915-)[8]	5
J.F. Brandt(1802-1879)	4
J.C. Hasskarl (1811-1894)	3
L.E.T. Loesener (1865-1941)	3
F.R. Schlechter (1872-1925)	3
P.E.O.W. Knuth (1854-1899)	3
K. Hoffmann (1802-1883)	3
G. Lindau (1866-1923)	3

Botanist (dates)	Number of names
L.A.T. Radlkofer (1829-1927)	3
K.F.A.H. Wolff (1866-1929)	3
J.R. Perkins (1853-1933)	3
P. Rohrbach (1846-1871)	3
A. Berger (1871-1931)	3
F.E. Wimmer (1881-1961)	2
F.W. Klatt (1825-1987)	2
R. Muschler (1883-1957)	2[9]
A. Brand (1863-1930)	2
C.G.O. Drude (1852-1933)	2
H.G. Hallier (Hall. f.) (1868-1932)	2
G.W.J. Mildbraed (1879-1954)	1
J.C. Huber (1830-1913)	1
R.E. Kunze (1838-1919)	1
O. Warburg (1859-1938)	1
W.G.B.A. Brehmer (1883-?)[10]	1
W.O.E. Ruhland (1878-1960)	1
F.A.G. Bitter (1873-1927)	1
F. Markgraf (1897-1987)	1
K.A.O. Hoffmann (1853-1909)	1
F.K.J. Vaupel (1876-1927)	1
H.A.R. Grisebach (1814-1879)	1
H. Dammann (-1892-)[11]	1
E.F. Knoblauch (1864-1936)	1
K. Lewin (-1922-)[12]	2
O.E. Schulz (1874-1936)	1

8. Charlotte Gilg-Benedict, for many years assistant to E.G. Gilg and joint author (Gilg & Benedict) of many species in Capparaceae, later Gilg's wife as Gilg-Benedict.
9. Only two of R. Muschler's names are recorded as representing Eritrean or Ethiopian plants if the methods defined in this paper are used; for a more in-depth discussion, see Ryding (2001).
10. Barnhart (1965) indicates only year of birth.
11. Name mentioned without further information by Barnhart (1965).
12. According to Barnhart (1965) K. Lewin was born in Berlin in 1892, but there is no mentioning of him among Berlin botanists. Year of death is not ascertainable. He was author of a large paper on *Haplocarpha* and *Arctotis* (Asteraceae) in 1922, but the paper does not contain any biographical information.

try. Had closer connections with France been established, it would have counterbalanced the pressure from Egypt. However, the French government decided not to follow the proposals through. Schimper did not collect much during this time. His political and administrative duties probably restricted his possibilities for travelling and plant collecting. Gillett (1972) has, however, recorded plant collecting activities by Schimper in 1842, 1847-1848 and 1850. In 1855, his father-in-law, Dejazmach Wube, was killed in a battle with Ras Tewodros, who later became emperor. In February of the same year, Schimper's house in Adua was looted and his specimens and manuscripts were destroyed. Tewodros ordered that he should be confined to the surroundings of Adua, and not be allowed to travel or collect in other areas. Specimens exist from the Adua region for the years 1856, 1861, 1862, and 1863. Most of these specimens went to the Botanical Museum in Berlin (B), where the original set of most of these collections, including many types, was held. Unfortunately many of these were destroyed in the Second World War and the duplicates that were distributed often had very scanty labels. A certain Captain Pullen brought an original set of some of the collections from this period to England; most of these plants are at Kew. In 1868, Schimper was imprisoned at Tewodros' fortification at Magdala together with other Europeans. He was released in that same year by the British expedition led by Napier. An original set of specimens went to the Natural History Museum, London (BM), in gratitude for his release. There is no record of collecting activity by Schimper after 1868. He died at Adua in 1878. Many duplicates and perhaps also first sets of his collections were stored at the Natural History Museum in Strasbourg, where they were destroyed by the bombardment of Strasbourg in 1870.

The great diffusion of Schimper material collected from both Ethiopia and Eritrea became widely available to almost anyone interested. Botanists carrying out taxonomic revisions of broader groups would have had Schimper material available, and a large number of specialist studies were carried out.

German botanists of the Engler period

As described above, Schimper continued to collect until 1863 and sent collections to Berlin, London and Strasbourg at least until that date. Many of these later collections were used in Berlin for the description of new taxa (Table 3), for example in A. Engler's *Hochgebirgsflora* (Engler 1892). However, material from other collectors was also received at Berlin. Throughout the Engler-period there was a small number of other German (or German speaking) collectors who visited northern and central Ethiopia as well as the Harar region (Harerge). The best known of these collectors are H. Steudner, who collected in northern Ethiopia and Eritrea in 1861-1862, G. Rohlfs & A. Stecker, who collected in years 1880-1883, J.M. Hildebrandt, who collected in 1872, G. Schweinfurth, who collected, especially in Eritrea and in the border area between Sudan and Ethiopia, in the years 1863-1866, and again in 1891-1894. Kammel von Hardegger & P. Paulitschke, who were in eastern Ethiopia in 1884-1885, were Austrian, and their collections are only in Vienna. A. Keller was Swiss and took part in the big game hunting expedition of the Italian Count Ruspoli in 1891; Keller's collections are at Zurich with very few duplicates found elsewhere.

The most important German field work, apart from Schweinfurth's, was the trips to southern Ethiopia by H. Ellenbeck in 1900-1901, O. Neumann in 1900-1901 and F. von Rosen in 1905-1906. F.J. Bieber, who went to Kefa in 1904-1905, was an Austrian envoy and his collections, which are unicates, are in Vienna where Cufodontis (1948) as the first studied them nearly 50 years later. Kew has

some duplicates of Steudner's collections, but only the collections of Schweinfurth were much distributed to institutions outside Berlin: Index Herbariorum reports 20 herbaria holding his collections (Hettie Vegter 1986). Later in the period the collections made by a number of Italian collectors were studied by German botanists, especially collections from eastern Ethiopia, such as the plants from the trips made by Robecchi-Bricchetti in 1888-1889 and 1891 and Ruspoli & Riva in 1892-1893 in Harar and Sidamo. Collections from royal or noble big-game hunting expeditions also entered the Berlin herbarium. Schweinfurth, for example, identified the collections made by the Romanian princes D. & N. Ghika-Comanesti in eastern Ethiopia and Somalia during the years 1895-1896, and the Ruspoli & Riva expedition was also a big game expedition.

A special problem is presented by a number of new names proposed and validated by L. Buscalioni and R. Muschler said to be collected by the Duchess Helene of Aosta. The types of these names are stated to come from localities in modern Tanzania, Zambia and Zimbabwe, but in fact the descriptions of at least some of these taxa are based on material collected by Schweinfurth in Eritrea (Ryding 2001).

At Berlin there was a group of botanists interested in floristics, systematics and plant geography. Africa, South America and the Pacific were important areas of interest, as can be seen from the series *Die Vegetation der Erde*, of which 5 volumes are dedicated to Africa. The flora of Ethiopia was just one of many interests. Engler was the leading exponent of this school; he was from 1889 to 1921 the director of the Berlin Botanical Garden. Not surprisingly, he was also the most productive in the naming of material from the Flora area with a production of 91 names.

Schweinfurth was a private botanist associated with the Berlin Botanical Garden; he was the only herbarium botanist who also did field work in the Flora area and had a dedicated personal interest in northeastern tropical Africa. Table 3 shows that 54 German botanists named 483 plants from the Flora area. There are some slight complications with nationality: The only information we have traced about K. Lewin is that he was born in Berlin and published in Berlin, but is not mentioned among the Berlin botanists; we have therefore considered him

Table 4. Mostly British botanists associated with the Flora of Tropical Africa-period (1868-1932), or at least the period before the Flora of Tropical East Africa, and the number of plants they named from the FEE-area. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
G. Bentham (1800-1884)	61
J.G. Baker (1834-1920)	41
N.E. Brown (1849-1934)	30
C.B. Clarke (1832-1906)	21
D. Oliver (1830-1916)	20
J.D. Hooker (1817-1911)	18
O. Stapf (1857-1933)	16
W.P. Hiern (1839-1925)	15
T. Anderson (1832-1870)	10
E.G. Baker (1864-1949)	9
J. Hutchinson (1884-1972)	7
H.N. Ridley (1855-1956)	6
M.T. Masters (1833-1907)	3
A.B. Rendle (1865-1938)	3
S. Moore (1850-1931)	3
C.H. Wright (1864-1941)	3
H.B. Christian (1871-1950)	3
J. Britten (1846-1924)	2
C.E. Hubbard (1900-1980)	2
T.A. Sprague (1877-1958)	2
M. Ashby (1923-)	1

German. J. Perkins was an American lady, but she was a student of the Engler-school and worked in Germany; she is therefore listed under German botanists. Penzig was a German, who became an Italian citizen and was for many years professor and director of the Botanical Garden at Genoa; he is, a bit arbitrarily, counted here.

Flora of Tropical Africa and associated British publications

The major work dealt with in this section is the *Flora of Tropical Africa* (1868-1937). The editor of the first three volumes of this work (FTA) was D. Oliver, followed by W. T. Thiselton Dyer, D. Prain, and A. W. Hill. Several taxa based on material collected in the Flora area were first described in FTA or in papers associated with it, see Table 4. This Flora was part of the series of "colonial floras" to be published by the Royal Botanic Gardens, Kew. However, there were rather few British collectors who went to Eritrea and Ethiopia; most British collecting was a side product of other activities in Ethiopia. The collections, which W.C. Plowden made from northern Ethiopia in 1848-1860, were a side product of his activities as a British Consul in Ethiopia. The collections, which Capt. M.S. Welby made in eastern and southern Ethiopia in 1894 and in 1898-1899, were a side product of his big game hunting. The same was the case with the collections made by F.L. and W.D. James and J.G. Thrupp in Harerge in 1885, and the collections of Lord Delamere made in eastern and southern Ethiopia in 1896-1897. A surprisingly large number of the previously undescribed taxa from Ethiopia and Eritrea in the FTA were still based on the material from Schimper and other collectors from the middle of the 19th century.

The number of new names based on material from Eritrea and Ethiopia described in the early volumes of the FTA is slightly smaller than the contemporary output from Berlin: 21 botanists named 276 plants. Not all were born British: Stapf lived in Austria until 1890, when the Royal Botanic Gardens, Kew, employed him. An important factor behind the lower British level of activity was that the British focused their interest elsewhere in Africa. An example can illustrate this: Spencer Moore is a well known authority in a number of families of African plants, but his species are mainly described from East Africa, the *Flora Zambesiaca* area, or what is currently the *Flora of Somalia* area.

The period 1860-1940 elsewhere with the exception of Italy

The interest in the Flora area outside the German countries and Britain was rather limited in this period, especially when compared with the previous period. Table 5 lists 21 continental European, but non-German botanists who named 96 plants. The list of national affiliations is rather mixed, including Belgian, Danish, Dutch, French, Swedish, Swiss and Russian botanists. The Schimper collections seem to have dried out as a source of undescribed taxa, and the new German and Italian collections were not nearly as widespread as the Schimper material.

Even after the beginning of the 20th century there was still limited interest in the Flora area in botanical centres outside Europe. An American collector, E.A. Mearns, passed through Ethiopia with the Th. Roosevelt expedition to hunt big game. The rather few collections are, as far as we know, at the Smithsonian Institution in Washington DC. An American traveller, A. Donaldson-Smith, travelled through eastern and southern Ethiopia in 1894-1895 and brought back material from southern Ethiopia, but this was worked on at the British Museum in London. E.B. Babcock and E.E. Sherff, both American monographers of large genera of composites, published 5 names in this period. The only other American botanist active on Ethiopia was Perkins, who worked in Berlin.

Table 5. Botanists from various European countries outside Britain, Germany and Italy, and the number of plants they named from the FEE-area in the period 1860-1940. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
H. Schinz (1858-1941)	13 (nearly all with Th. Durand)
Th. Durand (1855-1912)	11 (all with H. Schinz)
C.E.B. Bremekamp (1888-1984)	10
M. Gandoger (1850-1926)	10
C.A. Cogniaux (1841-1916)	9
J.I. Briquet (1870-1931)	5
R.E. Fries (1876-1966)	5
R.H. Chodat (1865-1934)	4
H.E. Baillon (1827-1895)	4
C. Sacleux (1856-1943)	3
T.C.E. Fries (1886-1930)	3
P.E.L. van Tieghem (1839-1914)	3
S.S. Murbeck (1859-1946)	3
C.E. Gustafsson (1868-1939)	3
J.E. Planchon (1823-1888)	3
B.P.G. Hochreutiner (1873-1959)	1
P. Aellen (1896-1973)	1 sp. & 1 var. name
C. von Friesen (-1933-)[13]	1
A. Thellung(1881-1928)	1
E. Warming (1841-1924)	1
A.I. Malzev (1879-1948)	1

13. Not mentioned by Barnhart (1965).

Italian interests and collections

With the annexation of Venice in 1866 and of papal Rome in 1870, Italy had united into one nation under a constitutional monarchy. At the same time the new nation began to take an interest in establishing colonies. In 1869, the Italian government purchased the Red Sea town of Assab to be used as a port and in 1885, the government occupied the harbour of Massawa. Then in 1889, the Italian government and the new emperor of Ethiopia, Menelik II, acknowledging the Italian possessions along the Red Sea, signed the treaty of Uchalli. Shortly after, the Italian Red Sea possessions were proclaimed the Colony of Eritrea from 1 January 1890. However, already in March 1890, Italy broke the treaty and invaded Ethiopia, but was defeated by Menelik II at Adua. At the subsequent peace treaty *status quo* was confirmed. The Italian botanical studies were part of this political development. At the Colonial Botanical Institute in Rome an attempt was made to write a *Flora della Colonia Eritrea* (Pirotta 1903-1908). It is notable at those early days of womens' admission to the world of science that four of the six botanists contributing to this work were women: Dr. Riccarda Almagia, Dr. Beatrice Armari, Dr. Eva Boselli, and Dr. Ernesta di Capua.

The first Italian botanical collectors that came into Ethiopia were O. Antinori and V. Ragazzi who were directors of the Italian Geographical Research Station based near Ankober in Shewa: Antinori collected from 1876 to 1882 and Ragazzi from 1884 to 1890). L. Traversi travelled with Nakari and Antonelli in the Rift Valley region in 1885-1888 (Nakari was apparently Finnish by birth, but nothing more is known about him). L. Robecchi-Bricchetti travelled in eastern Ethiopia in 1888-1889 and 1891, G. Ostini travelled with E. Chiovenda in Gonder and Gojam in 1908, G. Negri travelled partly with E. Chiovenda in central Shewa and Arsi in 1909-1910 and L. Buscalioni chiefly in Gojam, Shewa and Harar in 1916. A much longer list, although with some overlap, can be enumerated for Italian collectors in Eritrea. A very prolific example is A. Pappi who collected throughout Eritrea in

1892 and between 1902 and 1934. After the Italian fascist government had occupied Ethiopia in 1936, over 30 botanical collectors studied the flora. In southern Ethiopia, in what the Italians called "Galla-Sidama", the Italian field work was sometimes organised in large, multidisciplinary field trips with lorries, camps and porters. The result of this intensive collecting activity was preserved in a limited number of herbaria in Italy, including the Colonial Institute in Rome and the Colonial Botanical Garden in Palermo. Now, the Italian collections from Ethiopia, Eritrea and Somalia are almost all found in two institutions in Florence, the Erbario Tropicale (FT) and the Museo Botanico (FI), while some specimens remain in the herbaria of the botanical garden of Palermo (PAL), Catania (CAT), Bologna (BOLO), Turin (TO) and Modena (MOD). Very few of the collections have duplicates distributed outside Italy. A notable exception is the more widely distributed material of R.E.G. Pichi-Sermolli.

As can be seen in Table 6, 16 Italian botanists have named 470 plants. However, E. Chiovenda proposed more than half of these names and there is, therefore, no doubt that he is by far the most prolific Italian authority for taxa described from Ethiopia and Eritrea. Unfortunately, some of his work was done hastily. Moreover, he was too isolated from his botanical colleagues in other countries, as can be seen from a number of cases where he described species in wrong families (de Wilde 1968; Friis 1981b, 1985a, 1985b, 1987, 2001; Friis & Vollesen 1980; Vollesen 1985).

This list in Table 6 contains almost exclusively botanists of Italian origin. However, G. Cufodontis was born of Greek parents in Trieste, and he spent the last half of his life in Austria working in Vienna. He kept his keen interest in the flora of the Horn of Africa and produced the impressive *Enumeratio Plantarum Aethiopiae Spermatophyta* (Cufodontis 1953-1972). He also named new taxa based on modern collections made by German collectors from Gojam, Sidamo and Arsi (Cufodontis 1958a, 1958b, 1960, 1962, 1965, 1966 and 1969).

Penzig, who was professor at Genoa, is listed under German botanists of the Engler period.

There is no doubt that the table underestim-

Table 6. Mostly Italian botanists and the number of plants they named from the FEE-area mainly before the Second World War. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
E. Chiovenda (1871-1941)	268
G. Cufodontis (1896-1974)	74
R.E.G. Pichi-Sermolli (1912-)	31
D. Lanza (1868-1940)	23
A. Fiori (1865-1950)	23
U. Martelli (1860-1934)	18
G.E. Mattei (1865-1943)	12
O. Beccari (1843-1920)	6
A. Todaro (1818-1892)	4
A. Terraciano (1861-1914)	2
F. Parlatore (1816-1877)	2
G. Lusina (1893-1963)	2
B. Armari (-1904-)[14]	1
E di Capua (-1904-)[15]	2
C. Avetta (1861-1941)	1
R. Pirotta (1853-1936)	1
T. Caruel (1830-1898)	1

14. This is Beatrice Armari, author of a number of families in *Flora della Colonia Eritrea*, and not mentioned in Barnhart (1965).
15. This is Ernesta di Capua, author of a number of families in *Flora della Colonia Eritrea*, and not mentioned in Barnhart (1965). According to the IK on CD-ROM there are no taxa described by Riccarda Almagia and Eva Boselli.

ates the production of infraspecific names by Italian botanists, as can be seen from the *Enumeratio*.

The beginning of the Flora of Tropical East Africa

According to the Foreword to the *Flora of Tropical East Africa* (Turrill & Milne-Redhead 1952), the project to prepare this Flora stemmed from meetings almost immediately after the Second World War, when a committee recommended that a Flora of Uganda, Kenya and Tanzania should be prepared at the Royal Botanic Gardens, Kew. To this should be connected an expansion of collecting activities in East Africa and the building of a new wing to the Coryndon Museum in Nairobi, now the East African Herbarium (EA), part of the National Museums of Kenya. The botanists engaged in the writing of the Flora of Tropical East Africa had no immediate responsibility for the flora in Ethiopia and Eritrea, but since many of the taxa that occur in the Flora of Tropical East Africa area were first described from Ethiopia and Eritrea, there was some common interest. One of these sources of common interest was the boundary commission demarcating the borders between British Somaliland and Ethiopia in 1931-1933 (Gillett 1941), and another commission demarcating the border between Kenya and Ethiopia in 1952-1953.

The new group of British botanists was almost entirely based at Kew, spending extended periods collecting in East Africa, and most of them appear in Table 7. Undoubtedly, the Ethiopian Flora Project would not have fared as well as is the case had there not been a much bigger flora project already based at the Royal Botanic Gardens, Kew, dealing with the more species-rich flora of a neighbouring area. Since there was no obligation comparable to that of the FTA team to describe new species from Ethiopia, the list in Table 7 is not very long: 14 British botanists named 39 plants from the Flora area over 25 years. There was, however, a renewed interest in botanical collecting in Ethiopia and Eritrea during this period. This is first of all reflected in the collections of H.F. Mooney who founded the National Herbarium (ETH) in Addis Ababa (Mesfin Tadesse 1991). Mooney also encouraged Ethiopian collectors, *e.g.* Tekle H. Hagos.

Table 7. Mostly British botanists, who were associated with the Flora of Tropical East Africa during 1952 to 1980 and the number of plants they named from the FEE-area. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
G.W. Reynolds (1895-1967)	8
E.A. Bruce (1905-1955)	6
J.B. Gillett (1911-1995)	5 sp. & infrasp. names
F.G. Davies (1944-)	3
A. Radcliffe-Smith (1938-)	1 sp. & 2 var. names
J.P.M. Brenan (1917-1985)	2
V.S. Summerhayes (1987-1974)	2
W.B. Turrill (1890-1961)	2
P.R.O. Bally (1895-1980)	1
W.D. Clayton (1926-)	1
E.W.B.H. Milne-Redhead (1906-1996)	1
G.E. Wickens (1927-)	1 var. name
R.A. Graham (1915-1958)	1
J.D. Snowdon (1886-1973)	1

The Flora of Ethiopia and Eritrea; the beginning of scientific botany in Ethiopia and Eritrea

The history of the start of the Ethiopian Flora Project is given in the Preface to Volume 3 of the Flora of Ethiopia (Hedberg & Tewolde 1989). The collecting activity and the start of involvement of Ethiopian botanists are as follows.

Table 8. Botanists associated with the Flora of Ethiopia and Eritrea and the number of plants they named from the FEE-area up to 1996. The position of some, who has contributed both to the Flora of Tropical East Africa before 1980 and the Flora of Ethiopia and Eritrea, is of necessity somewhat arbitrary. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
M.G. Gilbert (1943-)	68 sp. & infrasp. names
M. Thulin (1948-)	25 sp. & infrasp. names
K. Vollesen (1946-)	24 sp. & infrasp. names
S.M. Phillips (1945-)	19 sp. & infrasp. names
B. Verdcourt (1925-)	16 sp. & infrasp. names
S. Carter (1933-)	15 sp. & infrasp. names
R.M. Polhill (1937-)	14 sp. & infrasp. names
P.J. Cribb (1946-)	8 sp. & infrasp. names
I. Friis (1945-)	7 sp. & infrasp. names
A.G. Miller (1951-)	6 sp. & infrasp. names
P. Goldblatt (1943-)	6 sp. & infrasp. names
R.B. Faden (1942-)	6 sp. & infrasp. names
B. Jonsell (1936-)	5 sp. & infrasp. names
H. Riedl (1936-)	5
O. Sebald (1929-)	2 sp. & 3 var. names
S. Thomas (-1996-)	5 sp. & infrasp. names
I. Nordal [I. Bjørnstad] (1942-)	4 sp. & infrasp. names
K.A. Lye (1940-)	4 sp. & infrasp. names
O. Ryding (1951-)	2
C. Jeffrey (1934-)	3 sp. & infrasp. names
L.E. Kers (1931-)	2 sp. & 1 var. name

Botanist (dates)	Number of names
S. Liede (1957-)	2 sp. & 1 subsp. name
O. Hedberg (1923-)	3 infrasp. names
B. Stedje (1956-)	2 sp. & infrasp. names
J.J.F. de Wilde (1932-)	2 sp. and infrasp. names
M.N. Hadidi (1934-)	2 sp. & var. names
R.D. Meikle (1923-)	1 sp. & 1 var. name
B. Stannard (1944-)	1
C. Grey-Wilson (1944-)	1
C. Puff (1944-)	1
C.M. Wilmot-Dear (1952-)	1
D. Bridson (1942-)	1
G. Moggi (1927-)	1
H.J. Venter (1938-)	1
I. Hedberg (1927-)	1
M.J.S. Sands (1938-)	1 var. name
Sebsebe Demissew (1953-)	20 sp. & infrasp. names
Mesfin Tadesse (1951-)	14 sp. & infrasp. names
Dawit Abebe (-1989-)	4
Ensermu Kelbessa (1952-)	3 sp. & infrasp. names
Asfaw Hunde (1940-)	2 sp. & infrasp. names
Getachew Aweke (1937-)	1

A number of European and American collectors, worked in the 1960s and 1970s. Following the foundation collection of Mooney, particularly large collections with duplicates associated with the National Herbarium have been made by J. Ash, M.G. Gilbert, O. Hedberg, I. Friis, K. Vollesen, M. Thulin, C. Puff, and about 15 more. There is now a long list of Ethiopian collectors of whom Ensermu Kelbessa, Getachew Aweke, Mesfin Tadesse and Sebsebe Demissew each have made over 1000 collections, mostly more. The other important collections in Ethiopia are those based in Alemaya University of Agriculture (ACD). W. Burger collected in Ethiopia in 1961-1965 and he was followed by a group of Dutch botanists mainly from Wageningen. These include J.J. Bos, E. Westphal, P.C.M. Jansen, J.J.F. de Wilde, and W.J.J.O. de Wilde. Burger and the Dutch at Alemaya University encouraged the early Ethiopian collectors, Tadesse Ebba and Amare Getahun. A few other European collectors (*e.g.* A. Ambjörn who collected in Shewa 1946-1947, and H. Smeds who collected in central and

Table 9. Botanists not directly contributing accounts to the Flora of Ethiopia and Eritrea and the number of plants they have named from the FEE-area up to 1996. Due to the sources of error mentioned in the chapter "Materials and methods; sources of error" the list of people and the new names they have proposed is not to be regarded as complete.

Botanist (dates)	Number of names
J.P. Lebrun (1932-)	7
M. Hedrén (1956-)	5 sp. & subsp. names
J.O. Kokwaro (1940-)	4 sp. & infrasp. names
A. Stork (1937-)	3
D.C.H. Plowes (-1986-)	3
E. Gamal-Eldin (1943-)	3 subsp. name
L.E. Newton (1936-)	3
N. Hepper (1929-)	3
R.B. Fernandes (1916-)	2 subsp. & 1 var. name
A. Anderberg (1954-)	2
D. Wiens (1932-)	2
E.B. Alexeev (1946-1976)	2
G.R. Michelozzi (1928-)	2 sp. & 2 var. names
H. Scholz (1928-)	1 sp. & 1 subsp. name
I.C. Hedge (1928-)	2
J.H. Kirkbride (1943-)	2
J.R.I. Wood (1944-)	2
O.M. Hilliard (1926-)	2
P.E. Brandham (1937-)	2
P.S. Masinde (-1993-)	2
R.H. Willemse (-1979-)	2
S. Wattimah [now S. Simiyu] (-1994-)	2 var. names
T. Reilly (-1995-)	2
H. Heiniger (-1953-)	2
A. Gilli (1904-)	1
A. Lourteig (1913-)	1 subsp. name
A.J. Paton (1963-)	1
B. Mathew (1936-)	1
C. Baden (1952-)	1 subsp. name
D. Field (1937-)	1
D.R. Hunt (1938-)	1
E. Benvenuto (1947-)	1 var. name
F.N. Rasmussen (1948-)	1
F.X. Ayobangira (-1987-)	1 var. name
G. Wagenitz (1927-)	1 subsp. name
H. Freitag (1932-)	1 subsp. name
H. Robinson (1932-)	1
H.D. Schotsman (1921-)	1

Botanist (dates)	Number of names
H.W. Lack (1949-)	1
H.Y. Liu (-1989-)	1
J. Raynal (1933-1979)	1
J. Shah (1948-)	1
J.H. Seyani (1948-)	1
J.M. Lock (1942-)	1 subsp. name
J.N. Brunken (-1977-)	1 subsp. name
K. Balkwill (1958-)	1
K. Mtotomwema (-1990-)	1 subsp. name
L. Boulos (1932-)	1
L.B. Smith (1904-)	1
L.C. Leach (-1971-)	1
M.J. Musselmann (1943-)	1
M. Hjertson (1961-)	1
M.N. Chaudhri (1932-)	1
P. Bruyns (1957-)	1
P. Goetghebeur (1952-)	1
P. König (-1988-)	1
P. Vorster (1945-)	1
P.A. Fryxell (1927-)	1
R.K. Brummitt (1937-)	1
R.M. Harley (1936-)	1
R.M. King (1930-)	1
C.X. Furtado (1897-1980)	1
S. Abedin (-1986-)	1 var. name
S. Ousted (1948-)	1 subsp. name
G.S. Serrato-Valenti (-1971-)	1 var. name
T.A. Cope (1949-)	1
T.G.J. Rayner (1963-)	1
V. Marais (1929-)	1 var. name
V.P. Botchantsev (1910-1990)	1
J.A.R. Paiva (1933-)	1
H. Wild (1917-1982)	1
R. Wilczek (1903-1984)	1
S.M.A. Kazmi (1926-)	1
J.H. Ross (1941-)	1
S.J. Mayo (1949-)	1
U. Meve (-1994-)	1 subsp. name

southern Ethiopia 1953-1954 and again 1957-1958) have kept their specimens in their home herbaria in Europe without distributing duplicates. A preliminary survey of collectors since the beginning of the 1960s can be found in an Appendix entitled *List of Collectors and their Collections since 1960.*

The start of the Flora Project relied on European taxonomists because the Ethiopian scientists were mostly away on training. Thus, as shown in Table 8, 36 non-Ethiopian botanists named 257 plants, many of them in the 1980s. The people on the list are American, Austrian, British, Danish, Dutch, Egyptian, German, Norwegian, South African and Swedish. By 1999, there were six Ethiopian taxonomists in the National Herbarium, one associated with agricultural research in Ethiopia, and one in Asmara University. Of these, six have named 44 plants, which is 15% of all the newly described taxa which we here associate with the Flora Project. We think this is impressive.

The Flora Project is closely connected with the growth of the National Herbarium in Addis Ababa, which now has over 70,000 specimens, including a number of types for new taxa described for the Flora. The collection of types includes duplicates made by Schimper over 100 years ago.

Other botanical activity in the recent years

We have also accumulated the names of botanists who have not contributed family accounts or parts of family accounts to the Flora project, but who have named plants from the Flora area. These are listed in Table 9, which is the longest of all lists in this paper: 76 botanists have named 118 plants. These botanists include Americans, Belgians, British, Chinese, Danes, Germans, Italians, Kenyans, Malawis, Pakistanis, Portuguese, Russians, South Africans, Swedes and Swiss. There are some for whom we have been unable to detect the nationality.

Without the collecting of Mooney and the others from the 1960s onwards, this naming activity would not have been possible. In some ways the situation resembles the situation just after 1838-1850. Around that time Schimper's collections provided the new material and the flora was *Tentamen Florae Aethiopiae.* Now it is largely the scientific material collected in association with the Flora Project, and the flora is called *Flora of Ethiopia and Eritrea.*

Conclusions

Overall, our impressions are that in the first half of the 19th century naming activities occurred in a number of British, French and German centres, with some in smaller counties like Switzerland. Then in the second half of the 19th century, naming was dominated by Britain, particularly Kew, and Germany, particularly Berlin. At the same time there was a decline in the French interest. Italian interests corresponded with the beginning of colonial interests on the Red Sea coast and were particularly strong in the first half of the 20th century. After 1950 there was a renewed British interest, partly connected with the beginning of writing of the *Flora of Tropical East Africa*, and a growing interest elsewhere, for example in Germany and several smaller European countries, especially the Netherlands and in Scandinavia. This period has also seen the emergence of scientific taxonomic botany in Ethiopia and Eritrea.

The long perspective in this development shows the importance of two types of activity for progress:

1. Active and competent field work, the collections from which are made widely available to those seriously interested in studying them, and
2. International collaboration and open contact between botanists across institutions and political borders.

Schimper became so important because he knew the country and the people, and because his material, especially the early material, became so widespread. To work in isolation, as happened increasingly in Italy towards the start of the Second World War, meant lack of mutual inspiration and constructive criticism from colleagues. The Flora Project has attempted both to support growth of science in Ethiopia and to foster friendly international collaboration. Perhaps this was due to an unrecognised lesson from the history that we have just outlined here.

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Appendix: List of Collectors and their Collections since 1960

In connection with the preparation of family accounts for the Flora, and through searches in Ethiopian herbaria, the present authors have recorded names of collectors, together with information about their year(s) of collection, the floristic regions in which they collected, and the whereabouts of their collections. The information is preserved in an alphabetically arranged text file, which is being continuously updated. It is hoped that readers that have additions or corrections will contact us. We are aware that the information in this list cannot be fully correct or complete, so please help us to improve it.

The information is presented in this order: Name of collector. Nationality and employment (where known). The designation "Ethiopian students" also refers to students at Asmara University up to Eritrean independence. Floristic provinces in which the collector is known to have been active. Herbaria (abbreviations according to Index Herbariorum) in which collections are known to have been deposited. Collections made by multiple collectors are recorded and reference made to the person responsible for the numbering series. Collectors who have worked before 1960, but are not fully treated by the previous review of Ethiopian collectors by Cufodontis (1962) are included in square parentheses.

Abeba T. – Ethiopian student. 1975. GD Coll. at ETH.

Abdurahman Ab. – Ethiopian student. 1972. HA. Coll. at ACD (4 nos.).

Aberu Dagnew – Ethiopian student. 1974. HA. Coll. at ACD (48 nos.).

Abiya Eshtu – Ethiopian student. 1974. HA. Coll. at ACD, ETH.

Abraham Woubshet – Ethiopian student. 1974. Coll. at ACD (2 nos.).

[Adefris Bellehu – Ethiopian (deceased), employed at the Desert Locust Service throughout its existence, later first Director of DLCOEA (Desert Locust Control Organization East Africa) in the 1950s, 1960s and early 1970s. 1950. WU. Coll. at EA.]

Afeworki Gebrai & Mehret Abebe – Ethiopian students. 1983. EW. Coll. at ETH, Asmara.

Ahmed M. Sherif. – Ethiopian, works for Min. of Agriculture Weed Science Division. Resident collector since 1985. SU, GJ. Coll. at ACD (21 nos.), ETH.

Aklilu K. Mariam – Ethiopian student. 1961. HA. Coll. at ACD (7 nos.).

Albers, C.C. – British (?) forester. Pre 1962. Mostly SU (many cultivated plants). Coll. at K, ETH.

Alemayehu Haile – (numbers in SW. Ethiopia Forestry Inventory Series). Ethiopian forestry assistant. 1976. AR. Coll. at EA, ETH, K.

Alemu Mengistu – Ethiopian student. 1971. HA. Coll. at ACD (10 nos.).

Alemayehu, Merga & Zinna – (in SW. Ethiopia Forestry Inventory Series). Ethiopian forestry assistants. 1976. SU. Coll. at ETH, EA.

Ali Hussen – Ethiopian student. 1976. HA. Coll. at ACD (7 nos.).

Allen, J. & Hammersley, J. – British natural history students. 1972. SU, HA (Ogaden). Coll. at K, ETH.

Amanuel Boru – Ethiopian student. 1974. GJ. Coll. at ACD (1 no.).

Amare Abebe – Ethiopian student. 1974. HA. Coll. at ACD (40 nos.).

Amare Getahun – Ethiopian agricultural scientist at Alemaya Agricultural University, later with international employment. 1959 to ca. 1965. Mainly collections from HA, fewer from many other administrative regions. Coll. at ACD (more than 10,000 nos.), ETH, K. Often also distributed as from IECAMA (see this) without the collectors name, *e.g.* the K set.

[Ambjörn, I. – Swedish agronomist and botanist. 1946-1947. SU. Coll. at S, UPS.]

Amdemariam G. M. – Ethiopian student. 1965. HA. Coll. at ACD (2 nos.).

Anderberg, A. – Swedish botanist, curator at the National Swedish Museum of Natural History. 1982. IL, SU, BA. Coll. at ETH, S.

Araya Sileshi – Ethiopian student. 1965. HA. Coll. at ACD (1 no.).

[Archer, W. – British. 1950-51. WU, SU, BA, HA, GJ. 1954. GD, WG, KF. Coll. at K.]

Asfaw Hunde. with Friis *et al.* 1970; with M. Thulin 1980. Ethiopian biologist with long association with the Universities of Copenhagen and Uppsala. A.H. has used European style of name in publications.

Ash, J.(Mrs. Jonquil). – British resident artist and botanist; husband an ornithologist, employed by N.A.M.R.U. (US Navy Medical Research Unit). 1969-1977. C., W. & S. Ethiopia (at least including KF, AF, SU, WG). Coll. at EA, ETH, MO & K. Mrs. Ash has collected ca. 3600 nos. from many parts of Ethiopia.

Aschalew Bekele – Ethiopian student. 1974. HA. Coll. at ACD (70 nos.), ETH.

[Ashall, C. – British research entomologist, with the Desert Locust Service and with DLCOEA (Desert Locust Control Organization East Africa) for about 20 years from beginning of 1950s, later Deputy Director of COPR (Centre for Overseas Pest Research). 1956-1957. HA. Coll. at K, EA.]

Ashebir Aselae – Ethiopian student. 1975. GD Coll. at ETH.

Asrat Feleke – Ethiopian student. 1960. HA. Coll. at ACD (1 no.).

[Assefa Abebe – Ethiopian, reasearch assistant with Desert Locust Service, later DLCOEA. 1959. HA. Coll. at ACD (1 no.).]

[Assefa Bogale – Ethiopian student. 1958. HA. Coll. at ACD (9 nos.).]

Aweke, G.: See Getachew Aweke. (Getachew Aweke has used European style of personal name usage for his earlier collections).

Ayele Bekeri – Ethiopian student. 1974. HA. Coll. at ACD (43 nos.).

Ayele Gebre Mariam – Ethiopian student. 1987. BA. Coll. at ETH.

Badege Bishaw – Ethiopian student. 1986. HA. Coll. at ACD (4 nos.).

Badege, G. – Ethiopian. 1973. Ethiopia. Coll. at ETH.

Bally, P.R.O. – Swiss botanist residing in Kenya, particularly interested in succulent plants. [1943-1944. SU, KF, AR, SD, HA. 1949. EW, EE. 1954. HA. 1957. HA.] 1963. SD, SU. 1967. SU, HA. Coll. at EA, K.]

[Bally, P.R.O. & Reynolds, G.W. – 1953. SD. Coll. at EA, K. Reynolds: See separate entry.]

Barkley, F.A. – British. 1962. SU. Coll. at K.

Barnes, C.I. – British, possibly associated with D.L.C.O.E.A. [1959-]1960. HA. Coll. at EA, FT.

[Barnes, G. T., with H. A. L. Ferguson. – British. 1953. Ethiopia.]

Basham, C. – British. 1960. HA. Coll. at ACD (3 nos.).

Batt, G.R. – British, attached to the British Army Expedition Survey? 1969-1970. EE (Dahlac Ils.). Coll. at K.

Beals, E. – American ecologist, lecturer at the university in Addis Ababa, also in charge of the National Herbarium after H.F. Mooney. 1964-1966. AF, SU, SD, WU. Coll. at ETH, FT, K.

Bekele Sissay – Ethiopian forage specialist. 1965. HA. Coll. at ACD (11 nos.).

Belay Shiferaw – Ethiopian student. 1981. HA. Coll. at ACD (1 no.).

Bentsson,.?. – Swedish agriculturalist attached to C.A.D.U. (Chilalo Agricultural Development Unit). 1968-1969 AR. Coll. at EA.

[Berhane Berhe – Ethiopian student. 1958. HA. Coll. at ACD (3 nos.).]

Berhane G. Kidan – Ethiopian student. 1965. Coll. at ACD (24 nos.).

Berhe W. Aregay – Ethiopian student. 196?. HA. Coll. at ACD (1 no.).

Beyene Kidane – Ethiopian student. 1974. HA. Coll. at ACD (1 no.).

Bidgood, S. – British botanist, working at K. 1995, 1996, 1997, 1998, 2000. TU, GD, GJ, WG, KF, IL, GG, SD. Collections mainly with I. Friis (q.v.) and others. Coll. at ETH, K, BR, C, EA, FT, MO, WAG.

Biru Abebe – Ethiopian student. 1968. HA. Coll. at ACD (1 no.).

Bisrat Gebru – Ethiopian student. 1982. EE\EW Coll. at ETH.

Bolton, M. – British expert working for the Ethiopian Wildlife Dept. 1969-c. 1972. IL (travelled widely but made few collections). Coll. at ETH.

Bonnefille, R.[Raymonde] – French palynologist, working on the vegetation history of East Africa. 1968, 1973. SU, GG (Omo Valley). Coll. at EA.

Bos, J.J. – Dutch botanist, born 1939, associated with WAG, now director of the Botanical Garden of Wageningen Agricultural University. Stationed at Alemaya 1974-1975. SU, SD, AR, HA. Coll. at ACD (ca. 1400 nos.), WAG (ca. 2500 nos.).

Boudet, G. & Rippstein, G. – French ecologists involved in rangeland survey. 1972-1973. GG, SD, BA, HA?. Coll. at ALF, K (a few). Report with restricted circulation: Boudet, G. & G. Rippstein, *Southern rangeland livestock development project. Ecological Range Survey (Ethiopia)*. A.G.R.O.T.E.C. (Rome), C.R.G. (Florence), S.E.D.S. (Paris) & I.E.M.V.T. (Maisons-Alfort). 175 pp. (1973).

Boulos, L. – Egyptian botanist, working (in Ethiopia) at ILCA and several other places in the Middle East and Africa. 1977. WU, SU, HA. (Some coll. with Amare Getahun). Coll. at ETH, K, and the herbarium of the International Livestock Centre for Africa (ILCA) in Addis Ababa.

Brehme, K.L. – ?Swedish or German forester. (partly in Mooney's number series, q.v.) 1961-?1962. EE, KF, AR, SU. Coll. at ETH, FT, K.

Brown, F. – British wildlife expert. 1971. GG, SD. Coll. at EA, K.

Brummitt, R.K. – British botanist working at K. 1970. SU (a few collections from Addis Abeba Airport). Coll. at K.

Brunt, M. – British forester, working for the Overseas Development Agency, Land Resources Division. (in SW. Ethiopia Forestry Inventory) 1974. AR. Coll. at ETH, K.

Buer, C. – American Peace Corps Volunteer working in Awash National Park and later at the Bale Mountains Nat. Park. 1967. SU Coll. (included in Balley's number series) at K.

Burger, W.C. – American botanist, Assistant Professor at the then I.E.C.A.M.A. (now Alemaya University of Agriculture) at Harimaia between Harer and Dire Dawa (later scientist at the Field Museum, Chicago). 1961-1965. HA, KF, AF, GD, SD (early coll. made with Amare G., q.v.). Coll. at ACD (Alemaya University of Agriculture, complete set, ca. 3800 nos.), C (a few), EA (a few), ETH, FT, K (ca. 3500 nos.), US. The vast majority of Burger's collections were made within 150 km of Alemaya University of Agriculture. He published Families of Flowering Plants in Ethiopia, (1967).

[Cambridge University Expedition – (field trip to the Choke Mts., GJ). 1957. GJ Coll. at. K (ca. 630 nos.), ETH (a few). The botanical collectors of this expedition (all British biology students) include J.M. Evans, J.R. Flenley, R.G. Hillier, C.L.A. Leakey, J.N. Lythgoe and W.J. Balantine. They collected both independently and in various combinations under the one number series.]

Campbell, .?. – British; associated with the Omo Valley archaeological excavations.1967. GG Coll at EA, K.

Carr, C.(Claudia) J. – American ethnologist attached to the Omo Valley archaeological excavations. 1967-1970. SW Ethiopia, lower Omo Valley (KF, GG). Coll. at EA, K, ETH (a few).

Chaffey, D.R. – British forester working for the Overseas Development Administration/Ethiopian Forestry Research Institute. (in SW Ethiopia Forestry Inventory). 1974-1977. SU, AR, IL, KF, SD, BA. Coll. at ETH (nearly complete set, ca. 1000 nos.), K (nearly complete set, as ETH), EA.

Cheke, Anthony. S. – British. 1966. KF. Coll. at K.

Chonacki, S. – Polish art historian and ethnologist, founder of the Institute of Ethiopian Studies in Addis Ababa. (usually in Mooney's number series). 1959-1962. SU, AR, SD, EW, WU. Coll. at ETH, K.

Coady, … – British. … Ethiopia. Coll. where?.

[Colville, J.W. 1954. EW, EE. Coll. at K (ca. 110 nos.), FT. British.]

Cooper: See Omer-Cooper.

Corrà, M. – Ethiopian ecologist, based in France, sometimes working for the International Livestock Centre for Africa (ILCA). 1976. HA. Coll. at ETH, K, and International Livestock Centre for Africa (ILCA). Corrà uses the European style of personal names.

[Curle, A.T. – British diplomat (ex army), resident in Addis Ababa. 1951. SU. Coll. at BM.]

[Curle, A.T. & Schelpe, E.A.C.L. 1952. SU, AR. Coll. at BM. Schelpe was a South African botanist working at Cape Town and mainly interested in ferns.]

Dagnachew Yirgu – Ethiopian, plant pathologist, worked with the FAO Coffee Mission under F.G. Meyer (q.v.). 1964-1965. HA. Coll. at ACD (7 nos.).

[Damon E. G – Ethiopian student. 1959. HA, KF. Coll. at ACD (32 nos.).]

Damtaw Teferra – Ethiopian botanical artist and editor; resident, but has moved abroad. 1984-1988. Collected with I. Friis (q.v.), M.G. Gilbert (q.v.) and S.M. Phillips (q.v.).

[Daniel Gelata – Ethiopian student. 1958. HA. Coll. at ACD (1 no.).]

Dawe, Janice. with C. Puff. 1982.

Dawit Abebe – Resident collector working with medicinal plants since 1980 for Min. of Health. SU, HA, BA. Coll. at ETH.

Demeke K – Ethiopian student. 1980. SU. Coll. at ETH.

Demel Teketay – Ethiopian student. 1986-1988. Later Ph.D. at the Swedish University of Agricultural Sciences, Umeå, in 1996. Lecturer at Alemaya University and director of ACD. Now director of Forestry Research in EARO (Ethiopian Agricultural Research Organisation), Addis Ababa. Mainly HA. Coll. at ACD (at least 1000 nos.), some duplicates at ETH.

Desaling Dessisa – Ethiopian student. Later project assistant. with Fantahun Simon, Tesfay Awas & Gashaw Gibre-Hiwot.

Desta Hundessa – Ethiopian botanist and agriculturalist, worked for the Min. of Agriculture, assisted Perdue (q.v.). 1968. SU. Coll. at ETH, EA, K.

Ebba, Tadesse: See Tadessa Ebba.

Edwards, S. [Sue] – British botanist, resident in Ethiopia since 1968, collecting since 1968, often with other collectors. (Collections with numbers below 100 distributed under the name of Sue Gilbert). SU, WG, IL, BA (Bale Mts. & Gode Research Station), HA; since 1983 EE and EW. Coll. at ETH, K, UPS, C, MO, EA.

[Ellis, P.[Peggy] E. – British entomologist (retired), researcher on locust behavior at the Anti-Locust Research centre in Britain (British Colonial Office), several research trips to arid areas of Eritrea and Eastern Ethiopia. Later with COPR (Centre for Overseas Pest Research). 1953-1955. EW, HA. Coll. at K (ca. 400 nos.), FT.]

[Emanuel Boru. 1958. HA. Coll. at ACD (1 no.).]

Ensermu Kelbessa – Ethiopian botanist, lecturer at ETH. Resident, collecting from 1980, often in collaboration with others, e.g.: Ensermu K. & Tamrat Bekele (1980-1983); Ensermu K. & Zerihun Woldu (1983); Ensermu K., Tamrat Bekele, Sahle G/K. & Vishwanatan (1984); Ensermu K. (1985); Ensermu K. & Melkie Tesfa (1986); Ensermu K. & Petros E. (1987); Ensermu K., Zemede Asfaw & Petros E. (1987); Ensermu K. (1991); Ensermu K. & Kifle Dagne (1992); Ensermu K. & Melaku W. (1995); Ensermu K., Zoe Gowler & Lemessa K. (1995); Ensermu K. & Dessalegn D. (1996); Ensermu K. & Aschalew G. (1998)) – TU, WU, GD, GJ, SU, AR, WG, IL, KF, GG, SD, BA, HA. Coll. at ETH, UPS, K (some).

Epherem Mamo – Ethiopian student. 1981. HA. Coll. at ACD (1 no.).

Erich, J. – French ecologist. 1982. SU. Coll. at ETH.

[Eriksson, J. – Swedish medical doctor and amateur botanist. 1958. KF, AR, BA, SD. Coll. at S, UPS, partly published by O. Hedberg in Arkiv för Botanik, Ser. 2,4 No. 13d: 421-435, (1962).]

Ermias Dagne – Ethiopian phytochemist at Addis Ababa University. Resident, collecting 1987-, often with other collectors, particularly M.G. Gilbert, Mesfin Tadesse and Sebsebe Demissew. BA, SD. Coll. at ETH.

[Esplen, ..., with H.A.L. Ferguson – ?British. 1953. Regions? Coll. where?]

[Evans, J.M. & Lythgoe, J.N. In exp. Univ. Cambridge. 1957. q.v. British students of biology.]

[Evans, J.M. & Flenley, J.R. (in the number series of exp. Univ. Cambridge). 1957. GJ. Coll. at K, ETH (a few). British. Natural history students from Cambridge University.]

Fekadu Abebe – Ethiopian student. 1980. SU. Coll. at ETH.

Fekadu Kassaye – Ethiopian student. 1984. SU. Coll. at ETH.

Feleke Gezahegne ? – Ethiopian student. 1986. HA. Coll. at ETH. ?Working for Min. of Agriculture.

[Feleke Tabor – Ethiopian student. 1958. HA. Coll. at ACD (4 nos.).]

[Ferguson, H.A.L., Esplen, ... & Barnes, G.T. 1953. GD. Coll. at K (ca. 140 nos.). British.]

Fesseha Berhe – Ethiopian student. 1963. HA. Coll. at ACD (48 nos.).

Fesseha Izaz – Ethiopian student. 1960. HA. Coll. at ACD (24 nos.).

[Flenley, J.R. & Hillier, R.G. (in exp. Univ. Cambridge). 1957. GJ. Coll. at K. British. Natural history students from Cambridge University.]

Frahm-Lélieveld, J.A. – ?Dutch/Swedish.1962. SU, KF. Coll. at WAG, K.

Frank, G. – Austrian railway engineer interested in succulent plants. 1985, 1988. SU, HA. Coll. at ETH, ?WU.

Freiw, ... 1979 SU Coll. at ETH. ?, presumably plant pathologist.

Friis, I. 1970 onwards. Danish botanist, lecturer, later professor of botany at the Botanical Museum and Library, Univ. of Copenhagen (C); frequent botanical visitor to Ethiopia and closely associated with Ethiopian Flora Project (on Editorial Board). Number series with more than 10,000 collections, mostly in teams with other collectors. – With Asfaw Hunde & Jakobsen, K. 1970. KF, IL. Coll. at C, ETH, K, BR. – With Rasmussen, F.N. & Vollesen, K. 1972-1973. Partly with Gilbert, M. G.: SU, SD Partly with Getachew Aweke: KF, IL. Coll. at C, ETH, K, BR, FT. (The 1970 and 1972-1973 collections were partly published by Friis, Rasmussen & Vollesen in Opera Botanica 63: 1-70 (1982)). Asfaw Hunde: Ethiopian botanist resident in Uppsala, Sweden, see separate entry. K. Jakobsen was a Danish university lecturer and botanist at Copenhagen University. F.N. Rasmussen is a Danish University lecturer and botanist at Copenhagen University. K. Vollesen: Danisk/British botanist at R.B.G., Kew; see separate entry. – Friis, I., Mesfin Tadesse & Vollesen, K. 1982. SD, BA. Coll. at ETH, C, K, UPS. Mesfin Tadesse & K. Vollesen: See separate entry. – Friis, I., Zerihun Woldu & Vollesen, K. 1982. IL. Coll. at ETH, C, K, UPS. Zerihun W.: See separate entry. – Friis, I., Damtaw Teferra, Gilbert, M.G. & Vollesen, K. 1984. IL, KF, BA. Coll. at C, K, ETH, UPS. M. G. Gilbert and Damtaw Teferra: See separate entries. – Friis, I. 1986. KF, IL, EW. Coll. C, ETH, K. – Friis, I. & Lawesson, J. 1988. GD, GJ. Coll. at C, ETH, K. Lawesson is a Danish Botanist at the Biology Department, University of Aarhus. – Friis, I., Zeri-

hun Woldu, Sebsebe Demissew & A. Michelsen. 1988. BA (Bale Mountains National Park). Coll. at C, ETH, K. [nos. 5611-5765]. Sebsebe Demissew: Se separate entry. – Michelsen, A.: Danish ecologist at the Botany deaprtment, University of Copenhagen. – Friis, I., Bidgood, S., Høst, P., Melaku Wondafrash, Desalign Sessisa & Shigulte Kebede. 1995. WU, TU, GD, IL, KF. – Friis, I., Bidgood, S., Fantahun Semon, Michael Jensen & Menassie Gashaw. 1996. GJ, WG IL. – Friis, I., Tesfay Awas & Gashaw Gibre-Hiwot. 1997. IL, WG, SU. – Friis, I., Michael Jensen, Menassie Gashaw, Desaling Dessisa, Fantahun Simon, Tesfay Awas & Gashaw Gibre-Hiwot 1997. IL. – I. Friis, S. Bidgood, Malaku Wandefrash & Gashaw Gibre-Hiwot (in part with Malaku Legesse). 1997. SU, SD, GG. Coll. at C, ETH, K. – I. & V. Friis & Ensermu Kelbessa 1998. SU. Coll. at C, ETH, K. – I. & V. Friis, Sebsebe Demissew & Negist Asfaw. 1998. GD, WU, SU. Coll. at C, ETH, K. – Friis, I., Bidgood, S., Malaku Wondefrash, Amsalu Ayana & Fantahun Simon. 1998. KF, IL, WG, SU. Coll. at C, ETH, K. – Friis, I., Bidgood, S., Malaku Wondefrash & Getu Tefera 1998. SU, SD, GG. Coll. at C, ETH, K. – Friis, I., Bidgood, S., Ermias Getachew & Mulugeta Gichile. 2000. KF, IL, SU. Coll. at C, ETH, K. – Friis, I., Bidgood, S., Ermias Getachew & Malaku Wondefrash. 2000. SU, SD. Coll. at C, ETH, K.

Fröman, B. & Persson, S. – Swedish forage agronomist and animal scientist, respectively. Produced a manual of Ethiopian grasses, Fröman & Persson, *An illustrated Guide to the Grasses of Ethiopia*. CADU, Asella. (1974). 1970-1974. AR. Coll. at K (ca. 60 nos. (mainly grasses)), EA, UPS.

Fukui, K. & M. – Japanese primatologist & anthropologist. 1973-1976. KF (chiefly Omo River Valley). Coll. at EA, K, ETH.

Gebrehiwet Medhanie – Eritrean botanist, lecturer at Asmara University. Resident collecting from 1996 -. EE, EW, WU. Coll. at UPS and Asmara University.

Gelahun Abati & Zerihun Woldu – Ethiopian. 1976. WU. Coll. at ETH. Gelahun A. is a practitioner of traditional medicine who worked in ETH. 1973-1983. Zerihun W. (q.v.).

Gelahun Abati & Tewolde Berhan Gebre Egziabher. – Ethiopian. 1973. SU. Coll. at ETH. Tewolde Berhan: see separate entry.

Gérard, ... – ?French. 1960. SU. Coll. at FT.

Gereau, R.E. – American botanist at MO. 1984. GG, KF (along the Omo River Valley). Coll. at ETH, K, MO.

Getachew Aweke. Resident collector from 1972. WE, EE, GD, GJ, TU, GG (partly with Friis, Rasmussen & Vollesen, partly with M. G. Gilbert, and with H. C. D. de Wit). Coll. at ACD (209 nos.), ETH, C, K, WAG. Ethiopian botanist at ETH, now retired.

Getachew Aweke & Weinert, E. 1980. SU. Coll. at ETH. Weinert: see separate entry.

Getachew Berta – Ethiopian student. 1974. HA. Coll. at ACD (5 nos.).

Getachew Teka – Ethiopian student. 1976. HA. Coll. at ACD (21 nos.).

[Getachew Tekle Haimanot – Ethiopian student. 1959. HA. Coll. at ACD (6 nos.).]

Getachew Zeleke – Ethiopian student. 1987. KF. Coll. at ETH.

[Ghebre Selassie Mebratu – Ethiopian student. 1959. HA. Coll. at ACD (1 no.).]

Gilbert, E.[Elisabeth] F. – American botanist in charge of the herbarium (ETH) 1966-1968. 1966-1968. KF, SU. Coll. at ETH, K.

Gilbert, M.G. – British botanist, resident in Ethiopia and in charge of herbarium (ETH) 1968-1976, worked at East African Herbarium, Nairobi (EA), 1977-1982, then full-time contributor to to the Flora of Ethiopia, working at Kew (K), and frequent visitor to Ethiopia until 1991, now working for MO at BM on the Flora of China project. Collections from all regions, ca. 5000 nos., often with other collectors, including S. B. Gilbert, Getachew Aweke, Gelahun Abate, Tewolde Berhan Gebre Egziabher, R. Bonnefille, T. Jefford, D. Rankin, C. I. Gilbert, K. Vollesen, Sebsebe Demissew 1986. SD, BA. Nos. 8052-8327. 1988. SD, BA. 8506-8832. 1989. SU. Nos. 9302-9308.), Ensermu Kelbessa, I. Friis, Ermias Dagne, Damtaw Teferra, S. Phillips. Coll. at ETH, K, EA, C, UPS. – Collections made with B. M. G. Jones, M. Thulin and J.J.F.E. de Wilde are each numbered separately. – Gilbert, M.G. & Jones, B.M.G. 1975. A separate series of numbers from BA, SD. Ca. 200 nos. Coll. at ETH, K. Jones, B.M.G.: British botanist. – Gilbert, M.G. & Thulin, M. 1975 (ca. 1500 nos.), 1978. SD (a few numbers only, most collections on this trip were made in Kenya). A separate series of numbers from SU, GG, WG, SD, HA. Coll. at ETH, K, UPS, EA, MO. Thulin, M.: Swedish botanist, see separate entry.

Gilbert, S. See Edwards, S.

Gilliland, H.G. – British/South African plant ecologist, worked sometimes with Desert Locust Service, main botanical collections from Somalia. See: Stower, W.J., Smith, K.D. & Gilliland, H.B.

Graff, N. van der – Dutch botanist/pathologist. 1974-1975. Ethiopia. Coll. at L.

[Greathead, D.J. – British entomologist (retired), carried out research on natural enimies of locust with ALRC (Anti-

Locust Research centre in GB), transferred to DLS (Desert Locust Survey), later DLCOEA (Desert Locust Control Organisation of East Africa). At first worked with G.B. Popov (q.v.) and W.J. Stower (q.v.). From 1962 with CIBC (Commonwealth Institute of Biological Control) and CAB (Commonwealth Agricultural Bureaux). Eventually director of IIBC (International Institute of Biological Control). 1953, 1955, 1957, 1958. 1964 (with FAO Coffee Mission under F.G. Meyer (q.v.)). 1975 (FAO mission studying insect attaks on *Olea*). GD, EW, EE. Coll. at BM, EA, ETH, K.]

Haberland, E. see Kuls *et al.*

Hagos, Teckle: See Teckle Hagos.

Hailu Mengesha [Probably identical with "Hailu M."] – Ethiopian student. 1960. GD, HA. Coll. at ACD (11 nos.).

Hailu Mirkanessa – Ethiopian student. 1974. GD, SU, HA. Coll. at ACD (13 nos.), ETH.

Hailu Yadete – Ethiopian student. 1960. HA. Coll. at ACD (13 nos.).

Hall, R.A. – British locust officer (deceased) with DLS (Desert Locust Survey), worked as assistant to G.B. Popov (q.v.). 1961. EE. Coll. at EA.

Hammersly, Jill, with J. Allen – British student. 1972. HA. Coll. ETH.

Handlos, Wayne – American Peace Corps Volunteer. 1962-1963. SU, AF. Coll. at ETH.

[Harrison, M. – British. ca. 1952. EW. Coll. at K (a few grasses). Harrison collected grasses mostly in the Sudan but one of the determination lists at K from 1952 indicates that he also collected in W Eritrea.]

Harlan, J. – American crop biologist. 1969. Collected sorghums. Coll. at Chicago, some at IBCR in Ethiopia.

Haugen, T. – Norwegian missionary. 1983-1985. SD, GG. Coll. at ETH, K (a few).

Headley, P.M. – British. Student in Oxford University exp. (q.v.). 1968. SU/AF. Coll. at K.

Hedberg, O. – Swedish botanist, professor of botany associated with UPS. European coordinator of the Ethiopian Flora Project. 1967, AR. 1973 SU, GD, BA (partly with Getachew Aweke) AR, GD. 1981 SU, WG, IL, BA. 1986 GD (Mt. Guna). Coll. at ETH, K, UPS. The 1967 collections are published by O. Hedberg in Webbia 26: 101-128 (1971).

Hedrén, M. Swedish botanist, at some time working at UPS, now lecturer at Lund University. 1982. SU, WG, IL, BA. Coll. at ETH, UPS.

[Hemming, C.F. – British ecologist (retired), attached to DLS (Desert Locust Survey), later D.L.C.O.E.A., travelled widely in Eritrea, Ethiopia and Somalia on vegetation surveys. 1952, 1954, 1956-1958. EE, EW, HA. Coll. at EA, K, ETH.]

Hendrickx, F.L. – Belgian. 19. SU. Coll. at BR.

Henning, E.M. – ?British. 19. SU. Coll. at K.

Hennock T. – Local medical officer. 1986 Coll. at ETH.

Hepper, F.N. – British botanist working at K. 1975. SU. Coll. at K (ca. 20 nos.).

Herbert, E.J. – British. 1962. BA. Coll. at K (ca. 80 nos.).

Hering, E.M. – British. 1959. SU. Coll. at K (ca. 140 nos.).

Hildebrandt, K. – German pharmacist resident in Ethiopia until he died ca. 1979. 1957-1970. SU. Coll. at ETH, W.

Hill, B.G. – American entomologist, lecturer at the Alemaya University of Agriculture. 1959-1960. SU, HA. Coll. at ACD (104 nos.), ETH.

[Hillier, R.G. – British natural history student. Collections in exp. Cambridge University. 1957. q.v.]

Hindorf, ... – ?German. 1970. Ethiopia. Coll. at K (ca. 45 nos.) Hindorf collected partly with Mogk (q.v.).

Hiremath, S.C. – Indian botanist. 1986-1987. Coll. at K (ca. 26 nos.) and probably elsewhere. Hiremath was interested in *Guizotia* and *Bidens* (Asteraceae), and his collections are all of these genera.

[Hodson, A.W. – British. 1923-1926. Ethiopia. Coll. at K (ca. 8 nos.).]

Hounerou, H.N. le – French ecologist, working at ILCA in Addis Ababa. 1976. HA. Coll. at ILCA (International Livestock Centre for Africa), ETH (a few).

Hovda, ... – Norwegian missionary. 1971-1972. SU, AR, SD. Coll. at UPS.

[Huddleston, J.A. – British research entomologist with ALRC (Anti-Locust Research Centre) in GB, travelled with P.E. Ellis and C.A. Ashall. 1955. Ethiopia. Coll. at K.]

Hundessa, Desta: See Desta Hundessa.

Hylander, K. [Kristoffer] & E. [Eva], & Adam Gobena – Swedish & Ethiopian. 1994. SU. Coll. (a few hundred) at ETH, UPS.

I.E.C.A.M.A. (this abbreviation covers a number of staff members at the then **I**mperial **E**thiopian **C**ollege of **A**griculture and **M**echanical **A**rts, often referred to as Alemaya College of Agriculture, now Alemaya University of Agriculture). 1957-1960. HA, KF. Coll. at ACD (the herbarium of

Alemaya University of Agriculture), EA, ETH, K. Duplicates of the same collections may have been distributed under this abbreviation but also as collected by Amare Getahun (q.v.).

Igersheim, A. with C. Puff. 1987.

Ingersol, R. – ?British or American. 1960. HA. HA. Coll. at ACD (5 nos.).

Jackson, J.A.D. – British forestry advisor. 1972, 1974. GG, SU/AF. Coll. at EA, K, ETH.

[Jackson, B.R. – ?British/American. 1956. SD. Coll. at ACD (9 nos.).]

Jago, N.D. – British research entomologist, worked with COPR (Centre for Overseas Pest Research) and later NRI (Natural resources Institute). 1975. BA. Coll. at K (ca. 30 nos.).

Jansen, P.C.M. – Dutch botanist, born 1943, stationed 1975-79 at Alemaya; associated with WAG, in charge of the PROSEA project at the Wageningen Agricultural University. 1975-1977. SU, WG, IL, KF, GG, SD, BA, AR, HA. (partly with H.C.D. de Wit and in IL with Getachew Aweke). Coll. at ACD (ca. 3400 nos.), WAG (ca. 5000 nos.).

Jefford, T. – British plant physiologist working at ETH. 1968-1976. SU (with M. Gilbert). Coll. at ETH.

Jember Debelle. – Ethiopian. 1974. SD. Coll. at ETH.

Jensen, M. – Danish ecologist. 1996-1999. WG, IL. Mostly with Menassie Gashaw (q.v.), I. Friis (q.v.) and others. Coll. at ETH, C.

Jimma Agricultural & Technical School (now Jimma Agricultural Junior College). 1957. KF. Coll. at ETH, K.

Jonas Z. – Ethiopian, ?on the staff of the Forestry Dept. 1978 IL Coll. at ETH.

Jones, B.M.G. – British botanist, working on teff breeding. 1972. BA. Coll. at ETH, K. Also collecting with M. Gilbert 1975.

Jones, Q. – British. 1969. Ethiopia. Coll. at K, UPS.

Joncheere, G.J. de – Dutch amateur botanist interested in ferns. 1970-1971. SU. Coll. at L, ferns in Herb. Pichi-Sermolli.

Joseph H. Selassie – Ethiopian student. 1972. HA. Coll. at ACD (10 nos.).

Joseph Keflemariam – Ethiopian student. … HA. Coll. at ACD (1 no.).

Kabwogi, I.L. – ?Nationality. 1974. HA. Coll. at ACD (69 nos.).

Kahurananga, J. – Tanzanian botanist, working at ILCA in Addis Ababa. ca. 1979-?1984. Coll. at International Livestock Centre for Africa (ILCA), ETH (a few).

Kaji, M. – Japanese primatologist/ ?anthropologist. 1979. GG. Coll. at ETH.

Kakimov, … – Russian phytopathologist. 1972, 1979 HA Coll. at ETH.

[Kassa W – Ethiopian student. 1957. KF. Coll. at ACD (17 nos.).]

[Kebede Koomsa – Ethiopian student. 1958. HA. Coll. at ACD (52 nos.), ETH.]

Kedir … HA. Coll. at ACD (18 nos.).

Kefale Gebre Mariam – Ethiopian student. 1979-1980. GJ, GG. Coll. at ETH.

Kidane Georgis – Ethiopian student. 1981. HA. Coll. at ACD (1 no.).

Kiloede, R. – ?Nationality. 1960. HA. Coll. at ACD (1 no.).

Kibreab F. – Ethiopian student. 1964. SU. Coll. at ETH.

Kifle H. Mariam – Ethiopian student. [1959-]1960. HA. Coll. at ACD (13 nos.).

Kiflemariam M. – Ethiopian student. 1981. HA. Coll. at ACD (1 no.).

Kiros … & Abadi … – Ethiopian. (Collections with IAR (Weed Research)). 1988. GJ. Coll. at ETH, K.

Klingel, … – ?German …?Year and ?regions. Coll. where?

Kloetzli, F. – Swiss ecologist. 1971-1973. GD (Semien Mts.). Coll. at EA, ZT.

Kokwaro, J. – Kenyan professor of botany at Nairobi University; Ethiopian collections made while student at Alemaya College. 1965-1966. HA. Coll. at ACD (239 nos.), EA, ETH.

Kuchar, P. – Canadian ecologist, working at South East Rangelands Project. ?1989-?1995. HA. Coll. at ETH, K, UPS and Eastern Ethiopia Herbarium.

Kukkonen, I. – Finnish botanist, born 1926, associated with H. ?year. ?Ethiopia. Coll. at H.

[Kuls, W. – German ethnologist. 1959-1960. GJ. Coll. at FR. Collections published in a detailed account by G. Cufodontis in *Senck. Biol.* **43***:* 301-330 (1962), *Senck. Biol.* **46***:* 115-120 (1965), *Senck. Biol.* **47***:* 273-282 (1966) & *Senck. Biol.* **50***:* 281-288 (1969). Kuls, W., Haberland, E. & Straube, H. (or any of these collectors in combination). 1954-1956. SU, SD, KF. Coll. at FR. German ethnologists. Collections published in a detailed account by G. Cufodontis in *Senck. Biol.*

39: 103-126, 289-314 (1958), *Senck. Biol.* **41***:* 367-392 (1960), *Senck. Biol.* **43***:* 273-300 (1962), *Senck. Biol.* **46***:* 89-114 (1965), *Senck. Biol.* **47***:* 251-271 (1966) & *Senck. Biol.* **50***:* 235-280 (1969).]

[Leakey, C.L.A. – British natural history student at Cambridge University (q.v.). (Collections in Exp. Univ. Cambridge), later tropical plant pathologist in Uganda and specialist at Cambridge. 1957. GJ. Coll. at K, ETH (a few).]

Legesse Negash – Ethiopian student. 1976. HA. Coll. at ACD (57 nos.).

Lemma G. Selassie – Ethiopian. Herbarium assistant at ETH. 1963-1970. WG, GJ, SU, SD, AR. Coll. at ETH.

Lemordant, D. – French. 1961. SU. Coll. at P.

Lewis, W.H. – American ethnobotanist. Ca. 1962. HA. Coll. at K.

Linnavouri, R. – Finnish zoologist. 1963. EE, EW, TU, WU, SU, SD, KF, HA. Coll. (ca. 130 numbers) at H. Itinerary published in *Ann. Zool. Fennici* **8:** 340-366 (1971).

Lisanewerk Nigatu & Mesfin Tadesse – 1986. BA (Harenna Forest). Coll. at ETH. Lisanewerk: Ethiopian botanist working at Jimma Agricultural Junior College, later at Alemaya University of Agriculture. Mesfin: see separate entry.

Longhitano, ... – Italian engineer. 1968 SU/HA Coll. at FT.

[Lulseged Asfaw – Ethiopian student. 1957. HA. Coll. at ACD (1 no.).]

Lundström, G. – Swedish volunteer working at ETH. 1969-1971. SU. Coll. at EA, ETH.

[Lythgoe, J.N. – Bristish natural history student. Collections in exp. Cambridge University. 1957. q.v.]

Määttä, K. – Finnish. 1972. GD. (E. of Lake Tana). Coll. (ca. 170 numbers) at H.

Makin, M.J. – British soil scientist working for the Overseas Development Administration. 1973. SD, GG. Coll. at K.

Makonnen Asres – Ethiopian student. 1964. HA. Coll. at ACD (45 nos.).

Mantell, Diana, with C. Puff. 1981.

Masresha Fetene – Ethiopian plant ecologist and physiologist. 1976. HA. Coll. at ACD (55 nos.). Lecturer in ecology at Addis Ababa University.

Maurel, ... – French. ?Year. HA. Coll. at P.

Mehret Abebe – Ethiopian student. with Afewirki Gebrai (q.v.). 1983.

[Melak H. Mengesha – Ethiopian student. Since c. 1970 in charge of gene bank at ICRISSAT, India. 1955. KF. Coll. at ACD (49 nos.).]

[McLoughlin, ... – South African army officer, mainly interested in succulent plants.1941 HA SU Coll. at PRE, K.]

Menassie Gashaw – Ethiopian ecologist, working with Ethiopian Wildlife Conservation Organisation. Resident, collecing 1996-1999, often with M. Jensen (q.v.), I. Friis (q.v.) and others. IL, WG. Coll. at ETH, C, K.

Mercier, J. – French ethnobotanist frequently visiting Ethiopia. 1968 to ?1993. GD, WU, SU. Coll. at ETH, K (a few), P, UPS.

Merga Gutetta. – Ethiopian forestry assistant. (Collections in SW Ethiopian Forestry Inventory). 1976. SD. Coll. at EA, ETH, K.

Mersai Ejigu – Ethiopian student. 1966. HA. Coll. at ACD (10 nos.).

Meseret Wondimu – Ethiopian plant pathologist/ecologist. 1981. HA. Coll. at ACD (1 nos.).

Mesfin Tadesse – Ethiopian botanist, at some time keeper of the National Herbarium (ETH) and lecturer of botany at ETH. Resident collector since 1977. EW, EE, AF, WU, GD, GJ, WU, SU, WG, IL, KF, GG, SD, AR, HA. Coll. at C, EA, ETH, K, MO, S, UPS, WAG, WU. Often collections together with others: Mesfin Tadesse & Sebsebe Demissew. 1978. Mostly IL, KF, WG. – Mesfin Tadesse & Zerihun Woldu. 1978-1979. Mostly GJ, GD. – Mesfin Tadesse, Gilbert, & S. Edwards 1979. SU. – Mesfin Tadesse & Olov Hedberg or Hedberg & Mesfin Tadesse 1979/1981. mostly AR, BA, SU. – Mesfin Tadesse & J. Mercier 1980. SU. – Thulin, M., Hunde, A. & Mesfin Tadesse. 1980. Moslty BA. – Mesfin Tadesse & Kagnew 1981-1982. GD, GJ, SU, WG, IL, KF. – Friis, Vollesen & Mesfin Tadesse 1982 – mostly SD. Mesfin Tadesse & Tewolde Berhan G.E. 1982. SD. – Mesfin, Sebsebe Demissew & Ensermu Kelbessa. 1985. Mostly SD, EW, EE. – Hedberg, O. & I. & Mesfin Tadesse. 1986. .GD. – Mesfin Tadesse, Puff, C., Ryding, O. 1988. Wof Washa (SU). – Mesfin Tadesse & Lisanework Nigatu. 1985-1987. BA, IL. – Mesfin Tadesse & Vollesen, K. 1986. SD, BA. – Mesfin Tadesse & Berhanu Abegaz. ?1990. SU. – Mesfin Tadesse & Ermias Dagne. 1991. Mostly BA. – Mesfin Tadesse, Lisanework Nigatu, Petros, Shukri, *et al.* (?) BA. – Mesfin Tadessa & Sebsebe Demissew 1986. EW/EE, TU. (nos. 3760-4040). – Mesfin Tadesse, Sebsebe Demissew & Ensermu Kelbessa 1985. SD (nos. 3123-3655). – Mesfin Tadesse, Sebsebe Demissew & Negist Asfaw 1989. BA. (nos. 5140, 5148, 5345). – Mesfin Tadesse, Sebsebe Demissew *et al.* 1986. EW/EE (nos. 3700-3759).

Meyer, F.G. – American botanist at the U.S. National Arboretum, Washington, D.C., who made two field trips in Ethiopia. On the early trip Meyer collected plants for the anti-cancer screening programme, as did Perdue (q.v.). On the second trip leader of FAO (Food and Agriculture Organisation) Coffee Misssion to Ethiopia in 1964. On this latter trip, he was accompanied by L.M. Fernie (British coffee breeder from Tanzania), R.L. Narasimhaswamy (Indian coffee breeder), L.C. Monaco (Brazilian plant geneticist), and the entomologist D.J. Greathead (q.v.). Ethiopian counterparts were Worku Makonnen (Ethiopian Coffee Board), Dagnatchew Yirgu (pathologist), Abebe Abeye (Ministry of Agriculture), and Yilma Yemane Berhan (Jimma Technical and Agricultural School). A report was published: Meyer, F.G. *et al.* (1968), *FAO Coffee Mission to Ethiopia 1964-65*. FAO, Rome. 200 pp. 1961-1962. WG, SU, AR, SD, KF. 1964. KF, IL. Coll. at NA, US, K.

Mhojo, A. – ?Nationality (West African). 1972. HA. Coll. at ACD (9 nos.).

Minta, M. – ?Nationality. 1971. SU. Coll. at ETH.

Mogk, M. – ?American. 1969. SU. Coll. at K.

Monod, T. – French biologist. ca. 1970. SU/AF. Coll. at P.

Mooney, H.F. – British forester and botanist, formerly of the Indian Forest Service, and founder of the National Herbarium of Ethiopia (ETH). Published a glossary of Ethiopian plant names: Mooney, H.F. (1963), *A Glossary of Ethiopian Plant Names*. Dublin University press. 79 pp. See also Mesfin Tadesse 1991. Dr. Herbert F. Mooney, founder of the National Herbarium of Ethiopia (ETH). *Taxon* **40**: 267-272. – 1953-1961 (series of expeditions). Collections from almost all parts of Ethiopia. Coll. at ACD (84 nos.), BR, ETH (most complete set), EA, FT, K (ca. 4500 nos.), WAG. Numbers above ca. 9300 are only at ETH.

Moult, P.[Pavela] H. – ?Nationality. 1974. IL. Coll. at K (ca. 70 nos.).

Mulosu Djote – Ethiopian student. 1963. SU. Coll. at ETH.

Mulugeta Negassa – Ethiopian student. 1974-1976. HA. Coll. at ACD (63 nos.), ETH.

Mulwany, P.M. – British natural history student, member of the Oxford University expedition 1968. 1968 GG. Coll. at K (ca. 160 nos.).

Mwambene, R.O.F. – ?Nationality (East African). 1971. HA. Coll. at ACD (33 nos.).

Nega W. ?-Ethiopian student. 1979 WU Coll. at ETH.

Nievergelt, S. – Swiss botanist. 1968-1969. GD (Simen National Park). Coll. at Z, with some duplicates at ETH.

Nigussie Jiru – Ethiopian student. 1983. KF. Coll. at ETH. At some time Ethiopian forestry assistant.

Nordal, I. – Norwegian; professor of botany associated with O. 1982, 1990, 1994, 1997. TU, GD, SU, SD, BA. Coll. at ETH, O [?elsewhere].

Ogada, F. – ?Nationality (East African). 1960. HA. Coll. at ACD (37 nos.).

Ouren, T. – Norwegian missionary. 1961. SU, AR. Coll. at BG, K.

Padwa, G. – Kenyan. 1953. GG/Sudan. Coll. at EA, K.

Palmer, M.C.L. – British natural history student. (Collection in Exp. Reading University). 1962. KF. Coll. at K.

Parker, C. – British tropical weed scientist, specialising in parasitic plants. (Collections in exp. Weed Research Organization). 1969, 1970. TU, SU, AR, HA. Resident in Ethiopia from 1986, after which collections, mainly weeds, from many parts of the country. Coll. at K, IAR (Institute of Agricultural Research), ETH.

Paskin, M. – British entomologist, associated with ALRC (Anti-Locust Research Centre) in Britain, later with COPR (Centre for Overseas Pest Research). Worked with P.E. Ellis and later on his own in Eritrea. 1961-1962. EE. Coll. at EA.

Patti, … – Italian.? … KF. Coll. at FT.

Perdue, R.E. – American economic botanist. 1964-1965. SU, AR, KF. Coll. at K (ca. 250 nos.), WAG, US (unlabelled set at ETH). Perdue collected plants for the anti-cancer screening programme as did Meyer (q.v.). The major part of the collections were made in Kenya and Tanzania.

Persson, S., with B. Fröman. – Swedish agronomist, associated with the CADU project. 1971. See Fröman.

Phillips, S.M. – British botanist, specialising in grasses, employed by the Ethiopian Flora Project to contribute an account of that family 1982-1994. 1989. GG Coll. at ETH, K, made with M.G. Gilbert (q.v.) and Damtew Teferra (q.v.).

Pichi-Sermolli, R.E.G. – Italian botanist, professor of botany at various Italian universities. 1966-1967. KF. Coll. (mainly or entirely ferns) in Herb. Pichi-Sermolli.

Piffard, F. – British. 1958. SU, WG, IL, KF. Coll. at K (c.114 nos.).

Polunin, O. – British amateur botanist and botanical author.1981. SU. Coll. at K (ca. 70 nos.).

Popov, G.B. – British ecologist and entomologist (deceased), worked for the Middle East Anti-Locust Unit during World War II, later with the DLS (Desert Locust

Survey) in Somalia, on Socotra and throughout Eastern Africa, later with F.A.O. and COPR (Centre for Overseas Pest Research). 1953-1954. EE, HA. Coll. at K, EA.

Prosser, M. – British teacher in Biology Dept., Addis Abeba (then H.S.I.) University. 1963-1964. Collected with E. Beals. S Ethiopia. Coll. at ETH.

Puff, C., Mantell, D.E. & Ensermu Kelbessa 1981, AF, GD, GJ, SU, WU. Coll. at ETH, WU, K (partly), UPS (partly). Puff is an Austrian botanist working at the Univ. of Vienna (WU), frequent visitor to Ethiopia. Diana Mantell was a British Ph.D. student at the Univ. of Vienna (now Dr. Mantell-Schachenmann). Ensermu: See separate entry. -Puff, C. Tewolde Berhan G.E., Edwards, S. & Ensermu Kelbessa 1981. SU. Coll. at ETH, WU, K (partly), UPS (partly). Tewolde: See separate entry. Edwards: See separate entry. – Puff, C. & Ensermu Kelbessa 1982. IL, KF, WG, Coll. at ETH, WU, K (partly), UPS (partly). – Puff., C., Dawe, J., Edwards, S. & Ensermu Kelbessa 1982. AR, BA, HA, SU. Coll. at ETH, WU, K (partly), UPS (partly). Janice Dawe was an American Ph.D. student at the Univ. of Vienna (now at Univ. of Alaska). – Puff, C. & Ensermu Kelbessa 1982-83. BA, GG, SD, SU. Coll. at ETH, WU, K (partly), UPS (partly). – Puff, C. & Ensermu Kelbessa 1986. IL, KF. Coll. at ETH, WU, K (partly), UPS (partly). – Puff, C., Igersheim, A., Ensermu Kelbessa & Sebsebe Demissew 1987. BA, SD, SU. Coll. at ETH, WU, K (partly), UPS (partly). Igersheim was an Austrian Ph.D. student at the Univ. of Vienna (now Dr. I. and employed at the Univ. of Vienna). Sebsebe Demissew: See separate entry. – Puff, C. & Sileshi Nemomissa 1988. GG, SD. 1996-1999. GD. Coll. at ETH, WU. Sileshi was a botany student at Asmara University, now lecturer of botany at ETH. See separate entry.

Pülschen, L. – German volunteer working at Debre Zeit Agricultural Research Station. 1984-1985. SU. Coll. at ETH.

[Raeder-Roitzsch, … – ?Nationality. (Collections partly in Mooney's number series). ca. 1958-1959. SU. Coll. at ETH.]

Rankin, D. [Dorothy] – American missionary, resident near Mezan Tefari to 1977, still teaching in Addis Abeba to ca. 1990. 1960-1977. KF. Coll. at ETH, K (18 ferns).

Reading University expedition. – ca. 1971. … Coll. at K (ca. 110 nos.). Members: A.J.S. Crees, C.E.D. Thomas, M.C.L. Palme.

[Reynolds, G.W. – South African amateur botanist, specialist in the genus *Aloë*. ca. 1956-7. Ethiopia. Coll. (mainly *Aloe*) at K (ca. 20 nos.). Route map in G. W. Reynolds, *The Aloes of Tropical Africa and Madagascar*, Mbabane, 1966.]

Richards, M.[Mary] – British amateur botanist, resident in East Africa, who made very extensive collections in SE tropical Africa. 1969. SU. Coll. at K. Collected in Ethiopia with Mrs. S.A. Robertson during short holiday visit.

Rippstein, G. – French ecologist. 197? SD, BA (with Boudet, G., q.v.). Coll. at ALF.

Robertson, S.A. [Mrs.] – British botanist (married to British entomologist working for the Desert Locust Control Organization of Eastern Africa). 1969-1971. EE, EW, TU, HA. Coll. at K (ca. 250 nos., but mostly from Kenya and Tanzania), ETH, EA.

Roos, D. [David] – Swedish. 1982. Ethiopia. Coll. of forestry – related specimens [several hundred] at ETH, UPS.

[Rosenius, K. – Finnish. 1954. AR, SU. Coll. (ca. 170 numbers) at H.]

Ryding, O. – Swedish botanist, trained at Uppsala University, working as university lecturer at Asmara University 1987-1990; since 1994 senior lecturer at C. 1987-90. EE EW (a few from SU WG IL KF GG SD). Coll. (ca. 1200 nos.) at ETH, Asmara, UPS, K, C (few). (A number collected with Sileshi Nemomissa, q.v., and others).

[Samuel Atnafu – Ethiopian student. 1957. HA. Coll. at ACD (48 nos.).]

Sandford, A. [Mrs.] in Ash's number series (q.v.). British, wife of R. Sandford (q.v.).

Sandford, R. – British agriculturist, born in Ethiopia, resident to ca. 1976. (Collections partly in Mooney's number series). 1959. SU. Coll. at BM, ETH.

Schelpe, E.A.C.L.E., with A. T. Curle. – South African Botanist working at Cape Town and mainly interested in orchids and ferns. 1952. Various parts of Ethiopia. Coll. at K.

Sebald, O. – German botanist at the Natural History Museum of Stuttgart. 1966. GD. 1968. GJ, SU. Coll. at ETH (some), STU (main set), M. Collections and travel accounts published by O. Sebald in *Stuttgarter Beitr. zur Naturkunde, Nr.* **194***:* 1-40 (1968); *ibid., Nr.* **206***:* 1-37 (1969); *ibid., Nr.* **222***:* 1-28 (1970) *ibid., Nr.* **236***:* 1-32 (1972) & *ibid., Nr.* **244***:* 1-41 (1972).

Sebsebe Demissew – Ethiopian botanist, lecturer, later professor of botany at ETH. 1978. GJ, SU. (nos. 1-64). 1978-79. SU. (nos. 65-198). 1979. GG. (nos. 199-304). 1989-1980. SU. (nos. 305-349). 1980. GD, GJ. (nos. 350-536). 1980-1981. SU. (nos. 540-543). 1981. EW/EE, GJ, SU, SD. (nos. 551-629). 1982. GD, GJ, SU, WG, IL, SD, BA. (nos. 1002-1003, 1034-1184, 1218-1249). 1983. AR. (nos. 1261-1264, 1369-1376). 1986. GD, GJ, SU. (nos. 1677-1729, 1845-1849). 1988. BA, SU. (nos. 2064-2154). 1989. HA, (nos. 2269-2352). 1991. SU. (nos. 2929-2930, 2936-2939). 1993.

SU. (nos. 3363, 3376, 4014-4027). 1994. WU, SU, BA. (nos. 4239-4346). 1995. WU, SU. (nos. 4423-4713). 1997. SU. (nos. 5124, 5362- ?). 1999. SU. (no. 5617). Main set at ETH, duplicates at C, K, and elsewhere. – Other collectors in the series of Sebsebe Demissew: N.N. in Sebsebe Demissew. 1990. SU. (nos. 2905-2908). – Tekle Haimanot in Sebsebe Demissew. 1997. TU, SU. (nos. 5499-5501). – Joint colletions: Sebsebe Demissew & Amha B. 1986. SU. (nos. 1673-1676). – Sebsebe Demissew & Berhanu Abegz. 1983. SU, KF, IL. (nos. 1446-1470). 1986. SU. (nos. 1730-1746). 1986. SU. (nos. 1880-1887). 1993. SU, WU, BA (nos. 3377-4013). – Sebsebe Demissew & Ensermu Kelbessa (q.v.) 1981. HA (nos. 975-1000). 1983. EW/EE, SU, WG, IL. (nos. 1265-1368). 1983. EW/EA, HA. (nos. 1377-1429). 1985. SU. (nos. 1501-1520). 1990. SD, SU (nos. 2596-2897). 1995. BA. (nos. 4714-4980). 1996. GG. nos. 5190-5361). 1997. GG. (nos. 5421-5483). – Sebsebe Demissew & Ermias Dagne (q.v.) 1989. SU. (nos. 2389-2397). 1990. SU. (nos. 2588-2595). – Sebsebe Demissew & I. Friis (q.v.) 1998. SU. (nos. 5582-5589). – Sebsebe Demissew & Melaku Wondefrash A. 1999. SU, KF. (nos. 5626-5736). 2000. SU. (nos. 5737-5740). – Sebsebe Demissew & Mesfin Tadesse (q.v.) 1986. EW/EE, GD, GJ, SU, HA. (nos. 1747 -1845). – Sebsebe Demissew & M.G. Gilbert (q.v.) 1990. KF. (no. 2411). – Sebsebe Demissew & Negist Asfaw – 1986. SU, GJ. (nos. 1889-1958). 1987. 1987. GG. (nos. 1959-2002). 1988 [1987?]. SU, BA, HA. (nos. 2005-2063). 1989. SU. (nos. 2398-2410). 1994. SU. (nos. 4132-4134). 1997. SU, IL. (nos. 5502-5525). 1998. SU. (nos. 5526-5530). – Sebsebe Demissew & Zemede Asfaw (q.v.) – 1981. GG, AR. (Nos. 621-773). – Sebsebe Demissew & Zerihun A. 1982. SU (nos. 1003-1033). – Sebsebe Demissew & Zerihun Woldu (q.v.) 1993. SU, WU. (nos. 4028-4058). – Sebsebe Demissew, Mesfin Tadesse (q.v.) & Ensermu Kelbessa (q.v.) 1985-1986. WG. (nos. 1521-1672). – Sebsebe Demissew, Tewolde Berhan G.E. (q.v.) & S. Edwards (q.v.) 1981. SU, SD. (Nos. 774-974). -Sebsebe Demissew *et al.* 1982. GD, SU. (nos. 1185-1217). 1983. GJ. (nos. 1250-1260). 1986. SU, HA. (nos. 1850-1879). 1988. SU, SD, KF (nos. 2155-2268). 1989. GJ, SU. (nos. 2377-2388). 1990. SU, AR, SD, BA. (nos. 2415-2587). 1991. TU, WU, SU, GG. (nos. 2940-3189). 1992. TU, SU. (nos. 3190-3198). 1992-1993. SU. (nos. 3276-3362). 1994. SU, SD. (nos. 4135-4239). 1995. SU, AR, BA. (nos. 4347-4422, 5125-5130). 1996. TU, GJ, GD, WU, SU. (nos. 5131-5189). 1997. SU, AR. (nos. 5484-5498). 1998. GD, GJ, SD. (nos. 5531-5581, 5592-5761). 1999. SU. (nos. 5620-5625). 2000. BA. (nos. 5741-5761). – Sebsebe Demissew, Ensermu Kelbessa *et al.* – 2000. KF, BA (nos. 5741-5761).

Seegeler, C.J.P. – Dutch botanist, born 1940, stationed 1971-1974 at Alemaya; later associated with WAG. 1971-1973. EW/EE, TU, GD, WU, GJ, SU, WG, IL, KF, SD, BA, AR, HA. Coll. at ACD (1100 nos.), WAG (1300 nos.).

Seifu H. Michael – Ethiopian student. 1964. HA. Coll. at ACD (79 nos.).

Sereke Berhan – Ethiopian student. 1988. SU. Coll. at ETH.

Sereke W.-Haimanot – Ethiopian student. 1974. HA. Coll. at ACD (46 nos.), ETH.

Seyoum Ayehunie – Ethiopian student. 1985. IL. Coll. at ETH.

Seyoum Leta – Ethiopian student. 1985. SU/AF. Coll. at ETH.

Siegenthaler, J.E. – American lecturer at Jimma Agricultural & Technical School (q.v.), published *Useful plants of Ethiopia*. C. 1965. 1956-1962. KF. Coll. at K.

Silberman, … – ?Nationality. ?Year. TU. Coll. at P.

Sileshi Nemomissa – Ethiopian student at the Asmara University, since 1988 collector in a range of montane and afro-alpine regions, including EW, EE, TU, GD, now lecturer at ETH. Often with others: C. Puff & Sileshi Nemomissa. 1988. GG, SD. 1996-1999. GD. O. Ryding & Sileshi Nemomissa. 1988-1989. EW, EE.

[Simmons, K. – ?American botanist or agriculturist at Alemaya (ACD). 1953-1956. HA. 1957. KF. Coll. at K, EA, ETH. Ogaden collections made with the anti-locust organization D.L.C.O.; it is possible that more than one person's collections are involved.]

[Smeds, H. – Finnish geographer. 1953-1954. KF. Coll. at H, some at K. 1957-1958. SU, KF, WG, BA. Coll. at FT, K (these two sets may not be duplicates of one another), ferns in Herb. Pichi-Sermolli. 1962. IL. Coll. where?, ferns in Herb. Pichi-Sermolli. The whereabouts of Smeds' collections, if any, made after 1962 are unknown.]

South West Ethiopian Forestry Inventory Project. – Collectors within this project, using one number series entitled as above, include: Alemayehu M., M. Brunt, D.R. Chaffey, Merga G., A.B.C. Thomerson, and Zinna.

[Staffen, R.M.B. – ?American. 1953. SU, SD. Coll. at ACD (41 nos.).]

Stauder, J.R. – ?British. 1962. Ethiopia, probably KF, IL or WG. Coll. at K (ca. 15 nos.).

[Stephenson, P.R. – British entomologist. Was in Uganda at the outbreak of World War II and was assigned to locust control during the war. At the end of the war he became Director of the DLS (Desert Locust Survey), later DLCOEA. 1949. EE. Coll. (included in P. Bally's number series) at K.]

Stewart, R.B. – American lecturer at Jimma Agricultural & Technical School (q.v.). 1956. KF. 1961. HA. Coll. at ACD (265 nos.), K (ca. 200 nos.), FT.

[Stower, W.J. & Smith, K.D. – British entomologists, associated with DLCOEA. 1949, 1951. EE. Coll. at BM or (included in P. Bally's number series) at K. See also following.]

[Stower, W.J., Smith, K.D. & Gililand, H.B. – British entomologists, associated with DLCOEA 1952. EE. Coll. at K. Gilliland is listed as subsidiary collector on sheets at K but sheets at EA with identical data are ascribed to Gilliland only.]

Straube: See Kuls & al.

Strecker, W.J.R. [Mrs.] – British anthropologist ca. 1972. GG/SD (lowlands near Kenyan border). Coll. at K (ca. 100 nos.).

Sutherland, J. [John] – ?British. 1969. Ethiopia. Coll. [a few hundred] at UPS.

Taddele & Ali – Ethiopian student. 1988. EW. Coll. at ETH, Asmara.

[Tadesse Abebe – Ethiopian student. 1959. Ethiopia. Coll. at ACD (37 nos.), ETH.]

Tadesse Ebba – Ethiopian lecturer at Alemaya. 1968. HA, SD. Coll. at ACD (240 nos.), ETH, K.

Tamrat Abebe – Ethiopian student. 1986. HA. Coll. at ACD (1 no.).

Tardelli, M. & Bigazzi, M. – Italian, associated with FT. 1987. GJ. Coll. at FT.

[Taye Bizuneh – Ethiopian student. 1959. HA. Coll. at ACD (11 nos.).]

Taye Zegeye – Ethiopian student. 1974-76. HA. Coll. at ACD (47 nos.).

Tekle Hawariat Hagos [usually cited as Tekle H. Hagos] – Ethiopian botanist, assistant to Mooney (q.v.) and first Ethiopian keeper of the National Herbarium (ETH), trained at K. & WAG. 1962. EE, EW, TU, SU, KF. Coll. at EA, ETH, FT, K (ca. 230 nos.).

Tedros A. & Tewolde Petros – Ethiopian students. 1985. EW. Coll. at ETH, Asmara.

[Telahun Abebe – Ethiopian student. 1959. HA. Coll. at ACD (1 no.).]

Tenagne Kebede – Ethiopian student. 1975. GD. Coll. at ETH.

Tesema ..., Kebede ... & Berhane ... – 1961. HA. Coll. at ACD (25 nos.).

Tesfaselassie G. Mariam – Ethiopian student. 1972. HA. Coll. at ACD (5 nos.).

Tesfay Awas – Ethiopian botanist, formerly at Teacher's Training College, Gambella, now working with the Institute for Biodiversity Conservation and Research (IBCR). Resident collector since ?1993. IL, KF. A few collections with I. Friis (q.v.). Coll. mainly at ETH.

Tesfaye Dagnew – Ethiopian student. 1976. HA. Coll. at ACD (7 nos.).

Tesfaye Haile – Ethiopian forestry assistant. (Collections in SW Ethiopian Forest Inventory). 1976. SD. Coll. at ETH, K.

Tesfaye Tessemma. – Ethiopian plant breeder and agronomist. 1975. GD. 1979. SU, HA. Coll. at ETH.

Tesfesse T. – Ethiopian student. ?1975. GD. Coll. at ETH.

Tewolde Berhan Gebre Egziabher. – Ethiopian plant ecologist, leacturer at ETH, president of Asmara University, and leader of Ethiopian Flora Project, 1980-1993. Resident, collecting since 1969, has often collected with others. Collections from all regions of Ethiopia and Eritrea at ETH, some at K.

Tezera Moges – Ethiopian student. 1960. HA. Coll. at ACD (12 nos.).

Theodoros Mesfin – Ethiopian student. 1981. HA. Coll. at ACD (1 no.).

[Thesiger, W. – British traveller. 1959. SD, GG. Coll. at BM.]

Thomas, C.E.H. – British natural history student. (Collections in exp. Reading University). 1962. SU, GJ, KF. Coll. at K.

Thomerson, A.B.C. – British forestry student working for the Overseas Development Administration/Ethiopian Forestry Research Institute. (Collections in SW. Ethiopia Forestry Inventory). 1975. KF, IL, BA. Coll. at EA, ETH, K.

Thulin, M. – Swedish, Professor of botany associated with UPS; first visit to Ethiopia on consultancy for C.A.D.U. (Chillalo Agricultural Development Unit) with a project on legumes, contributed a number of families for the Flora of Ethiopia and Eritrea, especially legumes. 1971. AR. Coll. at ETH, K, UPS. Thulin, M. & Gilbert, M.G. – 1975. S. Ethiopia. Coll. at UPS, K, ETH. See also Gilbert & Thulin. Thulin, M., Hunde, A. & Mesfin Tadesse. – Swedish and Ethiopian botanists. 1980. BA, AR, SD, SU. Coll. at UPS, ETH, K. Hunde: See under Friis. Mesfin Tadesse: See separate entry. Thulin, M. & A. Hunde. – Swedish & Ethiopian botanists. ?1982. GJ, SU. Coll. at ETH, K, UPS.

Tivell, A. – ?Swedish forester. 1977. WG. Coll. at EA.

Tompsett, B.P. – British. ca. 1960. Ethiopia. Coll. at K (ca. 30 nos.).

Tornay, S. – ?American, working with the anthropological expeditions to the Lower Omo Valley. 1967-197? Ethiopia (especially lower Omo River Valley). Coll. at EA.

Tsedale Waktola – Ethiopian soil scientist. 1981. HA. Coll. at ACD (1 no.).

Tsegaye Habte – Ethiopian student. 1986. HA Coll. at ETH.

Turton, D.A. – British anthropologist. 1970. (KF/GG). Coll. at K (ca. 300 nos.).

Uhlig, S.K. – German lecturer at Alemaya. 1986-87. BA, HA. Coll. at ACD (8 nos.).

Unger, J. – ?German. 1981. HA. Coll. at ACD (34 nos.).

Urban, E. – American ornithologist teaching in the Biology Dept. of The Addis Ababa (then H.S.I.) University. ca. 1968-1970. SU. Coll. at EA, K.

Vollesen, K. – Danish botanist, full-time collaborator with the Ethiopian Flora Project from 1981-86. 1986. BA. Coll. at K, ETH, C. Also numerous collections with Mesfin Tadess, I. Friis and M.G. Gilbert (q.v.).

Wakefield, ... – British. SD. Coll. at K.

Waterman, P. – British plant chemist based in Glasgow and often working with Chemistry Dept., Addis Abeba University. 1988. SU (with M. G. Gilbert & Ermias D.). Coll. at ETH, K.

Webb, H. – British. 1960. SU. Coll. at ACD (3 nos.).

Weinert, E. – German botanist residing in Ethiopia from 1978. 1980. SU, BA. Coll. at ETH.

Wendinov Bayov (with IAR (Weed Research)). ?Russian. 1988. WU. Coll. ETH, K.

West, O. – British (South African) army officer, later (probably) associated with the D.L.O.C. 1941. EE, WU. 1956. SU, HA. Coll. at EA, K.

Westphal, E. & Westphal-Stevels, J.M.C. Dutch botanists. Dr. E.W. born 1938, Dr. J.M.C. W.-S. born 1942. Associated with WAG, stationed at Alemaya 1967-68, later at Department of Tropical Crops, Wageningen, and member of the PROSEA team. 1967-1968. GD, WU, SU, WG, KF, GG, SD, AR, HA. Coll. 5550 numbers, but this includes herbarium specimens as well as seed collections, according to Anonymous (1976); coll. at ACD (ca 2500 nos.), WAG (main set), K, C.

Wiens, D. – American botanist, specialist on Loranthaceae and Viscaceae. 1974. TU, WU (with M. G. Gilbert & Getachew Aweke, also under own numbers). Coll. at K.

Wilde, J.J.F.E. de – Dutch botanist, brother of W.J.J.O. de Wilde, born 1932, now at WAG; associated with WAG, stationed at Alemaya 1968-1970. TU, GD, WU, GJ, SU, IL, GG, SD, BA, AR, HA. Coll. at ACD (ca. 2900 nos.), WAG (main set, ca. 7000 nos.), K. Wilde, J.J.F.E. de & Gilbert, M.G. 1969 (mainly Semien Mts., GD), 1971. GD, BA, SD, GG. Ca. 450 nos. Coll. at WAG, K (ETH set destroyed by fire). See also Wilde, W.J.J.O. de & Wilde-Dufjes, B.E. de.

Wilde, W.J.J.O. de & Wilde-Dufjes, B.E. de – Dutch botanists, 1965-66 based in Ethiopia, now working at L. 1965-1966. AF, WU, SU, WG, KF, SD, AR, HA. Coll. 5190 numbers, according to Anonymous (1976); most complete sets at ACD, ETH and WAG, duplicates at B, BR, C, DSM, EA, FHI, H, K, MO, P, PRE, UPS.

Willde-Dufjes, B.E. de – Dutch botanist, born 1936, based 1965-66 in Ethiopia, collected with husband, W.J.J.O. de Wilde (q.v.).

Wit, H.C.D. de – Dutch professor of botany at the Wageningen Agricultural University, Associated with WAG. 1978. Collected with Getachew Aweke. Coll. at ETH, WAG.

Willemse, R.H. – Dutch ?agronomist. 1971. SU. Coll. at K.

Wilson, R.T. – British agriculturist. 1975. TU. Coll. at K, ETH.

Wood, R.B. – British teacher in Biology Dept. of the Addis Ababa (then H.S.I.) University. 1964 (?or66) -1968. SD. Coll. at ETH.

Worku Negash – Ethiopian student. 1987. SU. Coll. at ETH.

Wudeneh Lechamo – Ethiopian student. 1988. HA. Coll. at ACD (120 nos.).

Yeneneh Taye – Ethiopian student. 1978. SU, HA. Coll. at ACD (1 no.), ETH.

Yihenew Makonnen – Ethiopian student. 1987. SU. Coll. at ETH.

Yilma Dejene & Getachew Aweke. – 1978. SD Coll. at ETH.

Yitbarek Negatu – Ethiopian student. 1981. HA. Coll. at ACD (1 nos.).

Yohannes Wolde Yesus – Ethiopian student. 1963. SU. Coll. at ETH.

[Yohannis Negash – Ethiopian student. 1959. HA. Coll. at ACD (3 nos.).]

[Yoseph Muletta – Ethiopian student. 1958. HA. Coll. at ACD (4 nos.).]

Zemede Asfaw – Resident Ethiopian, collector and researcher of cultivated plants since 1982. Has mainly collected cultivated plants. Coll. at ETH.

Zenna & Tesfaye – Ethiopian forestry assistants (in SW. Ethiopia Forestry Inventory). 1976. SU. Coll. at ETH, EA.

Zerihun Woldu – Resident Ethiopian, ecologist and sometimes collector since 1976, lecturer at ETH. Zerihun Woldu. With Gelahun Abati. – Ethiopia. 1976 onwards.

Zewdu Kebede – Ethiopian student. 1960. HA. Coll. at ACD (25 nos.).

Zewdu Kebede Banteyiwalu – Ethiopian student. 1987-88. IL, HA. Coll. at ACD (19 nos.).

Additions to the Yemen Flora

Mats Thulin, Abdulnasser Al-Gifri, Mohammed Abdullah Hussein & Saeed Gabali

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Fifty species of flowering plants new to the mainland of Yemen are reported from field trips undertaken in 1992, 1995 and 1998. The species roughly fall into three ecological groups, (1) species from the coastal zone of Hadramaut and Mahrah regions, (2) species from the escarpment mountains and plateau in Hadramaut and adjacent areas, and (3) species from the monsoon woodlands of eastern Mahrah close to the Oman border. The species in group (1) were previously mostly believed to be endemics either of Oman or Somalia. Most of the species in group (2) are previously known from Oman and/or Somalia, and sometimes also from eastern Ethiopia and beyond. The largest group is group (3), with species from the "Dhofar fog oasis". The fog moisture here supports a woodland that is denser than anywhere else in Yemen. This vegetation is well known in the Dhofar region in Oman, but in Yemen it has remained practically unknown up to now. Many of the species in this group have previously been regarded as endemics of the Dhofar region of Oman, but some of them have more or less wide distributions in tropical Asia or in north-eastern tropical Africa.

Mats Thulin, Department of Systematic Botany, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden. E-mail: mats.thulin@ebc.uu.se

Abdulnasser Al-Gifri, Zayed Complex for Herbal Medicine, P.O. Box 29300, Abu Dhabi, United Arab Emirates

Mohammed Abdullah Hussein, Biology Department, College of Education (University of Aden), Zingibar, Yemen

Saeed Gabali, University of Aden, P.O. Box 11038, Khormaksar, Aden, Yemen.

Introduction

Three major botanical field trips to the mainland of Yemen have been undertaken during the 1990's in collaboration between the Department of Systematic Botany at Uppsala University, Sweden, and the Department of Biology, University of Aden, Yemen. The first trip took place in October 1992, and concentrated mainly on the Hadramaut region in southern Yemen. The second trip took place in November 1995, and concentrated mainly on the Ibb and Taizz regions in northern Yemen. The third trip took place in November 1998, and concentrated mainly on the Mahrah region in southern Yemen. Various results from these field trips have so far been reported in the following papers: Thulin & Al-Gifri (1994), Thulin (1994a, 1994b), Hjertson (1995),

Thulin (1995a, 1995b), Thulin & Al-Gifri (1995), Thulin & Hjertson (1995), Petrusson & Thulin (1996a), Thulin (1998), Thulin (1999a) and Lönn (1999).

These papers mainly concern new species described from Yemen and other taxonomic novelties, but in Thulin (1995b) *Indigofera eremophila* Thulin was reported from Yemen for the first time on the basis of material collected in 1992, and Miller (1996a) reported *Commicarpus reniformis* Chiov. from Yemen for the first time, also on the basis of material collected on our trip in 1992.

In this paper 50 further species new to the mainland of Yemen are reported from these trips. The new records have all been made in southern Yemen, within the Arabian part of the Somalia-Masai regional centre of endemism (White & Léonard 1991), and in areas not covered by the recent *A handbook of the Yemen Flora* (Wood 1997). The area is covered by *Flora of the Arabian Peninsula and Socotra* of which the first volume has been published (Miller & Cope 1996). Another basic works for the area is *Flora des tropischen Arabien* by Schwartz (1939). The species in the present account are arranged alphabetically within the families, and the families are arranged alphabetically as well.

The species may also be arranged ecologically into the following three groups:

(1) species from the coastal zone mainly of the Hadramaut and Mahrah regions,
(2) species from the escarpment mountains and plateau (Jol) in Hadramaut and adjacent areas, and
(3) species from the monsoon woodlands of eastern Mahrah along the escarpments close to the Oman border.

The species in group (1) include *Basananthe berberoides, Cleome albescens (subsp. omanensis), Cocculus balfourii, Commiphora foliacea, C. playfairii, Conocarpus lancifolius, Gymnocarpos rotundifolius, Indigofera nephrocarpa, Microcharis disjuncta* (var. *fallax*), *Schweinfurthia spinosa, Suaeda moschata,* and *Zygophyllum smithii.* These all grow in the stony semi-desert plains, hillsides or wadis at more or less low altitudes along the coast of Hadramaut and/or Mahrah (Fig. 1 above), and most of them were previously believed to be endemics either of Oman or Somalia. Only *Microcharis disjuncta* has a wider distribution in Africa.

The species in group (2) include *Azima tetracantha, Bauhinia ellenbeckii, Ceratonia oreothauma, Cordia nevillii, Crotalaria dumosa, Cyclocheilon somalense, Indigofera sedgewickiana, Indigofera volkensii, Nannorrhops ritchieana, Pappea capensis,* and *Sporobolus ruspolianus.* Most of these species are found in Yemen either on the steep, periodically mist-covered escarpments above the coastal plain in Hadramaut, or on the plateau itself. *Indigofera sedgewickiana* is an exception, as it is so far only known from the mountains of Lahij rather than from Hadramaut. Phytogeographically it is a rather mixed group, but most of the species are previously known from Oman and/or Somalia (and eastern Ethiopia and beyond). Only *Pappea capensis* and *Azima tetracantha* are widespread species in Africa, with *Azima tetracantha* extending also to tropical Asia.

The largest group is group (3), which includes *Anogeissus dhofarica, Blepharis dhofarensis, Blepharispermum hirtum, Corallocarpus epigaeus, Commicarpus boissieri, Croton confertus, Cucumis sativus, Dhofaria macleishii, Diplocyclos palmatus, Dyerophytum indicum, Euphorbia smithii, Gossypium stocksii, Impatiens balsamina,*

Fig. 1. Above: view of Wadi Arf in the foothills near the coast of Hadramaut, with trees of *Conocarpus lancifolius* visible as dark dots along the wadi. Photo by M. Thulin, 5.X.1992. Below: view of the escarpment woodland in eastern Mahrah, near Sadfan, with branches of *Euphorbia smithii* in the foreground. Photo by M. Thulin, 11.X.1998. →

Jatropha dhofarica, Justicia diffusa, Lavandula dhofarensis, Leucas dhofarensis, Ocimum dhofarense, Ormocarpum dhofarense, Pulicaria omanensis, Remusatia vivipara, Rungia pectinata, Ruttya fruticosa, Sida cordata, Trichodesma hildebrandtii, Vatovaea pseudolablab, and *Withania qaraitica.* These species are all found on the fog-affected escarpment mountains of southern Arabia called the "Dhofar fog oasis" (Miller 1994), which are covered by dense woodlands on the seaward-facing slopes (Fig. 1). The area is in the monsoon belt and from about mid-June to mid-September each year the area comes under the influence of the south-west monsoon that causes dense fog to build up against the seaward-facing escarpments. The high quantities of drip-precipitation from fog moisture, in addition to the rainfall (Miller 1994), support woodland that is denser than anywhere else in Yemen. This vegetation is well known in the Dhofar region in Oman, and many of the plants found there are described and illustrated in the book by Miller & Morris (1988). In Yemen, where this vegetation covers a narrow band for about 30 km along the coast west of the Oman border, it has remained practically unknown because of the remoteness and inaccessibility of the area.

Our results show that all the dominant woody plants of these woodlands in Oman, such as *Anogeissus dhofarica, Blepharispermum hirtum, Croton confertus, Euphorbia smithii* and *Jatropha dhofarica,* are present and have the same role also in Yemen. Of these, all, except *Croton confertus,* which is known from Somalia, were previously believed to be endemics of Oman. Many other plants of these woodlands that were previously believed to be endemics of Oman are also present on the Yemen side, and surely there are still more to be found.

The monsoon woodlands in Yemen are still largely intact, although flatter areas have often been opened up for the cultivation of sorghum, etc. On the whole it is possible, though, that this unique vegetation is better preserved in Yemen than in Oman, where it is said to be under serious threat (Miller 1994).

During our trip in 1998 we also discovered some very isolated patches of a depauperate kind of monsoon woodland at about 800-850 m altitude near the top of Ras Fartak some 150 km from the Oman border. These woodland fragments contained fewer woody species than those close to the Oman border, and mainly *Acokanthera schimperi* (not seen closer to Oman), *Anogeissus dhofarica, Euclea schimperi, Croton confertus,* and *Olea europaea* subsp. *cuspidata,* were noted.

All the species listed above in this group are previously known from Oman, and many of them have been regarded as endemics of the Dhofar region of Oman. However, some of them, such as *Cucumis sativus, Dyerophytum indicum, Impatiens balsamina, Remusatia vivipara, Rungia pectinata* and *Sida cordata,* also have wider distributions in tropical Asia, and *Remusatia vivipara* is relatively widespread also in tropical Africa. *Ruttya fruticosa, Trichodesma hildebrandtii* and *Vatovaea pseudolablab* all have more or less wide distributions in north-eastern tropical Africa.

Acanthaceae

Blepharis dhofarensis A.G. Miller

Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9715 (K, UPS); escarpment NE of Hawf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9778 (K, UPS); near Yemen/Oman border crossing NE of Hauf, 16°40'N, 53°05'E, 12.XI.1998, *Thulin, Beier & Mohammed Hussein* 9748 (UPS).

Blepharis dhofarensis is known previously only from the Dhofar region in Oman (Miller in Miller & Biagi 1988; Miller & Morris 1988), where "it is restricted to the wet escarpment

woodlands where it prefers dense thickets on the steeper more inaccessible slopes" (Miller & Morris 1988). The three collections cited above were collected in escarpment woodland at 420-1000 m altitude, and the species also in Yemen has a preference for more rocky and steep situations. The large white flowers were seen visited by large wasps.

Justicia diffusa Willd.

Yemen. Mahrah: Ras Fartak, above Al Wadi, 15°40'N, 52°11'E, 7.XI.1998, *Thulin, Beier & Mohammed Hussein* 9603 (UPS); 28 km from Al Wadi along road to Tabut, 15°47'N, 52°00'E, 9.XI.1998, *Thulin, Beier & Mohammed Hussein* 9665 (UPS).

Justicia diffusa is a widespread species in southern Asia and Africa, but on the Arabian peninsula it was previously known only from the Dhofar region in Oman (Miller & Morris 1988). The two collections from Yemen reported here agree with the collections from Oman in being more or less prostrate, perennial plants with a more or less woody base. In other areas the species is an erect to ascending annual, and this difference should be studied further. In Yemen the plant was found on rocky slopes at 580-850 m altitude, where it was often growing in rock crevices.

Rungia pectinata (L.) Nees

Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9703 (K, UPS).

Rungia pectinata (L.) Nees (= *R. parviflora* (Retz.) Nees) is a tropical Asian species with its main area of distribution from India and Sri Lanka eastwards to China. On the Arabian peninsula it is known previously only from the Dhofar region of Oman (Miller & Morris 1988). The collection cited above was made on a rocky slope in *Anogeissus dhofarica* woodland at 420-540 m altitude.

Ruttya fruticosa Lindau

Yemen. Abyan: Awdhillah escarpment, Thirah pass, 17.VI.1967, *Lavranos & Smith* 882 (K). Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9712 (K, UPS).

Ruttya fruticosa has its main distribution in eastern and north-eastern tropical Africa, and on the Arabian peninsula it is known from the escarpment woodlands in the Dhofar region in Oman (Miller & Morris 1988). Miller & Morris also stated that the species occurs in Hadramaut, but to our knowledge there are no specified reports of it from there. However, the second collection cited above represents a new record of the species from Mahrah, where it was found on rocky slopes in *Anogeissus* woodland at 420-540 m altitude. Also, a previous collection from Abyan is cited above, made at about 1950 m altitude.

Araceae

Remusatia vivipara (Roxb.) Schott

Yemen. Mahrah: near Yemen/Oman border crossing NE of Hawf, 16°40'N, 53°05'E, 12.XI.1998, *sight record by M. Thulin*; along track NE of Hawf towards the Oman border crossing, 16°40'N, 53°05'E, 12.XI.1998, *sight record by M. Thulin.*

Remusatia vivipara is fairly widespread in western and central Africa, and a single record has also been made in western Ethiopia (Riedl 1997). The species is also distributed in southern Asia and in northern Australia. On the Arabian peninsula it is known previously only from the wet escarpment woodlands of Dhofar in Oman (Miller & Morris 1988), and the records from Yemen cited above are from the same vegetation type. In the first locality cited only a few individuals were seen at 850 m altitude, but the second locality, at 500 m altitude, had numerous plants. In both localities the species

was growing in rocky, shady situations. At the time of our visit the leaves had wilted, but the characteristic specialised bulbil-bearing shoots were present.

Arecaceae

Nannorrhops ritchieana (Griffith) Aitch.
Yemen. Mahrah: 213 km W of Al Ghaydah along track to Tarim, 16°26'N, 50°26'E, 16.XI.1998, *Thulin, Beier & Mohammed Hussein* 9830 (K, UPS).

Uhl & Dransfield (1987) gave the distribution of the monotypic genus *Nannorrhops* as "Iran, Afghanistan, Pakistan, and Arabia". They also provided a map that appears to show an Arabian distribution of the genus in Oman, as well as in the Hadramaut region of southern Yemen. Miller & Morris (1988) stated that "within Arabia it is recorded from Oman and S. Yemen", but without citing any specimens. As far as we are aware there is no, previously published, more exact record of this palm from Yemen. The collection cited above was made in the interior part of Mahrah region at about 670 m altitude, where *Nannorrhops* is common and locally dominant along wadis in the desert.

Asteraceae

Blepharispermum hirtum Oliv.
Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9717 (K, UPS).

Bleparispermum hirtum has previously been regarded as an endemic of the Dhofar region in Oman (Miller & Morris 1988; Eriksson 1992), where "it is common at lower altitudes in the escarpment woodlands" (Miller & Morris 1988). The collection from Yemen cited above was made on rocky slopes in *Anogeissus dhofarica* woodland at 420-540 m altitude.

Pulicaria omanensis Gamal-Eldin
Yemen. Mahrah: along road between Al Fatk and Damqawt, 16°33'N, 52°48'E, 10.XI.1998, *Thulin, Beier & Mohammed Hussein* 9685 (K, UPS).

Pulicaria omanensis was previously known only from the Dhofar region in Oman (Gamal-Eldin 1981; Miller & Morris 1988). This first record from Yemen was made on a rocky slope at about 100 m altitude.

Balsaminaceae

Impatiens balsamina L.
Yemen. Mahrah: along track NE of Hawf towards the Oman border crossing, 16°40'N, 53°05'E, 12.XI.1998, *Thulin, Beier & Mohamed Hussein* 9762 (UPS).

Impatiens balsamina is a native of tropical Asia that is widely naturalised in Africa, as well as in other tropical and subtropical regions (Grey-Wilson 1980, 1982). On the Arabian peninsula it is known previously only from the escarpment woodlands of the Dhofar region in Oman (Miller & Morris 1988). In the locality in Yemen cited above the plant grows in a rocky, shady slope at 500 m altitude, where it certainly gives the impression of being part of the native flora. At the time of our visit the plants were fruiting, but a few plants still in flower were seen at about 700 m altitude at 16°39'N, 53°03'E on 13 November 1998.

Boraginaceae

Cordia nevillii Alston
Yemen. Hadramaut: 13 km N of Hemiar in the Masila oil field, 15°50'N, 49°12'E, 11.X.1992, *Thulin, Eriksson, Gifri & Långström* 8293 (K, UPS).

Cordia nevillii is relatively widespread in Africa and Asia, and on the Arabian peninsula it is known previously from the Dhofar region in Oman, and it is also known from Socotra (Warfa 1990). Miller & Morris (1988), in their

account of the species in Oman, used the name *C. perrottetii* Wight. Verdcourt (1991) used the name *C. quercifolia* Klotzsch, based on a collection from Mozambique, for this species, but *C. quercifolia* was by Warfa (1990) regarded as a synonym of the variable *C. sinensis* Lam. and we prefer to follow this view. The collection from Yemen cited above was made on a rocky slope along a wadi at about 900 m altitude.

Trichodesma hildebrandtii Gürke
Yemen. Mahrah: escarpment NE of Hawf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9773 (K, UPS).

Trichodesma hildebrandtii is a species with a fairly wide distribution in Somalia, Ethiopia and northern Kenya (Verdcourt 1991), but on the Arabian peninsula it is known only from the Dhofar region in Oman (Miller & Morris 1988), where it for a long time was known as *T. cardiosepalum* Oliv. This first record from Yemen was made on the upper part of the escarpment at about 1000 m altitude, where *T. hildebrandtii* was found growing on rocky ground along with, *e.g. Monotheca buxifolia.*

Burseraceae

Commiphora foliacea Sprague
Yemen. Abyan: 30 km N of Zinjibar, 13°22'N, 45°20'E, 23.XI.1998, *sight record by M. Thulin.* Shabwah: 89 km from crossing near Lawdar towards Mahfis, 13°58'N, 46°35'E, 2.X.1992, *Thulin, Eriksson, Gifri & Långström* 7969 (Aden Univ., E, FT, K, UPS). Hadramaut: 23 km on the pipeline route starting 15 km NE of Riyan, 14°50'N, 49°31'E, 4.X.1992, *Thulin, Eriksson, Gifri & Långström* 8046 (UPS). Mahrah: 34 km from Sayhut along road to Qishn, 15°18'N, 51°24'E, 16.X.1992, *Thulin, Eriksson, Gifri & Långström* 8439 (K, UPS); 60 km from Al Wadi along road to Tabut, 15°33'N, 52°04'E, 9.XI.1998, *Thulin, Beier & Mohammed Hussein* 9676 (K, UPS).

Commiphora foliacea was regarded as an endemic of Oman by Miller & Morris (1988), but the species is actually widespread in Somalia (Thulin 1999c), as well as along the coast of southern Yemen. The collections cited above were made on rocky, stony, gravelly or sandy ground, often along wadis, where *C. foliacea* is a fairly common and locally dominant species at 100-400 m altitude.

Commiphora playfairii (Hook.f. ex Oliv.) Engl.
Yemen. Hadramaut: 26-27 km on the pipeline route starting 15 km NE of Riyan, 14°52'N, 49°30'E, 3.X.1992, *Thulin, Eriksson, Gifri & Långström* 8022 (K, UPS); 25 km on the pipeline road starting 15 km NE of Riyan, 14°52'N, 49°30'E, 4.XI.1998, *Thulin, Beier & Mohammed Hussein* 9524 (K, UPS).

Commiphora playfairii was known previously only from the coastal parts of northern Somalia (Thulin 1999c). The two collections cited above appear to be conspecific with the Somali plant and were made on open stony ground along small wadis at 200-220 m altitude.

Capparaceae

Cleome albescens Franch. subsp. ***omanensis*** Chamberlain & Lamond
Yemen. Mahrah: along road between Jadib and Damqawt, 16°36'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9723 (K, UPS); 13 km from Sayhut along road to Qishn, 15°15'N, 51°20'E, 16.X.1992, *Thulin, Eriksson, Gifri & Långström* 8412 (UPS).

Cleome albescens has long been regarded as an endemic of northern Somalia (Kers & Thulin 1993), but Chamberlain & Lamond (1994) published subsp. *omanensis* from Oman. Chamberlain & Lamond (1996) also recorded this taxon from southern Yemen on the basis of the collection *Guichard* KG/HAD/418 from Hadramaut, but this probably represents a dis-

tinct undescribed species. However, the collections from the Mahrah region cited above agree completely with *C. albescens* subsp. *omanensis*, and this taxon therefore is a member of the Yemen flora after all. The Yemeni collections were made on a rocky slope and along a wadi near the sea at 10-50 m altitude.

Dhofaria macleishii A.G. Miller
Yemen. Mahrah: escarpment NE of Hawf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9782 (E, K, UPS).

The monotypic genus *Dhofaria* was described as an endemic of the Dhofar region in Oman (Miller 1988, Miller & Morris 1988), but Nyberg (1996) also mentioned its occurrence in adjacent parts of Yemen. However, no specimens were cited. The collection cited above was made on a rocky slope with *Monotheca buxifolia* at about 1000 m altitude.

Caryophyllaceae

Gymnocarpos rotundifolius Petruss. & Thulin
Yemen. Hadramaut: 25 km W of Al Ridah, 14°56'N, 50°15'E, 4.XI.1998, *Thulin, Beier & Mohammed Hussein* 9531 (UPS).

Gymnocarpos rotundifolius was described by Petrusson & Thulin (1996a) from Oman, where it occurs on open, desertic, rocky ground and gravel plains at 0-100 m altitude (Petrusson & Thulin 1996a, 1996b). The collection from Yemen cited above is from a gravelly hillside at about 50 m altitude, some 350 km from the Oman border.

Chenopodiaceae

Suaeda moschata A.J. Scott
Yemen. Mahrah: 26 km from Al Wadi along road to Tabut, 15°47'N, 52°00'E, 9.XI.1998, *Thulin, Beier & Mohammed Hussein* 9661 (K, UPS); 28 km from Al Wadi along road to Tabut, 15° 47'N, 52° 00'E, 9.XI.1998, *Thulin, Beier & Mohammed Hussein* 9966 (K, UPS).

Suaeda moschata Scott (1981) was described from Oman, where it is known from sandy beaches, coastal dunes and wadi-beds at 0-600 m altitude (Boulos 1996). The two collections cited above are both from rocky slopes of the inland part of Ras Fartak at 450-580 m altitude, about 150 km from the Oman border.

Combretaceae

Anogeissus dhofarica A.J. Scott
Yemen. Mahrah: Ras Fartak, above Al Wadi, 15°40'N, 52°11'E, 7.XI.1998, *Thulin, Beier & Mohammed Hussein* 9606 (K, UPS).

Anogeissus dhofarica was described from Oman by Scott (1979), and Miller & Morris (1988) stated that "it is endemic to Dhofar and it is probably the commonest tree of the escarpment woodlands where it is frequently the dominant species, often forming almost pure stands". *A. dhofarica* is common and often dominant in the escarpment woodlands also where we saw it on the Yemen side of the border close to Oman, but the collection cited above is from one of the small isolated patches of woodland found at 600-850 m altitude on Ras Fartak, some 140 km from the Oman border.

Conocarpus lancifolius Engl. & Diels
Yemen. Hadramaut: 1 km above Al Barah village, 30 km on the pipeline route starting 15 km NE of Riyan, 14°58'N, 49°31'E, 5.X.1992, *Thulin, Eriksson, Gifri & Långström* 8083 (Aden Univ., E, K, UPS). Mahrah: Wadi Masilah, 15°19'N, 51°04'E, 15.X.1992, *Thulin, Eriksson, Gifri & Långström* 8396 (UPS).

Conocarpus lancifolius was described from northern Somalia and is also today generally assumed to be an endemic of Somalia (*e.g.* Wood 1997), although it is cultivated as a valuable tree in various other countries, for ex-

ample in Ethiopia, Kenya, and in various countries on the Arabian peninsula, including Yemen. However, the report of the species by Schwartz (1939) from Wadi Hadjr in Hadramaut, on the basis of the collection Wissman 1177, in our opinion most probably represents a native occurrence of *Conocarpus lancifolius* in Yemen. On our trip in 1992 we saw clearly native populations of the species along Wadi Arf in Hadramaut from Al Arshah and down to about 1 km above Al Barah (at about 250 m altitude). Particularly in the narrow uppermost part of Wadi Arf there are good stands of the tree (Fig. 1 above). Also along Wadi Masilah in Mahrah region at about 100 m altitude, obviously native stands of the tree were seen in 1992. On the basis of these findings Thulin (1993b) mentioned *Conocarpus lancifolius* as native in Yemen, but so far no details of this record have been published.

Cucurbitaceae

Corallocarpus epigaeus (Rottl.) C.B. Cl.
Yemen. Mahrah: escarpment NE of Hauf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9770 (K, UPS).

Corallocarpus epigaeus is fairly widespread in tropical Africa and is known also from Saudi Arabia (Collenette 1985), Oman, Pakistan and India (Jeffrey & Thulin 1993). The collection from Yemen cited here was made in *Anogeissus* woodland at about 700 m altitude.

Cucumis sativus L.
Yemen. Mahrah: near Yemen/Oman border crossing NE of Hawf, 16°40'N, 53° 05'E, 12.XI.1998, *Thulin, Beier & Mohammed Hussein* 9739 (K, UPS).

Miller & Morris (1988) described and illustrated a wild form of *Cucumis sativus* with bitter fruits from the "monsoon woodlands" of the Dhofar region in Oman. The same form is here reported from the escarpment woodlands in Yemen, where it is a common climber up to several meters long with very bitter, green fruits with whitish longitudinal lines. The collection cited above was made at 800-850 m altitude, but the species was seen down to about 400 m. Kirkbride (1993) stated *C. sativus* to grow wild in Burma, China (Yunnan Province), India, Sri Lanka and Thailand, but no mention was made of any occurrences on the Arabian peninsula.

Diplocyclos palmatus (L.) C. Jeffrey
Yemen. Mahrah: near Yemen/Oman border crossing NE of Hawf, 16°40'N, 53° 05'E, 12.XI.1998, *Thulin, Beier & Mohammed Hussein* 9740 (UPS).

Diplocyclos palmatus is widespread in the Old World tropics (Jeffrey 1967), but on the Arabian peninsula it has previously been recorded only from the Dhofar region in Oman (Miller & Morris 1988). The collection from Yemen cited here was made in *Anogeissus-Acacia etbaica* woodland at 800-850 m altitude.

Cyclocheilaceae

Cyclocheilon somalense Oliv.
Yemen. Hadramaut: 42 km along the pipeline route from the crossing with the Ressib road, 15°11'N, 49°16'E, 13.X.1992, *Thulin, Eriksson, Gifri & Långström* 8364 (Aden Univ., E, FT, K, UPS).

Cyclocheilon somalense has previously been regarded as an endemic of northern Somalia (Marais 1981), and this record from Yemen represents the first finding of a member of *Cyclocheilon* outside Africa. The genus, with its three species, was previously known only from Somalia and eastern Ethiopia (Marais 1981). In the Yemeni locality the plant was found on a rocky limestone slope at about 1250 m altitude.

Euphorbiaceae

Croton confertus Baker

Yemen. Mahrah: Ras Fartak, above Al Wadi, 15°40'N, 52°11'E, 7.XI.1998, *M. Thulin, sight record*; Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *M. Thulin, sight record.*

Croton confertus was described from Dhofar in Oman, where it "is common at lower altitudes in the wet escarpment woodlands" (Miller & Morris 1988). The species is also known from northern Somalia (Thulin 1993c). The first collection cited above was made in a patch of woodland near the top of Ras Fartak at 800-850 m altitude, whereas the second one was made in *Anogeissus dhofarica* woodland at about 500 m altitude.

Euphorbia smithii S. Carter

Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9713 (K, UPS).

Euphorbia smithii was previously regarded as an endemic of the Dhofar region in Oman, where it is said to be "one of the commonest small trees at lower altitudes in the escarpment woodlands" (Miller & Morris 1988). It is also common in the corresponding woodlands of eastern Mahrah in Yemen, where *E. smithii* seems to be particularly prominent on rocky slopes (Fig. 1 below).

Jatropha dhofarica A.R.-Sm.

Yemen. Mahrah: escarpment NE of Hawf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9767 (K, UPS).

Jatropha dhofarica was previously regarded as an endemic of the Dhofar region in Oman, where it is said to be "one of the most common and widespread species" (Miller & Morris 1988). This is equally true for the escarpment areas on the Yemen side of the border, where *J. dhofarica* is one of the dominant woody plants from near sea level up to about 800 m altitude.

Fabaceae

Bauhinia ellenbeckii Harms

Yemen. Hadramaut: Mola Matar area, near Bayn Al-Jibal, 14°47'N, 48°54'E, 6.X.1992, *Thulin, Eriksson, Gifri & Långström* 8130 (Aden Univ., E, FT, K, UPS); Mola Matar Pass, 16.VIII.1949, *Guichard* KG/HAD/199 (EA, photo at K).

Bauhinia ellenbeckii is in Africa known from Somalia and eastern Ethiopia (Polhill & Thulin 1983, 1988, Thulin 1993d). The species was said to occur also in Yemen by Thulin (1993d), but no specimens were cited. Two collections are now known, both from the Mola Matar area, one recent made among limestone rocks along a large wadi at 1950 m altitude, and one from 1949 from stony wadis at 1800 m altitude. The latter specimen was identified as "most probably *B. ellenbeckii*" by Brenan on a determination label from 24 Oct. 1960. The Mola Matar area is the area in Hadramaut with the highest altitude and presumably also the highest precipitation.

Ceratonia oreothauma Hillc., Lewis & Verdc. subsp. ***oreothauma***

Yemen. Hadramaut: Mola Matar area, Kawr Sayban, 14°51'N, 48°47'E, 7.X.1992, *Thulin, Eriksson, Gifri & Långström* 8159 (Aden Univ., E, K, UPS).

Ceratonia oreothauma was described by Hillcoat *et al.* (1980), with subsp. *oreothauma* in Oman and subsp. *somalensis* Hillc., Lewis & Verdc. in northern Somalia. Subsp. *oreothauma* was stated to occur also in southern Yemen by Thulin (1993d), but no specimen was cited. The collection cited above was made on limestone rocks in the mist zone at about 1900 m altitude. Only a single sterile tree was seen, 3 m tall, with a thick gnarled trunk.

Crotalaria dumosa Franch.

Yemen. Hadramaut: above Al Arshah, 15°00'N, 49°23'E, 13.X.1992, *Thulin, Eriksson, Gifri & Långström* 8383 (K, UPS).

Crotalaria dumosa is in Africa known from Somalia, Djibouti, eastern Ethiopia, and northern Kenya, but Polhill (1982) and Thulin (1993d) also stated it to occur in "Arabia". However, no record from Arabia seems to have been published previously and the species was not included in the checklist of legumes of West Asia by Lock & Simpson (1991). The collection from Hadramaut cited above was made on stony ground at about 900 m altitude.

Indigofera nephrocarpa Balf.f.
Yemen. Mahrah: Ras Fartak, 15°40'N, 52°13'E, 9.XI.1998, *Thulin, Beier & Mohammed Hussein* 9650 (UPS); 39 km from Jadib along road towards Al Fatk, 16°31'N, 52°43'E, 14.XI.1998, *Thulin, Beier & Mohammed Hussein* 9794 (UPS).

Indigofera nephrocarpa was originally described from Socotra, but has been recorded also from Oman and north-eastern Somalia (Miller & Morris 1988, Thulin 1993d), and from Pakistan (Small *et al.* 1988). This is the first record of the species from the mainland of Yemen. Both collections cited above are from rocky slopes at 5-20 m altitude near the sea.

Indigofera sedgewickiana Vatke & Hildebr.
Yemen. Lahij: Yaffa area, Wadi Yahar, above Harada, 13°47'N, 45°15'E, 9.XI.1995, *Thulin, Ghebrehiwet & Gifri* 9253 (E, K, UPS); Yaffa, X.1993, *Amira* 1 (UPS).

Indigofera sedgewickiana has previously been regarded as an endemic of northern Somalia (Thulin 1993d). The material cited here was in fruit when collected, but flowers have been produced on plants grown from seeds in the greenhouses of the Botanical Garden of Uppsala University. The Yaffa area used to be very isolated, but in the early 1990's a tarmac road was built reaching up to the mouth of the steep-sided gorge formed here by Wadi Yahar. *I. sedgewickiana* here grows in rocky gullies at 1600-1700 m altitude. The Yemeni population has relatively large leaves with more numerous leaflets compared to the Somali populations (most leaves with 9-13 leaflets versus often only 5-7 leaflets in Somalia), but the variation in these and other respects appears to be continuous.

Indigofera volkensii Taub.
Yemen. Abyan: near Juhayn, 13°34'N, 45°50'E, 18.X.1992, *Thulin, Eriksson, Gifri & Långström* 8458 (UPS). Hadramaut: 14 km from the turning to the Masila field on the road from Al Mukalla to Sayun, 15°01'N, 48°49'E, 7.X.1992, *Thulin, Eriksson, Gifri & Långström* 8179 (K, UPS).

Indigofera volkensii is widespread in eastern and north-eastern Africa (Thulin 1993d), but has not previously been recorded from the Arabian peninsula. The collections cited above were made on rocky hillsides at respectively 900 m and 1430 m altitude.

Microcharis disjuncta (Gillett) Schrire var. ***fallax*** (Gillett) Schrire
Yemen. Mahrah: 16 km from Sayhut along road to Qishn, 15°15'N, 51°21'E, 16.X.1992, *Thulin, Eriksson, Gifri & Långström* 8421 (K, UPS).

Microcharis disjuncta (= *Indigofera disjuncta* Gillett) was known previously from Namibia and adjacent parts of South Africa in southern Africa, and from Mauretania in the West to Sudan and Saudi Arabia in the East. There is also a population on Socotra that has been recognized as var. *fallax* (Gillett) Schrire. Var. *fallax* is said to differ mainly in having smaller leaves with some of the upper leaves 3-foliolate, whereas in var. *disjuncta* all leaves are simple (Gillett 1956). The collection from Yemen cited above is geographically nearest associated with the population on Socotra and also has small leaves with some of the upper leaves 3-foliolate. The Yemeni collection, which was made on a rocky slope along a wadi at about 75 m altitude, therefore is here placed in var. *fallax*.

Ormocarpum dhofarense Hillc. & Gillett
Yemen. Mahrah: near Yemen/Oman border crossing NE of Hawf, 16°40'N, 53°05'E, 12.XI.1998, *Thulin, Beier & Mohammed Hussein* 9746 (K, UPS).

Ormocarpum dhofarense was regarded as an endemic of the Dhofar region in Oman by Miller & Morris (1988). Lock & Simpson (1991) and Wood (1997) also reported it from northern Yemen, but the specimen cited by Wood (Wood 2012) is actually a lush specimen of *O. yemenense* Gillett. The collection cited above was made in *Anogeissus dhofarica-Acacia etbaica* woodland at 800-850 m close to the Oman border.

Vatovaea pseudolablab (Harms) Gillett
Yemen. Mahrah: along road between Jadib and Damqawt, 16°36'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9689 (K, UPS).

Vatovaea pseudolablab is fairly widespread in eastern and north-eastern Africa, where it is known from Sudan, Ethiopia, Somalia, northern Uganda, Kenya, and Tanzania (Thulin 1993d). On the Arabian Peninsula it has previously only been reported from the Dhofar region in Oman (Miller & Morris 1988). The collection from Yemen cited above was made on a rocky slope with *Commiphora* and *Jatropha dhofarica* at about 100 m altitude.

Lamiaceae

Ocimum dhofarense (Sebald) A. Paton
Yemen. Mahrah: escarpment NE of Hawf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9764 (K, UPS).

Ocimum dhofarense (= *Becium dhofarense* Sebald 1987) is known previously only from the escarpment woodlands of the Dhofar region in Oman, "where it frequently occurs as an understorey shrub below *Anogeissus dhofarica*" (Miller & Morris 1988). The collection from Yemen cited above was made in *Anogeissus dhofarica* woodland at 800 m altitude.

Lavandula dhofarensis A.G. Miller subsp. ***dhofarensis***
Yemen. Mahrah: along road between Jadib and Damqawt, 16°36'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9693 (K, UPS).

Lavandula dhofarensis is known previously only from the Dhofar region in Oman (Miller 1985, Miller & Morris 1988). Two subspecies are recognized, subsp. *dhofarensis* and subsp. *ayunensis* A.G. Miller. The collection cited above agrees with subsp. *dhofarensis*. The locality in Yemen is on a rocky slope with *Commiphora* and *Jatropha dhofarica* near the foot of the escarpment at about 100 m altitude.

Leucas dhofarensis Hedge & Sebald
Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9699 (K, UPS).

Leucas dhofarensis has previously been regarded as an endemic of the Dhofar region in Oman (Hedge & Sebald in Hedge 1982, Miller & Morris 1988). The collection from Yemen cited above was made on a rocky slope in *Anogeissus dhofarica* woodland at 420-540 m altitude.

Malvaceae

Gossypium stocksii Mast.
Yemen. Mahrah: along road between Jadib and Damqawt, 16°36'N, 52°56'E, 10.XI.1998, *M. Thulin, sight record.*

Gossypium stocksii was known previously from northern Somalia, Oman and Pakistan (Thulin 1999b). In Oman it is known from the coastal plains and foothills of the Dhofar region (Miller & Morris 1988), and the record cited above is from rocky ground near the mouth of a wadi close to the sea at about 20 m altitude.

Sida cordata (Burm.f.) Borss. Waalk.
Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9704 (K, UPS).

Sida cordata (= *S. veronicifolia* Lam.) is an Asian species that on the Arabian peninsula previously is known only from Oman (Miller & Morris 1988). The collection from Yemen cited above was made on a rocky slope in *Anogeissus dhofarica* woodland at 420-540 m altitude.

Menispermaceae

Cocculus balfourii Schweinf. ex Balf.f.
Yemen. Mahrah: Ras Fartak, above Al Wadi, 15°40'N, 52°11'E, 7.XI.1998, *M. Thulin, sight record.*

This species, regarded by Forman (1980) as "the most remarkable species in the Menispermaceae", was described from Socotra, but material believed to be conspecific from the Dhofar region of Oman was reported by Forman. Miller (1996b) stated that the species also occurs in southern Yemen, but no material was specified.

The record cited above from Yemen is from rocky limestone slopes at about 800 m altitude, but the plant was also seen at lower altitudes in several other places. The plants in Yemen agree with those in Oman in having relatively narrow cladodes, and it might still be questioned whether the form on the Arabian peninsula is conspecific with the form on Socotra.

Nyctaginaceae

Commicarpus boissieri (Heimerl) Cuf.
Yemen. Mahrah: escarpment NE of Hawf, 16°39'N, 53°03'E, 13.XI.1998, *Thulin, Beier & Mohammed Hussein* 9787 (K, UPS).

Commicarpus boissieri is known previously from Pakistan, India, Oman and Socotra (Miller 1996a). This first collection from the mainland of Yemen was made in *Anogeissus dhofarica* woodland at 700 m altitude close to the Oman border.

Passifloraceae

Basananthe berberoides (Chiov.) W.J. de Wilde
Yemen. Hadramaut: 12 km along road from Riyan to Al Mukalla, 14°45'N, 49°13'E, 3.X.1992, *Thulin, Eriksson, Gifri & Långström* 7993 (Aden Univ., K, UPS); near Zagfa, 7 km on the pipeline route starting 15 km NE of Riyan, 14°45'N, 49°31'E, 3.X.1992, *Thulin, Eriksson, Gifri & Långström* 8010 (Aden Univ., K, UPS); near Riyan airport, 14°39'N, 49°21'E, 9.X.1992, *Thulin, Eriksson, Gifri & Långström* 8223 (Aden Univ., K, UPS); 59 km from Hami along road to Sayhut, 14°59'N, 50°18'E, 9.X.1992, *Thulin, Eriksson, Gifri & Långström* 8240 (Aden Univ., E, K, UPS). Mahrah: 16 km from Sayhut along road to Qishn, 15°15'N, 51°21'E, 16.X.1992, *Thulin, Eriksson, Gifri & Långström* 8418 (Aden Univ., UPS); 31 km NE of Sayhut, 15°18'N, 51°24'E, 5.XI.1998, *Thulin, Beier & Mohammed Hussein* 9541 (UPS).

Basananthe berberoides is known previously from northern and central Somalia and from eastern Ethiopia (Thulin 1993a; de Wilde & Gilbert 1995). This record from southern Yemen is the first report of the genus *Basananthe* outside Africa. In Hadramaut and Mahrah *B. berberoides* grows on rocky hillsides, along wadis, and on stony or sandy plains close to the coast, and it is locally common. The known altitudinal range in Yemen is 10-75 m.

Plumbaginaceae

Dyerophytum indicum (Gibs. ex Wight) O. Ktze.
Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier &*

Mohammed Hussein 9718 (K, UPS); along track NE of Hawf towards the Oman border crossing, 16°40'N, 53°05'E, 12.XI.1998, *Thulin, Beier & Mohammed Hussein* 9761 (K, UPS).

Dyerophytum indicum is known previously from Oman, United Arab Emirates, western India and Socotra. The collections from Yemen cited above were made in rocky places in *Anogeissus dhofarica* woodland at 420-540 m altitude.

Poaceae

Sporobolus ruspolianus Chiov.

Yemen. Hadramaut: 6 km from the turning to the Masila field on the road from Sayun to Al Mukalla, 14°57'N, 48°53'E, 7.X.1992, *Thulin, Eriksson, Gifri & Långström* 8188 (Aden Univ., K, UPS).

Sporobolus ruspolianus is previously known from Ethiopia, Somalia, Socotra and Oman (Cope 1995, Phillips 1995). This first collection of the species (identification by T. Cope) from the mainland of Yemen was made on a rocky hillside on limestone at about 1300 m altitude.

Salvadoraceae

Azima tetracantha Lam.

Yemen. Hadramaut: 14 km from the turning to the Masila field on the road from Al Mukalla to Sayun, 15°01'N, 48°49'E, 7.X.1992, *Thulin, Eriksson, Gifri & Långström* 8182 (UPS); 42 km along the pipeline route from the crossing with the Ressib road, 15°11'N, 49°16'E, 13.X.1992, *Thulin, Eriksson, Gifri & Långström* 8347 (UPS). Mahrah: Ras Fartak, above Al Wadi, 15°40'N, 52°11'E, 7.XI.1998, *M. Thulin, sight record.*

Azima tetracantha is widespread in Africa and extends to India, Sri Lanka and the Philippines (Verdcourt 1968). On the Arabian peninsula it is previously known from Oman (Miller & Morris 1988). The two collections from Hadramaut cited above were made on rocky slopes at about respectively 1430 m and 1250 m altitude, whereas the sight record from Mahrah was made at about 800 m altitude.

Sapindaceae

Pappea capensis Eckl. & Zeyh.

Yemen. Hadramaut: 9 km W of Thilah al Ulya, 14°38'N, 49°02'E, 20.XI.1998, *Thulin, Beier & Mohammed Hussein* 9890 (K, UPS); Mola Matar area, Kawr Sayban, 14°51'N, 48°47'E, 6.X.1992, *Thulin, Eriksson, Gifri & Långström* 8141 (Aden Univ., UPS).

Pappea capensis is widespread in eastern Africa, where it is known from Eritrea, Ethiopia and Somalia in the north to South Africa in the south. On the Arabian peninsula it has previously been recorded from a single locality in Oman (Miller & Morris 1988: 258). The two collections from Hadramaut cited above were made in rocky limestone areas exposed to mist at about 640 respectively 1900 m altitude. In both localities only a single sterile tree was found.

Scrophulariaceae

Schweinfurthia spinosa A.G. Miller, M.J. Short & D.A. Sutton

Yemen. Hadramaut: 13 km on the pipeline route starting 15 km NE of Riyan, 14°47'N, 49°31'E, *Thulin, Eriksson, Gifri & Långström* 8016 (UPS); 23 km on the pipeline route starting 15 km NE of Riyan, 14°50'N, 49°31'E, 4.X.1992, *Thulin, Eriksson, Gifri & Långström* 8041 (K, UPS); 29 km on the pipeline route starting 15 km NE of Riyan, near Al Barah village, 14°57'N, 43°31'E, 4.X.1992, *Thulin, Eriksson, Gifri & Långström* 8054 (Aden Univ., K, UPS); 26 km along the pipeline route from the crossing with Ressib road, 15°18'N, 49°11'E, 13.X.1992, *Thulin, Eriksson, Gifri & Långström* 8322 (K, UPS); 25 km W of Al Ridah, 14°56'N, 50°15'E, 4.XI.1998, *Thulin, Beier & Mohammed*

Hussein 9533 (UPS). Mahrah: Al Ghaydah, wadi just E of town, 16°13'N, 42°12'E, 14.XI.1998, *Thulin, Beier & Mohammed Hussein* 9803 (UPS).

Schweinfurthia spinosa was known previously only from the Dhofar region in Oman (Miller, Short & Sutton 1982; Sutton 1988). The collections from Yemen cited above were made on stony ground along wadis and on rocky hillsides at 30-200 m altitude, except *Thulin* & al. 8322, which was collected on a gypsum hill on the Hadramaut plateau at about 1020 m altitude.

Solanaceae

Withania qaraitica A.G. Miller & J. Biagi
Yemen. Mahrah: Sadfan, along road between Jadib and Damqawt, then inland along track, 16°38'N, 52°56'E, 11.XI.1998, *Thulin, Beier & Mohammed Hussein* 9705 (K, UPS).

Withania qaraitica has previously been regarded as an endemic of the Dhofar region in Oman (Miller & Biagi 1988, Miller & Morris 1988, Hepper 1991). The collection from Yemen cited above was made on a rocky slope in *Anogeissus dhofarica* woodland at 420-540 m altitude.

Zygophyllaceae

Zygophyllum smithii Hadidi
Mahrah: 12 km NE of Itab, 15°25'N, 51°30'E, 5.XI.1998, *Thulin, Beier & Mohammed Hussein* 9553 (K, UPS); Ras Fartak, 15°40'N, 52°13'E, 9.XI.1998, *Thulin, Beier & Mohammed Hussein* 9649 (UPS).

When *Zygophyllum smithii* was described (El Hadidi 1980) it was known only from the type from the Masirah Island in Oman and since then two further collections have been made that are present at Kew. The two collections from Yemen cited above were made on stony hillsides at 280 m respectively 5-20 m altitude.

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Reno Muschler and the identity of his African labiates

OLOF RYDING

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A short biography of Reinhold Conrad (Reno) Muschler is provided, with emphasis on his botanical work and the scandal he caused in the botanical establishment of Berlin. A review of the attempts to rectify the irregularities in his publications is also provided. The author agrees with Muschler's colleagues in Berlin that Buscalioni's & Muschler's (1913) publication on new species of African plants purportedly collected in tropical Africa by the Duchess of Aosta is highly unreliable with respect to the data on provenance and collector of the type plants. Many are now believed to have in fact been collected by Schweinfurth in Eritrea and Yemen. However, in spite of the irregularities, the author argues that the types in this article should be cited in accordance with Muschler's original species description. The following nine species, described in the above-mentioned publication, and placed in Lamiaceae, are identified and found to be conspecific with the following species of Lamiaceae or Scrophulariaceae: *Coleus de-gasparisianus* Buscal. & Muschl. = *Plectranthus igniarius* Schweinf.; *C. helenae* Buscal. & Muschl. = *Plectranthus lanuginosus* (Hochst. ex Benth.) Agnew; *Geniosporum helenae* Buscal. & Muschl. = *Hebenstretia angolensis* Rolfe; *Lasiocorys de-gasparisiana* Buscal. & Muschl. = *Leucas nyassae* Gürke var. *nyassae*; *Ocimum superbum* Buscal. & Muschl. = *Ocimum spicatum* Deflers; *Orthosiphon de-gasparisianus* Buscal. & Muschl. = *Endostemon tereticaulis* (Poir.) M. Ashby; *Orthosiphon helenae* Buscal. & Muschl. = *Endostemon gracilis* (Benth.) M. Ashby; *Plectranthus emanueli* Buscal. & Muschl. = *Plectranthus longipes* Baker; *P. margeritae* Buscal. & Muschl. = *Plectranthus prostratus* Gürke. The names given after the equal-signs are to be used for the combined taxa. *Pycnostachys pseudospeciosa* Buscal. & Muschl. is accepted as the correct name of a species. The identity of *Sabaudia helenae* Buscal. & Muschl. is discussed. Neotypes and lectotypes of *Plectranthus igniarius* and most of Buscalioni's & Muschler's names of labiates are designated.

Olof Ryding, Botanical Museum and Library, Gothersgade 130, DK-1123 Copenhagen K, Denmark. E-mail: olofr@bot.ku.dk

Introduction

Reno Muschler, his life history and botanical work

In his biography, Plesske (1957) mentioned that Reinhold (Reno) Conrad Muschler was born in 1882, and was the only son of two singers at the Court Opera in Berlin. Initially, he intended to work with music. When he was 20 years old it was discovered that he suffered from lung tuberculosis. During the winters of 1902-1903, 1903-1904 and 1905-1906, he stayed in Egypt in the hope that the dry desert air would improve his health. During these journeys, he came in contact with the well-known botanists Paul Ascherson and Georg Schwein-

furth, who encouraged him to study the flora of the country. In 1904, he started to study Botany under Adolf Engler; and in 1908, he completed his PhD in Berlin (on African *Senecio* species). Immediately after his graduation, he was employed as a scientific labourer and later as an assistant at the Botanical Garden and Herbarium in Berlin (B). However, he had to leave his position in September 1913 (Zepernick & Timler 1979). According to Plesske (1957), Reno Muschler had a nervous breakdown caused by overwork and lack of sleep, but there are also other explanations for his resignation (see below). He stayed in Egypt during the First World War, later returning to Germany and earning his living as a music reviewer at a newspaper and later as author of novels, short stories and biographies. Reno Muschler died in 1957 (Zepernick & Timler 1979).

Reno Muschler was indeed a very ambitious and productive member of the staff at Herbarium and Botanical Garden in Berlin (B). Between the years 1906 and 1914, he had written at least 18 botanical publications including a Flora, alone and in co-operation with L. Buscalioni, E. De Wildeman, E.F. Gilg, O. Hoffmann and G. Schweinfurth. According to Plesske (1957), he wrote 65 scientific contributions. Altogether, he and his co-authors have described 10 new genera, about 380 new species and many new taxa of lower ranks. They also made about 50 new combinations on species level. However, in 1913, the reliability of Reno Muschler's botanical work was seriously questioned by his colleagues in Berlin (B). Schweinfurth (1915) and Engler *et al.* (1915) examined some of his articles and accused him of fraud. According to Schweinfurth (1915: 206) and Engler *et al.* (1915: 366), Reno Muschler was brought to court, but the law-suit against him was dismissed because he was said to have been in a state of unconsciousness or mentally disturbed, and unable to control his free will at the time of the deed.

Seven months after Muschler had resigned from his position in Berlin, Moore (1914) published a description of a new genus of Asteraceae that he named *Muschleria*. Moore (1914) wrote: "The generic name has been adopted in recognition of the work, especially on Compositae, of Dr. Reno Muschler." It would be interesting to know whether Moore was unaware of the scandal, regarded Muschler as innocent, or wanted to honour Muschler in spite of the irregularities.

Evaluations of Reno Muschler's botanical works; attempts to rectify his errors and identify his taxa

Muschler's (1906, 1907a, 1907-1908, 1911a, 1912b) early publications are not known to contain falsifications, but comparatively many of the new taxa described in these articles are now placed in synonymy. According to Volkens in Engler *et al.* (1915: 367), Muschler's (1909, 1911b, 1911c, 1914) articles on Asteraceae contain many misidentifications and other types of errors. Several of his new species could not be evaluated as the types could not be found. Volkens in Engler *et al.* (1915) also pointed out that Reno Muschler had benefited from the fact that the expert on the family Asteraceae in Berlin (B), O. Hoffmann, had identified many specimens in the herbarium as representatives of new taxa, but had died without having published his findings. According to Täckholm & Täckholm (1941), Muschler's largest work, his Egyptian Flora (1912a), has great deficiencies. According to Schweinfurth (1915), Muschler's (1907b) Flora of El-Tor (on Sinai) is fraudulent. Whereas Muschler gave the impression that some of the work was based on his own observations, Schweinfurth (1915) claimed that Muschler had never visited Sinai.

Buscalioni & Muschler (1913) is by far the most problematic of Muschler's contributions. In this article, Muschler and his co-author described a large number of new species on

the basis of plants purportedly collected by the Italian Elena de Francia, Duchess of Aosta, or her travel companions during their journey in tropical Africa in 1909-1911. The dates and provenance of the cited type collections match the itinerary of the Duchess of Aosta's expedition, but according to Engler *et al.* (1915), most of these plants have in reality been collected elsewhere and by others. Many of them are believed to have been removed from Schweinfurth's herbarium and to have come from Eritrea and Yemen. Engler *et al.* (1915: 368-369) also pointed out that the species descriptions in this article (apart from those of the legumes) in reality were written by Muschler alone. Although Luigi Buscalioni stands as the first author, there are no reasons to believe that he had been involved in the falsifications. In their joint article (Engler *et al.* 1915), several of the botanists at the herbarium in Berlin (B) evaluated or tried to trace the origin and rectify of the new taxa in Buscalioni's & Muschler's (1913) article. The following botanists treated the following families: F.L.E. Diels (Iridaceae), A. Engler (Moraceae), E.F. Gilg (Capparaceae, Vitaceae, Ochnaceae, Melastomataceae and Cucurbitaceae), P. Graebner (Cyperaceae), H. Harms (Fabaceae), G. Lindau (Acanthaceae), T. Loesener & R. Schlechter (Lamiaceae), R. Schlechter (Scrophulariaceae) and G.L.A. Volkens (Asteraceae). According to Harms in Engler *et al.* (1915: 370), the descriptions of new species of legumes in this article, that in reality were written by Buscalioni, are unproblematic and really based on plants from the Duchess of Aosta's expedition. The same apparently also applies to *Dorstenia piscicelliana* Buscal. & Muschl. (see Engler in Engler *et al.* 1915: 370). The Orchids in the same article, that have Buscal. & Schltr. as author are apparently also unproblematic (see Croix & Cribb 1998: 508). However, according to Friis & Jellis (1984), the above-mentioned problems apparently also apply to the Urticaceae in Buscalioni's & Muschler's article; the new species of that family were not investiged by Engler *et al.* (1915).

With reference to some old nomenclature rules, Engler *et al.* (1915: 366-367) claimed that many of plant names in Buscalioni & Muschler (1913) were invalid as they were meant to cause confusion by containing deliberately false data on collector and geographical origin. In accordance with this interpretation of the nomenclature rules, Gilg & Benedict (1915) regarded Buscalioni's & Muschler's four new species names of Capparaceae as invalid. However, their interpretation of these rules was questioned by Chiovenda (1916). Actually, according to the current botanical code (Greuter *et al.* 2000), plant names are not invalid for the reason given by Engler *et al.* (1915), but it is possible to propose rejection of these problematic names if they are found to have priority over other names of the same taxa. Buscalioni's & Muschler's plant names have been treated as valid in recent systematic works. The species names believed to have been based on material from north-east tropical Africa were included in Cufodontis' (1962, 1963, 1964, 1965, 1966, 1967) check-list.

According to White (1962: 184), some of the Duchess of Aosta's collections are preserved in Florence (FI or FT), but they have never been fully written up. He also mentioned that all but seven of Buscalioni's & Muschler's type specimens were destroyed in Berlin during the second world war. Fortunately, the species described by Buscalioni & Muschler (1913) have been illustrated, but many of the drawings are rather crude. As mentioned by Schubert & Troupin (1952, 1955), proofs of these drawings are deposited at the herbarium BR (in Brussels, now at Meise); most but not all of them were published by Piscicelli (1913). Many of the proofs (Fig. 1-5) carry the initials 'G.B.', but these initials do not appear on the illustrations

in Piscicelli (1913). On some labels attached to the herbarium sheets on which proofs are mounted, E. Robbrecht suggested that the proofs may have been sent by L. Buscalioni who corresponded with staff members at BR and met one of them in Berlin. However, it does also seem possible that the proofs have been received from Reno Muschler. The presence of an article (De Wildeman & Muschler 1913) shows that Reno Muschler co-operated with botanists in Brussels (BR). Schubert & Troupin (1952) were not able to identify the artist who had the initials GB. It seems possible that this artist is a woman called Miss Bartusch; she is mentioned in a letter from H. Harms (in Berlin) to E. De Wildeman (kept in the library at BR). Veldkamp (1968), Sebald (1980) and Friis & Jellis (1984) have identified some of Buscalioni's & Muschler's species of Oxalidaceae, Lamiaceae and Urticaceae by help of the proofs in BR or the illustrations in Piscicelli (1913). However, Ortiz & Rodriguez-Oubiña (1996) argued that the illustration of *Dicoma bangueolensis* Buscal. & Muschl. (Asteraceae) was not drawn from the type of this species name.

The reliability of data in Buscalioni & Muschler (1913)

As seen in the following examples, the provenance data of the labiates described by Buscalioni & Muschler (1913) are in many cases contradicted, not only by Loesener & Schlechter in Engler *et al.* (1915), but apparently also by an independent source of information, the known distributions of the taxa on the proofs from BR (Figs. 1-5). If these illustrations are based on Buscalioni's & Muschler's (1913) type plants, and Buscalioni's & Muschler's data on their provenance is correct, about nine out of the 11 of their types were collected outside the otherwise known distribution area and/or altitudinal range of their species; five of these represent isolated records in disjunct species distributions. These disjunct distributions do not match White's (1983) phytogeographical regions. According to Friis & Jellis (1984) and Ortiz & Rodriguez-Oubiña (1996), the purported types localities of *Pouzolzia piscicelliana* Buscal. & Muschl. [= *Australinia flaccida* (A. Rich.) Wedd., Urticaceae] and *Dicoma bangueolensis* Buscal. & Muschl. (Asteraceae) are widely separated from the rest of the distribution area of their species. Disjunct species distributions are not very uncommon, but it is remarkable that such a large proportion of the studied material seems to constitute geographically marginal or disjunct isolates. Moreover, most of the localities indicated by Buscalioni & Muschler (1913), such as Broken Hill, have been visited by many plant collectors. It seems unlikely that so many plant collectors would have failed to find so many of the species, if they really had been present in these areas. Hence, I agree with Engler *et al.* (1915) and White (1962) that there are strong reasons to distrust Buscalioni's & Muschler's (1913) information on the provenance of their species.

There is also some disagreement between the illustrations on the proofs from BR and Loesener's & Schlechter's identifications in Engler *et al.* (1915) which may be explained by misidentifications. The possibly confused species (*Plectranthus longipes* and *P. hadiensis* plus *Hebenstretia angolensis* and *H. oetesii*) are superficially similar.

How should the types in Buscalioni & Muschler (1913) be cited

Cufodontis (1963, 1964, 1965), Jeffrey (1995: 27, 52) and Ortiz & Rodriguez-Oubiña (1996) have regarded the type material cited by Buscalioni & Muschler (1913) and the material to which these plants are believed to have belonged as parts of the same collections, although the two gatherings of plants have been given different collector's names and numbers.

For example, although the *von Aosta* 515 is cited as the type in the original description, Jeffrey (1995: 27) cited *Schweinfurth* 582 as the type of *Melothria pulchra* Buscal. & Muschl.; this was made on the basis of Gilg's correction in Engler *et al.* (1915: 373). I disagree with the above-mentioned authors' concept of what is a collection. I think that specimens with different collector's names and/or numbers should always be treated as separate collections, although they may be presumed to have belonged to the same original collection. This is particularly important as we cannot be completely sure that the Berlin botanists have matched all of "the Duchess of *Aosta*'s" plants correctly when trying to trace their origin with the help of comparisons. Hence, despite the irregularities, we have to accept Buscalioni's & Muschler's own circumscriptions of their original material, and cite the types of their species as if they had been collected by "*von Aosta*". In normal cases, the collections from which Muschler's now destroyed "*von Aosta*" types are believed to have been removed, constitutes the most suitable material to serve as neotypes. However, under certain circumstances (see under *Coleus helenae* and *Plectranthus margeritae*), other collections may be more suitable as neotypes.

Identities of the labiates described in Buscalioni & Muschler (1913)

Buscalioni & Muschler (1913) described 11 new species and one new genus of Lamiaceae. Loesener & Schlechter in Engler *et al.* (1915: 371-372) regarded most of these descriptions as very problematic and tried to identify and trace the origin of these plants. However, their corrections do not seem to be unproblematic either. As mentioned by Chiovenda (1916), several of the so-called correct names are unpublished, and were apparently only known from the labels on some of Schweinfurth's collections. The labiates collected by Schweinfurth were destroyed in Berlin along with Muschler's types, but duplicates of some of these specimens have been preserved in Geneva (G-BOIS). In some cases, Loesener's & Schlechter's identifications in Engler *et al.* (1915) do not match the descriptions in Buscalioni & Muschler (1913) and/or the illustrations on the proofs from BR. Due to these inconsistencies, it seems necessary to reconsider Loesener's & Schlechter's identifications with the help of the presently available sources of information: Buscalioni's & Muschler's (1913) descriptions, duplicates of some Schweinfurth's collections in G-BOIS, and the illustrations on the proofs from BR.

1. *Coleus de-gasparisianus ("C. De Gasparisianus")*

Buscalioni & Muschler (1913) claimed that the type of *C. de-gasparisianus* was collected at the "Mbusi River" (the Buzi River in Mozambique), and mentioned that the plant was a shrub that lacked leaves at the flowering time. They regarded it as closely related to *Plectranthus igniarius* (Schweinf.) Agnew but differing by lacking hairs and having 20-35 mm long petiolate leaves. However, according to Loesener & Schlechter in Engler *et al.* (1915), the type of *C. de-gasparisianus* was removed from *Schweinfurth* 506 from the Haddes Valley in Eritrea, and belonged to *C. erythraeae* Schweinf. However, the latter name was never published. I have found no duplicates of Schweinfurth's collection, but Gürke, who was at the Berlin Herbarium (B) before Schweinfurth's herbarium was destroyed, has identified two collections at FT as *C. erythraeae*; these collections (*Ruspoli & Riva* 323 and 799) belong to *P. igniarius*. Apart from having leaves and flowers at the same time, the plant on the proof in BR (Fig. 1 Left) strongly resembles *P. igniarius*. *P. igniarius* is not known in Mozambique or Zimbabwe, but seems to be rather common in Eritrea. *P. igniarius* has mostly the leaves pubescent with

short hairs and less than 20 mm long pedicels, but the collection *Pappi* 2993 (at FT) from Mt. Dijot in Eritrea (not very far from the Haddes Valley) has very sparsely pubescent leaves with up to over 20 mm long pedicels. Pappi's collection lacks flowers, and *Schweinfurth & Riva* 1398 from a place not very far from Mt. Dijot, that has flowers but no leaves, is here chosen as neotype of *C. de-gasparisianus*.

Typification of Plectranthus igniarius

Schweinfurth (1867) did not indicate the collector's number of the type of *Coleus igniarius* (= *P. igniarius*), and the same applies to the other Schimper collections cited in his article. The original material was probably destroyed in Berlin. According to Cufodontis (1963), *Schimper* 527 is the type of this name, but specimens with that collection number have not been traced. The type of *P. malinvaldi* is based on material collected by the same collector (Schimper), the same day and at the same locality, but it has another collector's number (529). The same also applies to *Schimper* 1623, and a collection in Paris (P) is unnumbered. All this material may have belonged to the same collection, and the different numbers may have been added afterwards. Nevertheless, I find it advisable to regard these specimens as different collections. It cannot be decided which one of these three Schimper collections that is most close to the lost type in Berlin. Of the three collections, it is *Schimper* 529 that is the most widespread in the herbaria, but in order to avoid having two names attached to the same type collection, I designate *Schimper* 1623 as neotype of *P. igniarius*.

Conspectus of present taxonomy:

Plectranthus igniarius *(Schweinf.) Agnew,*
Upland Kenya Wild Flowers: 638 (1974); *Coleus igniarius* Schweinf., Beitr. Fl. Aethiopiens: 121 (1867). Type: Ethiopia, Gondar Region, "auf 4000' hohen Bergen bei Dehli-Dikeno", 23 X 1854, *Schimper* (B holotype destroyed). Neotype: Ethiopia, Gondar Region, "4000' … über meer auf Bergen Dehli Dikeno", 23 X 1854, *Schimper* 1623 (P neotype designated here; C photo of neotype).

P. malinvaldi Briq., Bull. Herb. Boissier 2: 125 (1894); *Coleus malinvaldi* (Briq.) Briq., Annuaire Conserv. Jard. Bot. Genève 2: 240 (1898), **synon. nov**. Type: Ethiopia, Gondar Region, "Dehli Dikeno", 23 X 1854, *Schimper* 529 (G-DC lectotype designated here; FT, P isotypes; C photo of lectotype).

Coleus de-gasparisianus Buscal. & Muschl., Bot. Jahrb. Syst. 49: 487 (1913), (as *C. De Gasparisianus*), **synon. nov**. Type: "Grassteppe am Ufer des Mbusi" (Manica e Sofala in Mozambique; but in reality probably from Mahio in Haddes Valley, Eritrea), "14 XII 1909", *von Aosta* 151 (B holotype destroyed). Neotype: Eritrea, Vallé Arrot, au sud de Aidereso, 4 IV 1892, *Schweinfurth & Riva* 1398 (FT neotype designated here; BR, G, P, S isoneotypes; C photo of neotype).

Coleus erythraeae Schweinf. ex Loes. & Schltr., Bot. Jahrb. Syst. 53: 372 (1915), nom. nud.

Coleus guidottii Chiov., Atti Reale Accad. Italia, Mem. Cl. Sci. Fis.11 (2): 54 (1940), **synon. nov.** Type: Eritrea, "Habab, Cub-Cub presso Nacfa", III 1936, *Guidottii* 776 (FT holotype; C photo.).

2. Coleus helenae

Buscalioni & Muschler (1913) claimed that the type of *C. helenae* was collected in the swamps at Lake Bangweulu in Zambia, but only few *Plectranthus* species grow in this type of damp habitats. According to Loesener & Schlechter in Engler *et al.* (1915), the plant was removed from *Schweinfurth & Riva* 1182 (from near Sageneti in Eritrea). They regarded this collec-

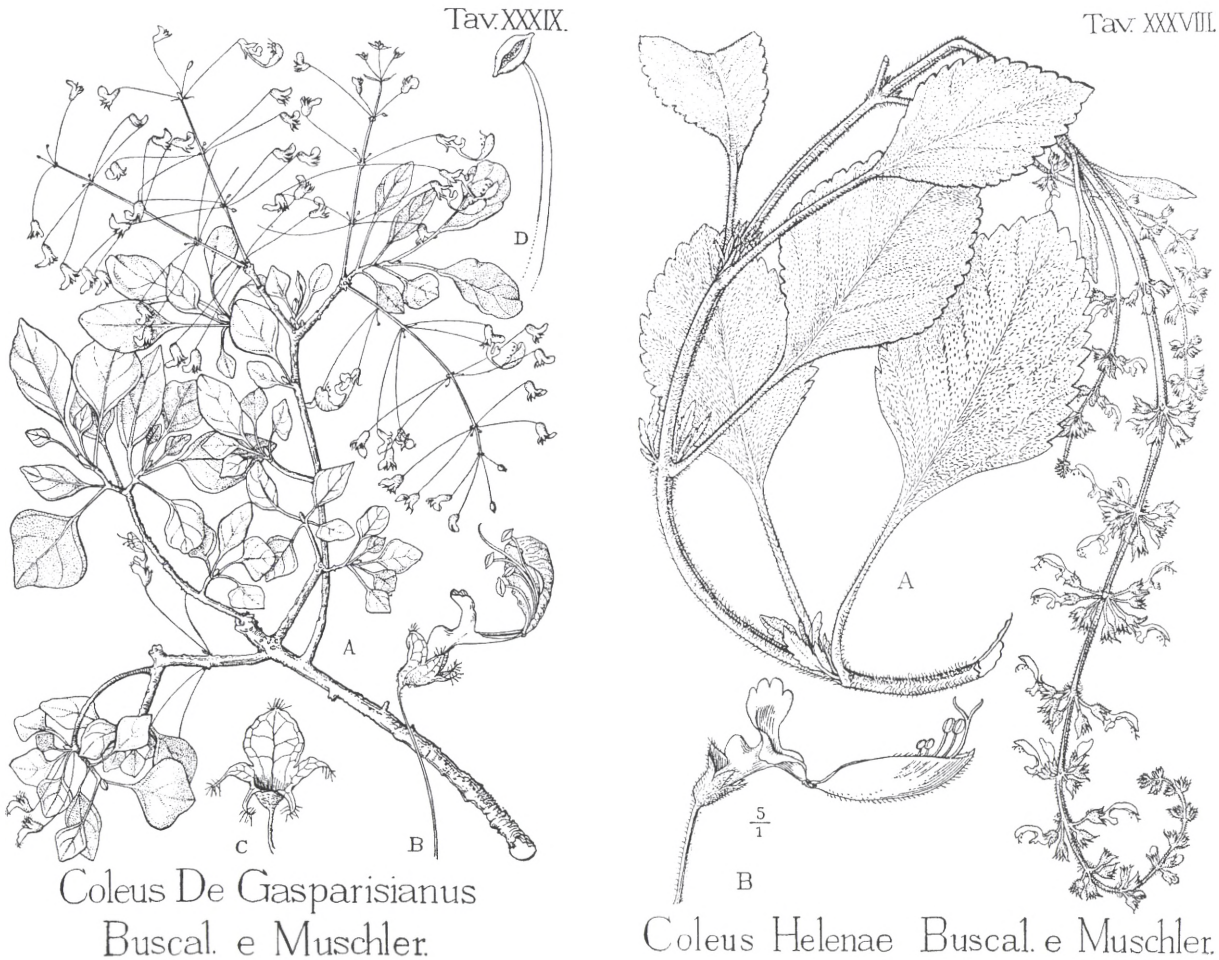

Fig. 1. Published and unpublished proofs in the herbarium BR with illustrations of species described by Buscalioni & Muschler (1913). Magnification: x 0.68. **Left**: *Coleus de-gasparisianus*. A: habit. B: Flower. C: Calyx. D: stamen. **Right**: *C. helenae*. A: habit. B. flower. The illustration to the right was published by Piscicelli (1913).

tion as conspecific to *P. ghindanus* Schweinf. ex Baker. This species is now commonly known under the older name *P. tenuiflorus* (Vatke) Agnew, but according to Ryding & Paton (submitted), it should be known as *P. aegyptiacus* (Forssk.) C. Chr. The presently available material of Schweinfurth's & Riva's collection (at G-BOIS) is mixed, consisting of a flowering plant of *P. lanuginosus* and some plants of *P. tenuiflorus* with mature fruiting calyces. Buscalioni's & Muschler's (1913) description matches *P. lanuginosus* better than *P. tenuiflorus*. It mentions that the plant has long-petiolate leaves and short pedicels, and does not mention the hall-mark of *P. tenuiflorus*, the long stamens that protrude well beyond the lower lip of the corolla. The plant on the proof in BR (Fig. 1 Right) is similar to *P. lanuginosus* and rather different from *P. tenuiflorus*. Unlike *P. tenuiflorus*, its has long petioles, no peduncles in the cymes, rather short pedicels and the stamens not or only very slightly longer than the lower

lip of the corolla. In the drawing, the corolla tube appears to be straight and to have a hump on the dorsal side. No *Plectranthus* are known to have such a hump and the drawing is probably slightly incorrect. However, the hump in the drawing resembles the spur-like outgrowth in the strongly bent corolla-tubes of *P. lanuginosus*. Neither, *P. tenuiflorus* nor *P. lanuginosus* are known from the area near Lake Bangweulu in Zambia, and neither of the two species grows in damp habitats. It remains uncertain whether Muschler's type of *C. helenae* consisted of *P. lanuginosus, P. tenuiflorus* or was a mixture of both these species. Fortunately, both the species epithets "*lanuginosus*" and "*tenuiflorus*" have priority to "*helenae*". Mixed collections, such as *Schweinfurth & Riva* 1182 (from which Muschler is supposed to have removed his type material) are not well suited to serve as neotypes. A collection of *P. lanuginosus*, *Schweinfurth & Riva* 1184, that was collected in a neighbouring locality a few days later, is here selected as neotype of *P. helenae*.

Conspectus of present taxonomy:

Plectranthus lanuginosus (Hochst. ex Benth.) Agnew,
Fl. Upland Kenya: 638 (1974); *Coleus lanuginosus* Hochst. ex Benth. in DC., Prodr. 12: 79 (1848). Type: Ethiopia, Tigray Region, Adua, *Schimper* III/1915 (K lectotype; BM, FI, KIEL, P, UPS isolectotypes; C photo of the lectotype).

Coleus helenae Buscal. & Muschl., Bot. Jahrb. Syst. 49: 487 (March 1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat.: 124, Fig. at p. 125 (November 1913), **synon. nov.** Type: "Sümpfe am Banguelo-See," (Zambia, Northern Region; but in reality probably from Mai Golgol near Segeneti in Eritrea), "8 III 1910", *von Aosta* 862 (B holotype destroyed). Neotype: Eritrea, Sageneti, cote du nord vers Selet, 12 III 1892, *Schweinfurth & Riva* 1184 (FT neotype designated here; BR, K, P isoneotypes; C photo of neotype).

There are additional synonyms in Ethiopia and Somalia.

3. Geniosporum helenae

Buscalioni & Muschler (1913) placed *G. helenae* in Lamiaceae, but their description suggests that it may belong to a different family. Loesener & Schlechter in Engler *et al.* (1915) identified the plant as *Hebenstretia polystachya* Harv. ex Rolfe (Selaginaceae or Scrophulariaceae s. lat.). Roessler (1979) does not mention *G. helenae* in revision of *Hebenstretia*, but includes *H. polystachya* in *H. oetesii* Rolfe subsp. *oetesii*. The plant on the proof from BR (Fig. 2 Left) is definitely a *Hebenstretia*, but it differs from the serrate-leaved Southern African *H. oetesii* by having remotely serrate to entire leaves. The illustrated plant is definitely more similar to the widespread tropical to Southern African *H. angolensis* Rolfe that usually has a similar leaf margin. According to Buscalioni & Muschler (1913), *G. helenae* was collected near the Buzi River (below 500 m in Mozambique). Loesener & Schlechter in Engler *et al.* (1915) apparently distrusted this information, perhaps because the genus *Hebenstretia* is not known from such low altitudes in tropical Africa, but they could not establish its origin with certainty.

4. Lasiocorys de-gasparisiana ("L. De Gasparisiana")

Buscalioni & Muschler (1913) claimed that the type of *L. de-gasparisiana* was collected at the "Mbusi River" (the Buzi River in Mozambique). Loesener & Schlechter in Engler *et al.* (1915) apparently distrusted this information but could not establish its origin with certainty. They identified it as *Leucas nyassae*, and I agree with Sebald (1980: 163-164) that the plant on the proof from BR (Fig. 2 Right) belongs to the same species (and to the var. *nyassae*). However,

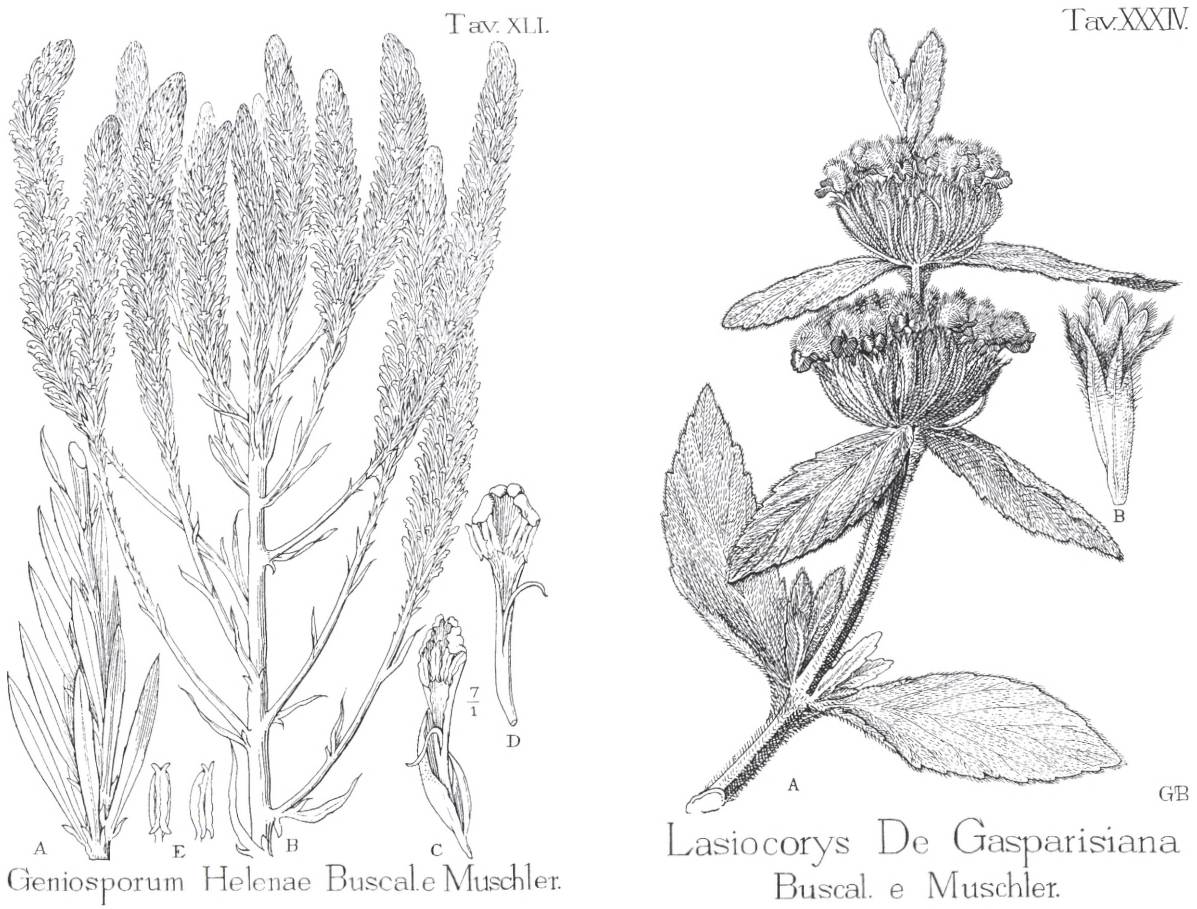

Fig. 2. Unpublished proofs in the herbarium BR with illustrations of species described by Buscalioni & Muschler (1913). Magnification: x 0.68. **Left**: *Geniosporum helenae*. A: part of a shoot. B: habit. C: flower. D: corolla. E: anthers. **Right**: *Lasiocorys de-gasparisiana*. A: habit. B: calyx.

Buscalioni's & Muschler's (1913) description may match many *Leucas* species but hardly *L. nyassae*. Whereas *L. nyassae* is an up to 1 m tall herb with 40-80-flowered verticillasters, the description mentions that *L. de-gasparisiana* is a *c.* 1.5 m tall shrub with 10-12-flowered verticillasters. There is obviously a conflict between the different sources of information, but when all the available data is taken into consideration, it seems more probable that the lost type of *L. de-gasparisiana* belonged to *L. nyassae* than that it belonged to the unknown species of the description. Hence, Muschler may have confused the plant material. According to Sebald (1980: 47, 163-165), *L. nyassae* is not known from the Buzi River in Mozambique, but has been recorded from neighbouring parts of Zimbabwe, not very far from this river. In the absence of more reliable sources of information on the provenance of the type material, I have designated a collection from the latter country as neotype of this name.

Conspectus of present taxonomy:

Leucas nyassae Gürke,
Bot. Jahrb. Syst. 22: 137 (1895); Sebald, Stuttgarter Beitr. Naturk. Ser. A. 341: 163 (1980). Type: Malawi, Southern Region, "Shire Highlands", *Buchanan* 255 (K syntype); "Shire Highlands", *Buchanan* 460 (K syntype).

var. ***nyassae***

Lasiocorys de-gasparisiana ("*L. De Gasparisiana*" Buscal. & Muschl., Bot. Jahrb. Syst. 49: 483 (1913). Type: "Steppe am Mbusi-Fluß (Mossambik)" (Manica e Sofala Region in Mozambique; but in reality probably from elsewhere), "7 VII 1909", *von Aosta* 82 (B holotype destroyed). Neotype: Zimbabwe, Central Region, Salisbury District, Lake Mac Ilwaine near Game Park, 21 III 1963, *Loveridge* 619 (K neotype designated here; SRGH isoneotype not seen; C photo of neotype).

A complete list of synonyms has been provided by Sebald (1980).

5. Ocimum superbum
Buscalioni & Muschler (1913) claimed that the type of *Ocimum superbum* was collected in Zambia, and gave a description that matches *O. gratissimum* L. They mentioned that the plant was 3 m tall, has hairs simple and leaves acute or subacute at the apex and attenuate at the base. On the basis of this evidence, Paton (1992) placed *O. superbum* as a synonym under *O. gratissimum*. However, according to Loesener & Schlechter in Engler *et al.* (1915), the plant was removed from the collection *Schweinfurth* 1199 from Yemen, and belonged to *O. cylindrostachys* Schweinf. The latter name has not been validly published, but *Schweinfurth* 1199 and other collections identified by that name (*e.g.* by Schwartz 1939) belong to *O. spicatum*. The plant on the proof from BR (Fig. 3 Left) is very similar to *O. spicatum*. Unlike *O. gratissimum* and in conflict with Buscalioni's & Muschler's (1913) description, it has obtuse leaves with a cuneate base. Whereas *O. gratissimum* has simple hairs only, the illustrations hint that the type plant had branched hairs. The very dense inflorescences, strongly recurved calyces with the upper lip pointing straight downwards are more typical of *O. spicatum*. There is obviously a conflict between the different sources of information, but when all the available information is taken into consideration, it seems more probable that the lost type of *O. superbum* belonged to *O. spicatum* than that it belonged to *O. gratissimum*. If the latter conclusion is correct, Muschler seems to have confused the plant material. *O. spicatum* is not known from Zambia, and a duplicate of the collection from Yemen, from which the type material was said to have been removed, is here selected as a neotype of *O. superbum*.

Conspectus of present taxonomy:

Ocimum spicatum *Deflers*,
Bull. Soc. Bot. Fr. 43: 226 (1896). Type: Yemen, Jabal Masna'ah, 17 IV 1890, *Deflers* 599 (K lectotype, P isolectotype, C photo of isolectotype).

O. superbum Buscal. & Muschl., Bot. Jahrb. Syst. 49: 488 (March 1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat. 134, Fig. at p. 135 (November 1913), **synon. nov**. Type: "Baumsteppe zwischen Buana Mukuba und Sekontui, 1200 m ü. M." (Central Region in Zambia; but in reality probably from Wabi Chnoiet in Yemen), 26 I 1910, *von Aosta* 421 (B holotype destroyed). Neotype: Yemen, Wadi Chnoiet, 1889, *Schweinfurth* 1199 (G-BOIS neotype designated here, C photo of neotype).

O. cylindrostachys Schweinf. ex Loes. & Schltr., Bot. Jahrb. Syst. 53: 372 (1915), nom. nud.; O. Schwartz, Fl. trop. Arab.: 231 (1939), nom. nud.

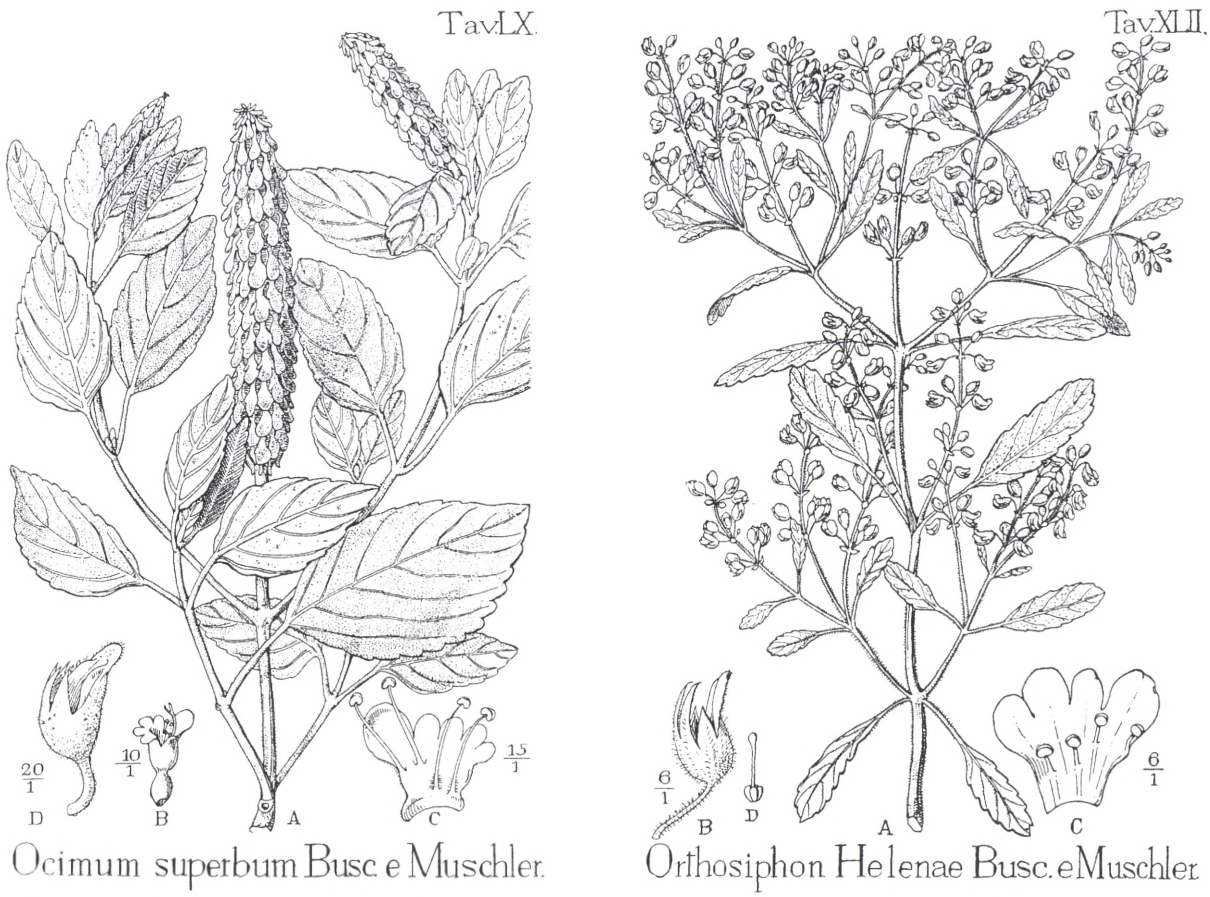

Fig. 3. Proofs in the herbarium BR with illustrations of species described by Buscalioni & Muschler (1913). Magnification: x 0.68. **Left**: *Ocimum superbum*. A: habit. B: corolla. C: dissected flower. D: fruiting? calyx. **Right**: *Orthosiphon helenae*. A: habit. B: calyx. C: dissected flower. The two illustrations were published by Piscicelli (1913).

6. Orthosiphon helenae

Buscalioni & Muschler (1913) claimed that the type of *O. helenae* was collected at Broken-Hill in Zambia, but according to Loesener & Schlechter in Engler *et al.* (1915), the plant was removed from *Schweinfurth* 820 that was collected in Okeber (Yemen). Schweinfurth's collection was identified as *O. melhanensis* Schweinf., but this name has not been validly published. As mentioned by Wood (1997), the correct name of this species is *Endostemon gracilis*. The presently available material of Schweinfurth's collection belongs to the Arabian form of this species, a form that is characterised by having comparatively narrow leaves. The same apparently also applies to the illustration of *O. helenae* on the proof from BR (Fig. 3 Right). Buscalioni's & Muschler's (1913) statement that *O. helenae* is annual or biennial, provides some additional support to believe that it belonged to *E. gracilis*. *E. gracilis* is not known from Zambia, and as far as known, the African material of this species differs from the illustrated plant in having broader leaves. Hence, a duplicate of Schweinfurth's Arabian collection, from which Muschler is believed to have removed the type

material, is here selected as neotype of *O. helenae*.

Conspectus of present taxonomy:

Endostemon gracilis (Benth.) M. Ashby, J. Bot. 74: 127 (1936); A.J. Paton *et al.*, Kew Bull. 49: 701 (1994); J.R.I. Wood., A Handbook of the Yemen Flora: 247 (1997); *Ocimum gracile* Benth., Labiat. gen. spec.: 12 (1832). Type: Zanzibar, *Bojer* s.n. (K lectotype).

Orthosiphon helenae Buscal. & Muschl., Bot. Jahrb. Syst. 49: 490 (1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat.: 130, Fig. at p. 131 (1913), **synon. nov**. Type: "Steppe bei Broken Hill" (Central Region in Zambia; but in reality probably from Okeber in Yemen), "12 I 1910", *von Aosta* 284 (B holotype destroyed). Neotype: Yemen, Okeber, am Gebel Melhan, 28 I 1889, *Schweinfurth* 820 (G-BOIS neotype designated here, B isoneotype destroyed, C photo of neotype).

Orthosiphon melhanensis Schweinf. ex Loes. & Schltr., Bot. Jahrb. Syst. 53: 372 (1915), nom. nud.; O. Schwartz, Fl. trop. Arab.: 232 (1939), nom. nud.

Additional synonyms have been given by Paton *et al.* (1994: 701).

7. Orthosiphon de-gasparisianus ("O. De Gasparisianum")

Buscalioni & Muschler (1913) claimed that the type of O. *de-gasparisianus* was collected in Zambia, but according to Loesener & Schlechter in Engler *et al.* (1915), the plant was removed from the collections *Schweinfurth* 244 and/or 278, both from Eritrea and identified as *O. erythraeum* Schweinf. However, the latter name has not been validly published, and is not known to have applied to other herbarium specimens. No duplicates of these collections have been found, and the latter name was never published or found on any herbarium labels. Fortunately, the habit illustration (Fig. 4 Left) is unmistakable, showing a plant belonging to *Endostemon tereticaulis*; but the flower is slightly atypical showing a divided upper lip. The species is widespread in tropical Africa but not known from Zambia. A neotype is here selected among material of *E. tereticaulis* from Eritrea, the country from which the original material is believed to have originated.

Conspectus of present taxonomy:

Endostemon tereticaulis (Poir) M. Ashby, J. Bot. 74: 129 (1936); A.J. Paton *et al.*, Kew Bull. 49: 711 (1994); J.R.I. Wood., A Handbook of the Yemen Flora.: 247 (1997); *Ocimum tereticaule* Poir. in Lam., Encycl. suppl. 1: 592 (1811). Type: West Tropical Africa, *Herb. Desfontaines.*

Orthosiphon de-gasparisianum Buscal. & Muschl., Bot. Jahrb. Syst. 49: 490 (March 1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat.: 132, Fig. at p. 133 (November 1913), **synon. nov.** Type: "Baumsteppe bei Broken Hill, 1000 m ü. M." (Central Region in Zambia; but in reality probably from near Ginda in Eritrea), "12 I 1910", *von Aosta* 282 (B holotype destroyed). Neotype: Eritrea, Nefasit, at the base of Mt. Bizen, just above the town, 25 XI 1989, *Ryding et al.* 2035 (UPS neotype designated here, ASMU, ETH isoneotypes; C photo of neotype).

Orthosiphon erythraeum Schweinf. ex Loes. & Schltr., Bot. Jahrb. Syst. 53: 372 (1915), nom. nud.

Additional synonyms have been provided by Paton *et al.* (1994: 771).

8. Plectranthus emanueli

Buscalioni & Muschler (1913) claimed that the

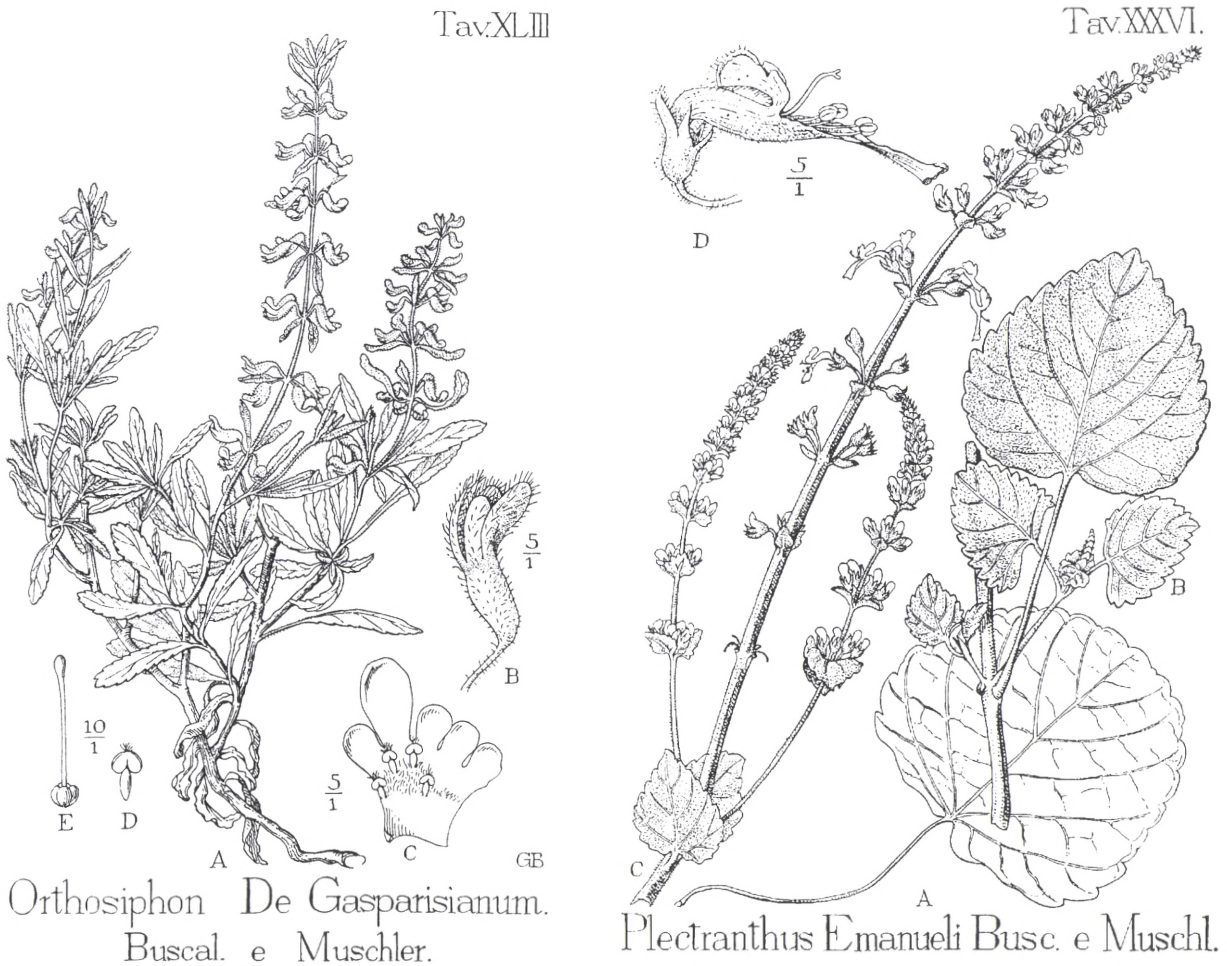

Fig. 4. Proofs in the herbarium BR with illustrations of species described by Buscalioni & Muschler (1913). Magnification: x 0.68. **Left**: *Orthosiphon de-gasparisianus*. A: habit. B: fruiting calyx. C. dissected flower. D: anther. E: pistil. **Right**: *Plectranthus emanueli* (right): A, leaf; B, part of shoot; C, inflorescence; D, flower. Slightly modified versions of the two illustrations were published by Piscicelli (1913).

type of *P. emanueli* was collected in Kenya, but Loesener & Schlechter in Engler *et al.* (1915) stated that this plant was removed from Schweinfurth's herbarium and is conspecific to *P. hadiensis* (Forssk.) Schweinf. ex Sprenger. However, other information on this plant suggests that it was more similar to *P. longipes* than to *P. hadiensis*. The description in Buscalioni & Muschler (1913) is rather uninformative, but disagrees with *P. hadiensis* in mentioning that *P. emanueli* has bracts. The drawing of *P. emanueli* (Fig. 4 Right) is more similar to *P. longipes* than to *P. hadiensis*. The illustrated plant resembles *P. longipes* (at least the material from Eritrea) in having both the upper and the lower lips of the corolla rather long; the stamens much shorter than the lower lip; bracts persistent; and the leaf blades being slightly notched at the peti-

Fig. 5. Proofs in the herbarium BR with illustrations of species described by Buscalioni & Muschler (1913). Magnification: x 0.68. **Left**: *Plectranthus margeriatae*. A: habit. B: flower. **Right**: *Pycnostachys pseudospecoisa*. A: habit. B: bract? C: corolla. D: upper part of style. Slightly modified versions of the two illustrations were published by Piscicelli (1913).

ole. *P. hadiensis* has the upper lip of the corolla slightly shorter; the stamens up to almost as long as the lower lip of the corolla; bracts usually early deciduous; and leaves slightly attenuate and not notched near the petiole. The three collections *Cufodontis* 359, 417 and 712 at FT, identified as *P. emanueli* by Lanza (1939), belong to *P. longipes*. However, it is uncertain whether Lanza had seen the type of *P. emanueli*. He might have compared his plants with the illustration in Piscicelli (1913). *P. longipes* is known from Kenya, but if Loesener & Schlechter in Engler *et al.* (1915) are right in that the plant comes from Schweinfurth's herbarium, it seems to be more probable that the type material comes from Eritrea. According to Cufodontis (1963), the type was collected by Schweinfurth in Eritrea and cultivated in Hortus Panormitano (in Palermo, Italy), but this material has not been traced by

the author. It might also have been removed from the Berlin isotype of *P. longipes* (*Schweinfurth* 178). In order to avoid attaching two names to the same collection, the neotype of *P. emanueli* has been selected among other material of *P. longipes* from Eritrea.

Conspectus of present taxonomy:

Plectranthus longipes Baker
in Dyer., Fl. trop. Afr. 5: 406 (1900). Type: Eritrea, Ginda, 17 II 1891, *Schweinfurth* 178 (K holotype; C photo.).

Coleus emanueli Buscal. & Muschl., Bot. Jahrb. Syst. 49: 484 (March 1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat. 472, Fig. at p. 473 (November 1913), **synon. nov**. Type: "Tal des Guasso Nyiro" (Kenya; but in reality perhaps from elsewhere), "22 XI 1910", *von Aosta* 1558 (B holotype destroyed). Neotype: Eritrea, Nefasit, at the base of Mt. Bizen, just above the town, 25 XI 1989, *Ryding et al.* 2034 (UPS neotype designated here; ASMU, ETH isoneotypes; C photo of neotype).

9. Plectranthus margeritae
Buscalioni & Muschler (1913) claimed that the type of *P. margeritae* was collected at Neumann's Camp NE of Mt Kenya, but in Piscicelli (1913) it was stated that it comes from near Marsabit, *c.* 200 km north of this site, and Loesener & Schlechter in Engler *et al.* (1915) stated that the plant was removed from *Schweinfurth* 282 from Yemen, and identified as *P. quadridentatus*. *P. quadridentatus* is conspecific to *P. prostratus*, a species that is only known from Africa, but the name has also been applied for the Arabic *P. arabicus* E.A. Bruce. The collection *Schweinfurth* 282, that was identified as *P. quadridentatus*, is sterile. Apart from having atypically large leaves, it is very similar to *P. arabicus*, but due to the absence of flowers and fruits I cannot confirm the identification by Loesener's & Schlechter (1915) with complete certainty. The question of the identity of *P. margeritae* seems to be more complicated than suggested by Loesener & Schlechter in Engler *et al.* (1915). The abundance of adventitious roots in the illustrated plant (Fig. 5 Left) agrees better with the prostrate *P. prostratus* than with the usually more upright *P. arabicus*. Buscalioni & Muschler (1913) claim that their species is heterophyllous, and that also applies to the plant on the proof from BR (Fig. 5 Left). One part of the illustrated plant has large subsessile and pinnatifidly lobed leaves, and is very similar to the collection *Schweinfurth* 282; the other part has smaller petiolate and only shallowly crenate leaves, and is very similar to the characteristic African *P. prostratus*. *P. arabicus* and *P. prostratus* are closely related and perhaps not very distinct, but as far as known, the leaves of the two species are not very variable within the same plants. However, according to A. Paton (pers. com.), a related species from coastal Kenya seems to have the leaves larger on sterile shoots, and heterophyly could perhaps occur in *P. prostratus* as well. When all available information is taken into consideration, it cannot be decided whether the type of *P. margeritae* belonged to *P. arabicus*, to *P. prostratus*, or was mixed and contained material from both these species. The species epithet *margeritae* is older than *arabicus* but younger than *prostratus*. In order to avoid unnecessary name changes, I prefer to attach the name (*P. margeritae*) to *P. prostratus*. The latter species is known from Kenya, but I have seen no material from the localities mentioned by Buscalioni & Muschler (1913) or in Piscicelli (1913). As many of Muschler's collections seem to have been removed from Schweinfurth's herbarium, it is perhaps more probable that this part of the type originates from Eritrea where Schweinfurth has collected the type of *P. quadridentatus* (synonym of *P. prostratus*). In order not to attach two names to the same collection, the

neotype of *P. margeritae* has been selected among other material of *P. prostratus* from Eritrea.

Conspectus of present taxonomy:

Plectranthus prostratus Gürke,
Bot. Jahrb. Syst. 19: 206 (1894). Types: Tanzania, Pare Distr., "Kilimandscharogebiet, am fuß der Nashornhügel am Panganiübergang", *Volkens* 484 (B syntype destroyed); North Mara Distr., Ukira, *Fischer* 497 (B syntype destroyed).

P. quadridentatus Schweinf. ex Baker in Dyer., Fl. trop. Afr. 5: 409 (1900). Type: Eritrea, Mt. Alam Kale, NW of Aidereso, 5 IV 1892, *Schweinfurth & Riva* 2086 (K holotype; FT, P isotypes).

P. margeritae Buscal. & Muschl., Bot. Jahrb. Syst. 49: 485 (March 1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat.: 470, Fig. at p. 471 (November 1913), **synon. nov.** Type: "Neumann-Camp" (Northern Frontier Region in Kenya; but in reality probably mixed with one part from E or NE Africa and one from Gebel Bura in Yemen), "11 I 1911", *von Aosta* 1688 (B holotype destroyed). Neotype: Eritrea, Nefasit, at the base of Mt. Bizen, just above the town, 30 XII 1989, *Ryding et al.* 2095 (C neotype designated here, ASMU, ETH, UPS isoneotypes).

10. Pycnostachys pseudospeciosa
Buscalioni & Muschler (1913) claimed that the type of *P. pseudospeciosa* was collected at Lake Bangweulu in Zambia, and there is a fragment from this plant in the Kew Herbarium (K). Loesener & Schlechter in Engler *et al.* (1915) did not include this species in their list of corrections. In her revision of *Pycnostachys*, Bruce (1939) recognised *P. pseudospeciosa* as the correct name of a distinct species. The plant on the proof in BR (Fig. 5 Right) can be identified as *P. pseudospeciosa*, and this confirms Bruce's (1939) application of the name. The species is indeed known from the area near Lake Bangweulu, and the type plant may well have been collected on the Duchess of Aosta's expedition, but the collection number (1002) was probably added by Muschler. However, in the light of all the irregularities, doubt may also be attached to the provenance of this type collection.

Conspectus of present taxonomy:

Pycnostachys pseudospeciosa Buscal. & Muschl.,
Bot. Jahrb. Syst. 49: 486 (March 1913); Buscal. & Muschl. in Piscicelli, Reg. Laghi equat.: 258, Fig. at p. 259 (November 1913); Bruce, Bull. Misc. Inform. 1939: 584 (1939). Type: Zambia, Northern Region, "steppe, am Bangueolo-See, 1300 m ü. M.", 23 III 1910, *von Aosta* 1002 (B holotype destroyed, K lectotype, designated here, C photo of lectotype).

11. Sabaudia helenae
Buscalioni & Muschler (1913) described the new genus *Sabaudia* and claimed that the type of the single species, *S. helenae*, was collected in Zambia, but according to Loesener & Schlechter in Engler *et al.* (1915), the plant was removed from the collection *Schweinfurth* 491 from Yemen. Chiovenda (1917) recognised *Sabaudia* as a distinct genus, and included two more species (*S. atriplicifolia* (Benth.) Chiov. and *S. erythraeae* Chiov.). He also recognised *S. helenae* as distinctly differing from the other two species by having bracteoles at the base of the calyces. Apart from having bracteoles, the illustration of *S. helenae* in Piscicelli (1913) is very similar to the Arabian *S. atriplicifolia* and is not very different from the *S. erythraeae* from Eritrea. As there are no other records of *Sabaudia* (and the related *Lavandula*) from Zambia and the neighbouring countries, it seems unlikely that the type of *S. helenae* should originate from this part of Africa. It is also uncertain whether the alleged difference between *S. hele-*

nae and *S. atriplicifolia* is consistent or significant enough to justify the separation of *S. helenae* as a different species. In recent works, the genus *Sabaudia* is included in *Lavandula*. A decision on the systematic status of *S. helenae* will be made by Dr. T. Upson (unpubl.) in connection with a revision of *Lavandula*.

Acknowledgements

Study visits have been made to the herbaria BM, BR, FT, HBG, K, P, S and UPS (abbreviations according to Holmgren *et al.* 1990). Material from some of these herbaria and G, G-BOIS, G-DC has been obtained on loan. B, FT, M, NY, US, WU, Z, ZT were consulted in the search for lost type material or photos of such material, but no material was found. Duplicates of some of the cited collections have been deposited in ASMU (the herbarium of Asmara University, Eritrea) and ETH. Prof. E. Robbrecht (at BR) has kindly provided me with copies of letters and allowed me to publish proofs of plant illustrations deposited in BR. I wish to thank the directors and curators of all these herbaria. I am also indebted to Dr A. Paton (at K) for critically reading and providing valuable suggestions to improvement of my manuscript.

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Diversity and endemism in the flora of Ethiopia and Eritrea – what do the published Flora volumes tell us?

Ib Friis, Sue Edwards, Ensermu Kelbessa & Sebsebe Demissew

Friis, I., Edwards, S., Ensermu Kelbessa & Sebsebe Demissew. 2001. Diversity and endemism in the flora of Ethiopia and Eritrea – what do the published Flora volumes tell us? *Biol. Skr.* **54**: 173-193. ISSN 0366-3612. ISBN 87-7876-246-4.

Data on the distribution of 2959 indigenous taxa dealt with in Flora of Ethiopia and Eritrea, Vol. 2(2), 3, 6 and 7, has been analysed. In this sample Sidamo has the highest diversity of flowering plants, and the total number of endemics or near-endemics to the Flora area (*i.e.* either restricted to the Flora area or also found in an immediately adjacent country) is 827. There is a maximum of both narrow endemics, country endemics and near-endemics in Sidamo. The diversity of the regions follows a pattern with a marked centre in SE Ethiopia (Sidamo, Bale and Harerge), a slightly less marked centre in the highlands from Shewa to Eritrea, and a poorly marked centre in SW & W Ethiopia. A comparison of the floras of the floristic regions by cluster analysis shows two very well defined clusters consisting of (1) a species-poor cluster of lowland of Eritrea and Afar; (2) a species-rich cluster consisting of all the other floristic regions. Within group (2) there are notable clusters of (2.1) Arsi, upland Shewa, Gonder, Gojam, and the upland of Tigray and Eritrea, (2.2) Welega, Kefa and Illubabor, and (2.3) Gamo Gofa, Sidamo, Bale and Harerge. The latter three regional clusters agree largely with the centres of endemism. Diversity gradually increases with altitude from *c.* 350 taxa between 0 and *c.* 300 m to a maximum of *c.* 1600 taxa between *c.* 1200 and 1500 m a.s.l. Then diversity gradually declines again to *c.* 400 taxa between *c.* 2700 and 3000 m, and to well below 100 on the highest mountain peaks. The number of country endemics or near-endemics is relatively high up to *c.* 1500 m, but the highest number is found between 1200 and 1500 m (where the total number of taxa is also highest). The total number of endemics and near-endemics declines with further increase in altitude, while the percentage increases. The flora is most diverse in open habitats, less so in forest, evergreen scrub, lakes, rivers, and in the open sea. The highest numbers of endemic and near-endemic taxa occur in open habitats. – The patterns found in plants agree reasonably well with patterns found in other organisms, *e.g.* birds.

Ib Friis, Botanical Museum and Library, Gothersgade 130, DK-1123 Copenhagen K, Denmark. Email: ibf@bot.ku.dk.

Sue Edwards, National Herbarium, P.O. Box 3434, Addis Ababa, Ethiopia. Email: sustain@telecom.net.et.

Ensermu Kelbessa, National Herbarium, P.O. Box 3434, Addis Ababa, Ethiopia. Email: nat.heb@telecom.net.et.

Sebsebe Demissew, National Herbarium, P.O. Box 3434, Addis Ababa, Ethiopia. Email: nat.heb@telecom.net.et.

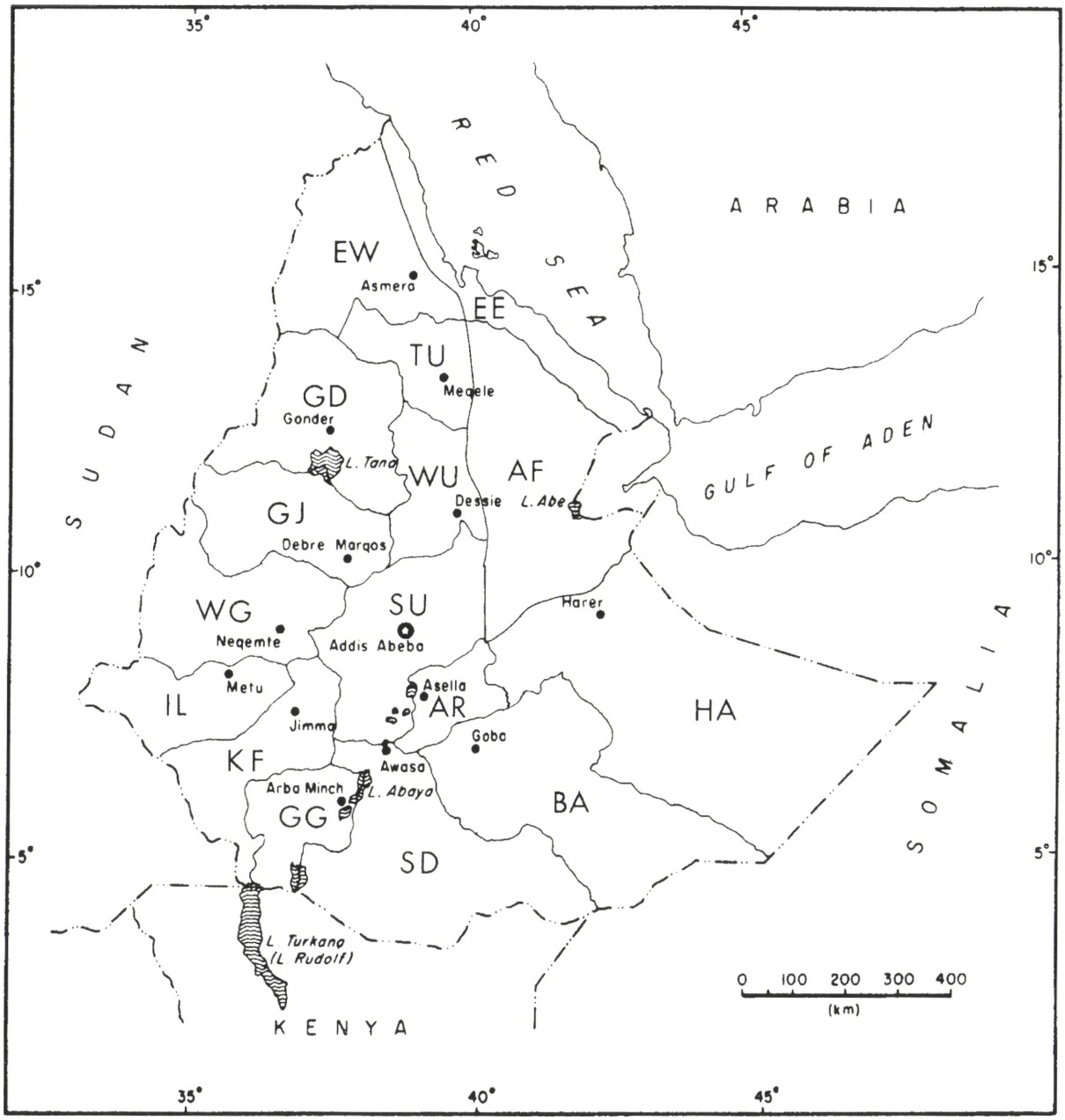

Fig. 1. Floristic regions of Ethiopia and Eritrea used for recording distributions in the Flora and in this study. EW: western Eritrea (above the 1000 m contour). EE: eastern Eritrea, below the 1000 m contour. AF: Afar. TU: upland Tigray; the previous Tigray region above the 1000 m contour. WU: upland Welo, the previous Welo region above the 1000 contour. GD: the previous Gonder region. GJ: the previous Gojam region. SU: upland Shewa, the previous Shewa region above the 1000 m contour. AR: the previous Arsi region. WG: the previous Welega region. IL: the previous Illubabor region. KF: the previous Kefa region. GG: the previous Gamo Gofa region. SD: the previous Sidamo region. BA: the previous Bale region. HA: the previous Harerge region. Reproduced with permission from the *Flora of Ethiopia and Eritrea.*

Introduction

In this paper the distribution- and habitat-data in the four published volumes of the *Flora of Ethiopia and Eritrea* are analysed. The purpose is to ascertain what such analyses can tell us about plant diversity, distribution and endemicity in the Flora area. We also intend to analyse what can be said about the external plant geographical relations of the flora. A detailed analysis of the forests and forest trees of Ethiopia, Eritrea, Djibouti and Somalia was published by Friis (1992). An analysis of certain features of the flora of Ethiopia and Eritrea based on the data available in Vol. 3 of the *Flora of Ethiopia and Eritrea* was presented at the XIIIth Plenary Meeting of AETFAT in Zomba, Malawi (Friis 1994). This was done as part of an overview of some general features of the montane flora of Northeast tropical Africa (Sudan, Eritrea, Ethiopia and Somalia). When the Editorial Board of the FEE met in 1998 in Addis Ababa and discussed the preparations for this symposium it was felt that an updated and, if possible, extended version of some of the analyses of Friis (1992, 1994) would be of interest. It should take into account all information included in the volumes of the Flora published since then, that is Vol. 2(2), Vol. 6 and Vol. 7. The taxa dealt with in the published volumes are expected to be approximately half the total number of taxa in the entire Flora.

An additional reason for redoing the analysis now is the much improved capacity of personal computers and the software they can handle. In Friis (1994) it was sometimes necessary to select subsamples of the material of the 1016 taxa accounted for in Vol. 3, and it was even in some calculations necessary to apply altitudinal zones of 700 m instead of 305 m in order to avoid overflow due to computer limitations. No such limitations have been encountered in the present analyses dealing with almost three times as many taxa. However, other basic limitations in the original data remain, such as the very different size of the floristic regions used for registration of distributions in the *Flora of Ethiopia and Eritrea* (Fig. 1). Also the very different degree of completeness with which the plant distribution in various floristic regions has been recorded is still a serious limitation. The floristic regions are based on the old administrative regions of imperial Ethiopia (incl. Eritrea), as shown in Table 1.

Table 1. Area in square.km. of the old administrative regions of imperial Ethiopia (incl. Eritrea) on which the floristic regions used in the *Flora of Ethiopia and Eritrea* are based. Also indicated are the number of taxa recorded in FEE, Vol. 2(2), 3, 6 & 7 from the floristic regions that more or less match the old administrative regions. The number indicated for Eritrea is the sum of the numbers for EE+EW minus the number of taxa in common. For Tigre, Welo, Shewa and Harerge (indicated with * in the table, the lowland parts of the old administrative regions have been omitted, but the number of taxa omitted by this is probably limited.

Country & Region	Area	Number of taxa		Country & Region	Area	Number of taxa
Eritrea	125750	1062		Welega	77250	561
Tigray	60250	*929		Ilubabor	53500	579
Gonder	80250	863		Kefa	53500	892
Gojam	62250	582		Gamo Gofa	39500	764
Welo	93500	*368		Sidamo	111750	1423
Shewa	82000	*1245		Bale	131250	820
Arsi	21500	523		*Harerge	261250	1113

The Flora area has a number of rather unique geographical features: it is basically a very large dissected, dome-shaped mountain massif consisting of two plateaux which are divided by the Rift Valley. Each plateau has peaks rising from the dome; in the southeastern plateau the highest peak is 4370 m, and in the northwestern plateau the highest peak is 4620 m a.s.l. In the Afar depression, a low-lying and extremely hot and dry northern extension of the Rift Valley, there are extensive salt deposits in exceptionally hot and arid land as low as 126 m below sea level. It is a feature of the *Flora of Ethiopia and Eritrea* that land plants can have an altitudinal range from *c.* 100 m below sea level to *c.* 1000 m above sea level. This is for example the case with the palm *Hyphaene thebaica* (L.) Mart. on p. 522 of FEE, Vol. 6. The Ogaden and Borana regions make up another hot lowland area. The former region is shared between Ethiopia and Somalia. The two regions have altitudes between *c.* 250 and *c.* 1500 m. The western lowlands of Ethiopia and Eritrea have altitudes between 300 and 1000 m above sea level, and have a more humid climate than the eastern lowlands.

Contrasting with these hot and rather inhospitable areas are the extensive highland areas on the plateaux. The areas above 1500 m in the Flora area are the largest in tropical Africa. As mentioned above, due to the separation formed by the Rift Valley they fall in two parts:

1. The North-western Ethiopian Highlands, which are subdivided into a northern and a southern part by the extensive and up to 1000 m deep and 10-50 km wide Blue Nile (Abay) Valley. The northern part is highly dissected, but with altitudes between *c.* 2000 and *c.* 3000 m, they are generally higher than the southern highlands, which are less dissected and have extensive areas between *c.* 1500 m and *c.* 2000 m.
2. The Southeastern highlands are mainly located in Ethiopia, but a narrow mountain chain continues into northern Somalia. Together, these two plateaux measure 1200 to 1500 km across, and span over 16° latitude and 12° longitude. Most of the two highlands consist of Tertiary volcanic rocks, including all the exposed rocks on the plateau and mountain peaks, but not the rocks in the deep river gorges.

The following review of the rainfall regimes is based on Mesfin Wolde Mariam (1970), Daniel Gamachu (1977) and Liljequist (1986). The precipitation on the large, fractured dome is highly dependent on the position in relation to the main rain-bearing winds (Liljequist 1986). The highest rainfall is in the extreme southwestern corner of the North-western Ethiopian Highlands, especially between the towns of Maji, Mezan Tefari and Dembi-Dollo, where there is rain in all months of the year, and the total average annual rainfall ranges between 2200 and 2400 mm (Mesfin Wolde Mariam 1970). Due to the orographic conditions the rainfall is high, locally up to 1500 mm, on the whole western escarpment of the North-western Ethiopian Highlands almost to the border with Eritrea (Liljequist 1986), and generally increasing with increasing altitude up to a certain elevation. The altitude of the rain maximum is variable, but according to the information in the works cited above it is probably in most parts of the Flora area found between 1500 and 2500 m above sea level. The rainfall of the escarpment declines and becomes more and more seasonal, with a more and more marked summer peak, as one moves to the north. The rainfall also declines and becomes more and more seasonal as one moves away from the escarpment and over the Ethiopian Highlands in a north-easterly direction. In the southern and central part there is a marked peak of rainfall in the summer, often with a short dry season separating the "small rains" from the "larger rains". There is a tendency for

rain shadow to develop on the eastern escarpment, except in the northern part of Ethiopia. In Eritrea there is an area with winter rain on the eastern escarpment and on the adjacent parts of the plateau. This pattern is to some degree repeated on the South-eastern Ethiopian Highlands, except that the orographic rain on the western slopes is not so clearly marked. There is more marked tendency to bimodal rainfall in a zone of southern Ethiopia stretching from the southern part of the Gambella lowland through southern Gamo Gofa, Sidamo, Bale and Harerge. This bimodalism is very pronounced in the lowlands, but occurs also in the Bale Highlands, where it, for example, is recorded around the town of Robe.

The vegetation is closely correlated with the rainfall and altitudes, with bushland, thicket, woodland and wooded grassland dominating the lowlands on all sides of the central highland (Friis 1992). The highest concentration of broad-leaved forest is in the high rainfall area in the south-western part of the North-western Ethiopian Highlands. There is a pattern of forest patches, which gradually declines in species richness towards the east, but occurring in a mosaic of forest, evergreen scrub, and montane woodland and wooded grassland on the plateaux. A more detailed, but still brief review of the overall geomorphological structure, climate and vegetation of the Flora area has been summarised in the introduction to Friis (1992).

Material and methods

In order to produce an updated analysis of the available floristic information, all data available on the distribution of 2959 indigenous taxa dealt with in the published volumes of the *Flora of Ethiopia and Eritrea* (Vol. 2(2), 3, 6 and 7) have been entered in a database. The fields in this data base include floristic regions within the Flora area, altitudes, total range of the species, and a crude indication of habitat range within the flora area. The database used was Microsoft Access 97, part of the Microsoft Office 97 packet.

The fields of the database are the following:

1. Taxon names (names of genus, species and infraspecific taxa; text field);
2. There are 16 fields for the distribution on floristic regions in the Flora area (logical fields: yes/no);
3. There are 15 fields for the distribution on the arbitrarily defined altitudinal zones (logical fields: yes/no); one field for endemism in the Flora area (logical field: yes/no), one field for near-endemism in the Flora area, *i.e.* occurring in the Flora area and one neighbouring country only (logical field: yes/no), 12 fields for distributions outside the Flora area, *i.e.* known from the Flora area AND the following geographical areas: "East Africa" (one or more of the following countries: Kenya, Uganda, Tanzania, Rwanda, Burundi; not Kenya only), "South-central Africa" (one or several of the following countries: Angola, Zambia, Zimbabwe, Malawi, Botswana), "tropical South Africa" (Namibia and the tropical part of South Africa, including the previous Transvaal and Natal), "Cape" (the extratropical South Africa), "Mediterranean", "Europe", "Madagascar and the Mascarenes", "West Africa" (the savanna and the sahel parts of western Africa from the Central African Republic to Senegal), "Guineo-Congolian region" (the rain forest region of West Africa, Cameroon, Gabon, Congo-Brazzaville, Congo-Kinshasa), "mainland Asia", "Indonesia, Philippines, New Guinea, Australia, Oceania", and "New World" (all logical fields: yes/no);
4. There are 6 fields for habitats in which the taxa occur in the Flora area: "open habitats", *i.e.* woodland, wooded grassland, grassland, deciduous bushland, "forest", "evergreen scrub", "weedy sites", "fresh water habitats",

"coastal and marine habitats" (all logical fields: yes/no).

The taxa in the analyses are species, subspecies and varieties. The floristic regions used in the *Flora of Ethiopia and Eritrea* appear in Fig. 1, where there is also a list of the abbreviations used. The arbitrarily defined altitudinal zones cover a vertical range of 305 m (*c.* 1000 ft.), which is the definition originally used by Hamilton (1975) in his studies of zonation in Uganda, and later by Friis (1992, 1994) on studies of Ethiopian zonation.

The definition of near-endemic is admittedly problematical, but was the only one feasible with the *Flora of Ethiopia and Eritrea* as the source of the data set. This definition means that species with their main distribution outside the Flora area (but restricted to a single country), and only one record from inside the Flora area, are counted as near-endemics. Such extreme examples are probably rare in reality, but less extreme ones are probably not so rare. It is necessary to keep this problem in mind when interpreting the results. Later, when the distributions of all species in the Flora area are known from reliable distribution maps, or from records in suitably small geographical units, such as squares the size of one degree or less, it may be possible to apply better definitions of endemism.

The analyses consist of enquiries made to this database; subsequent analyses were made with the statistical and graphic programme SigmaPlot Vers. 4.0, and the clustering programme NTSYSpc Vers. 2.02 (Rohlf 1998), a package of programmes designed for numerical classification of taxonomic and plant sociological data. Various modules in the NTSYS package have been used here. They are mentioned below under the section "Floristic similarity between the FEE floristic provinces."

Results

The analyses reported on in this paper include the following:

1. The floristic composition of the 16 floristic provinces used for recording distributions in the Flora was studied; this involved a study of richness of taxa which was done by simple counting of the scores of presence in the fields in question in the database.
2. The floristic similarity between the 16 floristic provinces used for recording distributions in the Flora was analysed by extracting a rectangular presence/absence data matrix from the database, with the columns representing the 16 floristic regions and the rows the 2959 taxa. Subsequently, the floristic similarity of the regions as represented in the matrix was analysed with various similarity indices and clustering methods.
3. The floristic composition of the 15 arbitrarily defined altitudinal zones of 305 m was analysed in the same way as the floristic provinces, that is analyses of species richness, using the same methods.
4. The floristic composition of the 6 major habitat types was analysed in the same way as the floristic provinces, that is analyses of species richness, using the same methods.
5. In all the analyses of floristic composition, studies were also made on the frequency of endemic and near-endemic taxa and, for the regions, also the frequency of single floristic-region endemics.
6. The floristic composition of groups of taxa with identical or similar total range of species (in 12 categories or groups) was analysed in the same way as the floristic provinces. The analyses include number of species in the groups, and floristic similarity between the groups (endemic and near-endemic taxa obviously excepted), using the same methods.
7. Differences in floristic affinities with areas

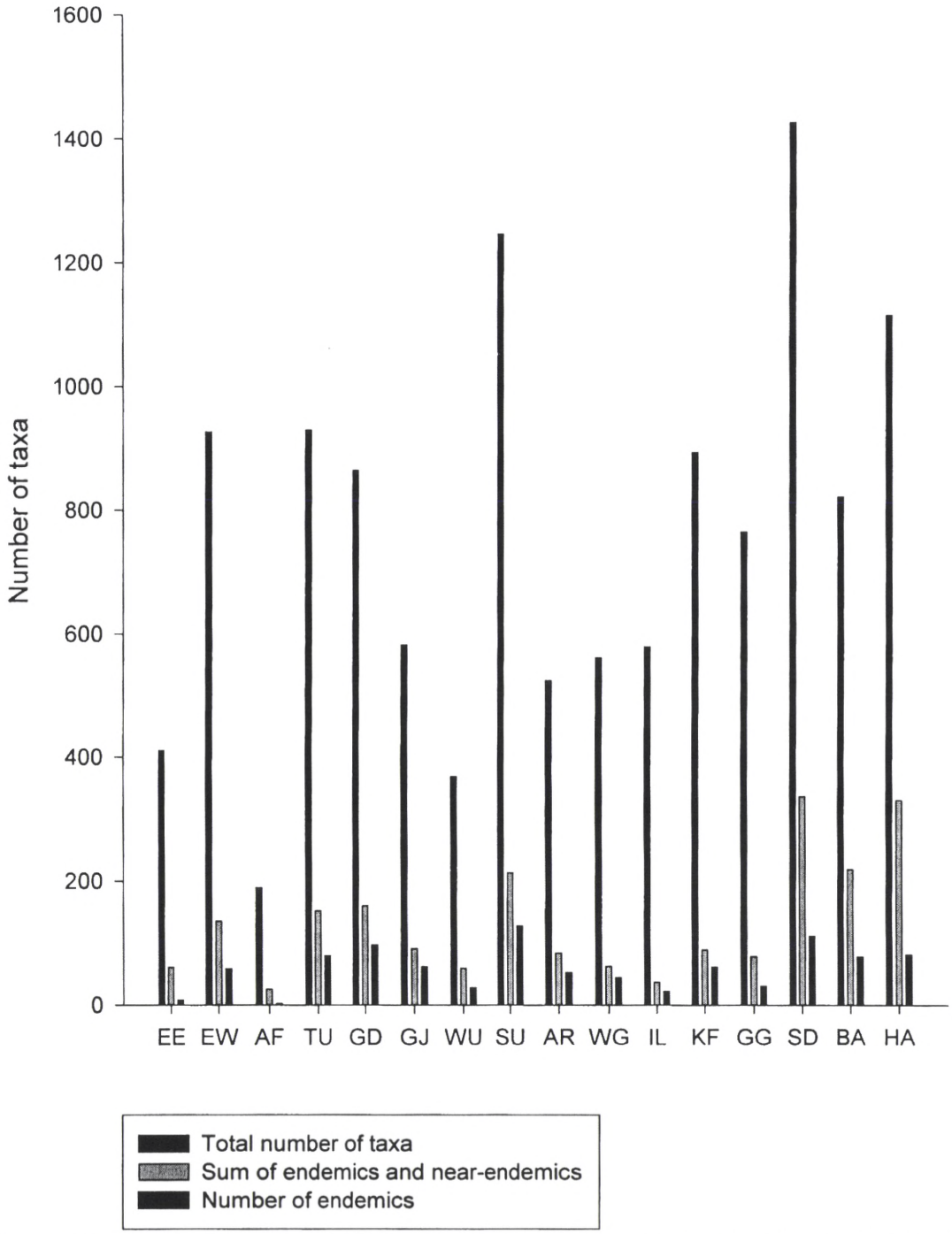

Fig. 2. Bar chart showing the total number of taxa (left bar in each group), sum of endemics and near-endemics (middle bar), and strict Flora area endemics (right bar) in the floristic regions used in the *Flora of Ethiopia and Eritrea*. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. Abbreviations as in Fig. 1.

outside the flora area were analysed with regard to the northern and the southern parts of the flora area.

Number of taxa and endemism in floristic regions

The term Richness of Taxa was used in Friis (1992) as a simple expression of plant diversity; here we will use Number of taxa. As mentioned, the whole area has a total of 2959 taxa recorded in the sample. The result of our analysis of the total number of taxa in each floristic region is shown as the left hand columns in the bar chart in Fig. 2.

The highest taxonomic diversity, measured as number of taxa, in the floristic regions of Fig. 1 is found in Sidamo (SD), with *c.* 1450 indigenous taxa. This is followed in declining sequence by upland Shewa (SU; *c.* 1300 taxa), Harerge (HA; *c.* 1100 taxa), upland Tigray (TU) and upland (and western) Eritrea (EW; each *c.* 950 taxa), Kefa (KF) and Gonder (GD; each *c.* 850 taxa), Bale (BA) and Gamo Gofa (GG; each *c.* 800 taxa), Illubabor (IL), Arsi (AR), Gojam (GJ) and Welega (WG; each *c.* 600 taxa), the eastern lowland of Eritrea (EE) and the uplands of Welo (WU; each *c.* 350-400 taxa), and Afar (AF; almost 200 taxa). The numbers are illustrated in Fig. 2.

The most prominent feature in the analysis seems to be the centre of diversity in SD. SU is the floristic region where Addis Ababa is located, and therefore the region where the most intensive collecting activity has taken place. It may be premature to indicate SU as a centre of diversity in the highlands. Quite likely, many of the other floristic regions with large highland areas are underrecorded, and future analyses may change the picture in Fig. 2 considerably. It seems, however, that SD, not a particularly central and well-collected floristic province, will maintain its strong position. The rather poorly recorded HA is likely to strengthen its position. The low figure from BA, geographically placed between the two richer provinces of SD and HA, would appear to indicate that that region is strongly underrecorded. The rather well collected KF with good rainfall has a surprisingly low number of taxa; the even lower numbers in WG and IL could be due to underrecording. These areas have good rainfall, as has KF, and IL has in places even higher and more well distributed rainfall than KF. Moreover, the rainfall in the western lowlands of IL (the Gambella region) is high in places (see Jensen & Friis 2001). According to the Flora, GJ has nearly 200 taxa fewer than the fairly well collected GD, which might be due to underrecording in GJ.

The total number of taxa strictly endemic to the Flora area or near-endemic (*i.e.* also found in one or more immediately adjacent countries) is 827 (28%) in the sample. The analysis of the database for endemic and near endemic taxa is shown as the middle columns in the bar chart in Fig 3. Also with regard to the sum of endemic and near-endemic taxa there is a maximum in SD (*c.* 330 taxa). The other regions follow in declining sequence: HA (*c.* 300 taxa), BA (*c.* 210 taxa), SU (*c.* 200 taxa), GD (*c.* 160 taxa), TU (*c.* 150 taxa), EW (*c.* 130 taxa), GJ and KF (each *c.* 90 taxa), and AR, GG, WG, and WU (each with between *c.* 80 and *c.* 60 taxa), IL (*c.* 40 taxa), and AF (*c.* 25 taxa). These figures seem to confirm that there are two main areas with high representation of endemic and near-endemic taxa. These are: (1) the south-eastern part of Ethiopia (SD, BA and HA), and (2) a somewhat less rich area in the highlands from SU to EW; the endemic and near-endemic taxa are less numerous in the south-western and western areas.

The total number of strictly endemic taxa in the sample is 368 (12.5%). The figures from the various floristic regions are indicated as the right-hand column in the bar chart in Fig. 2. It is seen that the distribution of the strict

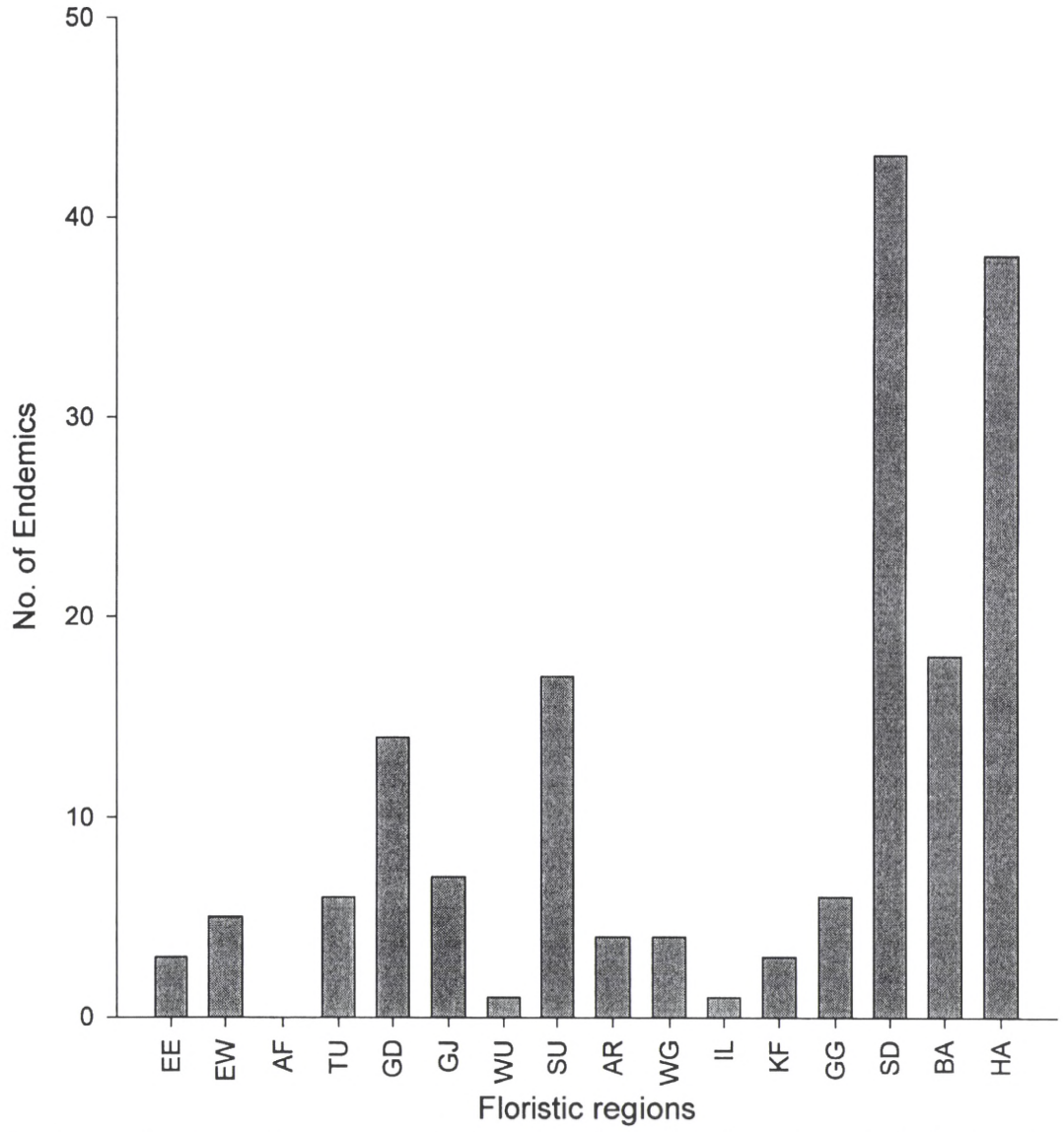

Fig. 3. Bar chart showing the number of narrow endemic taxa in each floristic region. A narrow endemic is here defined as a taxon restricted to a single floristic region. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. Abbreviations as in Fig. 1.

endemics neither follows the distribution of the total number of taxa nor the number of near-endemics. The latter are very numerous in southern and south-eastern regions of SD, BA and HA, where many taxa just cross the border into Kenya or Somalia. The plateau and highland endemics of upland TU, GD, GJ and upland SU make up a larger fraction of the sum of endemics and near-endemics.

Taxa, which are only known from a single

floristic region, have been recorded as narrow endemics. The distribution of these follows largely the pattern indicated above, and a review of the numbers in each region is given in Fig. 3. The highest number of narrow endemics is found in SD (43), followed by HA (38), BA (18), SU (17), and GD (14). The remaining regions have less than 10 narrow endemics each.

It was tried in the floristic regions to analyse the number of taxa, near-endemics or strict endemics that occurred below or above certain critical altitudes. However, such analyses do not give meaningful results because the altitudinal range for the taxa have been scored for the whole Flora area, not for the individual Floristic regions. This means for example that it is possible from the data base to find taxa that occur in EE above 1000 m (which is the upper altitudinal limit used to define eastern lowland Eritrea). The only condition for this absurdity is that the taxon occurs in EE and above 1000 m in some other places within the Flora area. Such analyses can only be carried out when the altitudinal range of the taxa has been recorded individually for each floristic region.

Floristic zonation: number of taxa and endemism in altitudinal zones

As mentioned in the introduction, analyses of floristic zonation have been carried out, based on arbitrarily defined altitudinal zones with a width of 305 m (1000 ft). The analysis of the database with regard to number of taxa, sum of near-endemics and strict endemics is shown in Fig. 4.

The altitudinal distribution of the taxa shows gradually increasing figures from *c.* 350 taxa in the zone from 0 to *c.* 300 m to a maximum of *c.* 1600 taxa between *c.* 1200 and 1500 m. Then the number is gradually falling off to *c.* 400 taxa between *c.* 2700 and 3000 m. There is a long "tail" of gradually declining figures to the highest mountain peaks at *c.* 4500 m. A similar skew bell-shaped figure was found by Friis (1992) in his analysis of the forest tree data, based on more detailed studies of 260 species of forest trees in Ethiopia, Djibouti and Somalia.

The sum of near-endemic and strict endemic taxa is comparably high in the lowermost altitudinal zone between 0 and 305 m (*c.* 100 taxa, or 20-25% of the total number of taxa in the zone). At gradually higher altitudes this figure does not increase nearly as markedly as the total number of taxa. The highest number of endemic or near-endemic taxa (*c.* 300) is found in the zone between 1200 and 1500 m, where the total number of taxa is also highest, but the endemic and near endemic taxa only make up *c.* 18% of the total number of taxa in the zone. The number of endemic or near endemic taxa keeps declining with increasing altitudes, but the percentage of the total increases again towards the highest values towards the mountain peaks. This agrees with an observation made below that the highest number of widespread Afromontane taxa occurs at the intermediate altitudes. The highest rainfall is almost everywhere in the Flora area between 1500 and 2500 m, which is the zone with the highest number of taxa.

From a comparison between the sum of the near-endemic taxa and the strict endemic taxa it can be seen that the number of strict endemic taxa is small in the lowlands, while the endemic high-altitude taxa are nearly all strict endemics. This is not surprising, because the lowlands mainly occur along the periphery of the Flora area. The locally distributed taxa in the lowlands are therefore very frequently shared with a neighbouring country, while the high altitude taxa of local distribution are only found in the central part of the Flora area. The high rainfall zone between 1500 and 2500 m, which is the zone with the highest number of endemics, is not the zone with the highest percentage of endemism.

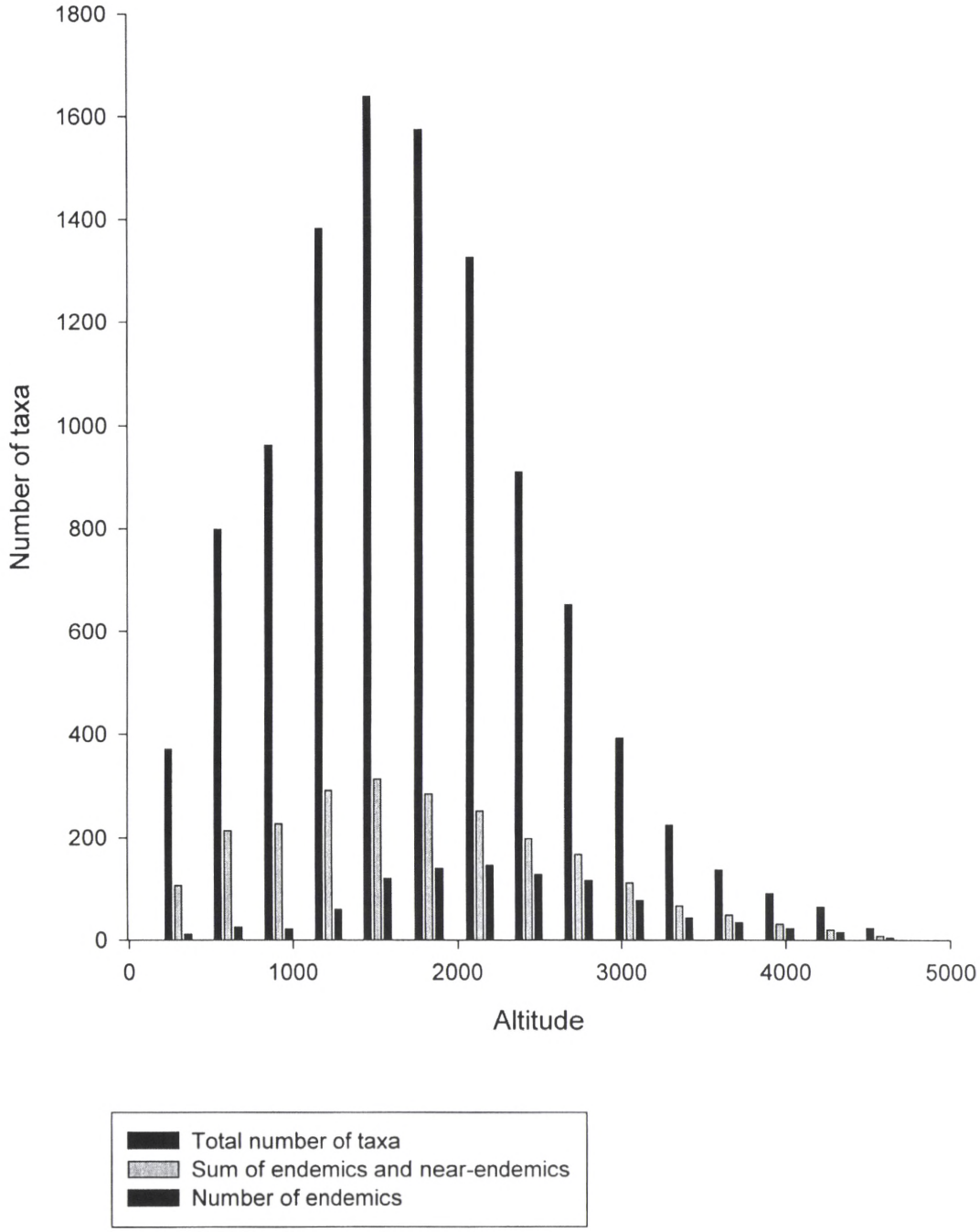

Fig. 4. Bar chart showing the total number of taxa (left bar in each group), the sum of endemics and near-endemics (middle bar), and strict Flora area endemics (right bar) in each of the artificially defined altitudinal zones used in this and a number of previous studies. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. The altitudinal zones have a range of 305 m, and they are indicated by their upper boundary.

Floristic similarity between the FEE floristic provinces

Lists of taxa recorded from all floristic regions of the Flora area were extracted from the data base. This resulted in a 16 x 2959 matrix with presence and absence data for 2959 taxa in the 16 FEE floristic regions. The matrix was analysed with the NTSYSpc package. All similarity coefficients available for two-state data in the SimQual-module were tried. Very similar results were obtained for most of these coefficients when the resulting similarity-matrices were clustered with the UPGMA (Unweighted Pair-Group Method, Arithmethic average) or the WPGMA (Weighted Pair-Group Method, Arithmethic average) methods in the SAHN module. The major differences between the results with the various coefficients and the UPGMA or the WPGMA methods were the highly changing position of WU on the resulting trees. Rather robust clusters found by this method were (1) the eastern lowlands of EE and AF. This group formed a cluster joining the cluster consisting of all the other floristic regions at a very low level of similarity. Within the larger group there are notable clusters of floristic regions at intermediate levels of similarity. Some of these are (2) WG, KF and IL, (3) GG, SD, BA and HA, and (4) AR, SU, GD, GJ, TU and EW. Within (4) more vaguely marked groups of (5) TU and EW, and (6) GD and GJ were noticed. Particularly the groupings (1), (2), (3) and (4) would seem geographically meaningful. The clusters (3) and (4) agree with the centre of high taxon diversity and endemism pointed out above under the analysis of the bar charts. A typical example of these trees, based on the well-known Jaccard similarity index and UPGMA clustering, both default methods in the NTSYS-package, was very similar to the trees obtained in Friis (1994).

Rohlf recommends in the text of the NTSYS package that the results obtained by UPGMA and WPGMA be tested by the use of the single-link and the complete-link methods in the SAHN module. If the results of these clustering methods are very similar the clusters must be very distinct. The similarity between the results of the single-link and the complete-link methods can be tested by the calculation of a strict consensus tree with the help of the Consen module. For most of the similarity coefficients for two-state data in the NTSYS package there was considerable difference between the results obtained by the single-link and the complete-link methods. Trees obtained with the single-link method showed in these cases a strong tendency to "chaining", *i.e.* one region at the time joining a steadily growing, unresolved cluster. In most of these cases the consensus tree between the single-link and the complete-link trees collapsed to a comb-like structure, and a low consensus index was calculated. However, good consensus trees with rather high consensus indices were obtained from trees calculated with Kulczynski's coefficient no. 2 (K2), the Phi coefficient, the Yule coefficient (Y), the Ochiai coefficient (O), and Rohlf's "unnamed coefficient no 4" (UN4). The highest consensus index between the results of the single-link and the complete-link was obtained with Rohlf's "unnamed coefficient no 5" (UN5), with the highest consensus index (Colless' index. = 0.857) found in the entire analysis. A strict consensus tree based on these calculations is shown in Fig. 5. The clusters mentioned above and obtained with the UPGMA and WPGMA clustering methods reappear in these resolved strict consensus trees. The grouping (1) EE-AF versus the rest of the regions is clearly defined in even the most collapsed strict consensus tree. The groups (2) WG-KF-IL and (3) SD-BA-HA are present (while GG is more loosely associated) in most strict consensus trees, and also the central highland complex, (4) AR-SU-GD-GJ-

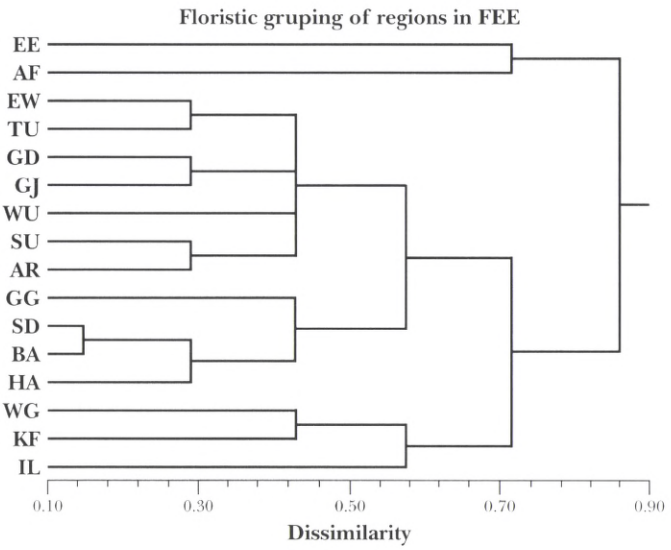

Fig. 5. Cluster diagram showing the floristic grouping of the provinces of Ethiopia and Eritrea used for recording distributions in the Flora and in this study. The diagram is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. This diagram is a strict consensus tree of single- and complete-link trees based on Rohlf's Unnamed Coefficient UN5. Abbreviations as in Fig. 1.

TU-EW, is rather well marked. Within (4) the more vaguely marked groups of (5) TU-EW, and (6) GD-GJ frequently also appear clearly.

Major habitat types: number of taxa and endemism

As mentioned in the introduction, analyses of the flora of the major habitat types have been carried out. The result entailed a certain judgement from the information given in the Flora accounts, and it turned out to be very difficult to distinguish between the open habitats: woodland, wooded grassland, deciduous bushland, *etc.*, for which reason they had to be lumped together. The analysis of the database with regard to number of taxa, sum of near-endemics and strict endemics in these categories is shown in Fig. 6.

The flora of the major habitat/vegetation types shows a strong preponderance of the open habitats from which 2174 taxa are recorded. 534 taxa have been recorded from forest. 350 taxa have been recorded from evergreen scrub. Approximately 140 taxa are from freshwater habitats. Approximately 200 are taxa of weeds of cultivated or fallow land, and *c.* 45 are associated with coastal vegetation or are marine taxa.

By far the highest sum of endemic and near-endemic taxa (*c.* 670; almost 30% of the total number of taxa in these habitats) occur in the open habitats. Only *c.* 90 endemic and near-endemic taxa (less than 20% of the total number of taxa in this habitat) occur in forest habitats. Approximately100 taxa occur in evergreen scrub (nearly 30% of the total number of taxa in this habitat), 9 are coastal plants. 8 taxa are freshwater plants, and *c.* 10 endemic or near endemic taxa are weedy in cultivated or fallow land. The results emphasise the importance of open habitats and evergreen scrub as important habitats for strict or near endemics.

The numbers of strict endemics make up a much greater percentage of the sum of endemic and near-endemic taxa in the forest and evergreen scrub than in the open habitats. The explanation of this is probably the same as mentioned above. The open areas are frequent in the lowlands in the periphery of the Flora area, whereas forests and evergreen scrub occur in the central part of the countries.

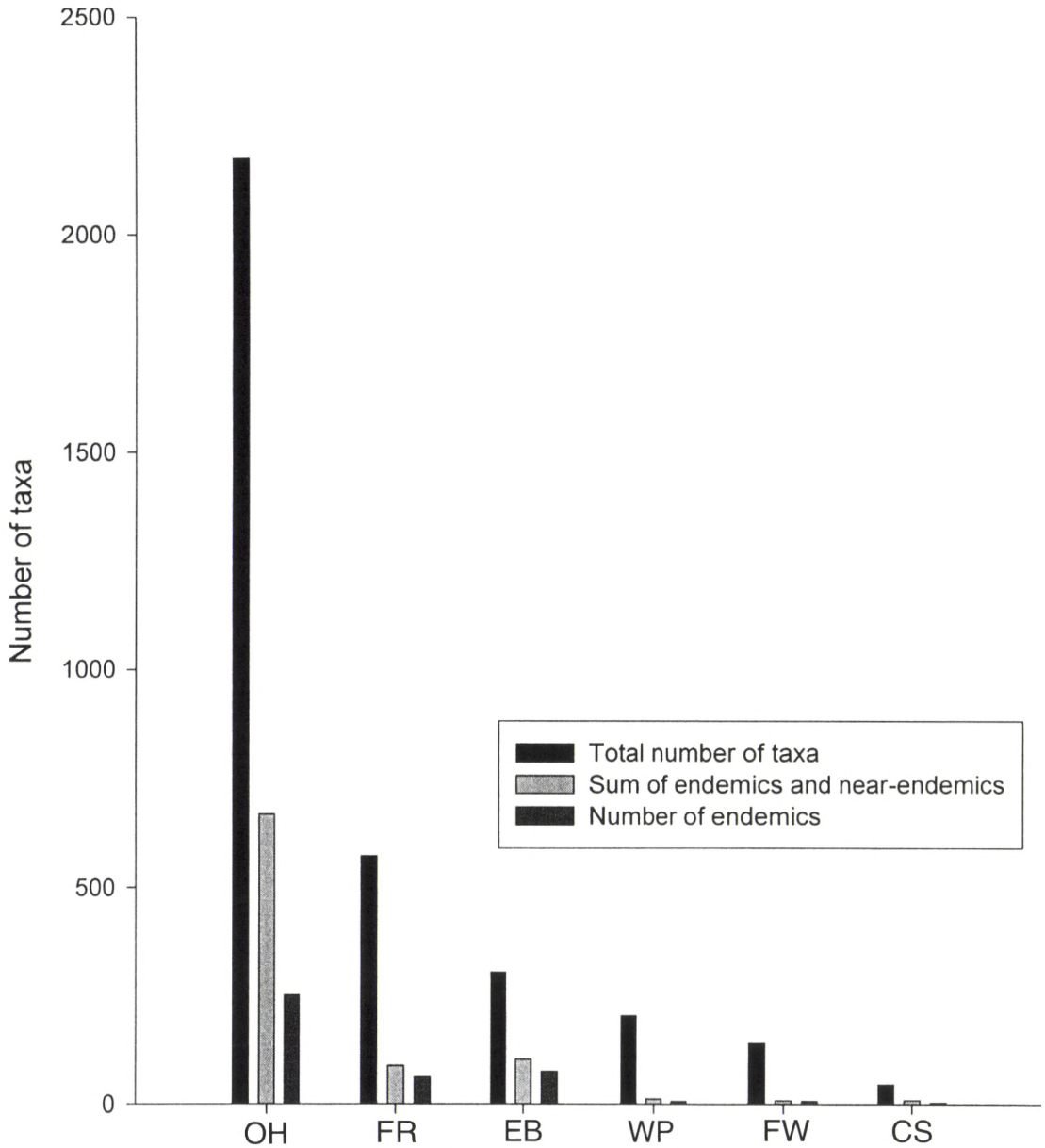

Fig. 6. Bar chart showing the total number of taxa (left bar in each group), the sum of endemics and near-endemics (middle bar), and strict Flora area endemics (right bar) in major habitat types. OH: Open habitats, including woodlands, wooded grasslands, deciduous bushland, grasslands, semi-desert grasslands, etc. FR: Evergreen and semi-evergreen forests. EB: Evergreen bushland, including secondary evergreen bushland. WP: Weedy or ruderal places. FW: Fresh water habitats, incl. permanent swamps, rivers and lakes. CS: Coastal vegetation, incl. marine plants, and saline areas near the sea shores. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7.

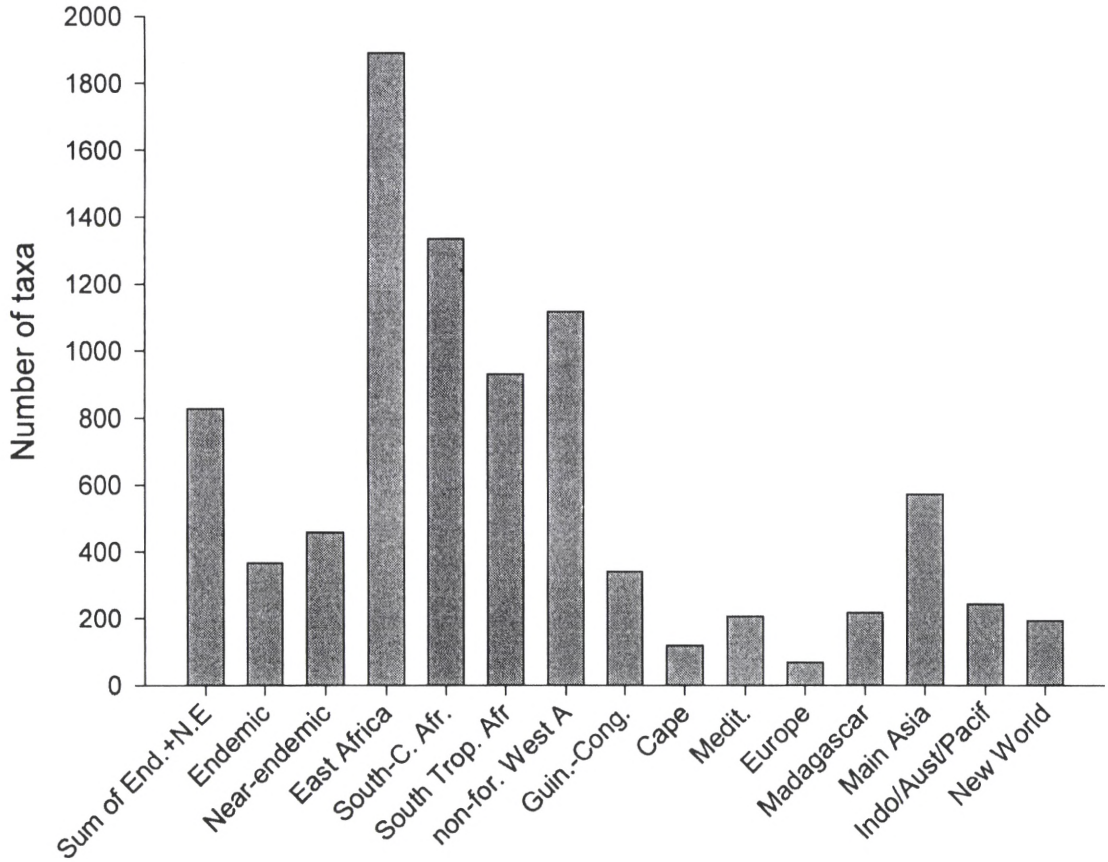

Fig. 7. Bar chart showing the number of taxa in the Flora area which also occur in particular areas outside the Flora area. The left column indicates the sum of endemic and near endemic species. *South-C. Afr.* (south central Africa) includes southern tropical Africa as approximately covered by *Flora Zambesiaca. South Trop. Afr.* (Southern tropical Africa) includes approximately the area covered by *Flora of Southern Africa*, excluding the winter rainfall area, which is indicated as *Cape. Medit* (the Mediterranean) includes approximately the area with cultivation of *Olea europaea. Europe* is excluding the Mediterranean part. *Main Asia* is mainland Asia. *Indo/Aust/Pacif* covers the Indonesian Islands, Australia and Oceania. *New World* covers North and South America. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7.

Overall range of taxa in the Flora

As mentioned in the introduction, analysis of the general distribution patterns of the taxa outside the Flora area has been carried out, based on the information on the total range of the taxa in the flora accounts. This has, as for the habitat types, entailed a certain judgement when the information was entered in the data base. The analysis of the database with regard to number of taxa in the categories of overall distribution mentioned in the introduction is shown in Fig. 7.

The closest phytogeographical connection for the entire sample is with East Africa (*c.* 1900 taxa). The link with the South-central African region is less pronounced (*c.* 1300 taxa). The links are even less pronounced with the following areas, which have been arranged

in declining order of similarity: non-forested West Africa (*c.* 1100 taxa), South tropical Africa (*c.* 930 taxa), Asian mainland, inc. India, the Himalayas, China and Indochina (*c.* 570 taxa), forest zone of lowland Congo and the Gulf of Guinea (*c.* 340 taxa), Indonesia, the Philippines, New Guinea, Australia and Oceania (*c.* 240 taxa), Madagascar and the Mascarene Islands (*c.* 220 taxa), the New World (*c.* 190 taxa), extratropical South Africa (*c.* 120 taxa), and Europe (*c.* 70 taxa).

Differences between phytogeographical affinities of northern and southern Ethiopia

In a paper presented at the second plenary meeting of AETFAT held in 1953 Gillett (1955: 463) ventured a generalisation. His statement was: "... the flora of southern Ethiopia [south of a line roughly from the Blue Nile to Harerge and Djibouti, roughly the southern limit of FEE regions GJ, WU and AF] is much more like that of Kenya and Uganda than it is like that of northern Ethiopia." Contrarily, Thulin (1986) concluded on the basis of study of the distribution of 151 species of Leguminosae that there is no such "Gillett's line". Thulin provided the explanation of Gillett's result that the flora of the southern highlands of Ethiopia, especially the flora of the high mountains of Arsi and Bale, was very poorly known when Gillett wrote his paper, and that Gillett's sample was therefore biased. What does the much greater data set in FEE Vol. 2(2), Vol. 3, Vol. 6 and Vol. 7 show? Is it possible to say that the flora south of Gillette's line is much more like that of Kenya and Uganda than the flora north of the line, or does an analysis based on the present data set confirm the findings of Thulin (1986)?

We have redone the analysis undertaken for Fig. 7 with the material divided into the 7 floristic regions north of Gillette's line and the 9 Floristic regions south of the line. The phytogeographical spectra of the northern and the southern parts of the Flora area are shown in Fig. 8.

The number of taxa found in the sample from the northern part of the Flora area is only 62% of that from the southern area, and a comparison in absolute numbers is therefore not meaningful. The various elements in the northern and southern profiles are in Fig. 8 shown as a percentage of the total flora in the respective part. It can be seen that the differences between the particular elements in the profiles of the northern and the southern parts of the Flora area are generally only a few percent, indicating that there is very little difference. A difference of more than 5% is seen in the number of near-endemic taxa, where the southern part has the highest values, agreeing with the high number of near-endemic taxa in for example the Ogaden of HA.

It is perhaps surprising that the flora of the northern part of the study area has a higher percentage of species which reach the area of South-central Africa and the South Tropical Africa than has the southern part of the Flora area, which are geographically nearer these areas. The explanation of this must be that the taxa involved are widespread and make up a slightly larger percentage in the north (only just above 5% for the South Tropical African taxa, less than 5% more for the South-central African taxa).

The same can probably be said about the non-Guineo-Congolian species, which reach West Africa. Also in this element the value is about 5% higher in the northern part of the Flora area than in the southern part, indicating that a relatively high proportion of widespread Sudano-Sahelian taxa reach Northern Ethiopia and Eritrea.

Gillett emphasised the species common with the Mediterranean in northern Ethiopia, but such taxa only make up *c.* 4% more of the flora in the northern part of the Flora area than in

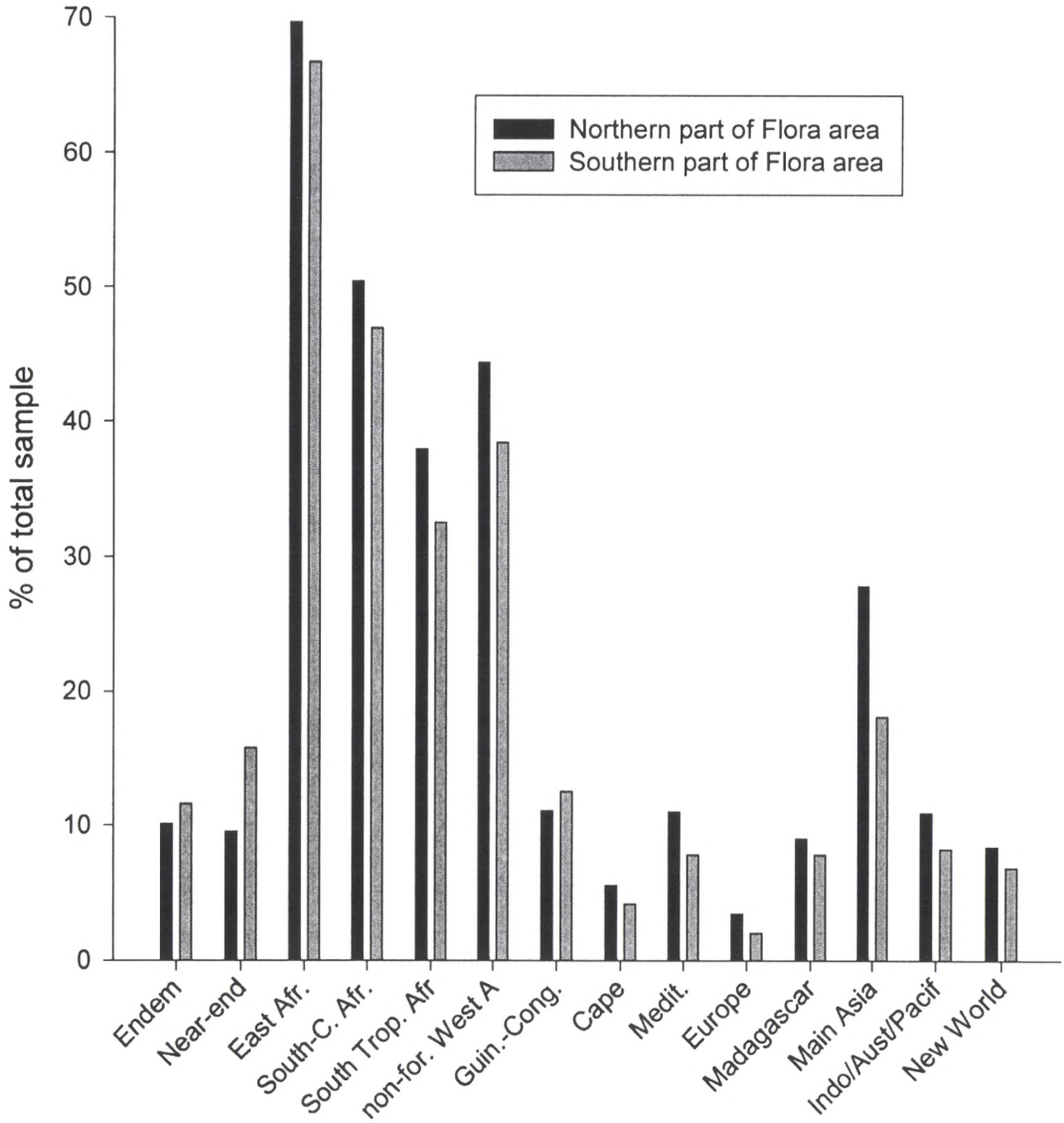

Fig. 8. Bar chart showing percentages of taxa with the same or similar overall range in the northern (left bar in each group) and southern (right bar) part of the Flora area (separated by a line at c. 10° N). The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. The phytogeographical groups are the same as those used in Fig. 7.

the southern. The differences with regard to taxa that also occur in Europe are very small.

The most striking difference between the phytogeographical profiles of the two parts of the flora area is found in the elements that also occur in mainland Asia (beyond Yemen). This element is more than 9.5% stronger in northern than in the southern part of the Flora area, an observation which does not seem to have been made before. There are also slightly

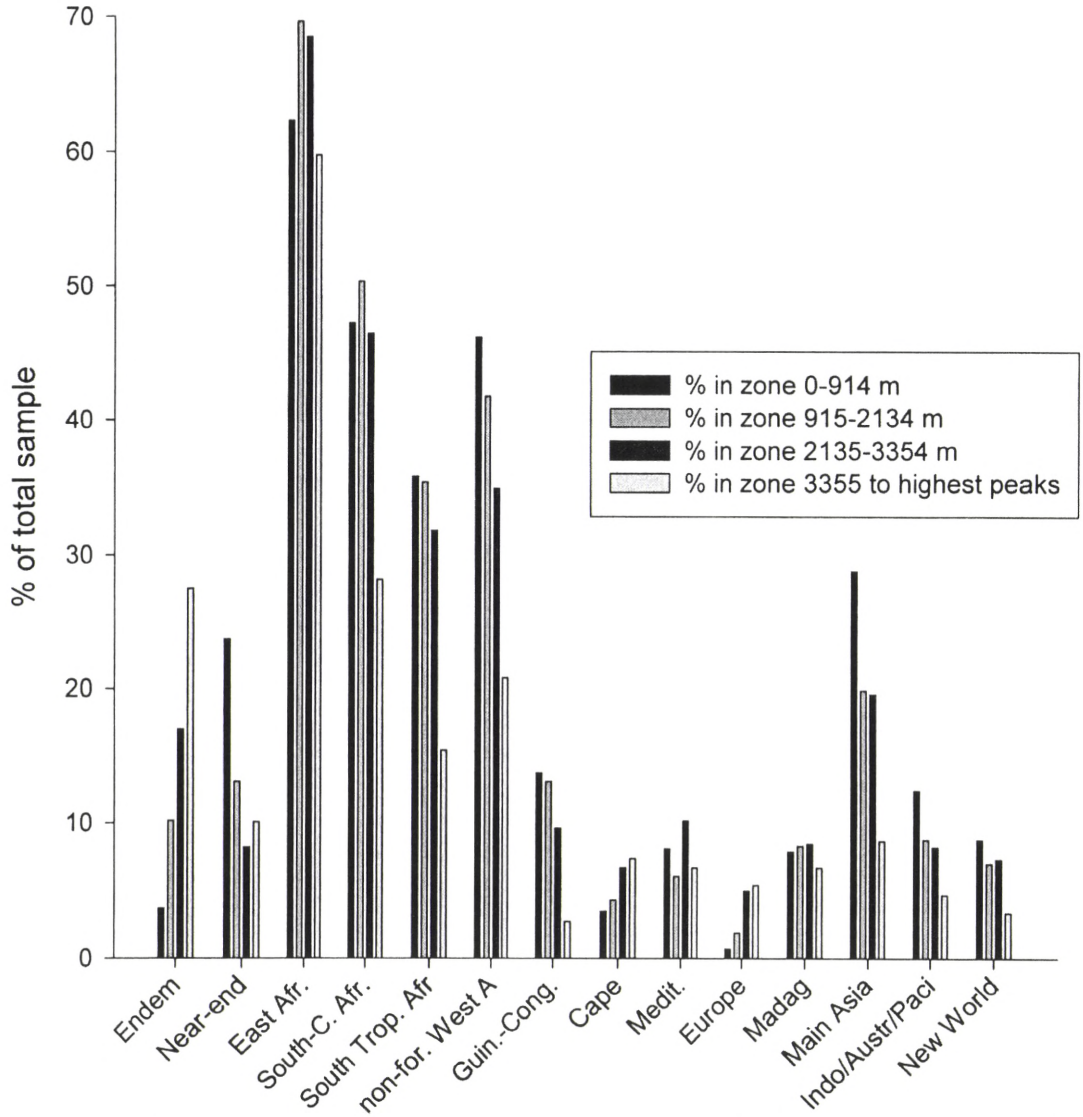

Fig. 9. Bar chart showing percentages of taxa with the same or similar overall range in four arbitrarily defined altitudinal zones (0-914 m a.s.l. (left bar in each group); 915-2134 m a.s.l. (middle left bar); 2135-3354 m a.s.l. (middle right bar); 3355-4500 m a.s.l. (right bar)) in the Flora area. The bar chart is based in the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. The phytogeographical groups are the same as those used in Fig. 7.

stronger elements of Indonesian-Australian-Pacific taxa and New World taxa in the north than in the south. However, these differences are minimal in comparison with the difference with regard to Mainland Asian taxa, of which there are nearly as many in absolute figures in the north as in the south. With the higher absolute number of taxa in the south, this results in a higher percentaged Asian representation in the north.

Differences between phytogeographical affinities at different altitudes

The data from the data base used in Fig. 7 was also reanalysed in order to discover differences in the floristic affinities of the flora in four arbitrarily defined altitudinal zones which cover all altitudes in the Flora area (0-914 m; 915-2134 m; 2135-3354 m; 3355-4500 m). The phytogeographical spectra of the four altitudinal zones are shown in Fig. 9.

There are striking differences between the altitudinal zones with regard to strict country endemics, where the lowest frequency is found at altitudes below 915 m, and the highest at altitudes above 3355 m. Almost a completely opposite trend is shown by the near-endemics. Contrary to these two trends, there are little differences between the altitudinal zones with regard to East African affinities. South-central African, West African and Guineo-Congolian affinities are notably less frequent in the highest altitudinal zone than in the lower zones. The opposite is the case with the Cape-, Mediterranean and European affinities. All this is to be expected. Affinities with Madagascar seem unchanged with altitude. The affinity with mainland Asia is much more pronounced in the lowermost zone than in the upper ones. This trend is less prominent for the affinities with Indonesia, Australia, Oceania and the New World.

Discussion and conclusions

The study shows that results obtained from much smaller data sets are surprisingly robust to the inclusion of additional data and the use of more rigorous methods. The results of this study largely confirm the conclusions of Friis (1992), based on a sample of forest trees from Ethiopia, Eritrea, Djibouti and Somalia, and Friis (1994) which was based on Vol. 3 of the *Flora of Ethiopia and Eritrea* only (1016 taxa). Friis (1994) conclude that the floristic provinces used for indicating the distribution of taxa in the *Flora of Ethiopia and Eritrea* fell into four major groups. The study was based on floristic similarity of a randomly selected sample of 400 taxa of the 1016 recorded in Vol. 3 of the *Flora of Ethiopia and Eritrea*. These four major groups were: (1) a species-poor group of EE and AF, and (2) a species-rich group consisting of all the other floristic regions. Within group (2) notable clusters were (3) AR, SU, GD, GJ, TU and EW, (4) WG, KF and IL, and (4) GG, SD, BA and HA. This result is almost identical with our findings, based on the 2959 indigenous taxa reported in the four volumes that have now been published.

There is a fairly good agreement between areas of high species diversity and a high number of endemics, both the near-endemics, the country-endemics and the single floristic region endemics.

1. The southern regions, with a centre in Sidamo, come out strongly according to both the criteria based on taxa richness and the criteria based on a high number of endemics. SD has the highest number of taxa and the highest number of single floristic-region endemics, whereas it competes with SU for the highest number of country-endemics. This agrees reasonably well with the bird data (Fjeldså & de Klerk 2001), as there is also a well-marked centre of narrow bird endemism in Borana (Sidamo), marking the transition from the Ethiopian highlands to the desert areas east of Lake Turkana. Also in other parts of the Somalia-Masai region of southern Ethiopia and Somalia there are a number of endemic birds which occur singly or in small groups of a few species together in an apparently complex pattern.
2. The south-western regions, centred on Kefa, come out in the floristic survey as a less

important centre according to both the taxon-richness criteria and the total number of Flora endemic and near-endemic taxa, and rather poor with regard to single floristic-region endemics. According to Fjeldså & de Klerk (2001), the south-western region is not a marked centre in birds.

3. The upland/highland regions from Shewa and northwards form a reasonably important centre of diversity and endemism in plants. Among the highland regions, SU, TU and GD have the highest number of taxa. SU has the highest total number of endemics and near endemics and the highest number of single floristic-region endemics. TU has a slightly higher number of taxa than GD, but the situation with regard to all kinds of endemism is the reverse. GJ, and especially WU, seem to be understudied. According to Fjeldså & de Klerk (2001), the Ethiopian highlands form the region's most important and coherent centre of endemism, having a higher number of endemic taxa than any other area, but the endemic birds of the plateaux are widespread in the highlands. This pattern in birds agrees with the comparatively high figures we have found for country-endemic plants in the central part of the Ethiopian highlands, but the data on the distribution in the highlands are as yet not sufficient for a more detailed comparison. It is, however, our impression that there is good agreement between plants and birds in this respect.
4. The zone between *c.* 1200 and 1500 m a.s.l. has both the highest number of species and the highest number of endemics in plants; the zonation in bird endemism is not so easy to analyse, and an analysis has not been presented by Fjeldså & de Klerk, but according to Fjeldså (pers. com.) the highest number of widespread endemic species is probably found above 1500 m a.s.l., while the restricted endemic species are found at lower altitudes.
5. The importance of open habitats as centres of diversity and endemism is prominent in plants, but open habitats seem less important as centres of endemism in birds (Fjeldså & de Klerk 2001).
6. The strong affinity with East Africa is found both in plants and in birds.
7. The observations do not support the suggestion by Gillett that there is much stronger similarity between the floras of southern Ethiopia and East Africa than between northern and southern Ethiopia.
8. However, it seems to be a new observation that the element of species which reach mainland Asia (beyond Yemen) is considerably stronger in northern Ethiopia and Eritrea than in southern Ethiopia. There is a notable change of floristic overall affinity with changing altitude.
9. The flora of Ethiopia and Eritrea seems to have better representation of taxa distributed in the Mediterranean region, Europe and mainland Asia than does the non-migrant bird fauna.

The concentration of fairly widespread highland endemics in the Ethiopian highlands of both plants and birds is perhaps not surprising, considering the large extension and the general isolation of the Ethiopian highlands. But the possible reasons for the concentration in SD, HA and BA of narrow endemics in both plants and birds are not yet clear. Counterparts of this concentration of narrowly endemic species are found in Somalia near the Ceerigaabo (Erigavo) escarpment in northern Somalia, near Hobyo (Obbia) and near Muqdisho (Mogadishu) on the coast, and near Buulobarde (Bulo Burti) between Muqdisho and the Ethiopian border (Thulin 1994). The geological and edaphic explanations for endemism in Somalia, for example the existence of areas or isolated outcrops of limestone and gypsum and very species-rich sand dunes

(Thulin 1986, 1994), do probably not hold for other organisms, including birds. As mentioned in the paper by Fjeldså & de Klerk (2001), the Borana area (SD) has possibly had more stable conditions for a long time (with low interannual variability) than the surrounding area, allowing persistence of relict bird taxa. But that explanation does not explain the very local centres of endemism also found in Somalia. There is certainly scope for further observations on and theories about this subject.

Acknowledgements

Jean Oelkers and Anne-Marie Bürger recorded the data that could be entered unambiguously from the published *Flora of Ethiopia and Eritrea* volumes. Anne-Marie Bürger entered the more complex data, which involved an interpretation of the information provided, such as the total range of the taxa outside the Flora area and the habitat range of the taxa, in collaboration with Ib Friis. We wish to acknowledge the painstaking efforts that Ms. Oeckers and Bürger have made during this lengthy work. We should also like to thank Dr. Mats Thulin for critically reading the manuscript.

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Distribution patterns of Cyperaceae in East and Northeast Tropical Africa with special emphasis on local endemism

KÅRE ARNSTEIN LYE

LYE, K.A. 2001. Distribution patterns of *Cyperaceae* in East and Northeast Tropical Africa with special emphasis on local endemism. *Biol. Skr.* **54**: 195-212. ISSN 0366-3612. ISBN 87-7876-246-4.

A total of 500 species of Cyperaceae have been recorded from East and Northeast Tropical Africa. Of these 450 are known from Tropical East Africa (Kenya, Uganda and Tanzania) and 268 from Tropical Northeast Africa (Eritrea, Ethiopia and Somalia). While about one half of the species has an African (mostly panafrican and East-South African) distribution, there are about 50 species with a pantropical distribution, 53 species with an Afro-Asian distribution, 13 species with an Afro-American distribution, while 13 species have European affinities. Distribution patterns within Africa are also discussed, and species listed in an appendix. There are 112 species endemic to the region, of which 65 are endemic to East Africa and 41 to Northeast Africa. Of these, 53 species are here classified as narrow endemics and are mostly endangered species. The percentage of species endemic to the two regions is approximately the same, with 14.4% for East Africa and 15.3% for Northeast Africa. However, endemicity varies greatly from nation to nation with only 0.9% and 1.3% endemic species in Uganda and in Eritrea, 8.7% in Tanzania and 30.3% in Somalia. Endemicity in Somalia is outstanding and is in tropical Africa only surpassed by that of Madagascar (37.7%). Endemicity in our region is also compared to that of other African countries.

Kåre Arnstein Lye, Dept. of Biology and Nature Conservation, Agricultural University of Norway, P.O. Box 5014, N-1432 Aas, Norway. E-mail: kare.lye@ibn.nlh.no

Introduction

This paper deals with the countries of *Flora of Tropical East Africa* (Uganda, Kenya and Tanzania), *Flora of Ethiopia and Eritrea* (Eritrea and Ethiopia) and *Flora of Somalia* (South and North Somalia) with notes on neighbouring countries.

About 500 sedges are known from this area. Like grasses, sedges have their greatest diversity in the region of seasonal rainfall between forest and desert, but unlike grasses they only dominate the vegetation in certain permanent swamps.

The generic concept adopted here is the same as that used for *Flora of Ethiopia and Eritrea* (Lye 1997d) and *Flora of Somalia* (Lye 1995). It differs much from that adopted for *The Families and Genera of Vascular Plants* (Goetghebeur 1998). The differences of opinion mainly concern the genus *Cyperus* where Goetghebeur (1989, 1998) recognises the segregate genera *Courtoisina*, *Ascopholis*, *Alinula*, *Pycreus*, *Queens-*

landiella and *Kyllinga*. However, recent molecular work (Muasya *et al.* 1998) has convincingly shown that such segregates are phylogenetically unacceptable. On the other hand it is possible that many other genera now widely accepted as separate from *Cyperus* should also be merged with that genus, viz. *Remirea*, *Oxycaryum* (Lye 1971), *Sphaerocyperus* (Lye 1972a), *Kyllingiella*, *Ascolepis* and *Lipocarpha*.

General distribution patterns

The total number of Cyperaceae from tropical Africa is about 800, while the number for tropical East and Northeast Africa is 497 (or about 500 when some undescribed taxa are included). Tropical East Africa has 450 species while 268 species are known from tropical Northeast Africa

Knowledge of African distribution patterns is best documented through the 1334 distribution maps published in *Distributiones Plantarum Africanarum* (until 1994). Other important general plant geographical publications are presented by White (1965, 1971, 1977, 1979, 1983, 1993), Friis (1983, 1993, 1994), and for afroalpines by Hedberg (1957, 1994), but none of the plants mapped in any of theses publications are members of Cyperaceae. Wickens (1976) includes distribution maps of three sedges (but apparently based on Kew material only); these are *Cyperus rigidifolius* Steud., *Cyperus* (*Kyllinga*) *chlorotropis* and *Cyperus* (*Pycreus*) *mundtii*. Raynal (1967, 1971) mapped the distribution of two species of *Scleria* (*S. glabra* and *S. poaeoides*) and all African species of *Rhynchospora* (nine occur in our region), and Vorster (1983) has mapped *Cyperus* (*Mariscus*) *deciduus*. Otherwise the distribution of species of Cyperaceae in our area is mostly known only from general enumerations of countries or regions.

The highest number of Cyperaceae in Africa is recorded from southern Tanzania and adjacent Zambia and Congo (Kinshasa). From this area the number decreases both southwards, westwards and northwards. The total number of species in the whole of West Africa is 304 (Hooper & Napper 1972) while Tanzania alone has 389 species. Nigeria with 221 species (Lowe & Stanfield 1974) is the West African country with the highest number of species, followed by Ghana and Senegal with 181 and 176 species respectively (Hooper & Napper 1972). The whole of North Africa has about 80 species (Maire 1957), see Figs. 1-2.

Nations receiving low rainfall in central and southern Africa also have relatively few Cyperaceae, *e.g.*, 79 species in Niger (Raynal 1976b), 131 species in Tchad (Raynal 1972) and 138 species in Namibia (Clarke & Mannheimer 1999). The two countries in Eastern Africa with a low rainfall, viz. Eritrea and Somalia have 77 and 89 species of Cyperaceae respectively (Lye 1995 & 1997d). The small South African country Swaziland has 75 species (Compton 1976).

The distribution patterns of wetland and dryland sedges are on the whole very different. While numerous wetland sedges have a pantropical distribution and a few species in our region even a temperate-subtropical distribution, many dryland sedges have restricted distributions and are often endemic to fairly small geographical regions. However, species with very restricted distributions are not necessarily endemic to a single nation, *e.g.* Ruwenzori endemics occur in Uganda and Congo (Kinshasa), Virunga endemics occur in Uganda and Rwanda, and Elgon endemics in Uganda and Kenya.

Of the 500 sedges known from our area, about one half (250 species) has an African (mostly panafrican or East-South African) distribution. Of these 12 species have their main distribution in West Africa, 8 species are more common in North Africa to Arabia, and 12

species are most common in southern Africa. About 50 species have a pantropical and 54 species an Afro-Asian distribution, while 13 species have an Afro-American distribution. Only 13 species are found in Europe, but several of these occur in Asia also. In addition there are 112 species endemic to the region.

Distribution within countries

Sudan

Knowledge of Cyperaceae in the Sudan is rather scanty. According to Andrews (1956) there are 142 species; two of these are narrow endemics, viz. *Coleochloa schweinfurthiana* and *Coleochloa glabra*, which are each endemic to a single South Sudanian mountain, Jebel Bangenze (Yambio district) and Jebel Oda (Nelmes 1953). When better investigated, the number of sedges is likely to be in the order of 160-180. This is still a low number compared to its large size; it is the biggest country in Africa (bigger than Congo Kinshasa, which has about 400 species).

Eritrea

Being a dry country with little and often erratic rainfall, Eritrea's flora includes few Cyperaceae. The total number of species recorded is 77 (Lye 1997d), of which only one (1.3%) is endemic, viz. *Cyperus schweinfurthii*. Another rare sedge, *C. holostigma*, is shared with Ethiopia only.

Ethiopia

With 206 species of sedges (Lye 1997d) Ethiopia has a much higher number than the Sudan and Eritrea, and compared to West and North African countries it certainly has a much richer sedge flora. However, Uganda, Kenya and Tanzania have an even higher number of sedges. Ten species are endemic to Ethiopia (4.9%); three of these are narrow endemics known only from one 1 degree grid. The most interesting ones are *Cyperus clandestinus*, which is sometimes placed in a monotypic genus *Chamaexiphium* or in *Ficinia*, and *Ficinia borealis* (Lye 1996f), which has its nearest relatives in South Africa.

Somalia

As this country is mostly very dry with a very prolonged dry season and often erratic rain, sedges are uncommon and mostly occur in small populations. Despite this, Somalia is the country in mainland tropical Africa with the highest percentage of endemic species (27 species out of 89), *i.e.* 30.3% (Lye 1995). Endemicity in Somalia is outstanding and it is in tropical Africa only surpassed by that of Madagascar (37.7%). Of the 27 endemics, 15 are known from only one 1 degree grid. The highest concentration of such species is found in the Mogadiscio grid with three species, and the Erigavo and Las Anod grids with two species. The latter two grids are not well collected. However, the Mogadiscio grid is possibly the best collected in Somalia, so the presence of the three endemics here may be explained by the distribution of collectors.

Uganda

Although this country has a very large sedge flora with 234 species (in fact it has one of the highest numbers per area), it has only two endemic species (0.9%), *Isolepis ruwenzoriensis* (Lye & Haines 1974) and *Kyllingiella ugandensis* (Haines & Lye 1978). *Isolepis ruwenzoriensis*, which is endemic to the Ugandan side of Mt. Ruwenzori, may not be a real national endemic species as it is likely to be found on the Congo side of the Ruwenzori also. However, *Isolepis ruwenzoriensis* is probably very rare as it has been recorded only once, and has been unsuccessfully searched for recently. Another species, *Carpha eminii*, has a similar distribution, but is also recorded on the Congo side of Mt. Ruwenzori (Robyns 1955).

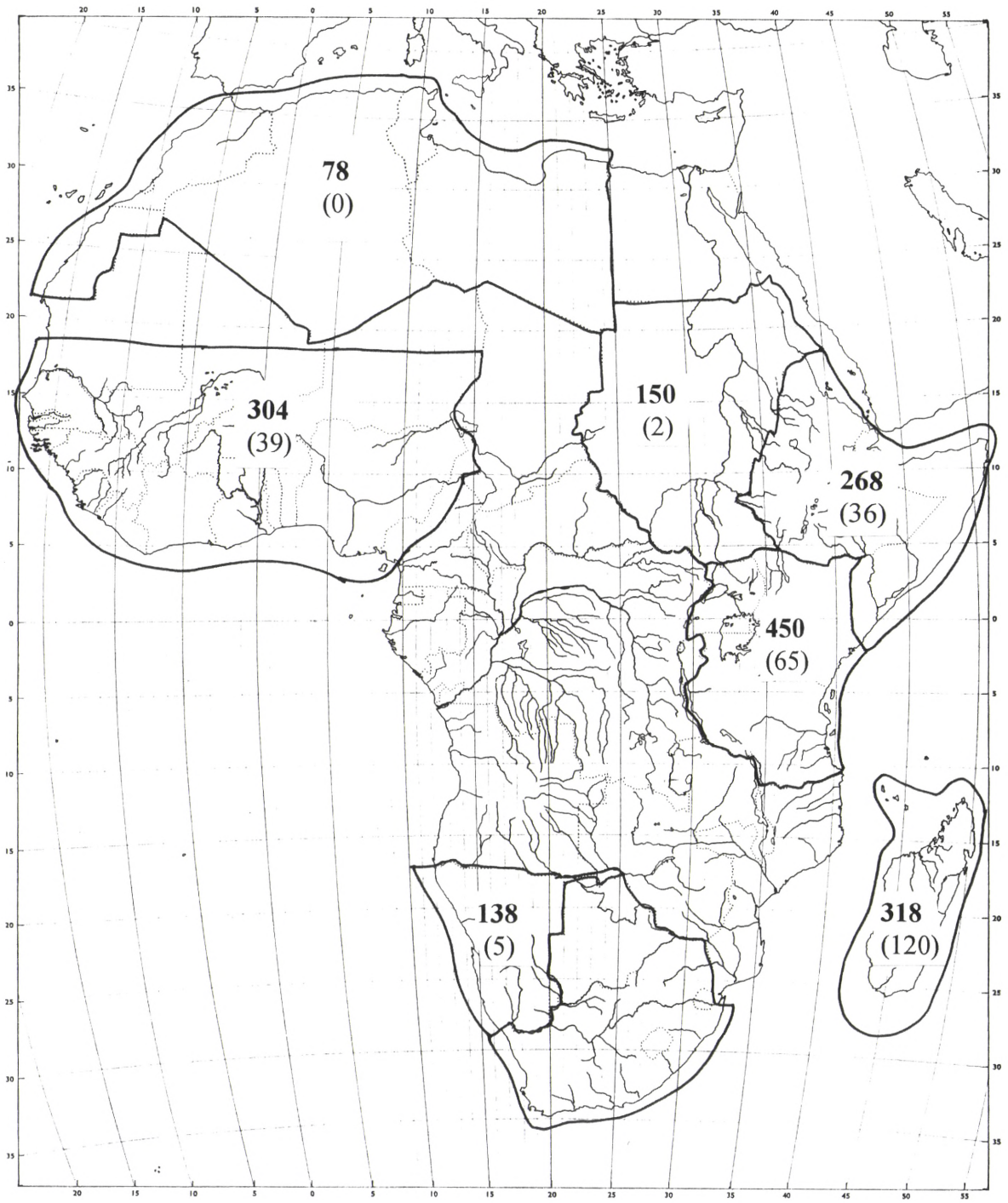

Fig. 1. Map of Africa showing number of species of Cyperaceae for major regions. Numbers in brackets indicate number of endemic species.

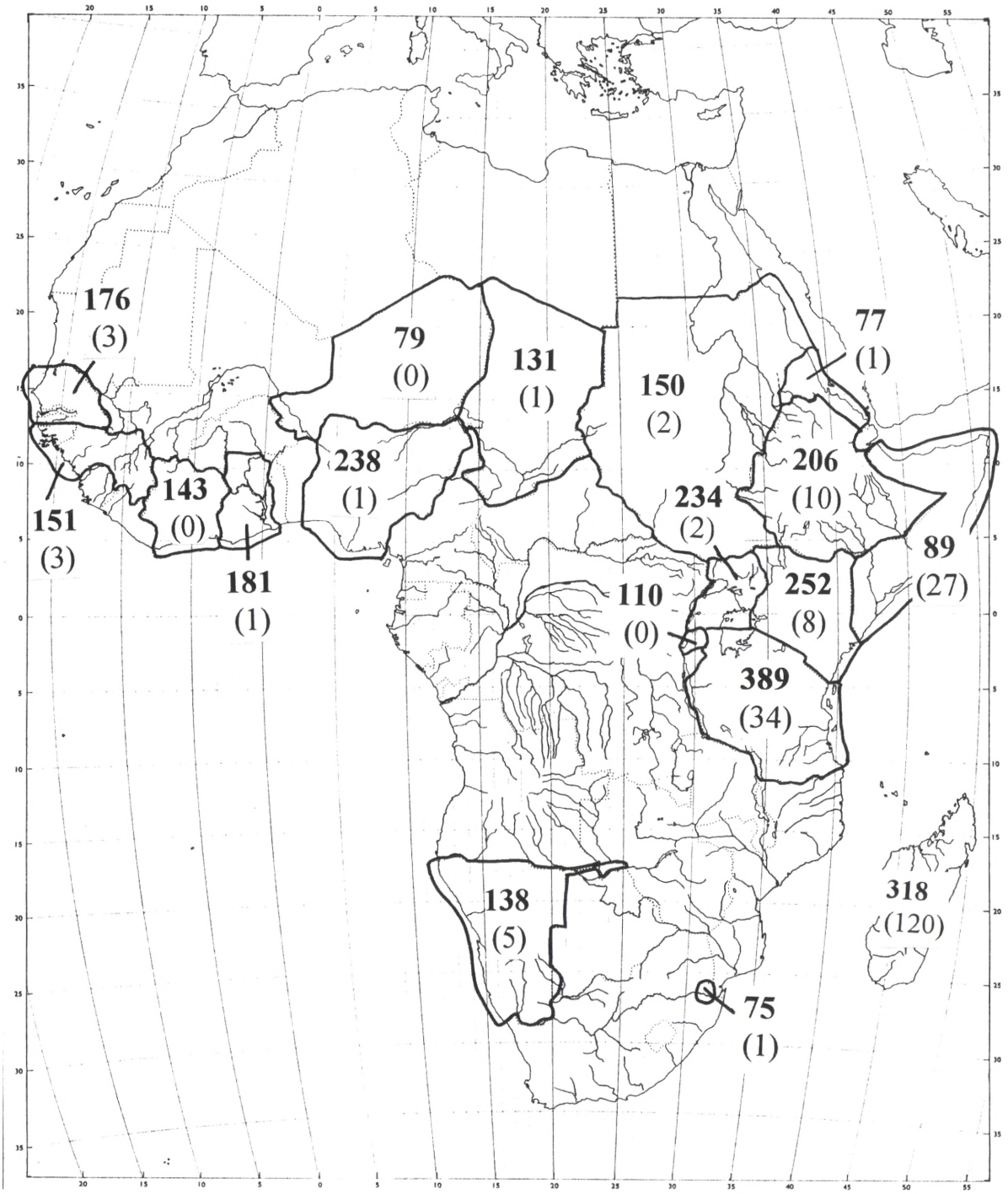

Fig. 2. Map of Africa showing number of species of Cyperaceae in individual African nations. Numbers in brackets indicate number of endemic species.

Kyllingiella ugandensis is probably a very rare and endangered species known from a single locality on the southern side of the Imatong Mountains.

Kenya

In our region Kenya is only surpassed by Tanzania in richness of species. It has 252 species of Cyperaceae (Haines & Lye 1983), of which 8 are endemic, all known from only one 1-degree grid (3.2%). The highest concentration of such species is found in the Kwale grid with three endemic species, viz. *Cyperus kwaleensis*, *C. boreobellus* and *C. microumbellatus*. It is possible that the high number of narrow endemics in the Kwale grid is due to extensive collecting. However, it is interesting that Linder (1998) investigated 794 species found this grid (but enlarged to cover a 2.5 x 2.5-degree square) the second richest in narrow endemic species in tropical Africa (only surpassed by the Dar es Salaam grid). *Isolepis keniaeensis* is known only from Mt. Kenya, and has no known close relatives.

Tanzania

This country has an extremely rich sedge flora and with 389 species (Haines & Lye 1983) is in tropical mainland Africa possibly surpassed by Zambia and Congo (Kinshasa) only. No fewer than 34 species are endemic (8.7%), and of these 23 are narrow endemics known from just one 1 degree grid. The highest concentration of such species are found in the Dar es Salaam grid with four species, and the Songea, Mbeya and Sumbawanga grids all with two species. Although the Dar es Salaam grid square is one of the best investigated in Tanzania, it is interesting that Linder (1998) found that the same grid square (but enlarged to cover 2.5 x 2.5 degrees) is the richest in narrow endemic species in tropical Africa, viz. 22 narrow endemics out of 794 investigated species.

Rwanda

The flora of Rwanda includes 110 species of Cyperaceae (Maquet 1988). There are no endemic species. It shares *Bulbostylis ugandensis* (Lye 1974b) with Uganda and *Carpha angustissima* with SW Uganda and adjacent parts of Congo. Other species are more widespread.

Burundi

The Cyperaceae flora of Burundi is not well studied. It contains at least one narrow endemic, *Bulbostylis nemoides* (Goetghebeur 1984).

Congo (Kinshasa)

The Cyperaceae flora of Congo (Kinshasa) is rich and varied as is expected from such a vast country with many different climatic regimes. It contains one endemic genus, *Nelmesia* (van der Veken 1955) and many endemic species. Many rare species are shared with Zambia and adjacent parts of Tanzania. It probably has about 400 species of Cyperaceae. For example the genus *Fimbristylis* has 18 species in Congo (Goetghebeur & Coudijjzer 1984) as against 14 species in Tanzania (Haines & Lye 1983).

Zambia

The sedge flora of Zambia is very rich and has many endemics as well as undescribed species. It could possibly have more numerous species of Cyperaceae than Tanzania. For example the genus *Scleria* has 57 species in Zambia (Robinson 1966) as against 44 species in Tanzania (Haines & Lye 1983). *Scleria calcicola* E. A. Rob., *S. zambesica* E. A. Rob., *S. polyrrhiza* E. A. Rob., *S. fulvopilosa* E. A. Rob., *S. procumbens* E. A. Rob., *S. lucentinigricans* E. A. Rob., *S. xerophila* E. A. Rob. and *S. arcuata* E. A. Rob. are all endemic.

Zimbabwe

The sedge flora of Zimbabwe is rich and has a greater affinity with the South African flora than have the East African countries. However,

Table 1. Genera and subgenera of Cyperaceae in eastern and northeastern tropical Africa, their total number of species (tot.), number of endemic species in each country (end.) and percentage of endemic species.

Genus or subgenus	**Eritrea**		**Ethiopia**		**Somalia**		**Kenya**		**Uganda**		**Tanzania**	
	tot.	end.	tot.	end.	tot.	end.	tot.	end.	tot.	end.	tot.	end.
Fuirena	1	0	5	0	3	3	10	0	5	0	14	2
Schoenoplectus subg. *Actaeogeton*	1	0	4	0	4	0	6	0	7	0	9	0
S. subg. *Bolboschoenus*	0	0	1	0	1	0	1	0	0	0	1	0
S. subg. *Schoenoplectus*	2	0	4	0	3	0	3	0	4	0	5	0
Eleocharis	2	0	5	0	3	0	6	0	9	0	14	0
Websteria	0	0	0	0	0	0	0	0	0	0	1	0
Fimbristylis	4	0	8	0	4	0	9	0	8	0	14	0
Abildgaardia	1	0	1	0	0	0	2	0	1	0	2	0
Bulbostylis	7	0	16	1	5	1	25	2	17	0	32	10
Nemum	0	0	0	0	0	0	0	0	1	0	0	0
Isolepis	2	0	8	2	0	0	6	1	5	1	8	1
Ficinia	0	0	1	1	0	0	1	0	0	0	2	0
Oxycaryum	0	0	1	0	0	0	0	0	1	0	1	0
Kyllingiella	2	0	2	0	0	0	2	0	2	1	2	0
Cyperus subg. *Alinula*	0	0	1	0	0	0	1	0	1	0	1	0
C. subg. *Anosporum*	0	0	1	0	1	0	2	0	2	0	2	0
C. subg. *Chamaexiphium*	0	0	1	1	0	0	0	0	0	0	0	0
C. subg. Courtoisina	1	0	1	0	0	0	1	0	1	0	2	0
C. subg. *Cyperus*	30	1	56	3	59	19	78	3	57	0	89	9
C. subg. Fimbricyperus	0	0	0	0	0	0	0	0	0	0	1	0
C. subg. *Kyllinga*	10	0	19	0	12	0	23	1	20	0	33	6
C. subg. *Marisculus*	0	0	1	0	0	0	1	0	0	0	1	0
C. subg. *Pycnostachys*	3	0	10	0	7	2	16	1	19	0	23	3
C. subg. *Pycreus*	8	0	16	1	4	1	16	0	19	0	28	0
C. subg. *Queenslandiella*	0	0	0	0	1	0	1	0	0	0	2	1
C. subg. *Sorostachys*	0	0	1	0	2	1	1	0	1	0	1	0
Sphaerocyperus	0	0	0	0	0	0	0	0	0	0	1	0
Remirea	0	0	0	0	0	0	0	0	0	0	1	0
Lipocarpha	0	0	5	0	0	0	5	0	4	0	8	0
Ascolepis	0	0	3	1	0	0	2	0	3	0	8	0
Schoenus	1	0	0	0	1	0	0	0	0	0	0	0
Rhynchospora	0	0	2	0	0	0	1	0	5	0	9	0
Tetraria	0	0	0	0	0	0	0	0	0	0	1	0
Carpha	0	0	0	0	0	0	0	0	2	0	1	0
Cladium	0	0	0	0	0	0	1	0	1	0	1	0
Machaerina	0	0	0	0	0	0	0	0	0	0	1	0
Hypolytrum	0	0	0	0	0	0	0	0	1	0	2	0
Scleria	0	0	14	0	0	0	13	0	20	0	44	0
Diplacrum	0	0	0	0	0	0	0	0	1	0	1	0
Coleochloa	1	0	1	0	0	0	1	0	1	0	4	1
Schoenoxiphium	0	0	2	0	0	0	3	0	3	0	3	0
Carex subg. *Carex*	2	0	6	0	2	0	6	0	7	0	7	1
C. subg. *Indocarex*	0	0	6	0	0	0	4	0	3	0	7	0
C. subg. *Primocarex*	0	0	2	0	0	0	3	0	1	0	1	0
C. subg. *Vignea*	1	0	2	0	0	0	2	0	2	0	1	0
Number of Cyperaceae species	77	1	206	10	89	27	252	8	234	2	389	34
Percentage of endemic species	1.3		4.9		30.3		3.2		0.9		8.7	

it lacks many of the species found in Zambia and southern Tanzania. The Chimanimani Mountains, so rich in endemics (41 species according to Wild 1964), do not have any endemic species of Cyperaceae.

Malawi

The sedge flora of Malawi is rich and, like that of Zimbabwe, has a closer affinity with the South African flora than have the East African countries. The South African genus *Tetraria* has its other non-South African species here, viz. *T. mlanjensis*.

Species endemic to East and North East Africa

112 species of Cyperaceae are endemic to tropical East and Northeast Africa. Of these, 65 species are endemic to East Africa (14.4%) while 41 are endemic to Northeast Africa (15.3%). For individual nations the numbers are given in Table 1. The total numbers of endemic species for the regions are higher than the added numbers of endemic species for countries. This is due to some species being endemic to two or more countries or to both regions considered together.

In a work on grasses Clayton & Cope (1980) identified a centre of endemism in Ethiopia, but this is not so for Cyperaceae, where Somalia and Tanzania are the two nations richest in endemic species.

Narrow endemics

Here we shall define 'narrow endemics' as species confined to a one-degree square or grid (latitude and longitude). There are 53 such species in eastern and northeastern tropical Africa, and they are enumerated in Table 2. There are 23 such species in Tanzania, 15 in Somalia, eight in Kenya, four in Uganda (with neighbours), three in Ethiopia, and none in Eritrea. Such species are generally very vulnerable and most species are endangered and need some sort of protection to avoid extinction. It is true that not all species known from a single one-degree grid are vulnerable, but in Cyperaceae the great majority is.

Most of the narrow endemics have been described fairly recently by Goetghebeur (1984), Haines & Lye (1978), Hooper (1985), Lye (1972b, 1974a, 1974b, 1982a, 1982b, 1982c, 1982d, 1982e, 1983a, 1983b, 1983c, 1985, 1987, 1992, 1994, 1996a, 1996b, 1996c, 1996d, 1996e, 1996f, 1996g, 1997a, 1997b, 1997c), Lye & Haines (1974) and Simpson (1990, 1994). Only a handful of narrow endemic species were described much earlier (Schumann 1895, Clarke 1901, Chermezon 1935, Kükenthal 1936, Nelmes 1939).

As shown in Fig. 3, the highest concentration of narrow endemic species is found in three coastal grids, *i.e.* (1) the Dar es Salaam-Zanzibar grid in Tanzania with four endemics, *Bulbostylis taylorii*, *Cyperus micromariscus*, *C. gigantobulbes* and *C. stramineo-ferrugineus*, (2) the Kwale grid south of Mombasa in Kenya with three endemics, viz. *Cyperus kwaleensis*, *C. boreobellus*, and *C. microumbellatus*, and (3) the Mogadiscio square in Somalia with three species, viz. *Cyperus baobab*, *C. somalidunensis* and *C. scabricaulis*. The two first grids are part of Clarke's (1998) 'new regional centre of endemism in Africa'.

The six grids encompassing the Erigavo Mountains, the Las Anod area (both Somalia), the Mt. Ruwenzori (Uganda/Congo), and the

Fig. 3. Map of eastern and northeastern tropical Africa showing presence of narrow endemic species of Cyperaceae for each one-degree square. Large dot = 3 or 4 narrow endemic species per square. Medium dot = 2 narrow endemic species per square. Small dot = 1 narrow endemic species per square. →

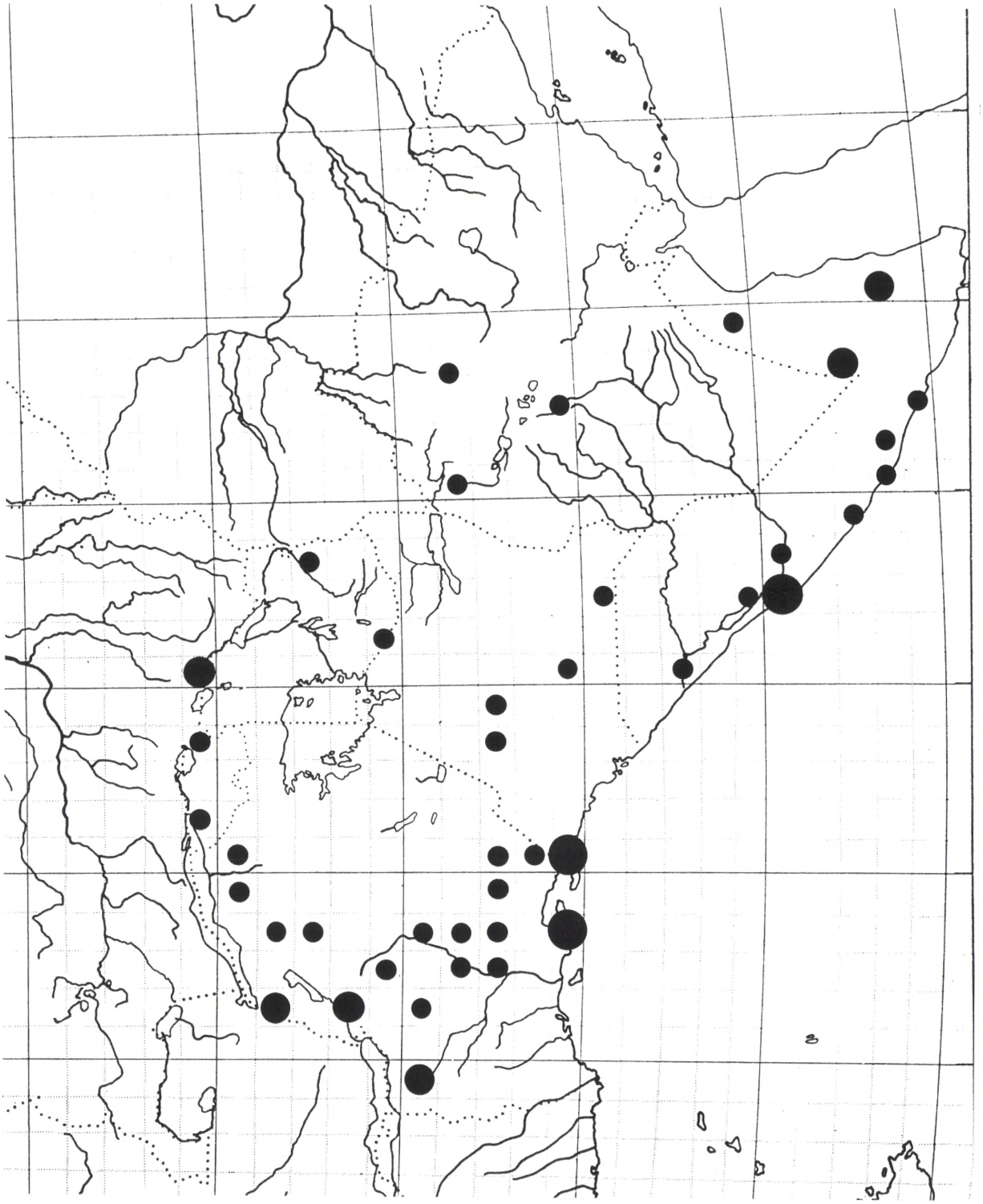

Table 2. The narrow endemic species of Cyperaceae in eastern and northeastern tropical Africa, country and latitude and longitude of their distribution areas.

Species	Country	Lat. Long.	Species	Country	Lat. Long.
Bulbostylis angustespicata	Tanzania	8°S 33°E	*Cyperus gypsophilus*	Somalia	8°N 47°E
B. elegantissima	Tanzania	7°S 34°E	*C. kwaleensis*	Kenya	4°S 39°E
B. leiolepis	Tanzania	4°S 30°E	*C. kyllingaeformis*	Kenya	1°N 34°E
B. longespicata	Ethiopia	5°N 36°E	*C. longi-involucratus*	Tanzania	7°S 36°E
B. microcarpa	Tanzania	4°S 37°E	*C. microbracteatus*	Tanzania	10°S 35°E
B. microrotundata	Tanzania	5°S 30°E	*C. microbulbosus*	Tanzania	5°S 37°E
B. nemoides	Burundi	3°S 29°E	*C. micromariscus*	Tanzania	6°S 39°E
B. squarrosa	Kenya	2°N 40°E	*C. micromedusaeus*	Somalia	7°N 49°E
B. tanzaniae	Tanzania	6°S 31°E	*C. micropelophilus*	Somalia	2°N 44°E
B. taylorii	Tanzania	6°S 39°E	*C. microumbellatus*	Kenya	4°S 39°E
Carex papillosissima	Tanzania	7°S 36°E	*C. mudugensis*	Somalia	5°N 48°E
Carpha angustissima	Uganda Rwanda Congo	1°S 29°E	*C. nyererei*	Tanzania	6°S 32°E
			C. ossicaulis	Somalia	4°N 47°E
			C. pluricephalus	Somalia	3°N 45°E
C. eminii	Uganda Congo	0°N 29°E	*C. poecilus*	Somalia	4°N 44°E
			C. purpureoviridis	Tanzania	6°S 37°E
Cyperus afropumilus	Tanzania	8°S 33°E	*C. recurvispicatus*	Somalia	6°N 48°E
C. alba-purpureus	Tanzania	8°S 31°E	*C. scabricaulis*	Somalia	2°N 45°E
C. baobab	Somalia	2°N 45°E	*C. somalidunensis*	Somalia	2°N 45°E
C. bifolius	Ethiopia	8°N 36°E	*C. stramineo-ferrugineus*	Tanzania	6°S 39°E
C. boreobellus	Kenya	4°S 39°E	*Ficinia borealis*	Ethiopia	7°N 39°E
C. brunneoalbus	Kenya	2°N 40°E	*Fuirena boreocoerulescens*	Somalia	10°N 48°E
C. castaneobellus	Tanzania	10°S 35°E	*F. somaliensis*	Somalia	0°N 42°E
C. cremeomariscus	Tanzania	8°S 31°E	*F. striatella*	Somalia	10°N 48°E
C. densibulbosus	Somalia	8°N 47°E	*Isolepis keniaensis*	Kenya	0°S 37°E
C. flavoculmis	Kenya	1°S 37°E	*I. ruwenzoriensis*	Uganda	0°N 29°E
C. gigantobulbes	Tanzania	6°S 39°E	*I. trollii*	Tanzania	7°S 37°E
C. graciliculmis	Tanzania	6°S 36°E	*Kyllingiella ugandensis*	Uganda	3°N 32°E

Sumbawanga, Mbeya, and Songea areas (Tanzania) all have two narrow endemics found in the same square.

Isolated mountains or hills (in addition to Mt. Ruwenzori) with narrow endemics are Mt. Kenya (*Isolepis keniaensis*), Shimba Hills (*Cyperus microumbellatus*), Ukaguru Mountains (*Cyperus graciliculmis*), Nguru Mountains (*Cyperus purpureoviridis*) and the perhaps less isolated Mafinga (Sao Hill) area (*Carex papillosissima*).

Discussion

General history

It is unlikely that past geological history concerning continental drift and the old West Gondwanaland connections with South America (Raven & Axelrod 1972) has had a pronounced effect on present day distribution of tropical East and Northeast African sedges except for the occurrence of certain genera. Only 13 of our species are found in America (several are recent introductions by man) while more than 50 species are found in Asia. Therefore the eastern African sedge flora is much more closely related to that of India than to that of America. However, the African genus *Coleochloa* has its related genera in America and not in Asia, and could depend on past connections with America 45-60 million years ago.

The closer relationship between the sedge flora of Madagascar and eastern Africa as well as between India and eastern Africa could, however, at least in part depend on the past geographical position of Madagascar and India as part of or close to the African mainland.

Climate

It is the climate at present and during the more recent past, when continents occupied their present positions, which have set up modern patterns of vegetation and floras.

As most of present day tropical Africa was clothed with evergreen rainforest of tropical to warm temperate character 20 million years ago (Raven 1983), the evolution of most of our sedges must have occurred subsequently. The forest genus *Hypolytrum* could, however, be a remnant from that past continuous and unbroken forest.

Later thousands of metres of uplift have expanded habitats for plants characteristic of cooler areas and greatly enhanced the opportunities for north-south migration. The spreading aridity associated with the cool currents resulting from massive glaciation has reduced the forest flora and allowed savannas and savanna species to spread and develop at the expense of the rainforest and rainforest species. The forest genus *Mapania* probably became extinct in eastern Africa during this period.

The climatic fluctuations during later periods and particularly during much of the Quaternary Period (last 1.8 million years) must have affected the distribution of some genera and species of Cyperaceae.

It is, however, likely that it is first and foremost the climate and the climatic changes during the last 20 000 years which formed the diversity in Cyperaceae in our region. Warmer and more humid periods interchanged with colder and drier periods. During the last ice age maximum 18 000 years B.P. Morrison (1968) working in SW Uganda found the mean annual temperature to be 6° C lower than at present. Due to this lowering of temperature during this period numerous temperate and subalpine species of sedges probably had a much-extended distribution.

The opening up of the vegetation of Africa during this dry and cold period probably provided a migration route between the arid northeastern parts of our area and Namibia for plants adapted to dry conditions. Lowland rainforest in our area probably persisted on parts of the Tanzanian Arc mountains and possibly in the Kwale area in Kenya only. This could explain the presence of local endemic species on these mountains and hills.

The presence of many lowland coastal endemics in drier habitats is more difficult to explain. It is, however, likely that at least in Somalia there were dry regions with open vegetation throughout the interglacial as well as the post-glacial periods. Such areas could serve as refugia during periods when dense forest covered most other parts of tropical Africa.

On the whole distribution patterns among

endemic Cyperaceae are not easily explained from the African plant geographical regions described by White and others. A better correlation is found using the land-cover maps produced by Tucker *et al.* (1985).

Edaphic conditions

Although the bedrock in tropical countries is apparently less important for the distribution of plants than it is in temperate countries, hard rocks are important in forming habitats with shallow soils unsuitable for the colonization of trees and larger shrubs. Such habitats are often important habitats for many annual sedges or sedges with special adaptation for dry conditions, *e.g. Cyperus dubius.* and the genus *Coleochloe.* The importance of inselbergs in allowing the survival of open-country species at times of forest expansion has been highlighted by Barthlott & Poremski (1996, 1998).

Also sediments poor in nutrients, such as the almost pure silica-sand on the NW side of Lake Victoria are important habitats for sedges as they are too nutrient-poor for colonisation by shrubs and trees at least when regularly grazed, *e.g. Bulbostylis ugandensis, B. cardiocarpoides* Cherm., *Cyperus tenuiculmis* Böckel. and *C. tenax* Böckel. However, nutrient-poor soils are sometimes covered by extensive forests such as in SE Tanzania (Vollesen 1981).

In Somalia very local soils such as gypsum soils provide habitats for very rare and endangered species, such as *Cyperus gypsophilus.* Soils with high metal contents sometimes have very specialized endemics also, but such soils are mostly found in the Zambia-Katanga region (Malaisse 1983), *e.g. Bulbostylis metalliphila* (Lye 1985).

Also seasonal water logging or flooding is an important edaphic factor keeping trees and larger shrubs away (White 1977; Lock 1998) thus providing optimal conditions for many rare sedges, particularly in southern Tanzania and northern Zambia. Permanently wet habitats often contain extensive patches of sedges, but very rarely vulnerable or endangered species.

Dispersal mechanisms

Many sedges growing in permanently wet habitats have diaspores adapted to long-distance dispersal by birds (Ridley 1930), *e.g.* the genera *Fuirena, Schoenoplectus* (Raynal 1976a), *Eleocharis* and *Rhynchospora.* Such genera have a number of species with wide pantropical distributions, *e.g. Fuirena umbellata, Schoenoplectus maritimus, Eleocharis geniculata* and *Rhynchospora corymbosa.*

Many sea-shore species, particularly those growing immediately above the strand-line, have diaspores which float in sea-water and thus sometimes have very extensive pantropical distributions, *e.g. Fimbristylis cymosa, F. ferruginea* and *Remirea maritima.* Others have a widespread Afro-Asian distribution, *e.g. Fimbristylis polytrichoides* and *Abildgaardia triflora.*

Species growing in seasonally wet or in dry habitats and with diaspores without special development for long-distance dispersal sometimes have wide pantropical distributions also. Such distributions are difficult to understand particularly for dryland species unless they are considered as resulting from an old Gondwanaland continent or their diaspores being wind-blown during strong and unusual weather conditions, *e.g. Abildgaardia ovata, Bulbostylis hispidula, B. barbata* and *Cyperus laevigatus.*

During the last hundred years especially many species of sedges growing as weeds in cultivations and especially in rice fields, have been dispersed as weeds from continent to continent as contamination in crop seeds.

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Appendix 1. Major distribution patterns

Species in Uganda with West African affinities: *Cyperus fertilis* Böckel.; *C. mortonii* Lye; *C. renschii* Böckel. var. *scabrida* Lye; *C. socialis* C.B. Cl.; *C. submicrolepis* Kükenth.; *Fimbristylis gabonica* Cherm.; *Nemum spadiceum* (Lam.) Ham.; *Scleria globonux* C.B. Cl.

Species in Tanzania with West African affinities: *Cyperus clavinux* C.B. Cl.*; C. demangei* (Rayn.) Lye; *Hypolytrum testui* Cherm.

Species with South African affinities: *Bulbostylis striatella* C.B. Cl.; *Carpha glomerata* (Thunb.) Nees; *Cyperus fulgens* C.B. Cl.; *C. marginatus* Thunb.; *C. merxmuelleri* (Podl.) Lye; *C. vestitus* Krauss; *Ficinia gracilis* Schrad.; *F. stolonifera* Böckel.; *Isolepis natans* (Thunb.) A. Dietr.; *Schoenoxiphium caricoides* C.B. Cl.; *S. lehmannii* (Nees) Steud.; *S. sparteum* (Wahlenb.) Kük.

Species with North African to Arabian affinities: *Carex negrii* Chiov.; *Cyperus conglomeratus* Rottb.; *C. cruentus* Rottb.; *C. dives* Del.; *C. involucratus* Rottb.; *C. jeminicus* Rottb.; *C. macrorrhizus* Nees; *C. procerus* Rottb.

Species with European affinities: *Carex acutiformis* Ehrb.; *C. distans* L.; *C. divisa* Huds.; *C. longus* L.; *C. mundtii* (Nees) Kunth.; *C. rotundus* L.; *Fuirena pubescens* (Poir.) Kunth; *Isolepis cernua* (Vahl) Röm. & Schult.; *I. fluitans* (L.) R. Br.; *I. setacea* (L.) R. Br.; *Schoenoplectus lacustris* (L.) Palla; *S. maritimus* (L.) Lye; *S. mucronatus* (L.) Kerner; *Schoenus nigricans* L.

Afro-Asian species: *Abildgaardia triflora* (L.) Lye; *Bulbostylis densa* (Wall.) Han.-Mazz. s.lat.; *Cyperus alopecuroides* Rottb.; *C. aromaticus* (Ridl.) Mattf. & Kük.; *C. brevifolius* (Rottb.) Hasskn.; *C. bulbosus* Vahl; *C. corymbosus* Rottb.; *C. cyperoides* (L.) O. Ktze.; *C. denudatus* L. f.; *C. difformis* L.; *C. dubius* Rottb.; *C. exaltatus* Retz.; *C. hyalinus* Vahl; *C. imbricatus* Retz.; *C. iria* L.; *C. kyllingia* Endl.; *C. maderaspatanus* Willd.; *C. meeboldii* Kük.; *C. melanospermus* (Nees) Valc. Sur.; *C. metzii* (Steud.) Mattf. & Kük.; *C. mollipes* (C.B. Cl.) K. Schum.; *C. nitidus* Lam.; *C. niveus* Retz.; *C. nutans* Vahl var. *eleusinoides* (Kunth) Haines; *C. pseudokyllingioides* Kük.; *C. pulchellus* R. Br.; *C. pumilus* L.; *C. pygmaeus* Rottb.; *C. rubicundus* Vahl; *C. sanguinolentus* Vahl.; *C. triceps* Endl.; *C. zollingeri* Steud.; *Eleocharis dulcis* (Burm.f.) Heschel; *Fimbristylis bisumbellata* (Forssk.) Bub.; *F. dipsacea* (Rottb.) C.B. Cl.; *F. miliacea* (L.) Vahl; *F. polytrichoides* (Retz.) Vahl; *F. schoenoides* (Retz.) Vahl; *Fuirena ciliaris* (L.) Roxb.; *F. pubescens* (Poir.) Kunth; *Isolepis fluitans* (L.) R. Br.; *Lipocarpha chinensis* (Osb.) Kern; *L. hemisphaerica* (Roth) Goetgh.; *L. kernii* (Raymond) Goetgh.; *Rhynchospora brownii* Roem. & Schult. ssp. *brownii*; *R. rubra* (Lour.) Makino s. lat.; *Schoenoplectus articulatus* (L.) Palla; *S. lateriflorus* (Gmel.) Lye; *S. mucronatus* (L.) Kerner; *S. subulatus* (Vahl) Lye; *Scleria mikawana* Makino; *S. pergracilis* (Nees) Kunth; *S. poaeformis* Retz.; *S. tesselata* Willd.

Afro-American species: *Cyperus lanceolatus* Poir.; *C. niger* Ruiz & Pavon; *C. sphacelatus* Rottb.; *Lipocarpha micrantha* (Vahl) G. Tuck.; *Rhynchospora brevirostris* Griseb.; *R. candida* (Nees) Böckel.; *R. holoschoenoides* (L.C. Rich.) Hert.; *Scleria bambariensis* Cherm.; *S. bulbifera* A. Rich.; *S. distans* Poir.; *S. lagoënsis* Böckel.; *S. melanomphala* Kunth; *S. pterota* Presl.

Pantropical species: *Abildgaardia ovata* (Burm. f.) Kral; *Bulbostylis barbata* (Rottb.) C.B. Cl.; *B. hispidula* (Vahl) R. Haines; *Cladium jamaicense* Crantz.; *Cyperus amabilis* L.; *C. articulatus* L.; *C. brevifolius* (Rottb.) Hassk.; *C. compressus* L.; *C. cuspidatus* H.B.K.; *C. densicaespitosus* Mattf. & Kük.; *C. difformis* L.; *C. distans* L. f.; *C. esculentus* L.; *C. flavescens* L.; *C. haspan* L.; *C. imbricatus* Retz.; *C. laevigatus* L.; *C. macrostachyos* Lam.; *C. mundtii* (Nees) Kunth; *C. polystachyos* Rottb.; *C. rotundus* L.; *C. sesquiflorus* (Torr.) Mattf. & Kük.; *C. sphacelatus* Rottb.; *C. squarrosus* L.; *C. tenuispica* Steud.; *C. unioloides* R. Br.; *Eleocharis acutangula* (Roxb.) Schult.; *E. atropurpurea* (Retz.) Kunth; *E. geniculata* (L.) Röm. & Schult.; *E. mutata* (L.) Roem. & Schult.; *E. nigrescens* (Nees) Steud.; *E. retroflexa* (Poir.) Urban; *Fimbristylis complanata* (Retz.) Link; *F. cymosa* R. Br.; *F. dichotoma* (L.) Vahl; *F. ferruginea* (L.) Vahl; *F. littoralis* Gaud.; *F. squarrosa* Vahl; *Fuirena umbellata* Rottb.; *Isolepis setacea* (L.) R. Br.; *Oxycaryum cubensis* (Poep. & Kunth) Lye; *Remirea maritima* Aubl.; *Rhynchospora corymbosa* (L.) Britt.; *Schoenoplectus erectus* (Poir.) Rayn.; *S. maritimus* (L.) Lye; *Schoenus nigricans* L.; *Scleria lithosperma* (L.) Sw.; *Websteria confervoides* (Poir.) Hooper

Species with highly disjunct distributions: *Carex peregrina* Link**;** *Cyperus subparadoxus* Kük.*; Eleocharis decoriglumis* Bérhaut; *Isolepis cernua* (Vahl) Röm. & Schult.

Appendix 2. Endemic species in the various nations and geographical areas

Sudan: *Coleochloa glabra* Nelmes; *C. schweinfurthiana* (Böckel.) Nelmes.

Sudan and Somalia: *Cyperus nubicus* C.B. Cl.

Eritrea: *Cyperus schweinfurthii* (Chiov.) Kük.

Eritrea and Sudan: *Cyperus microbolbos* C.B. Cl.

Eritrea and Ethiopia: *Cyperus holostigma* Schweinf.

Ethiopia: *Ascolepis eriocauloides* (Steud.) Steud.; *Bulbostylis longespicata* (Lye) Lye; *Carex cognata* Kunth. var. *abyssinica* (Chiov.) Lye; *Cyperus atronervatus* Böckel. ssp. *angustifolius* Lye; *C. atronervatus* Böckel. ssp. *atronervatus*; *C. bifolius*

Lye; *C. boreohemisphericus* Lye; *C. clandestinus* Steud.; *C. maculatus* Böckel. ssp. *ogadensis* Lye; *C. pratensis* Böckel.; *Ficinia borealis* Lye; *Isolepis nervosa* A. Rich.; *I. omissa* Raynal.

Ethiopia and Sudan: *Carex thomasii* Nelmes.

Ethiopia and Somalia: *Carex brunnea* Thunb. subsp. *occidentalis* Lye; *Cyperus brunneofibrosus* Lye; *C. cunduduensis* Chiov.

Ethiopia, Somalia and Yemen: *Carex negrii* Chiov.

Ethiopia and Kenya: *Bulbostylis cruciformis* (Lye) R. Haines; *Cyperus costatus* Mattf. & Kükenth. ssp. *sidamoensis* (Mtoto.) Lye; *Fimbristylis keniaeensis* Kük.

Ethiopia and Uganda: *Scleria hispidior* (C.B. Cl.) Nelmes.

Ethiopia and Burundi: *Lipocarpha constricta* Goetgh.

Ethiopia and Tanzania: *Bulbostylis sphaerocarpa* (Böckel.) C.B. Cl.; *Isolepis kilimanjarica* R. Haines & Lye.

Somalia (N = north; S = south): *Bulbostylis hispidula* (Vahl) R. Haines subsp. *macroglumis* Lye (S); *B. somaliensis* Lye subsp. *confusa* Lye (S); *B. somaliensis* Lye subsp. *somaliensis* (S); *Cyperus altomicroglumis* Lye (S); *C. baobab* Lye (S); *C. benadirensis* Chiov.(S); *C. chaetophyllus* (Chiov.) Kük. (S); *C. commixtus* Kük. (N); *C. densibulbosus* Lye (N); *C. erectus* (Schumach.) Mattf. & Kük. subsp. *jubensis* (Chiov.) Lye (S); *C. gypsophilus* Lye (N); *C. medusaeus* Chiov. (S); *C. microglumis* D. A. Simps. (S); *C. micromedusaeus* Lye (N); *C. micropelophilus* Lye (S); *C. mogadoxensis* Chiov. (S); *C. mudugensis* D.A. Simps. (S); *C. obbiadensis* Chiov. (S); *C. oblongus* (C.B. Cl.) Kük. subsp. *jubensis* (Mtoto.) Lye (S); *C. ossicaulis* Lye (S); *C. pluricephalus* Lye (S); *C. poecilus* C.B. Cl. (N); *C. pseudosomaliensis* Kük. (N); *C. recurvispicatus* Lye (S); *C. rotundus* L. subsp. *divaricatus* Lye (N); *C. scabricaulis* Lye (S); *C. scleropodus* Chiov. (N); *C. somalidunensis* Lye (S); *C. somaliensis* C.B. Cl. (N); *Fuirena boreocoerulescens* Lye (N); *F. somaliensis* Lye (S); *F. striatella* Lye (N).

Somalia and Kenya (N = north Somalia; S = south Somalia): *Bulbostylis craspedota* Chiov. (S); *B. pallescens* Lye (S); *Cyperus afrodunensis* Lye (S); *C. chordorrhizus* Chiov. (S); *C. eximius* (C.B. Cl.) Mattf. & Kük. (S); *C. frerei* C.B. Cl. (S); *C. phillipsiae* (C.B. Cl.) Kük. (N + S).

Somalia and India (S = south Somalia): *Cyperus dwarkensis* Sahni & Naithani (S).

Kenya: *Bulbostylis afroorientalis* (Lye) R. Haines; *B. hispidula* (Vahl) R. Haines ssp. *intermedia* (Lye) R. Haines; *B. squarrosa* (Lye) Lye; *Cyperus boreobellus* Lye; *C. brunneoalbus* (Lye) Lye; *C. flavescens* L. ssp. *tanäensis* (Kükenth.) Lye; *C. flavoculmis* Lye; *C. kwaleensis* Lye; *C. kyllingaeformis* Lye; *C. microumbellatus* Lye; *C. sanguinolentus* Vahl ssp. *nairobiensis* (Lye) Lye; *C. soyauxii* Böckel. ssp. *pallescens* Lye; *Isolepis keniaeensis* Lye.

Kenya and Uganda: *Carex elgonensis* Nelmes; *C. runssoroensis* K. Schum.; *Cyperus afroalpinus* Lye; *C. crassivaginatus* Lye; *Isolepis graminoides* R. Haines & Lye.

Kenya and Tanzania: *Bulbostylis argenteobrunnea* C.B. Cl.; *Carex phragmitoides* Kükenth.; *C. vallis-rosetto* K. Schum.; *Cyperus globifer* (C.B. Cl.) Lye; *C. kilimandscharicus* Kükenth.; *C. oblongo-incrassatus* Kükenth.; *C. pseudo-hildebrandtii* Kükenth.; *C. rohlfsii* Böckel.; *C. songeensis* (Lye) Lye; *C. undulatus* Kükenth.

Uganda: *Carex bequaertii* De Wild. var. *maxima* Lye; *Cyperus fischerianus* A. Rich. var. *ugandensis* Lye; *C. flavescens* L. ssp. *microglumis* (Lye) Lye; *C. melanospermus* (Nees) Valck. Sur var. *hexalatus* Lye; *Fimbristylis miliacea* (L.) Vahl ssp. *macroglumis* Lye; *Fuirena pubescens* (Poir.) Kunth var. *abbreviata* Lye; *Isolepis ruwenzoriensis* R. Haines & Lye; *Kyllingiella ugandensis* R. Haines & Lye; *Scleria distans* Poir. var. *chondrocarpa* (Nelmes) Lye.

Uganda and Congo (Kinshasa): *Carpha eminii* (K. Schum.) C B. Cl.

Uganda and Tanzania: *Cyperus afromontanus* Lye.

Burundi: *Bulbostylis nemoides* Goetgh.

Burundi and Tanzania: *Ascolepis hemisphaerica* Goetgh.

Tanzania: *Ascolepis protea* Welw. ssp. *chrysocephala* Lye; *Bulbostylis angustespicata* (Lye) Lye; *B. elegantissima* (Lye) R. Haines; *B. hispidula* (Vahl) R. Haines ssp. *halophila* (Lye) R. Haines; *B. johnstonii* C.B. Cl.; *B. leiolepis* (Kük.) R. Haines; *B. macrostachya* (Lye) R. Haines; *B. microcarpa* (Lye) R. Haines; *B. microrotundata* (Lye) Lye; *B. rotundata* (Kük.) R. Haines; *B. tanzaniae* (Lye) R. Haines; *B. taylorii* (K. Schum.) C.B. Cl.; *Carex papillosissima* Nelmes; *Coleochloa microcephala* Nelmes; *Cyperus afropumilus* (Lye) Lye; *C. afrovaricus* Lye; *C. alba-purpureus* (Lye) Lye; *C. castaneobellus* Lye; *C. cremeomariscus* Lye; *C. endlichii* Kükenth.; *C. gigantobulbes* Lye; *C. graciliculmis* Lye; *C. longi-involucratus* Lye; *C. microbracteatus* (Lye) Lye; *C. microbulbosus* (Lye) Lye; *C. micromariscus* Lye; *C. nyererei* Lye; *C. obsoletenervosus* A. Peter; *C. purpureoviridis* Lye; *C. stramineo-ferrugineus* Kük.; *C. tanganyicanus* (Kük.) Lye; *C. tanzaniae* (Lye) Lye; *C. ugogensis* Peter & Kük.; *Fimbristylis miliacea* (L.) Vahl ssp. *pallescens* Lye; *Fuirena claviseta* A. Peter; *F. sagittata* Lye; *Isolepis trollii* (Kükenth.) Lye.

Tanzania and Zambia: *Ascolepis protea* Welw. ssp. *rhizomatosa* Lye; *A. pusilla* Ridley var. *echinata* S. Hooper; *Cyperus albogracilis* (Lye) Lye; *C. chinsalensis* Podlech; *C. longistolon* Peter & Kükenth.; *C. peteri* Kükenth.; *?Fuirena abnormalis* C.B. Cl.; *Schoenoplectus rhodesicus* (Podlech) Lye; *Scleria adpresso-hirta* E.A. Robinson; *S. delicatula* Nelmes.

Tanzania and Zimbabwe: *Ascolepis erythrocephala* S. Hooper; *Scleria pachyrrhyncha* Nelmes.

Tanzania and Malawi: *Carex cyrtosaccus* C.B. Cl.; *Coleochloa virgata* (K. Schum.) Nelmes.

Tanzania and Congo (Kinshasa): *Tetraria usambarensis* K. Schum.

Tanzania and Madagascar: *Cyperus subparadoxus* Kük.; *Machaerina flexuosa* (Böckel.) Kern.

The Commelinaceae of Northeast Tropical Africa (Eritrea, Ethiopia, Djibouti, Somalia and Kenya): Diversity and phytogeography

ROBERT B. FADEN

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Northeast Tropical Africa (NETA, comprising Eritrea, Ethiopia, Djibouti, Somalia and Kenya) is rich in Commelinaceae, with 95 species in 10 genera. Twenty-four species, all belonging to *Aneilema*, *Commelina* or *Cyanotis*, are endemic to the region, with country rates of endemism ranging from zero to 35%. Three of the six sections of *Aneilema* present in NETA have endemic species there, including section *Somaliensia*, which is wholly endemic to NETA. The forest genera of Commelinaceae in NETA comprise only 4% of the total species. NETA is richer in Commelinaceae than West Tropical Africa or Southern Africa. The most strongly represented flora element is the Somali-Masai flora element. NETA shares 12-13 species with the Arabian Peninsula and 14 species with India.

Robert B. Faden, Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0166, U.S.A. Email: faden.robert@nmnh.si.edu.

Introduction

The Commelinaceae are the fourth largest family of monocots in tropical Africa (after the Poaceae, Orchidaceae and Cyperaceae). Approximately 270 species in 18 genera occur on mainland tropical Africa and Madagascar (Faden 1983; Faden & Evans 1999). Generic diversity is highest in West and Central Africa, but species diversity is greatest in eastern Africa. Species occur in almost all habitats from sea level to about 4200 m.

Our knowledge of African Commelinaceae is constrained by a relative scarcity of modern floristic treatments and monographs. Floristic accounts have been published for West Tropical Africa (Brenan 1968); Senegal (Vanden Bergen 1988); Togo (Brunel *et al.* 1984); Sudan (Andrews 1956); Ethiopia and Eritrea (Ensermu & Faden 1997); Somalia (Faden 1995); Upland Kenya (Faden 1974b, 1994); Rwanda (Malaise 1988); Southern Africa (Obermeyer & Faden 1985); and Madagascar (Perrier de la Bâthie 1938). Only *Aneilema* has been monographed (Faden 1991). Despite these shortcomings, I believe that it is still meaningful to examine diversity within areas that are relatively well known floristically and to look for phytogeographic patterns.

Table 1. The number of species in genera of Commelinaceae in the floras of Djibouti, Somalia, Ethiopia and Eritrea, and Kenya (Northeast Tropical Africa). * = naturalised.

Genus	Djibouti	Somalia	Ethiopia/Eritrea	Kenya	Northeast Tropical Africa
Aneilema	1	7	18	28	34
Anthericopsis	–	1	1	1	1
Coleotrype	–	–	–	1	1
Commelina	4	13	19	30	36
Cyanotis	–	1	8	9	13
Floscopa	–	–	1	1	1
Murdannia	–	1	2	4	5
Pollia	–	–	2	1	2
Stanfieldiella	–	–	1	–	1
*Tradescantia**	–	–	–	1	1
Total:	5	23	52	76	95

The Study Area

Northeast Tropical Africa has been defined to comprise Sudan, Eritrea, Ethiopia, Djibouti and Somalia, or these countries excluding Sudan (Friis 1992). For the purposes of this paper I define Northeast Tropical Africa (NETA) differently herein, including Kenya and excluding Sudan. I have circumscribed the area thus for two reasons. First, the newly defined area much more closely matches the Somali-Masai regional center of endemism of White (1983) than do the earlier demarcations. Second, although there is a published flora of Sudan (Andrews 1956), but none for the whole of Kenya, the Commelinaceae of Kenya are much better known. The 1980 collections of Friis & Vollesen from the Imatong Mountains in Sudan – specimens studied at the University of Copenhagen – added at least two genera and seven species of Commelinaceae to Andrews' flora, clearly demonstrating how incomplete our knowledge is of the flora of that country. In contrast, my many years of collecting Commelinaceae in Kenya, studies of the family for *Upland Kenya Wild Flowers* (Faden 1974b, 1994), and ongoing work on the *Flora of Tropical East Africa* Commelinaceae have provided me with a detailed knowledge of the Commelinaceae of Kenya.

The propriety of including Kenya in NETA may be questioned further because Kenya is also part of Tropical East Africa. However, there are precedents for including African countries, or parts of countries, in more than one flora, such as Botswana in *Flora Zambesiaca* and *Flora of Southern Africa*, the Red Sea Hills in floras of Egypt and Sudan, and the former British Cameroons in both *Flora of West Tropical Africa* and *Flore du Cameroun*. The flora of the greater, arid part of Kenya clearly has affinities to the north. Similarly, many species of middle to high elevations in Kenya also occur in Ethiopia. Thus for a phytogeographic study of northeastern Africa, it is quite appropriate to also include Kenya.

Other floristic regions of White (1983) that are represented in the newly defined NETA are the Sudanian regional center of endemism (in western Ethiopia), the Afromontane and Afroalpine regional center of endemism (Kenya

and Ethiopia), the Lake Victoria regional mosaic (western Kenya) and the Zanzibar-Inhambane regional mosaic (southern Somalia and coastal Kenya).

The Commelinaceae of Northeast Tropical Africa

The Commelinaceae recognized from NETA are listed in Appendix 1. Ninety-five species and at least eight additional infraspecific taxa belonging to 10 genera have been recorded. Among these, the genus *Tradescantia* is neotropical, with several species cultivated, one of which, *T. zebrina*, is locally naturalized in Kenya. *Cyanotis axillaris* and *C. cristata* are mainly tropical Asian weedy species. The former is widespread but rarely collected in tropical Africa, where it may be considered an established, although perhaps not indigenous, species. *Cyanotis cristata* is known in mainland Africa from a single Eritrean collection made in 1969, so it may well have reached continental Africa recently. The remaining nine genera and 92 species of Commelinaceae are unquestionably indigenous to NETA.

When the species in NETA are summarized by regional flora (Table 1), the flora of Kenya is clearly much richer is species (76 species, or 80% of the total in NETA) than the other floras: Ethiopia and Eritrea together: 52 species (55%); Somalia: 23 species (24%); Djibouti: 5 species (5%). When area is taken into account, there is one species of Commelinaceae per 25,955 km sq for NETA as a whole. The species per km sq for the individual floras are: Kenya (1/7671), Ethiopia and Eritrea together (1/23498), Somalia (1/27724) and Djibouti (1/4640). Thus Kenya, which is a little less than half the area of Ethiopia plus Eritrea, is approximately three times as rich in species as Ethiopia plus Eritrea. Djibouti appears rich in species, but that is an artifact of its small size: it contains a few widespread species.

The bulk of the Commelinaceae species in NETA (83 species or 87% of the total species) belong to only three genera, *Aneilema*, *Commelina* and *Cyanotis*. These genera comprise 100% of the species in Djibouti (Lebrun *et al.* 1989), 91% of the Commelinaceae of Somalia, 87% of the species of Ethiopia and Eritrea, and 88% of the Kenya species. Country size and habitat diversity within NETA countries appear to have had little bearing on the floristic dominance by these three genera.

Endemism

The taxa of Commelinaceae that are endemic to NETA are indicated in Appendix 1. Twenty-four species (25%) are endemic to NETA. Endemism per regional flora is variable, with none of the five species endemic to Djibouti, eight of 23 species (35%) endemic to Somalia, four of 52 species (8%) endemic to the *Flora of Ethiopia and Eritrea* area (with none in Eritrea), and six of 76 species (8%) endemic to Kenya. In addition to one-country endemics, *Aneilema gillettii* and *A. sebitense* are endemic to Ethiopia and Kenya, and *Aneilema lamuense* is known only from Kenya and Somalia. Curiously, no species are shared solely between Ethiopia and Somalia. Three species occur exclusively in Ethiopia, Somalia and Kenya: *Aneilema somaliense*, *A. pusillum* and *Commelina stefaniniana*.

The 24 species of Commelinaceae that are endemic to NETA all belong to *Aneilema*, *Commelina* or *Cyanotis* (Appendix 1). Both *Aneilema* and *Commelina* have high rates of endemism in NETA: 13 of 34 species (38%) of *Aneilema* endemic; 10 of 36 (28%) of *Commelina* endemic. *Cyanotis*, however, has just one endemic species, *C. polyrrhiza*, out of 13 species present (8%).

A measure of the distinctness of the flora of a country within a region comprising several countries, such as NETA, is the number of species that occur exclusively in the country, whether or not the species are endemic to the

Table 2. The number and percentage of Northeast Tropical African species, and the number of endemic Northeast Tropical African species in the sections of *Aneilema*.

Section	Total number of species	Number of Northeast Tropical African Species	% of total number of species	Species endemic to Northeast Tropical Africa
Amelina	8	6	75	2
Rendlei	4	3	75	–
Somaliensia	5	5	100	5
Lamprodithyros	14	13	93	6
Brevibarbata	17	2	12	–
Pedunculosa	9	5	56	–

country. For example, none of the species that occur in Djibouti are exclusive to that country within NETA. In Eritrea, one of the 11 species (9%) occurs only in that country, but it is not endemic. When Eritrea is combined with Ethiopia, only eight of the 52 species (15%) do not occur elsewhere in NETA, and half of those eight species comprise the four Ethiopian endemics. Because Somalia is wholly surrounded by other countries of NETA, it is hardly surprising that all eight of the species of Commelinaceae that are exclusive to it are also endemic, these eight constituting 35% of the total species present. Kenya is unusual in that it has a high rate of exclusivity (30 of 76 species (39%) not occurring elsewhere in NETA), but only six of those species are endemic to Kenya. Among the 24 exclusive, non-endemics, only three, *Aneilema lanceolatum*, *Murdannia clarkeana*, and the introduced *Tradescantia zebrina*, do not also occur in Tanzania. Seven of the species shared between Kenya and Tanzania are endemic to these two countries (*Aneilema brenanianum*, *A. calceolus*, *A. clarkei*, *A. taylorii*, *Coleotrype brueckneriana*, *Commelina trilobosperma*, *Murdannia axillaris*), as compared with six species that Kenya shares exclusively with Ethiopia and/or Somalia.

The significance of endemics in a region can be understood best when phylogenetic relationships of the species are known. In *Commelina* and *Cyanotis*, species relationships are largely unknown, and even the division of these genera into sections is unsettled. Although the monograph of *Aneilema* (Faden 1991) lacks a phylogenetic analysis, it clearly defines the sections of the genus. Moreover, some relationships among the species are evident. Therefore, only *Aneilema* endemics in NETA will be considered further here.

All six sections of *Aneilema* that are present in continental Africa have species in NETA (Table 2). Three of the four sections that are best represented in NETA, in terms of percentage of total species, have endemics in this area, including section *Somaliensia* which is wholly endemic to NETA. The fourth well-represented section, section *Rendlei*, has no endemics in the flora because the NETA species (*A. brenanianum*, *A. rendlei*, *A. taylorii*) occur mainly in southern Kenya, and all extend into northern Tanzania where the section is most diverse (Faden 1991).

The NETA endemics of *Aneilema* section *Amelina* are mainly Kenyan. *Aneilema ephemerum* is a yellow-flowered annual that is endemic to northeastern Kenya and is probably most closely related to the widespread (in Africa as a whole) forest perennial *A. aequinoctiale*. *Aneilema gillettii*, is restricted to a small area on both sides of the Kenya-Ethiopia border. It is most likely related to the widespread *A. hockii*.

Four species groups of section *Lamprodithyros*

have endemics in NETA. The first group is represented by *Aneilema sebitense* which occurs at moderate elevations in western Kenya and southern Ethiopia. It is clearly the sister species of *A. forskalii* of Ethiopia and seasonally moist hills along the Red Sea and the Gulf of Aden. *Aneilema trispermum*, a Somalian endemic, represents the second species group. Its closest relative may be *A. petersii*, which occurs from southern Sudan, southern Ethiopia and Kenya southwards. The three species of the third species group occur near or just interior to the Indian Ocean coast. *Aneilema benadirense* is endemic to Somalia and *A. tanaense* to Kenya. *Aneilema calceolus* occurs in Kenya and Tanzania. The fourth species group has a similar range to the third group. *Aneilema succulentum*, a Kenyan endemic, occurs in dry habitats, just interior to the coastal strip, whereas *A. clarkei* of Kenya and Tanzania, and *A. lamuense*, of Kenya and Somalia, occur in moister habitats nearer the coast.

Section *Somaliensia* comprises five species of geophytic perennials, which sort into three groups. The section as a whole is endemic to NETA, with the greatest taxonomic diversity in Somalia (Faden 1991). The first group consists of *A. somaliense*, which is characterized by its bracteoles non-perfoliate, seeds often more than two per ventral locule, and flowers polygamomonoecious. *Aneilema somaliense* occurs mainly in Kenya and Ethiopia, being rare in Somalia, unlike the other two groups.

The second species group comprises *A. obbiadense*, *A. longicapsa* and *A. grandibracteolatum*. The group is characterized by very long, pointed capsules, perfoliate bracteoles, and consistently two seeds per ventral locule. *Aneilema obbiadense* is confined to the coastal plain of Somalia, whereas closely related *A. longicapsa* occurs further inland in Somalia, except around Hobyo (Obbia), where both species are present. *Aneilema grandibracteolatum* is known from a single collection from the Ogaden area in Ethiopia.

The third group consists of *A. pusillum*, which is divided into four subspecies that are not always easily distinguishable. However, the most distinctive of the subspecies, subsp. *thulinii*, could possibly merit species rank. The *A. pusillum* group is characterized by the diminutive size of the plants, inflorescences, and flowers, very succulent leaves, and a basic chromosome number of $x = 14$ (versus $x = 16$ in the other two groups). Three of the four subspecies are confined to Somalia; the fourth, subsp. *variabile*, which is the most problematic taxonomically, extends to Kenya and Ethiopia.

Ecology of Northeast Tropical African Commelinaceae

Faden (1983) classified the African genera of Commelinaceae ecologically as forest and non-forest genera, according to the predominant habit of most species in the genus. In NETA, only three forest genera, *Coleotrype*, *Pollia*, and *Stanfieldiella*, are native, and these contain only four species (4% of the total Commelinaceae) in the area. The forest genera occur only in Ethiopia (*Stanfieldiella*), Kenya (*Coleotrype*) or both countries (*Pollia*). The species of *Stanfieldiella* and *Pollia* are confined to southwestern Ethiopia and western Kenya in forests that are known to have West African floral elements (Friis 1992). *Coleotrype brueckneriana* occurs in moist forest along the Kenya coast, a region also known to have West African species and affinities (Faden 1974a).

There are only twice as many non-forest genera (*Aneilema*, *Anthericopsis*, *Commelina*, *Cyanotis*, *Floscopa* and *Murdannia*) as forest genera in NETA, but the non-forest genera contain more than 20 times as many species. The two largest non-forest genera, *Commelina* and *Aneilema*, both contain forest species, *e.g.*, *C. albiflora* and *A. aequinoctiale*, but these represent only small percentages of the total species of these genera.

Comparisons with other African floras

The Commelinaceae of NETA may be compared with those of West Tropical Africa (WTA) and Southern Africa (Table 3). West Tropical Africa has one-third more indigenous genera than NETA because of the presence of four forest genera (*Amischotolype*, *Buforrestia*, *Palisota*, and *Polyspatha*) that do not extend to NETA, versus only one non-forest genus, *Anthericopsis*, in NETA that does not extend to WTA. The proportion of forest genera (7 of 12, or 58%, versus 3 of 9, or 33%) is accordingly much higher in WTA. The forest genera in WTA contain 22 species, or 28% of the species in the flora, as compared to only four species (4%) in NETA. Despite the greater diversity of forest genera and species of Commelinaceae in WTA, the three largest genera in both floras are the same, *Commelina*, *Aneilema* and *Cyanotis*, all non-forest genera. However, whereas these three genera comprise 83% of the species in NETA, they constitute only 57% of the species in WTA. The greater species diversity of these three genera in NETA than in WTA, especially of *Aneilema* and *Commelina*, more than offsets the paucity of forest genera and species in NETA. Thus NETA has more species (95 versus 78). When area is taken into account, NETA is more than twice as rich in species of Commelinaceae as WTA (1 species per 25955 square km in NETA versus 1/60000 square km in WTA).

The amount and distribution of endemism differ between NETA and WTA. Species endemism is slightly higher in NETA (24 species or 25% of total species endemic) than in WTA (16 species (21%) endemic), but endemics occur in only three of the nine

Table 3. The number and percentage of endemic species in genera of of Commelinaceae in Northeast Tropical Africa, West Tropical Africa and Southern Africa. total = total number of species; endem. = number of endemic species; % = percentage of endemic species.

	Northeast Tropical Africa			West Tropical Africa			Southern Africa		
	total	endem.	%	total	endem.	%	total	endem.	%
Amischotolype				1					
Aneilema	34	13	38	10	4	40	11	1	9
Anthericopsis	1								
Buforrestia				2	1	50			
Coleotrype	1			1			1		
Commelina	36	10	28	23	3	13	17	3	18
Cyanotis	13	1	8	11	5	45	7	3	43
Floscopa	1			9	1	11	3		
Murdannia	5			3			1		
Palisota				9	2	22			
Pollia	2			2					
Polyspatha				3					
Stanfieldiella	1			4					
Tradescantia	1						1		
Total	95	24	25	78	16	21	41	7	17

indigenous genera in NETA, as compared with six of the 12 genera in WTA. Two of the forest genera, *Buforrestia* and *Palisota*, in WTA have endemics, whereas none of the forest genera in NETA has endemic species. The non-forest genus *Cyanotis* has much higher endemism in WTA than in NETA, but *Aneilema* and *Commelina* have far fewer endemic species in the former. *Aneilema*, however, has about the same percentage endemism in both floras (13 of 38 species (38%) endemic in NETA versus 4 of 10 (40%) in WTA).

The flora of Southern Africa, a region that is largely extra tropical, is poorer in genera (seven) and species (41) of Commelinaceae than both NETA and WTA (Table 3). All six of its native genera also occur in the other two floras. Its relative strengths are the presence of more species of *Floscopa* than NETA and more *Aneilema* species than WTA. It also has the same number of *Coleotrype* species (one) as the other two floras, although each flora has a different species. *Coleotrype* is the only forest genus in Southern Africa, its single species constituting just 2% of the Commelinaceae in the region.

Overall, species endemism in Southern African Commelinaceae (17%) is lower than in NETA or WTA. Like NETA, endemics occur only in *Aneilema*, *Commelina* and *Cyanotis*. In Southern Africa endemism is high in *Cyanotis* (43%, much higher than in NETA (11%), about the same as in WTA (45%)), moderate in *Commelina* (18% versus 28% in NETA and 13% in WTA), and low in *Aneilema* (9%, compared to 38% in NETA and 40% in WTA).

Phytogeographic Patterns of Northeast Tropical African Commelinaceae

The phytogeography of the Commelinaceae in NETA might be summarized by listing all the species that are present in each floristic zone of White (1983) that occurs in NETA. However, the detailed distributions of most Commelinaceae species in NETA have not been compiled, so any such list would be very incomplete. Moreover, it is the total distribution of a species that determines its phytogeographic relationships, not just its distribution within NETA. NETA Commelinaceae species may occur primarily outside the region in floristic zones that are themselves not present in NETA. Thus the phytogeographic patterns of the Commelinaceae of NETA will be presented in terms of floristic elements, that is, the floristic zone, or combination of zones, that represents the broad distribution patterns of the species.

Widespread Species

Some Commelinaceae that occur in NETA are so widespread elsewhere in Africa, and sometimes also outside of Africa, that trying to characterize them phytogeographically, in terms of White's floristic zones (White 1983), would be meaningless. These include *Commelina africana*, *C. benghalensis*, *C. bracteosa*, *C. diffusa*, *C. erecta*, *C. forskaolii*, *C. subulata*, *Floscopa glomerata* and *Murdannia simplex*. All of these species, except *C. bracteosa* and *Floscopa glomerata*, are also recorded outside of Africa.

The Somali-Masai Element

White's Somali-Masai regional center of endemism covers the greatest area of any floristic zone in NETA. It also encompasses a diverse array of climatic conditions and habitats. Therefore, it is hardly surprising that the majority of Commelinaceae species in NETA occur in this region. The species that characterize the Somali-Masai floristic zone can be separated into three groups on the basis of their distributions.

The Somali Endemics – The flora of Somalia is poor in numbers of species of Commelinaceae but high in endemism (see above). The endemic species of *Aneilema* have been dis-

cussed above. The endemic species of *Commelina* in Somalia, like those of *Aneilema*, do not represent a single lineage. The one-seeded capsule locules and nearly linear lower petal in *C. somalensis* and *C. frutescens* suggest a possible relationship with *C. erecta* and *C. bracteosa*, but the Somalian endemics are too incompletely known to do more than speculate about their affinities.

The relationships of the two other endemic Somalian *Commelina* species are more certain. *Commelina arenicola* was first described as *C. africana* var. *circinata* by Chiovenda (1936) and accepted as such by Brenan (1964). However, its annual habit, buff-orange to apricot-pink flowers, and testa pattern all indicate a closer relationship with *Commelina subulata* and related species than with *C. africana* (Faden 1996). *Commelina arenicola* differs from other species of the *C. subulata* group by its bivalved (rather than trivalved) capsules and its occurrence at very low elevations near the coast.

Commelina sp. 8 of *Flora of Somalia* (Faden 1995) is very similar to and presumably closely related to *C. forskaolii*, differing chiefly by its putatively yellow flowers. This apparently new species is noteworthy because it would represent a local endemic within the very wide range of *C. forskaolii*.

Northern Somali-Masai Species – These species are confined to the Somali-Masai floristic zone within NETA but are not largely or entirely restricted to Somalia. They also do not extend south of the equator in Kenya. These species include *Aneilema somaliense*, *A. grandibracteolatum*, *A. gillettii*, *A. ephemerum*, *A. sebitense* and *Commelina stefaniniana*. The possible relationships of the *Aneilema* species have been discussed above. *Commelina stefaniniana* has so many unusual features, such as purple-spotted leaves, scented flowers and pubescent sepals, that its relationships are unclear.

Southern Somali-Masai Species – These species are restricted to the Somali-Masai floral zone within NETA and are entirely or chiefly in Kenya within the region, occurring at least partly south of the equator, or they extend south to Tanzania or west, at least to Uganda. Taxa that are mainly Kenyan but reach southern Ethiopia include *Aneilema rendlei* (also occurs in northern Tanzania), *A. indehiscens* subsp. *keniense* (also in Rwanda), *A. recurvatum* (also in Uganda and northwestern Tanzania), and *Commelina reptans* (extends to Rwanda, Burundi and northern Tanzania). Somali-Masai species in Kenya that do not reach Ethiopia include *Aneilema brenanianum* (extends to Tanzania), *A succulentum*, *A. tanaense*, *Commelina lugardii* (extends to eastern Congo (Kinshasa) and northern Tanzania), *C. melanorrhiza* (which has a sister species in Ethiopia: *C.* sp. 17), *C. nairobiensis* and *Murdannia clarkeana* (plants from Chad and Central African Republic may be conspecific).

The Sudanian Element

There are few Commelinaceae that are mainly restricted to the Sudanian floristic region in Africa as a whole. They constitute a group of five related species of *Aneilema* section *Brevibarbata* that is centered in West Tropical Africa (Faden 1991; Morton 1967). Only *A. lanceolatum* enters NETA where it is known from a single collection from the Lake Turkana region of Kenya in the Somali-Masai floristic zone.

The Zambesian Element

The Zambesian element in the NETA Commelinaceae species consists of those species that occur primarily to the south of NETA in the Zambesian regional center of endemism. These include *Aneilema hockii*, *A. johnstonii*, *Commelina petersii* and *C. kotschyi* that occur in NETA in the Somali-Masai floristic zone. Zambesian species requiring a higher rainfall, *e.g. Aneilema spekei* and *A. hirtum*, occur in the

Lake Victoria floristic zone in Kenya and Sudanian floristic zone in Ethiopia. A third group of Zambesian species, such as *Commelina imberbis*, *C. zambesica* and *Cyanotis foecunda*, are mainly Zambesian in their distributions but have apparently minor range extensions into West or Central Africa. A fourth group of Zambesian species reach Kenya but not Ethiopia. They may occur in the Somali-Masai floristic zone (*Aneilema nicholsonii*) or Lake Victoria floristic zone (*Cyanotis paludosa* and *Murdannia semiteres*). It is noteworthy that the latter two species are aquatic or semiaquatic.

The Sudanian/Zambesian Element

This flora element consists of species that are widespread in both the Sudanian and Zambesian floristic zones. They are best exemplified by *Cyanotis caespitosa*, *C. lanata* and *C. longifolia*. The aquatic, *Murdannia tenuissima*, also shows this general pattern, but it also occurs in the transitional zone to the Guineo-Congolian floristic zone. No *Aneilema* species shows this pattern, and the *Commelina* species that more or less exemplify it appear to be primarily Zambesian with much poorer representation in the Sudanian floristic zone, based on Brenan (1968), unless this is an artifact of undercollecting. They have been treated as Zambesian above.

The Afromontane Element

Although Commelinaceae have been recorded up to 4,200 m in Africa (see Ensermu and Faden 1997, for *Cyanotis barbata*), few species grow above 2000 m. The most characteristic species that occur in the Afromontane floristic zone in NETA are *Aneilema leiocaule* and *Cyanotis barbata* of Kenya and Ethiopia, *Aneilema minutiflorum* of Kenya and *Cyanotis polyrrhiza* of Ethiopia. The *Aneilema* species are forest plants, whereas the *Cyanotis* species grow in open, exposed situations. *Commelina africana* frequently occurs in open habitats in the Afromontane floristic zone, especially in Ethiopia, but it is also well-represented in the Somali-Masai and Zanzibar-Inhambane floristic zones. *Aneilema aequinoctiale* occurs in forest and at forest edges, but it occurs mainly outside the Afromontane floristic zone of White (1983). *Commelina foliacea* can occur in the Afromontane floristic zone in montane forest, but it is more common at lower elevations in other floristic zones, at least in Kenya. The sole collection of *Commelina* sp. 2 of Ensermu and Faden (1997) is recorded from montane forest.

The Zanzibar-Inhambane Element

The Zanzibar-Inhambane regional mosaic extends mainly along the coast from southern Somalia to southern Mozambique. The Commelinaceae that characterize this floristic zone in NETA are relatively local endemics, *e.g. Aneilema clarkei*, *A. calceolus*, *A. lamuense*, *A. taylorii* and *Murdannia axillaris* (see Faden 1991 for distribution maps of the *Aneilema* species). The *Aneilema* species are related to species from the Somali-Masai floristic zone. *Murdannia axillaris*, the only African *Murdannia* with biseriate seeds, is more closely related to the Asian *M. blumei* (Hassk.) Brenan than to any other African species.

The Guineo-Congolian Element

The Guineo-Congolian regional center of endemism (White 1983) does not occur in NETA. Consequently there are few Guineo-Congolian species of Commelinaceae in the flora. Six Guineo-Congolian species or subspecies extend from West and Central Africa to NETA: *Aneilema aequinoctiale* subsp. *aequinoctiale* (Ethiopia), *A. beniniense* (Ethiopia and Kenya), *Commelina capitata* (Kenya), *Pollia condensata* (Ethiopia and Kenya), *P. mannii* (Ethiopia) and *Stanfieldiella imperforata* (Ethiopia).

The Guineo-Congolian species are all

restricted in their distributions in NETA and are disjunct from their nearest localities to the west or south. Those species that are recorded from Ethiopia occur in moist forest, mainly between 1000 and 1300 m elevation. Such forests are afromontane in structure and species composition, but they include a number of Guineo-Congolian species, according to Friis (1992). Because of their low elevations, such forests lie in the Sudanian floristic zone of Illubabor and Kefa regions. In Kenya the Guineo-Congolian species are found mainly in the Kakamega Forest or nearby forests, between 1550-1680 m, in western Kenya in the Lake Victoria floristic zone. An endemic forest species in the Kakamega area, *Commelina albiflora*, might have Guineo-Congolian affinities, but its actual relationships are unclear.

Guineo-Congolian species or taxa related to them may also occur in coastal forests of Kenya and Tanzania in the Zanzibar-Inhambane floristic zone (Faden 1974a). *Aneilema nyasense*, known in NETA by a single collection from the Shimba Hills in coastal Kenya, occurs primarily in eastern Congolian forests, although it also is present in Tanzania, Malawi and Mozambique. *Coleotrype brueckneriana* Mildbr., known only from a single locality along the Kenya coast and two localities in eastern Tanzania, has a sister relationship with the Guineo-Congolian species *C. laurentii* K. Schum., which extends from West Africa to central Uganda. These are the only two white-flowered species of *Coleotrype*.

Relationships with the Arabian Peninsula and India

Fourteen species of Commelinaceae were recorded from Yemen by Wood (1997). I have not been able to find convincing records of other species from the Arabian Peninsula – *e.g.*, Migahid (1989) includes *C. boissieriana* C. B. Clarke from Saudi Arabia, but that apparently is a synonym of *C. imberbis* – so Wood's flora will serve as the basis for the following comparison. Two species, *Aneilema woodii* Faden and *Cyanotis nyctitropa* Deflers, were considered endemic to Yemen (Wood 1997). The remaining 12 species also occur in NETA (Table 4). Among these, five are clearly African species that extend only to the Arabian Peninsula: *Aneilema forskalii*, *Commelina africana*, *C. imberbis*, *C. latifolia* and *Cyanotis lanata*. The remaining seven also extend at least as far as India, if a broad interpretation of *Commelina erecta* is used (see below).

A further uncertainty concerns *Cyanotis nyctitropa*, which is exceedingly close, both morphologically and geographically, to *C. somaliense* of northern Somalia. They are at least very closely related, if not conspecific. Their relationships appear to be with African species such as *C. foecunda* Hassk. It may be noted here that the plant in horticulture under the epithet *C. somaliensis* is not conspecific with the Somalian plant.

The one certain endemic Commelinaceae in the Arabian Peninsula is *Aneilema woodii*, which presently is known from a single locality in Yemen. It naturally hybridizes with *Aneilema forskalii*, with the hybrids possibly competing with *A. woodii* for space and perhaps pushing it to the brink of extinction. Both *A. woodii* and *A. forskalii* belong to *Aneilema* section *Lamprodithyros* which is otherwise confined to Africa, so the African, especially Northeast Tropical African, relationships of *A. woodii* are certain.

A surprisingly large number of species (14, or 15% of total species in NETA) is shared between NETA and India (Table 4). This exceeds the number shared between NETA and the Arabian Peninsula. The seven species that occur in NETA and India, but are lacking from the Arabian Peninsula, are especially noteworthy. Two of these, *Cyanotis axillaris* and

Table 4. The Northeast Tropical African species of Commelinaceae with distributions in the Arabian Peninsula or India. * = conspecificity of the Asian and African plants is uncertain; ** = correct name is uncertain.

Species	Northeast Africa	Arabian Peninsula	India
Aneilema forskalii	+	+	
Commelina africana	+	+	
C. albescens	+	+	+
C. benghalensis	+	+	+
C. diffusa	+	+	+
*C. erecta**	+	+	+
C. forskaolii	+	+	+
C. imberbis	+	+	
*C. kotschyi**	+		+
C. latifolia	+	+	
C. petersii	+		+
C. subulata	+	+	+
*Cyanotis arachnoidea**	+		+
C. axillaris	+		+
*C. barbata/vaga***	+	+	+
C. cristata	+		+
C. lanata	+	+	
*C. somaliensis/nyctitropa**	+	+	
*Murdannia semiteres**	+		+
*Murdannia simplex**	+		+

C. cristata, are clearly Asian species with weedy tendencies that may have reached Africa only recently. Indeed, as noted above, *C. cristata*, which has also collected from Socotra, is known in continental Africa from a single, recent collection. *Cyanotis axillaris* has been found in Africa in Kenya, Tanzania, Malawi, Sudan, Chad and Cameroon, but there are few collections.

The two species of *Commelina* that are disjunct between NETA and India, *C. kotschyi* and *C. petersii*, have much more restricted Asian than African ranges. *Commelina kotschyi* ranges in Africa from northern Ethiopia south to Swaziland, South Africa and Botswana. Rao (1967) suggested that, in view of its scarcity in India, where it occurs only in the Western Ghats, *C. kotschyi* might have arrived there from Africa only recently.

Commelina petersii has only just been reported from the Indian subregion (Faden 2000). Until recently, the species was known in India and Sri Lanka as 'C. persicariaefolia Wight' (Clarke 1881; Hooker 1892, 1898), a later homonym for *C. persicariifolia* Delile. Rao (1967) correctly concluded that it was an African species, but misidentified it as *C. imberbis*, which is not found in India. In Africa *Commelina petersii* ranges from Eritrea to Botswana, Angola and Namibia. Its report from West Tropical Africa

by Brenan (1968) was based on erroneously determined collections, but I have seen a specimen from Sao Tomé in the Gulf of Guinea (*Figueiredo & Arriegas* 55, K), where perhaps it was introduced. In Asia, Rao (1967) recorded it from "very limited localities in Peninsular India." I found this species to be fairly common in Sri Lanka in 1976-1977. It is also reported from Burma (Clarke 1881; Hooker 1898).

The absence of *Commelina kotschyi* and *C. petersii* from the Arabian Peninsula is surprising. The occurrence of *C. kotschyi* in northern Ethiopia and *C. petersii* in Eritrea (Ensermu & Faden 1997) would anticipate their presence across the Red Sea. Wood (1997) treated a Schweinfurth record of *C. petersii* from Yemen as likely to have been *C. imberbis*, but neither he nor I have seen a Schweinfurth collection determined as *C. petersii* to confirm this.

The three other species that occur in NETA and India but ostensibly not in between, *Cyanotis arachnoidea*, *Murdannia semiteres* and *M. simplex*, all have taxonomic problems. There are varying degrees of uncertainty about the conspecificity of the Asian and African plants in each case. All are currently being investigated.

The remaining seven species present both in NETA and India also occur in Yemen. The only species that in controversial is *Commelina erecta*. This American and African species definitely occurs in Yemen. Morton (1967) concluded that *C. erecta* also occurred in India and Australia, with Indian *C. kurzii* being conspecific with *C. erecta*. Brenan (1968) and Rao *et al.* (1972) accepted Morton's distribution for *C. erecta*. My field observations of *C. kurzii* in Sri Lanka showed that it consistently has lilac to lavender flowers, whereas American and African *C. erecta* is blue-flowered. *Commelina kurzii* is a plant of shady locations, and has been reported as hexaploid and octaploid (see Rao *et al.* (1972) for a summary of published counts). *Commelina erecta* occurs mainly in more open habitats, at least in Africa, and has only been recorded as tetraploid (Faden unpublished; Rao *et al.* 1972). Thus, the conspecificity of African *C. erecta* and Indian *C. kurzii* is hardly established.

Discussion

A major problem in determining biogeographic patterns and relationships in a group is the certainty of the taxonomy. The taxonomy is reasonably well established for the overwhelming majority of Commelinaceae of NETA. Ten new species of *Aneilema* and five of *Commelina* (plus seven new subspecies within these genera) from this area have been described in recent years (Faden 1984, 1991, 1994, 1996). Yet others remain to be described, such as two species of *Commelina* from Ethiopia cited in Ensermu & Faden (1997).

The status of some taxa remains uncertain. For example, plants that have been called *Commelina velutina* in Kenya (Faden 1994) do not closely resemble typical plants of that species from Cameroon. The species that was called *Commelina elgonensis* in *Upland Kenya Wild Flowers* (Faden 1994) and *C. schweinfurthii* in *Flora of Ethiopia and Eritrea* (Ensermu & Faden 1997) is a member of a species group that has its center of morphological and taxonomic diversity south of our area. This species group has not been studied fully, so species limits and their nomenclatural consequences remain unclear. Similar problems exist in the *Commelina eckloniana* complex. The plants treated under this name in Ethiopia (Ensermu & Faden 1997) and in Upland Kenya (Faden 1994) may not belong to the same species.

Other taxonomic problems concern species that have been typified by non-African material, *e.g. Cyanotis arachnoidea* and *Murdannia semiteres*, which are both typified by specimens from India. The African plants treated under these epithets have yet to be shown convinc-

ingly to be conspecific with the Indian material.

Comparing the Commelinaceae of NETA with those of other floras has additional problems. The taxonomy of those authors has to be checked critically by examining specimens, when possible. Furthermore, distribution records from even the most recent floras soon become outdated as a result of active collecting, both within and outside the flora area.

The treatment of the Commelinaceae for the *Flora of West Tropical Africa* (Brenan 1968) may serve as an example. I have added two species to Brenan's total, an undescribed *Polyspatha* species, which was overlooked by Brenan, and *Commelina gambiae* C. B. Clarke, which was treated as a variety of *C. nigritana* Benth., but I now consider a distinct species. I have also deducted one species, *Commelina petersii*, because the cited specimens, when examined recently at Kew, proved to be *C. imberbis*. Brenan listed 20 species exclusively from the WTA area. That number has been reduced to 16 by collections from outside the WTA area.

More recent floristic treatments of Commelinaceae have had changes too. I now recognize *Commelina scandens* Welw. ex C. B. Clarke as distinct from *C. diffusa*, which adds one species to the *Flora of Southern Africa* (Obermeyer & Faden 1985). *Commelina* sp. aff. *erecta*, a robust plant from coastal Kenya with three dehiscent capsule locules, has been added to the Commelinaceae of Somalia (Faden 1995), based on the collection *Alstrup & Michelsen* 144 (C) examined in 1999. *Cyanotis* sp. 7 in *Flora of Ethiopia and Eritrea* (Ensermu and Faden 1997), which was reported only from Ethiopia, has recently been matched with a specimen in the Kew Herbarium from Ivory Coast (*Aké Assi* 6578). Whether it is a rare species with a widely disjunct distribution or an odd form of *C. lanata* that crops up occasionally remains to be determined, but it is not an Ethiopian endemic.

With 95 species, NETA is rich in Commelinaceae, especially when compared with West Tropical Africa and Southern Africa. However, Tropical East Africa (Kenya, Uganda and Tanzania) is richer still, with an estimated 133 species (Faden 1983), and Tanzania alone has approximately 100 species. The richness of all these floras is largely due to the diversity of species in the non-forest genera, especially *Aneilema* and *Commelina*.

The Somali-Masai floristic zone has been a source of origin of some groups of Commelinaceae and of the diversification of others. *Aneilema* section *Somaliensia* and perhaps section *Lamprodithyros* originated within NETA. A secondary radiation of *Aneilema* section *Lamprodithyros* species occurred in the Zanzibar-Inhambane floristic zone. The blue-flowered *Commelina* species belonging to Clarke's section *Disseocarpus* (Clarke 1881), *e.g. C. kotschyi*, *C. latifolia* and *C. petersii*, are well represented within NETA and may have diversified within the Somali-Masai floristic zone.

Endemism is relatively high in the Commelinaceae of NETA, but it is unevenly distributed. It is lacking in Djibouti and Eritrea, low in Ethiopia and Kenya, and high in Somalia. The endemics tend to be locally distributed, and only six of the 24 species endemic to NETA occur in more than one country. Many of the endemics are poorly collected and incompletely known.

The endemic Commelinaceae of Somalia are not only numerous but unusual morphologically. The roots of *Aneilema obbiadense* spread out just beneath the surface of the sand for up to 150 cm and are used locally for weaving containers. The spherical inflorescences are up to 30 cm in diameter-the largest in the genus-and function as tumbleweeds for seed dispersal (Faden 1995). The large papery spathes of *Commelina frutescens*, the only shrub-like species of *Commelina*, may also serve for wind dispersal. The yellow flower color

reported for this species and for *C.* sp. 8 is unusual in *Commelina*.

The major phytogeographic relationships of the Commelinaceae of NETA appear to be to the south, particularly with Tanzania. Relationships with West Africa are few, and are represented by small Guineo-Congolian and Sudanian flora elements. The Commelinaceae of the Arabian Peninsula are all species that occur in NETA or are related to NETA species. Some curious disjunctions between species in NETA and India may indicate occasional long-distance dispersal. Some reported African-Indian distributions might be due to faulty taxonomy.

A commonality of Commelinaceae in African floras is the preponderance of non-forest species, even in floras that contain large areas of lowland rainforest. This may be related to the usually greater extent of non-forest than forest habitats in the total flora area. In contrast, a probably incomplete tally that I have made of the Commelinaceae species of Gabon, a country that is mainly rainforest, includes 20 species of forest genera and only 13 of non-forest genera. Perhaps most striking is the overall low species diversity when non-forest habitats are scarce.

The non-forest genera have diversified ecologically into a much greater range of habitats than have the forest genera. Thus there are significant numbers of forest species of *Commelina* and *Aneilema*, some of which are very local and others widespread. The forest genera species, in contrast, always seem to need moisture or shade or both to succeed, even when they occur in disturbed situations, including cultivation. There are no non-forest species of forest genera.

Several lines of evidence support that rainforest was once more widespread in eastern Africa than it is at present. The numerous shared species and sister species relationships between the coastal forests of East Africa and the Guineo-Congolian forests led me to conclude that these forests had been directly connected in the past (Faden 1974a), probably during two different periods. Moreau (1966) came to the same conclusion based on bird distributions.

Palynological studies have provided much information about the climate of East Africa during the Pleiostocene. This evidence was reviewed by Hamilton (1974). A pollen core from Lake Victoria by Kendall (1969) showed that the period between 8000 and 3000 years B.P. showed the greatest forest expansion since 12500 B.P., but the extent of the forest is unknown.

Clear evidence of a wet forest in a presently non-forested region is supported by a middle Miocene flora from the Rift Valley of Kenya (Jacobs & Kabuye 1987). Macrofossils include a new species of *Pollia*, *P. tugenensis* Jacobs & Kabuye (Jacobs & Kabuye 1989). The 12.6 million year old fossils of a forest genus of Commelinaceae and other species unambiguously demonstrate the presence of wet forest. The temperature at the time of deposition appears to have been similar to present temperatures, but the rainfall must have been higher and less seasonal (Jacobs & Deino 1996).

The expansion and contraction of forests in Africa would have had profound effects upon the diversity of Commelinaceae. Expansion of the forest would have allowed the forest genera to expand their ranges and perhaps diversify. Whether most species of the non-forest genera would have just retreated, adapted to moister conditions, or become extinct is unclear.

The effects of the contraction of the forests are more predictable. Forest species would have retreated or become extinct. Those that found suitable habitat might have persisted, disjunct from the main populations. Those disjuncts would have speciated occasionally, *e.g. Coleotrype brueckneriana*. The expanding non-forest habitats would have provided much new territory into which the non-forest genera could radiate and diversify.

Commelina and *Aneilema* appear preadapted for success in seasonally dry environments. To withstand drought some species have developed annual or geophytic habits. The spathes in *Commelina* provide mechanical protection for the buds and developing fruits. Probably more significantly, the mucilaginous secretions produced within the spathes protect the buds and young fruits against desiccation, regardless of the external weather conditions. In *Aneilema* a similar role is played by the glands on the cup-shaped bracteoles that surround the youngest buds, by the glands on the sepals that in bud moisturize the inner floral whorls, and by the glandular hairs that cover the ovaries and young fruits in nearly all species.

Cyanotis also appears well adapted to dry conditions, but whether this was due to a preadaptation is unclear. A well developed adaxial hypodermis gives the leaves great water-storing capacity. Despite this, many of the species have developed a wide array of underground storage organs, such as rhizomes, root tubers, bulbs and corms, and a few are annuals. *Cyanotis* buds and fruits are protected by large, usually hairy, overlapping, shingle-like bracteoles.

The great richness of African Commelinaceae is mainly due to speciation of the non-forest genera. Only when we can thoroughly document present distributions, determine phylogenetic relationships, and compare these to shifting climates and vegetation patterns can we understand how and when this diversity arose.

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Appendix 1. The Commelinaceae of Northeast Tropical Africa.

FEE = Flora of Ethiopia and Eritrea (Ensermu & Faden 1997); FS = Flora of Somalia (Faden 1995); UKWF2 = Upland Kenya Wild Flowers (Faden 1994); + = species present in the country; * = endemic in the country or in countries in Northeast Tropical Africa.

Species	Djibouti	Somalia	Eritrea	Ethiopia	Kenya
Aneilema aequinoctiale (P.Beauv.) Loudon subsp. *aequinoctiale*				+	
A. aequinoctiale (P.Beauv.) Loudon subsp. nov.					+
A. benadirense Chiov.		*			
A. beniniense (P.Beauv.) Kunth				+	+
A. brenanianum Faden					+
A. calceolus Brenan					+
A. clarkei Rendle					+
A. ephemerum Faden					*
A. forskalii Kunth	+		+	+	
A. gillettii Brenan				*	*
A. grandibracteolatum Faden				*	
A. hirtum A.Rich.				+	+
A. hockii De Wild.				+	+
A. indehiscens Faden subsp. *indehiscens*					+
A. indehiscens Faden subsp. *keniense* Faden				+	+
A. johnstonii K.Schum.				+	+
A. lamuense Faden		*			*
A. lanceolatum Benth.					+
A. leiocaule K.Schum.				+	+
A. longicapsa Faden		*			
A. minutiflorum Faden					+
A. nicholsonii C.B.Clarke					+
A. nyasense C.B.Clarke					+
A. obbiadense Chiov.		*			
A. petersii (Hassk.) C.B.Clarke subsp. *pallidiflorum* Faden					+
A. petersii (Hassk.) C.B.Clarke subsp. *petersii*				+	+
A. pusillum Chiov. subsp. *gypsophilum* Faden		*			
A. pusillum Chiov. subsp. *pusillum*		*			
A. pusillum Chiov. subsp. *thulinii* Faden		*			
A. pusillum Chiov. subsp. *variabile* Faden		*		*	*
A. recurvatum Faden				+	+
A. rendlei C.B.Clarke				+	+
A. sebitense Faden				*	*
A. somaliense C.B.Clarke		*		*	*
A. spekei C.B.Clarke				+	+
A. succulentum Faden					*
A. tanaense Faden					*
A. taylorii C.B.Clarke					+
A. trispermum Faden		*			
A. zebrinum Chiov.				+	+
Anthericopsis sepalosa (C.B.Clarke) Engl.		+		+	+
Coleotrype brueckneriana Mildbr.					+

Species	Djibouti	Somalia	Eritrea	Ethiopia	Kenya
Commelina africana L.	+	+	+	+	+
C. albescens Hassk.	+	+	+	+	+
C. albiflora Faden					*
C. arenicola Faden		*			
C. benghalensis L.	+	+	+	+	+
C. bracteosa Hassk.					+
C. capitata Benth.					+
C. diffusa Burm.f.				+	+
C. echinosperma K.Schum.					+
C. eckloniana Kunth				+	+
C. elgonensis Bullock / *C. schweinfurthii* C.B.Clarke				+	+
C. erecta L.		+		+	+
C. foliacea Chiov. subsp. *amplexicaulis* Faden					+
C. foliacea Chiov. subsp. *foliacea*				+	+
C. forskaolii Vahl	+	+	+	+	+
C. frutescens Faden		*			
C. imberbis Ehrenb. ex Hassk.			+	+	+
C. kotschyi Hassk.				+	+
C. latifolia Hochst. ex A.Rich.			+	+	+
C. lugardii Bullock					+
C. melanorrhiza Faden					*
C. nairobiensis Faden					*
C. petersii Hassk.		+	+	+	+
C. reptans Brenan				+	+
C. sp. aff. erecta L.		+			+
C. sp. aff. imberbis Ehrenb. ex Hassk					+
C. sp. 8 of FS		*			
C. sp. 2 of FEE				*	
C. sp. 17 of FEE				*	
C. sp. D of UKWF2 (=C. sp. 5 of FS)		+			+
C. somalensis Chiov.		*			
C. stefaniniana Chiov.		*		*	*
C. subulata Roth			+	+	+
C. triangulispatha Mildbr.					+
C. trilobosperma K.Schum.					+
C. velutina Mildbr.					+
C. zambesica C.B.Clarke				+	+
Cyanotis arachnoidea C.B.Clarke					+
C. axillaris (L.) Sweet					+
C. barbata D.Don			+	+	+
C. caespitosa Kotschy & Peyr.				+	+
C. cristata (L.) D.Don			+		
C. foecunda Hochst. ex Hassk.				+	+
C. lanata Benth.				+	+
C. longifolia Benth.				+	+
C. paludosa Brenan					+
C. polyrrhiza Hochst. ex Hassk.				*	
C. somaliensis C.B.Clarke		+			
C. sp. A of UKWF2					+
C. sp. 7 of FEE				+	

Species	Djibouti	Somalia	Eritrea	Ethiopia	Kenya
Floscopa glomerata (Willd. ex Schult. & Schult.f.) Hassk.				+	+
Murdannia axillaris Brenan					+
M. clarkeana Brenan					+
M. semiteres (Dalz.) Santapau					+
M. simplex (Vahl) Brenan		+		+	+
M. tenuissima (A.Chev.) Brenan				+	
Pollia condensata C.B.Clarke				+	+
P. mannii C.B.Clarke				+	
Stanfieldiella imperforata (C.B.Clarke) Brenan var. *glabrisepala* (De Wild.) Brenan				+	
S. imperforata (C.B.Clarke) Brenan var. *imperforata*				+	
Tradescantia zebrina Hort. ex Bosse					+

Endemism and patterns of distribution of the genus Aloe (Aloaceae) in the flora of Ethiopia and Eritrea

Sebsebe Demissew, Inger Nordal & Odd E. Stabbetorp

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It is demonstrated that 35 (87%) of the 40 species of *Aloe* found in the area covered by the Flora of Ethiopia and Eritrea are endemic to this area. Most of the species are restricted to three rather well defined local centres of endemism. These are (1) a northern and central highland area, (2) an eastern highland area, and (3) a southern highland and lowland area. Each area has its own set of locally endemic species. The majority of the species of *Aloe* are either restricted to *Acacia-Commiphora* bushland, or to dry montane evergreen forest and scrub. The distribution of the Aloe species is compared with the African phytochoria recognised by White. Thirteen species (33%) belong to an Afromontane element; eight species (20%) are Afromontane/Somalia-Masai transgressors; eighteen species (45%) belong to a Somalia-Masai element. One species (2%) is a Sudanian/Somalia-Masai/Afromontane transgressor. In comparison with other areas of Eastern Africa, there is a notably high concentration of high altitude Afromontane species in the Flora area. Moreover, the genus reaches more than 1000 m higher above sea level in the Flora area than in Tropical East Africa. There seems to be a proliferation of the genus at higher altitudes in the Flora area. A somewhat similar trend is seen in Somalia, but not in Tropical East Africa.

Sebsebe Demissew, National Herbarium, Addis Ababa University, P.O. Box 3434, Addis Ababa, Ethiopia. E-mail: nat.heb@telecom.net.et

Inger Nordal, Biological Institute, University of Oslo, P.O. Box 1045, Blindern, N-0316 Oslo, Norway. E-mail: inger.nordal@bio.uio.no

Odd E. Stabbetorp, Norwegian Institute for Nature Research, P.O. Box 736, N-0105 Oslo, Norway. E-mail: odd.stabbetorp@ninaosl.ninaniku.no

Introduction

The genus *Aloe* (Aloaceae) consists of more than 360 species (Mabberley 1987). Almost all indigenous records of the species are from Africa south of the Sahara (including Socotra and Madagascar), except for a few species which extend into the Arabian Peninsula. The genus has been introduced to the West Indies and many other tropical countries.

G.W. Reynolds, a highly qualified South African amateur researcher of the genus *Aloe*, has produced two monumental publications of the genus. The first (Reynolds 1950) described the species of *Aloe* of South Africa, the second

one (Reynolds 1966) the species of tropical Africa and Madagascar. Together, these two books provide the information on the taxonomy and distribution of all African species, as they were known up to the date of publication. The two volumes spurred taxonomic, floristic and other types of research in various parts of the continent. Recent taxonomic studies in East and North-East Tropical Africa, including the Floras of Ethiopia and Eritrea, Somalia and Tropical East Africa, have indicated a large number of endemic or near-endemic species. For example in Tropical East Africa (Kenya, Uganda and Tanzania) 50 out of the 83 species known (60%) are endemic to the region (Carter 1994). In North-East Tropical Africa (Ethiopia, Eritrea, Sudan, Somalia and Djibouti) 77 species of *Aloe* have been reported to occur. Of these 59 (76%) are believed to be endemic to the region (Carter 1994; Lavranos 1995; Sebsebe Demissew 1996; Sebsebe Demissew & Gilbert 1997; Sebsebe Demissew & Gilbert 2000; Sebsebe Demissew & Dioli 2000).

Many species of *Aloe* are highly threatened. There are several reasons for this. Perhaps the most important reason is that many species, especially those that have a very restricted distribution area and only small populations, are very much sought after by succulent enthusiasts for cultivation as rarities. Other species are collected for their use in medicine and the cosmetic industry (Sebsebe Demissew 1996). All species of *Aloe* are on the CITES list number one in order to control the international trade in species of this genus as far as possible. It is therefore important to improve and explore the documented information on taxonomy, distribution and ecology of the *Aloe* species. This will help the conservation efforts and attempts at sustainable use, as well as further research in other relevant fields, such as the chemistry of the natural compounds. Therefore an analysis based on the recent flora contribution (Sebsebe Demissew & Gilbert 1997) and later research by the authors and others (Sebsebe Demissew & Gilbert 2000; Sebsebe Demissew & Dioli 2000) is presented here. Note that the recently described *A. bertemariae* has not been included in the review of geographical distribution patterns in Fig. 7.

Speciation and endemicity of Aloe species

In the area covered by the Flora of Ethiopia and Eritrea (FEE) 35 (87%) are endemic or near-endemic (that is have a restricted distribution in one or two neighbouring countries) of the 40 species known so far. Three of the species have been subdivided into subspecies; for two of these taxa all the infraspecific taxa are endemic or near-endemic. The average percentage of endemic and near endemic species for all vascular plants in the Flora area is approximately 27% according to calculations based on the volumes of the Flora published so far (Friis *et al.* 2001). The degree of endemism in the genus *Aloe* in the Flora area is therefore nearly three times as high as the average figure. Species of *Aloe* seem generally to have restricted distribution areas, both in the Flora area and in other areas. No suggestion for the reasons behind this prolific speciation and limited distribution of the species has been offered in the literature, but it could be speculated that the strange chromosome evolution of *Aloe* and its possible consequences might give clues for a possible explanation. According to Brandham & Doherty (1998) the family Aloaceae is one of the most stable angiosperm families with regard to having a uniform bimodal karyotype in all species and the same basic chromosome number of x=7, comprising four long chromosomes and three short ones. The same authors have indicated that despite the karyotypic uniformity, some variation between species and genera in overall chromosome size *i.e.* in nuclear DNA amount has been

observed. In the case of the genus *Aloe*, it has been shown that the increase in the DNA amount coincides with evolutionary advancement – the advanced species having higher amount of DNA. The same authors have also observed that structural changes in *Aloe* chromosomes are common, but do not occur as homozygotes and take no part in the speciation. The stable chromosome morphology, the constant basic number and the selection against structural changes of chromosomes getting fixed, coupled with the variations in the DNA amount in the different species, are factors which most likely play a significant part in the evolution of *Aloe* species. One could speculate that these factors might lead to the formation of homogenous populations with very limited hybridization with neighbouring populations, which would help accounting for the situations described and discussed in this paper.

Distribution of Aloe species in relation to vegetation types

The current paper will attribute the *Aloe* species to a number of ecological zones (vegetation types in a broad sense), and to phytogeographical categories.

The ecological zones used for this study represent a slight modification of the nine major vegetation types recognised in the National Conservation Strategy (CSE 1997) and the coastal vegetation (added here). These ecological zones are further discussed in another symposium paper (Friis & Sebsebe Demissew 2001). The ten major vegetation types are, starting from the lowermost altitude:

1. Coastal vegetation. This consists of a whole range of vegetation types extending from the littoral zone to various types of coastal bushland. It is found only along the Red Sea Coast.
2. Desert and semidesert scrubland. Usually an open vegetation type with scattered shrubs or small trees and annual herbs. Succulents can be present or frequent. Extensive areas with this vegetation type exist in Afar Depression, the Ogaden and the area around Lake Chew Bahir and the Omo Delta below *c.* 500 m.
3. Lowland semi-evergreen forest. The vegetation type is characterized by mainly semi-deciduous trees and shrubby species and grasses. The woody species mainly include tall emergent trees. This vegetation type, which occurs in the Gambella Region in western Ethiopia, has been described only recently (Friis 1992). It occurs at 450-650 m.
4. *Acacia-Commiphora* bushland. This vegetation type is characterized by drought tolerant trees and shrubs, which have either small deciduous leaves or leathery persisting leaves. The canopy may reach tree-size, but is often lower. The understorey mainly consists of shrubs, perennial herbs and grasses. The trees and shrubs include species of *Acacia*, *Balanites*, various species of *Commiphora*, *Capparis*, *Combretum* and *Terminalia*. *Acacia-Commiphora* bushlands occur mainly in the north, east, south, central parts of the country at 900-1900 m.
5. *Combretum-Terminalia* woodland. This vegetation type is characterized by trees and shrubs, with fairly large deciduous leaves and an understorey of herbs and grasses which grow tall in open areas and in valleys. The dominant trees and shrubs include various species of *Combretum*, *Terminalia*, *Boswellia*, *Lannea*, *Anogeissus* and *Stereospermum*. The bamboo, *Oxytenanthera abyssinica*, is prominent in river valleys in western Ethiopia. *Combretum-Terminalia* woodlands occur mainly in the northwestern and western parts of the country, particularly in Beni-Shangul and Gumuz, and Gambella

Regions, in the Tekeze Valley and Shire lowlands in the north, the Didessa Valley in western, in south and northern Omo in southwestern Ethiopia at (500-)900-1900 m.

6. Evergreen scrub. This vegetation consists of evergreen bushes, *e.g.* species of *Euclea*, *Rhus*, *Carissa*, *Maytenus*, *Dodonaea*, *etc.* This vegetation is a transition zone between forest and woodland or bushlands. It occurs in many parts of the FEE area, where it forms a natural transitional vegetation belt around forests. However, due to human interference it has now replaced large areas in the highlands, which were probably forested previously. A special type is the Ericaceous scrub, which occurs at the upper limit of montane forest and forms a transition between forest and sub-Afroalpine vegetation. Evergreen scrub occurs at *c.* 1400-3500 m.
7. Dry evergreen montane forest and grassland. This is actually a complex, which also includes glades of grassland and wooded grassland with certain species of montane *Acacia*, and in principle the montane evergreen scrub is part of the same complex (Friis 1992). The vegetation type is characterized by small to large sized trees, and the extensive grasslands are rich in legumes. The common tree species include *Juniperus procera* and *Olea europaea* subsp. *cuspidata*. In the *Acacia* woodland and wooded grassland *A. abyssinica*, *A. negrii* and *A. pilispina* are the most common trees. The dry evergreen montane forests, *Acacia* woodlands and grasslands occur in much of the highlands in northern, north-western, central and south-western parts of the country, particularly in Shewa, Wello, Tigray, Gojam, Gonder, Gamo Gofa, Sidamo, Harerge, and Bale. On the northwestern parts of the plateau this vegetation type is found at 1900-3400 m.
8. Moist evergreen forest. This vegetation type is characterized by tall emergent and medium sized trees and by understorey shrubs. Based on altitude and floristic composition, it can be subdivided into two subtypes: (1) typical moist Afromontane forest, and (2) transitional forest. Emergent tree species typical of moist evergreen forests include in the Afromontane forest *Aningeria adolfi-friedericii*, *Albizia gummifera*, *Macaranga capensis* and *Ocotea kenyensis*. Characteristic canopy trees in the transitional forest are *Aningeria altissima*, *Alstonia boonei*, and *Manilcara butugi*. Moist evergreen forests occur mainly in western, south-western and south-eastern parts of the country. In western and south-western parts, these vegetation types occur between 1000 (near Tepi and Mizan) and 2500 m.
9. Afroalpine vegetation, including sub-Afroalpine vegetation. This vegetation type is characterized by small trees, shrubs, shrubby herbs at the lower altitudes, giant and small rosette herbs, cushion-plants and grasses, many of them forming tussocks, at the higher altitudes. Typical shrubby forms at the lower altitudes include species of *Erica* and *Hypericum*. Among the giant and small rosette herbs at higher altitudes are included the giant lobelia, *Lobelia rhynchopetalum*, species of *Kniphofia* and various species of Asteraceae, including *Dianthoseris* and *Haplocarpha*. Species of *Helichrysum* are prominent among the cushion plants, and species of *Alchemilla* among the dwarf shrubs. The transition in Ethiopia between the *Erica* scrub and Afroalpine vegetation is less sharp than on the high East African mountains. In the latter, the Afroalpine zone is characterized by the presence of giant and acaulescent rosette plants, cushion plants and tussock grasses (Hedberg 1964). This vegetation type occurs above 3400 m, with a transition zone to forest and

Table 1. Distributional status of the species of *Aloe* in FEE. Abbreviations for distributions: EA = species extending to East Africa (Ethiopia plus Somalia, Kenya, Uganda and/or Tanzania). WA = species extending to West Africa. NC = species endemic or near-endemic to Ethiopia, occurring in the Northern Central part of the country. S = species endemic or near-endemic to Ethiopia, occurring in the Southern part of the country. E = species endemic or near-endemic to Ethiopia, occurring in the Eastern part of the country. (e) = endemic. (n) = near-endemic. Abbreviations for Phytochoria: S-M = Somalia-Masai. SUD = Sudanian. AFM = Afromontane.

	Distribution	Altitudinal range	Coastal. Sea level	Desert and semi-desert Below 500 m	*Acacia-Commiphora* woodland (500-) 900-1900 m	Dry evergreen montane forest, etc. 1900-3200 m	Sub-Afroalpine vegetation Above 3200 m	Phytochoria according to White (1983)
A. trichosantha **subsp.** *trichosantha*	**NC(?n)**	900-1700 m			•			S-M/AFM
A. trichosantha **subsp.** *longiflora*	**NC/E/S(e)**	1000-1950 (-2200) m			•	•		S-M/AFM
A. citrina	**S(n)**	275-1000 m		•	•			S-M
A. pubescens	**NC/E(e)**	1800-2550 m				•		AFM
A. eumassawana	**NC(e)**	Sea level	•					S-M
A. schoelleri	**NC(e)**	c. 1500 m				•		S-M/AFM
A. macrocarpa	**WA**	1400-2200 (-3000) m			•	•		SUD/S-M/AFM
A. lateritia	**EA**	c. 1500 m			•			S-M
A. ellenbeckii	**S(n)**	c. 1600 m			•			S-M
A. kefaensis	**NC(e)**	c. 1800 m				•		AFM
A. ruspoliana	**S/E(n)**	300-1450 m		•	•			S-M
A. retrospiciens	**E(n)**	c. 1000 m			•			S-M
A. mcloughlinii	**S/E(e)**	1050-1250 m			•			S-M
A. pirottae	**S/E(e)**	1300-1800 m			•			S-M
A. parvidens	**S(n)**	1200-1450 m			•			S-M
A. rugosifolia	**S(n)**	c. 1350-1700 m			•			S-M
A. harlana	**E(e)**	1650-2100 m			•	(•)		S-M/AFM
A. monticola	**NC(e)**	c. 2450 m				•		AFM
A. percrassa	**NC(e)**	2100-2700 m				•		AFM
A. debrana	**NC(e)**	2000-2700 m				•		AFM
A. steudneri	**NC(e)**	2600-3150 m				•	•	AFM
A. ankoberensis	**NC(e)**	3000-3500 m				•	•	AFM
A. pulcherrima	**NC(e)**	2450-2700 m				•		AFM
A. trigonantha	**NC(e)**	c. 2100 m				•		AFM

	Distribution	Altitudinal range	Coastal. Sea level	Desert and semi-desert Below 500 m	*Acacia-Commiphora* woodland (500-) 900-1900 m	Dry evergreen montane forest, etc. 1900-3200 m	Sub-Afroalpine vegetation Above 3200 m	Phytochoria according to White (1983)
A. rivae	**EA**	1350-2000 m			•	•		S-M
A. secundiflora	**EA**	1350-1550 m			•			S-M
A. otallensis	**S(e)**	1200-1600 m			•			S-M
A. elegans	**NC(e)**	1500-2400 m			•	•		AFM
A. camperi	**NC(e)**	550-2700 m			•	•		S-M/AFM
A. adigratana	**NC(e)**	2000-2700 m				•		AFM
A. sinana	**NC(e)**	1250-1950 m			•	•		S-M/AFM
A. calidophila	**S(n)**	1200-1620 m			•			S-M
A. megalacantha **subsp.** *megalacantha*	**E(n)**	1100-1850 m			•			S-M
A. megalacantha **subsp.** *alticola*	**E(e)**	2100-2150 m				•		AFM
A. gilbertii **subsp.** *gilbertii*	**S(e)**	1300-1800 (-1900) m			•			S-M/AFM
A. gilbertii **subsp.** *megalacanthoides*	**S(e)**	1200-1350 m			•			S-M
A. schelpei	**NC(e)**	1700-2450 m				•		AFM
A. yavellana	**S(e)**	1600-1900 m			•	•		S-M/AFM
A. jacksonii	**S(n)**	c. 1050 m			•			S-M
A. tewoldii	**E(e)**	?c. 1500 m				•		AFM
A. vituensis	**EA**	c. 1200 m			•			S-M
A. friisii	**S(e)**	c. 1000 m			•			S-M
A. bertemariae	**S(e)**	300-400 m			•			S-M

evergreen scrub in the lower part of its range. It occurs on the highest mountain peaks in Ethiopia.

10. Riparian and swamp-vegetation. This vegetation type is characterized by a range of tree and shrubby species and associated herbs and grasses. Swamps are dominated by sedges, grasses and many herbs.

The ten categories mentioned above have for this analysis been modified as follows to describe the vegetation types in which *Aloe* species occur in the FEE area. In most of these vegetation types species of *Aloe* frequently occur on rocky outcrops or on rock faces and cliffs without much other vegetation. However, in the *Acacia-Commiphora* bushland, species of

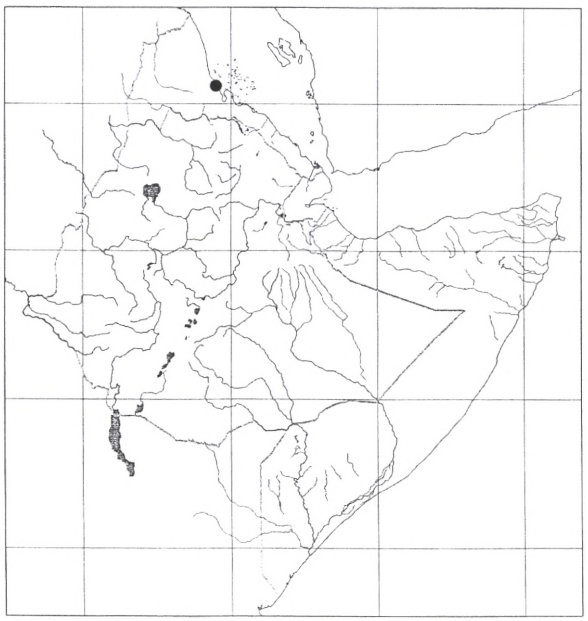


Fig. 1. Distribution of *Aloe eumassawana*.

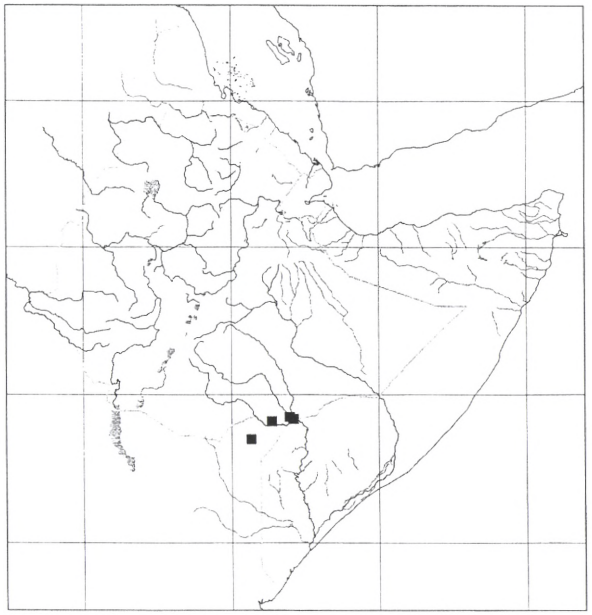


Fig. 2. Distribution of *Aloe citrina*.

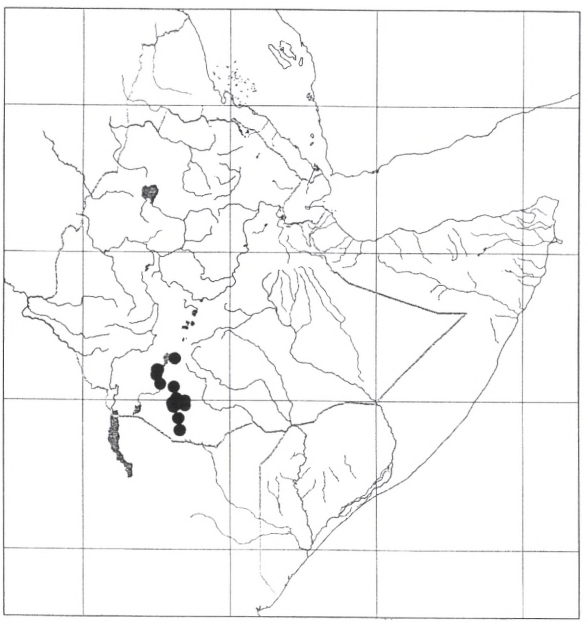


Fig. 3. Distribution of *Aloe otallensis*.

Fig. 4. Distribution of *Aloe harlana*.

Aloe frequently occur in shade under bushes. The modified vegetation types are:

1. Coastal vegetation.
2. Desert and semi-desert scrub.
3. *Acacia-Commiphora* bushland.
4. Dry evergreen montane forest and grassland. For the purpose of this paper, the evergreen scrub is included here.
5. Afroalpine vegetation, including sub-Afroalpine vegetation.

So far, no species of *Aloe* has been recorded from the five other vegetation types in the FEE area.

The distribution of all *Aloe* species known from the FEE area is recorded in Table 1. The species, and especially the endemic and the near-endemic species, occur mainly in two vegetation types: dry evergreen montane forest and grassland (including montane evergreen scrub) and *Acacia-Commiphora* bushland. With the exception of two species all *Aloes* in the FEE area occur above (500-)1000 m. These two species are *A. eumassawana* (Fig. 1), which occurs in coastal vegetation, and *A. citrina* (Fig. 2, 8), which occurs both in semi-desert vegetation and *Acacia-Commiphora* bushland). Two species occur above 3000 m; these are *A. steudneri* and *A. ankoberensis*, both of which reach into the sub-Afroalpine vegetation. This agrees with the observation that species of *Aloe* are rare in the semi-desert and the desert vegetation, and in sub-Afroalpine vegetation. Examples of species mainly occurring in *Acacia-Commiphora* bushland above 1000 m, are *Aloe otallensis* (Fig. 8), which occurs in Borana in the southern part of the FEE-area (Fig. 3), and *A. harlana* (Fig. 8), which occurs in the eastern part of the FEE area (Fig. 4), although the latter transgresses to the lower part of dry evergreen forest. A species, which typically occur in the evergreen forest and scrub of the central highlands, is *A. debrana* (Fig. 5, 8). A species, which typically is associated with sub-Afroalpine vegetation, is *A. steudneri;* it mainly occurs at high altitudes in the Simen Mts (Fig. 6, 8).

Distribution patterns of endemic and near-endemic Aloe species

The concentration of *Aloe* species in the FEE area to altitudes between (500-)900 and c. 3000 m, as demonstrated in Table 1, means that they are largely found in the highlands, the foothills of the highlands and in the Rift Valley. A limited number is found on the Borana-Ogaden Plain, a system of gently sloping plains towards Somalia and Kenya. A summary of localities of most endemic and near-endemic *Aloe* species is shown on Fig. 7 (note that the newly described *A. bertemariae* has not been included), and the distribution of the species within these three regions have been indicated in Table 1. A wedge-shaped high rainfall area with vegetation of evergreen forest or secondary vegetation derived from forest penetrates into the highlands from south-west; this wedge-shaped area has few or no *Aloe* species. The wedge-shaped high rainfall area covers large parts of the FEE floristic regions of WG, IL and KF. The western lowlands with *Combretum-Terminalia* woodlands and fierce and frequent grass fires are also apparently devoid of *Aloe* species.

Thus, the distribution areas of *Aloe* species in the FEE-area fall into three parts.

1. The northern and central highlands south to SU and north-eastern KF.
2. The eastern highlands, continuing into the mountain chain in northern Somalia.
3. The southern highlands, the Rift Valley, and the Borana-Ogaden Plain.

Hardly any species overlap the boundaries between these three areas, with *A. pubescens* and *A. macrocarpa* as the two most notable

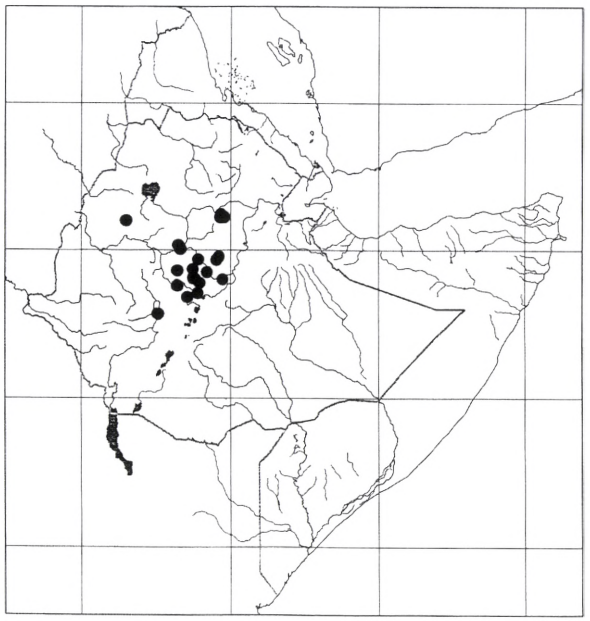


Fig. 5. Distribution of *Aloe debrana*.

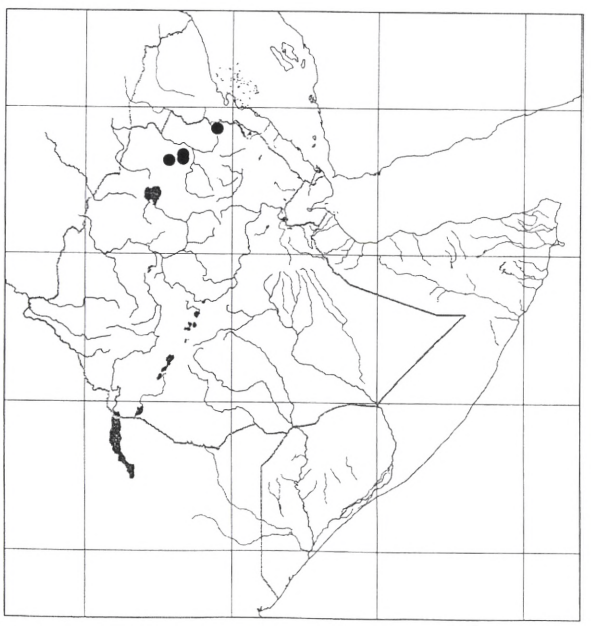


Fig. 6. Distribution of *Aloe steudneri*.

examples. These species, and others that occur in two or three of the three areas mentioned above, are excluded from the map in Fig. 7.

Aloe species and African phytochoria

One of the most characteristic features of the *Aloe* flora of the FEE area is the relatively high number of species, which mainly occur or are restricted to high altitudes (Table 1). Most high-altitude species are clearly restricted to the Afromontane region, and are thus Afromontane endemics according to the definition of White (1983). There is a number of high-altitude species associated with sub-Afroalpine vegetation; they are large, succulent rosette plants with no or only a short stem. Stemless succulent rosette-plants are not part of the normally accepted life forms of typical Afroalpine plants (Hedberg 1964), and they occur also in the vegetation zone immediately below. These *Aloe* species are therefore considered part of an Afromontane element, which reach or just transgress the border between the Afromontane and the Afroalpine zones.

The other notable endemic or near-endemic element in the *Aloe* flora of the FEE area includes the species that occur in the *Acacia-Commiphora* bushland in the Somalia-Masai regional centre of endemism (Table 2). They are thus Somalia-Masai endemics according to the definition of White (1983). A small number of these species transgress into the Afromontane region. *Aloe macrocarpa* is outside the FEE-area widespread in the Sudanian region, but in Ethiopia it behaves as a species, which transgress the border between the *Acacia-Commiphora* bushland and the dry montane evergreen forest; it is therefore recorded as SUD/S-M/AFM here (*Cf.* Table 1).

An enumeration of the phytogeographical elements indicated in Table 1 shows the following distribution:

Table 2. Elements in the *Aloe* flora of the FEE area.

Strictly Afromontane element	13 species	33%
Afromontane / Somalia-Masai transgressors	8 species	20%
Strictly Somalia-Masai element	18 species	45%
Sudanian/Somalia-Masai / Afromontane transgressor	1 species	2%
Total	40 species	

The data from the Flora of Somalia (Lavranos 1995) have been analyzed here in the same way. The results show that among the 30 indigenous species there seems to be no strict Afromontane element (see also Discussion). The ten species (33.3%), which occur at the highest altitude in Somalia, are probably best referred to as Afromontane/Somalia-Masai transgressors. These species occur mainly in

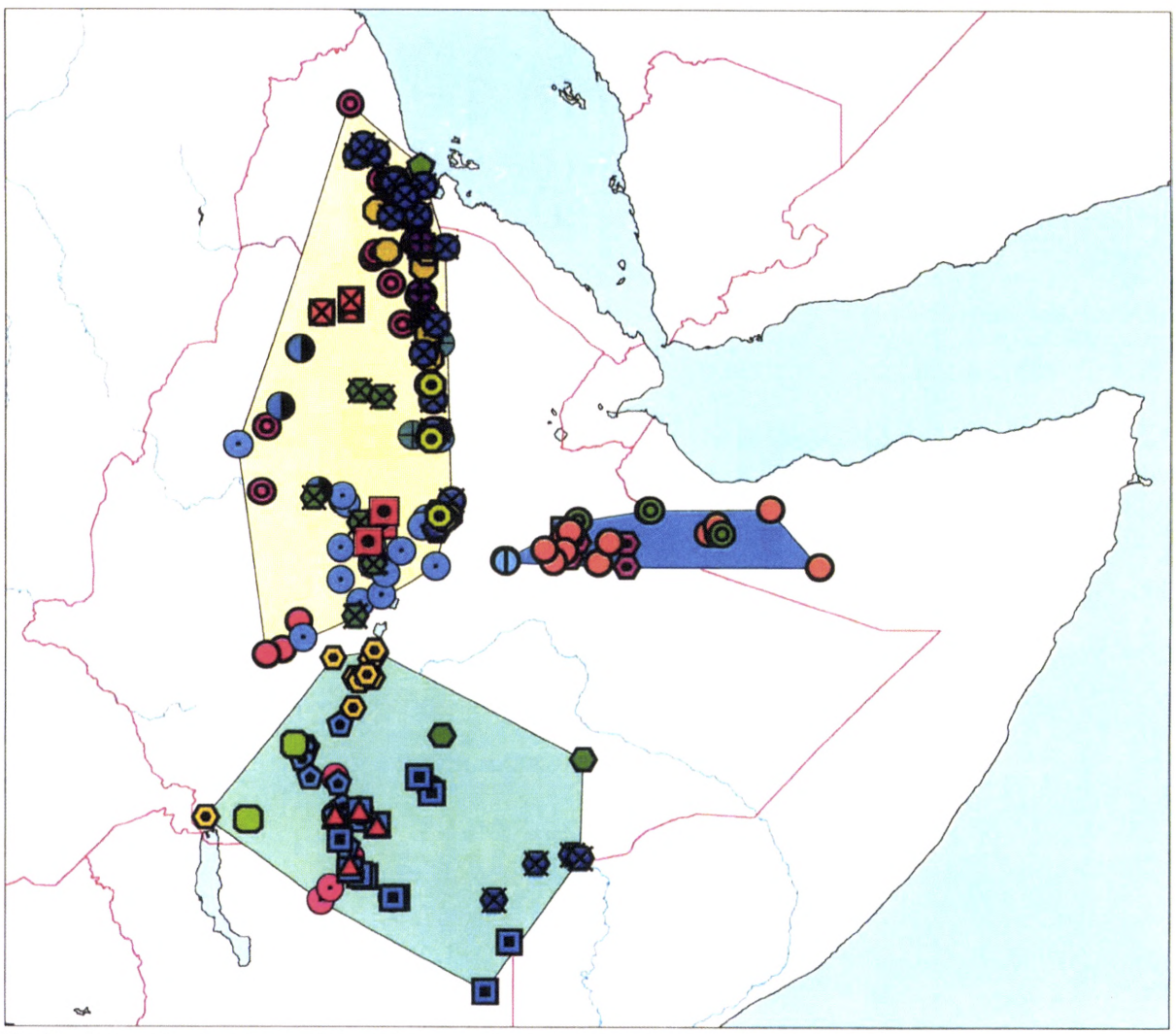


Fig. 7A. Geographical patterns of *Aloe* endemics and near-endemics in the FEE-area. Legends on opposite page.

the *Juniperus-Buxus* evergreen forest and associated evergreen scrub (Friis 1992) in the mountain chain in Northern Somalia. Nineteen species (63%) are distributed in *Acacia-Commiphora* bushland within the Somalia-Masai region and are strict Somalia-Masai endemics. One species (3%) is a Somalia-Masai/Zanzibar-Inhambane transgressor.

The 83 species in the Flora of Tropical East Africa (Carter 1994) have been analyzed in the same way. However, the result is complex, especially where the species in the Lake Victoria Regional Mosaic, the Zanzibar-Inhambane Regional Mosaic, and the Zambesian Region in southern part of the FTEA area are concerned. There are many species that would appear to occur in the transition zones between these phytochoria. We have therefore only analyzed the elements, which we also have studied from the FEE and the Flora of Somalia area, and only on a very tentative basis. Eight (10%) species seem to be strictly Afromontane in Tropical East Africa, and none of these occurs above 2650 m, which contrast with the two species reaching between 3000 and 3500 m in Ethiopia. Three species (4%) in Tropical East Africa seem to be Afromontane/Somalia-Masai transgressors. Thirty-seven (45%) species seem to be strictly endemic to the Somalia-Masai Region.

Thus, the FEE area has by far the highest concentration of Afromontane *Aloe* species in the entire Tropical East and Tropical North-East African Regions combined. But the mountains in Northern Somalia have a very notable element of *Aloe* species in the transition zone between the Somalia-Masai and the Afromontane regions.

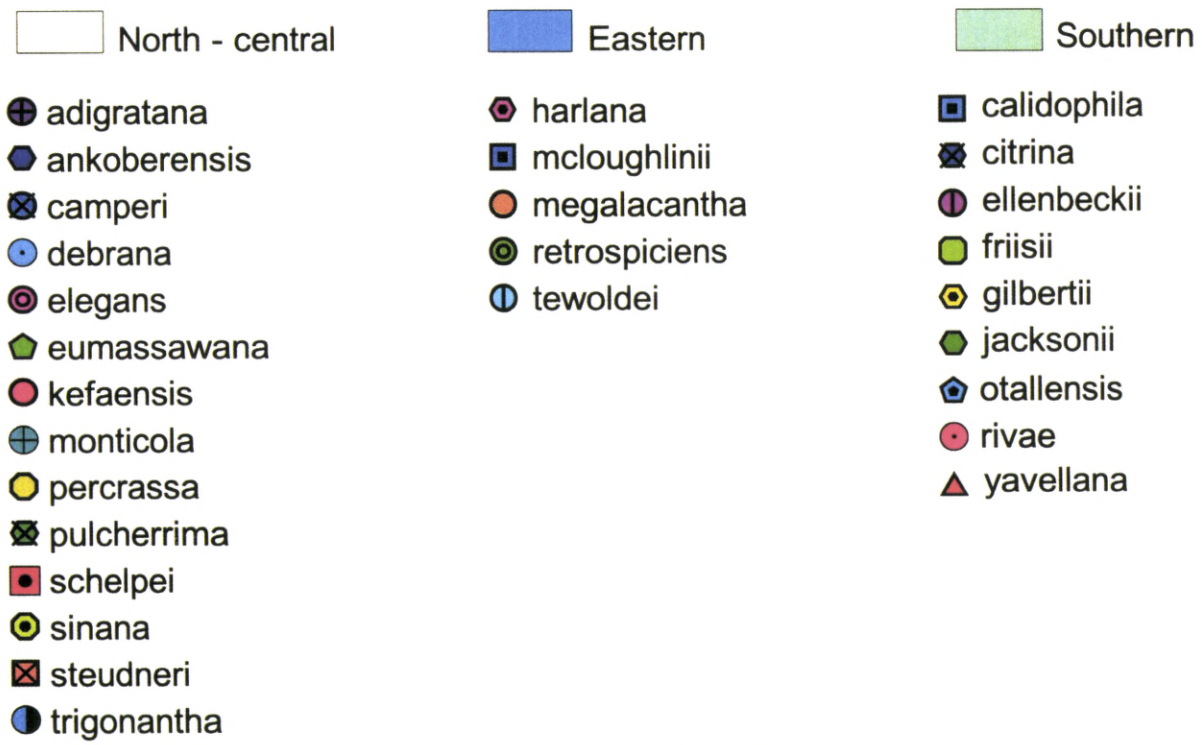
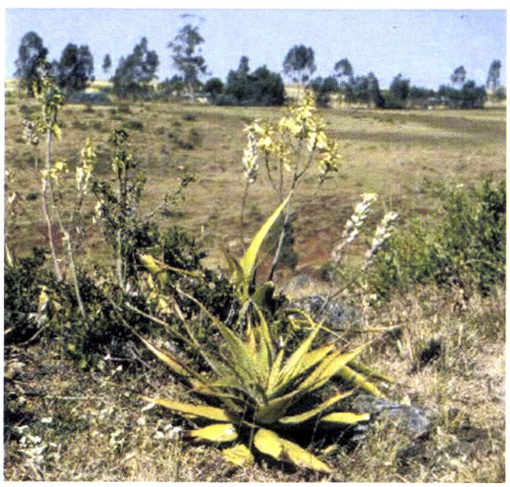


Fig. 7B. Geographical patterns of *Aloe* endemics and near-endemics in the FEE-area. Legends to map.



Discussion

The high representation of Afromontane *Aloe* species in the FEE region is partly due to the prolific speciation of two groups. The first group, comprising *A. ankoberensis*, *A. pulcherrima*, and *A. steudneri* (Fig. 8), are genuinely high-altitude species. The other group, which occurs also at slightly lower altitudes, includes *A. debrana* (Fig. 8), *A. percrassa*, and *A. trigonantha* (Fig. 8). Both groups occur within the unimodal rainfall area of the Ethiopian highlands where the rainfall is (probably) below 1000 mm, and the two groups have therefore speciated both at high altitude and low rainfall, a combination which is not so extensively represented in Tropical East Africa. The *Aloe* species of Somalia show a somewhat similar pattern, although the mountains in Somalia are lower than in Ethiopia, and dry high-altitude habitats do therefore not exist to the same extent. The endemic *Aloe* species in the Flora of Somalia region are largely found in typical Somalia-Masai vegetation types and well within the Somalia-Masai region, except the group which has speciated at higher altitudes. Here they are associated with *Buxus-Acokanthera* scrub and dry *Juniperus* forest, somewhat similar to the *Juniperus* forests in Ethiopia, which may be the main habitat for high-altitude speciation in Ethiopia. The high-altitude group in Somalia contains the following species: *Aloe jucunda* Reynolds, *A. peckii* Bally & Verdoorn, *A. albovestita* S. Carter & P. Brandham, *A. cremnophila* Reynolds & Bally, *A. gillettii* S. Carter, and *A. hildebrandtii* Bak. The exact phytogeographical position of the dry *Juniperus* forest and the *Buxus-Acokanthera* scrub in Somalia is not quite clear. White (1983) and Thulin (1986) have included these two closely associated vegetation types as an upper part of the Somalia-Masai region. Friis (1992) has found that it is worthy of being recognized as a transition zone between the Somalia-Masai and the Afromontane regions. Whatever the phytogeographical position, this zone is interesting because it is rich in endemics, a feature not usually found in phytogeographical transition zones according to White (1983).

There seems therefore to be speciation in relatively dry areas at higher altitudes in both Ethiopia and Somalia, while a similar trend does not seem to be prominent among *Aloe*-species in East Africa.

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← **Fig. 8**. Some endemic or near-endemic *Aloe* species from Ethiopia. The species in the left column, from top to bottom: *Aloe citrina*, SD, near Bokol Mayo towards Dolo Odo; 15 Dec. 1990. Photo by Sebsebe Demissew. *Aloe otallensis*, SD, NE of Yavello; 19 Nov. 1994. Photo by Sebsebe Demissew. *Aloe trigonantha*, GJ, near Yejube, SE of Debre Markos; 19 Dec. 1998. Photo by Sebsebe Demissew. The species in the right hand column, from top to bottom: *Aloe steudneri*, GD, Simen National Park. Photo by J.C. Hilman. *Aloe harlana*, HA, near Harla Village, between Dire Dawa and Dengego; 21 Apr. 1989. Photo by Sebsebe Demissew. *Aloe debrana*, SU, near Debre Berhan; 21 Dec. 1988. Photo by Sebsebe Demissew.

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Endemism in groups of Ethiopian geophytes ("Liliiflorae")

Inger Nordal, Sebsebe Demissew & Odd E. Stabbetorp

Nordal, I., Sebsebe Demissew & Stabbetorp, O.E. 2001. Endemism in groups of Ethiopian geophytes ("Liliiflorae"). *Biol. Skr.* **54**: 247-258. ISSN 0366-3612. ISBN 87-7876-246-4.

Altogether 33 endemic and near-endemic taxa are found within lilioid geophytes, giving a frequency of 31%. Twelve species are strictly endemic, giving a frequency of 12%. These relations correspond very well to the general aspect of the flora. It is shown that different families have different centres of endemic diversity and different altitudinal distribution of the endemic taxa. The genera with the highest numbers of endemic taxa are *Gladiolus* and *Chlorophytum*. The region richest in lilioid geophytic endemics is an area of Bale and Sidamo, including the Bale Mountains, their eastern slopes and the adjacent plains from Neghelle (in Sidamo) to Sof Omar (in Bale). To obtain information relevant for local conservation the 16 floristic regions defined in the Flora of Ethiopia and Eritrea, might be too broad-scaled to catch the more local evolutionary"hot-spots".

Inger Nordal, Department of Biology, P.O. Box 1045, Blindern, N-0316 Oslo, Norway. E-mail: inger.nordal@bio.uio.no

Sebsebe Demissew, National Herbarium, P.O. Box 3434, Addis Ababa, Ethiopia. E-mail: nat.heb@telecom.net.et

Odd E. Stabbetorp, Norwegian Institute for Nature Research, P.O. Box 736, Sentrum, N-0105, Oslo, Norway. E-mail: odd.stabbetorp@ninaosl.ninaniku.no

Introduction

A geophyte is a perennial herbaceous plant with a subterranean storage organ, particularly adapted to survive periods of stress. This underground storage will condition the plants for rapid sprouting when conditions ameliorate and the stress, being drought or cold, disappears. This strategy has evolved in several groups of both dicotyledonous and monocotyledonous plants. Lilies in the widest sense ("Liliflorae"), have particularly evolved strategies to survive more or less extreme dry periods by specialised organs, as bulbs, corms, fleshy rhizomes, roots with tubers or fleshy roots. The lilioid geophyte strategy is to sprout immediately with the first rains, and in particular before the grasses start dominating. The early appearance of the geophytes in areas with strong seasonality, as in large part of the Sudano-Zambesian tropical Africa, exposes them to heavy herbivory, by ungulates and other primary consumers. Most lilioid geophytes have accordingly developed chemical defence by *e.g.* alkaloids, anthraquinons, saponins, or glycosids.

The taxonomy of lilies in the wide sense has

changed considerably through the last 15 years (*cf.* Dahlgren *et al.* 1985; Kubitzki 1998a). Altogether nine families of the former "Liliiflorae", revised in the Flora of Ethiopia and Eritrea ("FEE", Edwards *et al.* 1997), include typical lilioid geophytes: Hypoxidaceae (Nordal 1997a, 1998), Anthericaceae (Nordal 1997b; Conran 1998), Asphodelaceae (Sebsebe Demissew & Nordal 1997; Smith & van Wyk 1998), Eriospermaceae (Sebsebe Demissew 1997a; Perry & Rudall 1998), Hyacinthaceae (Stedje 1997; Speta 1998), Alliaceae (Tewolde & Edwards 1997; Rahn 1998), Amaryllidaceae (Nordal 1997c; Meerow & Snijman 1998), Iridaceae (Goldblatt 1997, 1998), and Colchicaceae (Sebsebe Demissew 1997b; Nordenstam 1998).

Orchidaceae, a family that molecular analyses have nested within the traditional "Liliiflorae" families, certainly also includes geophytes (as well as epiphytes), but this family is not included in this analysis. Dioscoreaceae (Miège & Sebsebe Demissew 1997; Huber 1998) and Taccaceae (Lye 1997; Kubitzki 1998b), most often associated with wetter habitats than the typical "Liliiflorae" include more or less tuberous plants, but they are also excluded from this analysis.

Material and methods

The collections of the National Herbarium, Addis Ababa University (ETH); East African Herbarium, Nairobi (EA); Royal Botanic Gardens, Kew (K); Herbarium Vadense, Wageningen (WAG), British Museum – Natural History (BM); Botanischer Garten und Botanisches Museum, Berlin-Dahlem (B); Erbario Tropicale di Firenze (FT); Muséum National d'Histoire Naturelle, Paris (P); Jardin Botanique National de Belgique, Bruxelles (BR) have been screened for geographical and ecological information on endemic or near-endemic taxa in Ethiopia and Eritrea.

Near-endemic taxa are defined as taxa that reach Somalia, the northernmost part of Kenya (north of 3° N), the north-easternmost part of Sudan and/or Southwest Yemen. Plants endemic to the Horn of Africa (particularly Somalia), but not represented in Ethiopia or Eritrea are not taken into account in this study.

The geographical data were imported into a mapping system constructed by O. E. Stabbetorp and S. E. Sloreid (Norwegian Institute of Nature Research, Oslo), and further analyses were undertaken in the program Arcview (ESRI 1996). Around every record a circle with a radius of 100 km was constructed, and the number of overlaps recorded on the maps. The darker the area the more endemic species in the vicinity.

Results

Hypoxidaceae

The family includes two genera in Ethiopia and Eritrea with fleshy rhizomes or corms: *Curculigo* and *Hypoxis*. The former is represented by one widespread species *C. pilosa* (Schum. & Thonn.) Engl. This species is rare and highly disjunct in Ethiopia, but otherwise distributed through most of the Sudano-Zambesian phytogeographical region. The genus *Hypoxis* includes one diploid, sexual species, *H. angustifolia* Lam., also widespread in the Sudano-Zambesian region. Another taxon, possibly widespread, but in Ethiopia only recorded in Gonder, *H. schimperi* Baker, needs further study. All other representatives of the genus belong to a widespread polyploid apomictic aggregate, the "*H. villosa* complex", which certainly includes endemicity at a taxonomic level which might be referred to as "microspecies" or "agamospecies". Such taxa were denoted the "*abyssinica*" form, the "*boranensis*" form, the "*tristycha*" form and the "*neghellensis*" form in FEE (Nordal 1997a). The first two forms are fairly widespread within Ethiopia and Eritrea, and probably also found outside the area,

whereas the last two are narrow endemics in Sidamo, close to the centre of endemism for *e.g.* Anthericaceae (see below and Fig. 2). Polyploidy and apomixis always create taxonomic problems, more common in boreal and arctic regions, but there is increasing evidence for occurrence of these phenomena also in the tropical and subtropical regions. Due to the taxonomic problems, Hypoxidaceae is not included in the further analyses.

Anthericaceae

The family is represented by two genera in FEE, *Anthericum* and *Chlorophytum*. The generic delimitation was settled by Kativu & Nordal (1993), who transferred most of the African species of "*Anthericum*" to *Chlorophytum*. With this delimitation *Anthericum* is mainly a temperate Old World genus with few extensions to the Tropics in eastern Africa, and *Chlorophytum* mainly a tropical Old World genus.

In Ethiopia and Eritrea the genus *Anthericum* is characterised by short rhizomes and +/- thick roots. The species belong to seasonally waterlogged areas. One species is near-endemic, *i.e. A. jamesii* Baker (Fig. 1C), occurring in the Harerge region, West Somalia, and North Kenya, very close to the Ethiopian border. The remaining two African species, *A. angustifolium* Hochst. ex A. Rich. and *A. corymbosum* Baker, have a somewhat broader distribution, but with a clear concentration in North East Tropical Africa. The percentage of (near-) endemics in the genus is accordingly 33%.

The genus *Chlorophytum* was revised for the Horn of Africa by Nordal & Thulin (1993). They revealed that this region represents an important area of diversity and described 9 new species that were endemic or near-endemic to the Horn of Africa. The species show a great diversity in subterranean storage organs, +/- elongated rhizomes, corms (often joined in long links to so-called moniliform rhizomes), swollen roots or root tubers. The strict endemic species of Ethiopia and Eritrea are three: *C. neghellense* Cufod., in Sidamo and Bale (Fig. 1A); *C. ducis-aprutii* Chiov., scattered in West Eritrea, Bale and Harerge; and *C. pterocarpum* Nordal & Thulin, a narrow endemic in Bale (Sof Omar). Further, near-endemics are: *C. tetraphyllum* (L.f.) Baker, fairly common on disturbed ground in Ethiopia and Eritrea (Fig. 1B), reaching south-western Yemen; *C. bifolium* Dammer from Bale (in Ethiopia known only from the type specimen of unprecise locality) and adjacent Somalia and Kenya; *C. inconspicuum* (Baker) Nordal, in Shewa and Sidamo with extension to northern Somalia and Yemen; *C. zavattari* (Cufod.) Nordal in Sidamo and Bale, reaching adjacent Somalia and Kenya; *C. humifusum* Cufod. in Sidamo, Bale and with a Somalia/Kenya distribution similar to *C. zavattari*); and *C. pendulum* Nordal & Thulin also in Sidamo and Bale and adjacent Kenya.

Altogether the FEE (Nordal 1997b) included 23 species of the genus *Chlorophytum*. Since this publication, new information has been revealed, which will be communicated here:

1. *Chlorophytum tordense* Chiov. was recorded by Nordal (1997b) as a near-endemic species. Later examinations have lead to the conclusion that this taxon represents a slender form of the widespread *C. affine* Baker (Nordal *et al.* 1998).
2. *C. micranthum* Baker was recorded as a near-endemic by Nordal (1997b). Later studies (Nordal *et al.* 1998) have shown that this taxon has a wider distribution in eastern Africa (Uganda, Kenya, Burundi, and Sudan) than recorded in the FEE. It should, however, be remarked that the relation of this species to *C. gallabatense* Schweinf. ex Baker remains unclear. The former might represent a more or less hysteranthous ecotype with slightly smaller flowers compared to the latter.

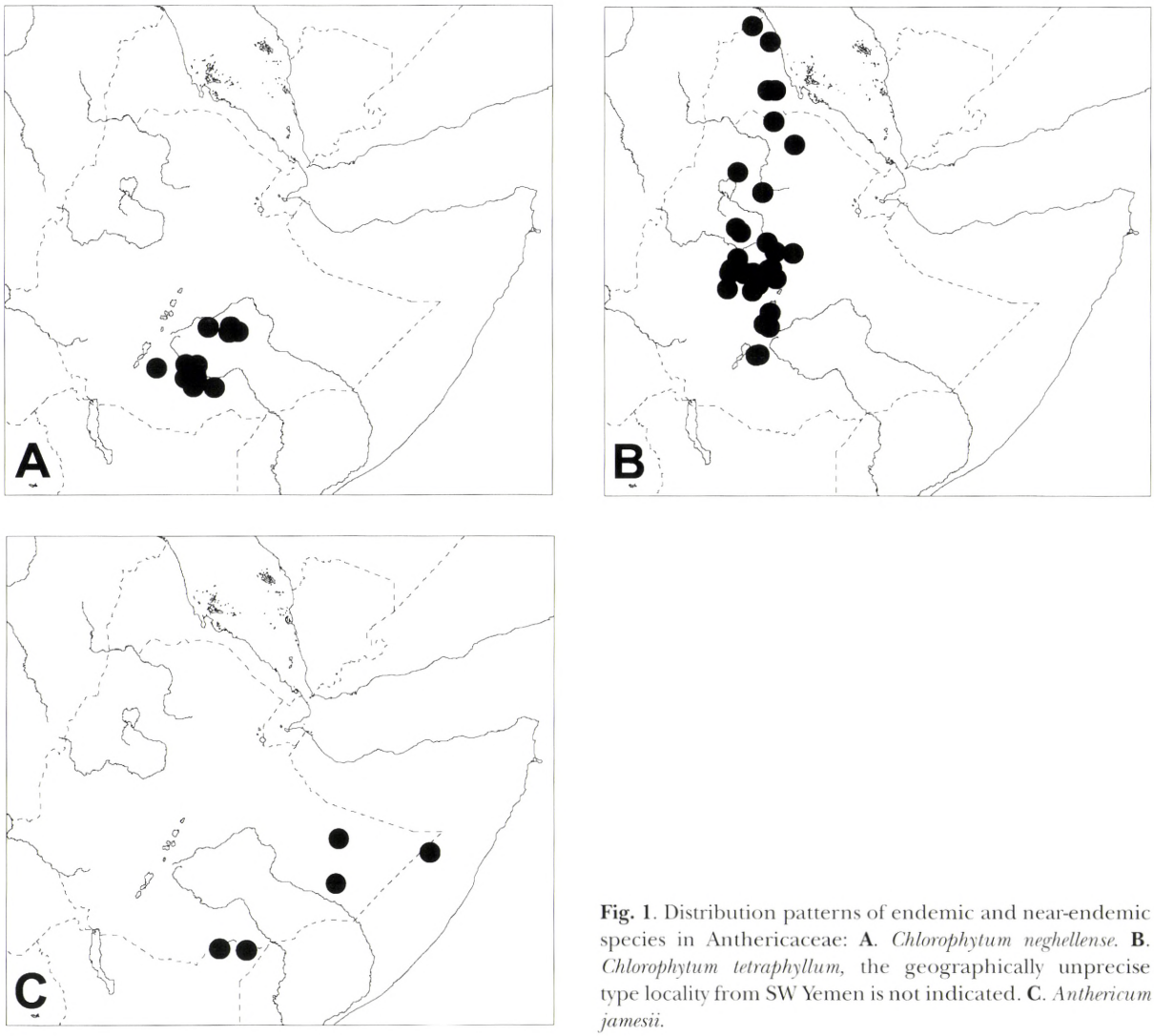

Fig. 1. Distribution patterns of endemic and near-endemic species in Anthericaceae: **A**. *Chlorophytum neghellense*. **B**. *Chlorophytum tetraphyllum*, the geographically unprecise type locality from SW Yemen is not indicated. **C**. *Anthericum jamesii*.

3. *C. floribundum* Baker, also a taxon closely related to *C. gallabatense*, is characterised by having a papillate rhachis (Nordal *et al.* 1998). The specimen Mooney 9739 (WAG) from Dibdiba in Sidamo (4° 55' N, 39° 30' E) exhibits this feature, and must be referred to this taxon. *C. floribundum* is widespread and occurs in Tanzania, Zambia, Malawi and Zimbabwe. Also in this case the specific delimitation towards *C. gallabatense* might be disputed.

4. *C. filipendulum* Baker is here recorded as new to Ethiopia. Through the studies of particularly the rain forest taxa of the genus (Nordal *et al.* 1998; Poulsen & Nordal work in prep.), the delimitation between *C. macrophyllum* (A. Rich.) Asch. and *C. filipendulum* has been settled. This delimitation was not clear at the time of the publication of the FEE (Nordal 1997b). The specimen, *Friis et al.* 3902 (C, K, ETH), from Kefa, Bebeka Cof-

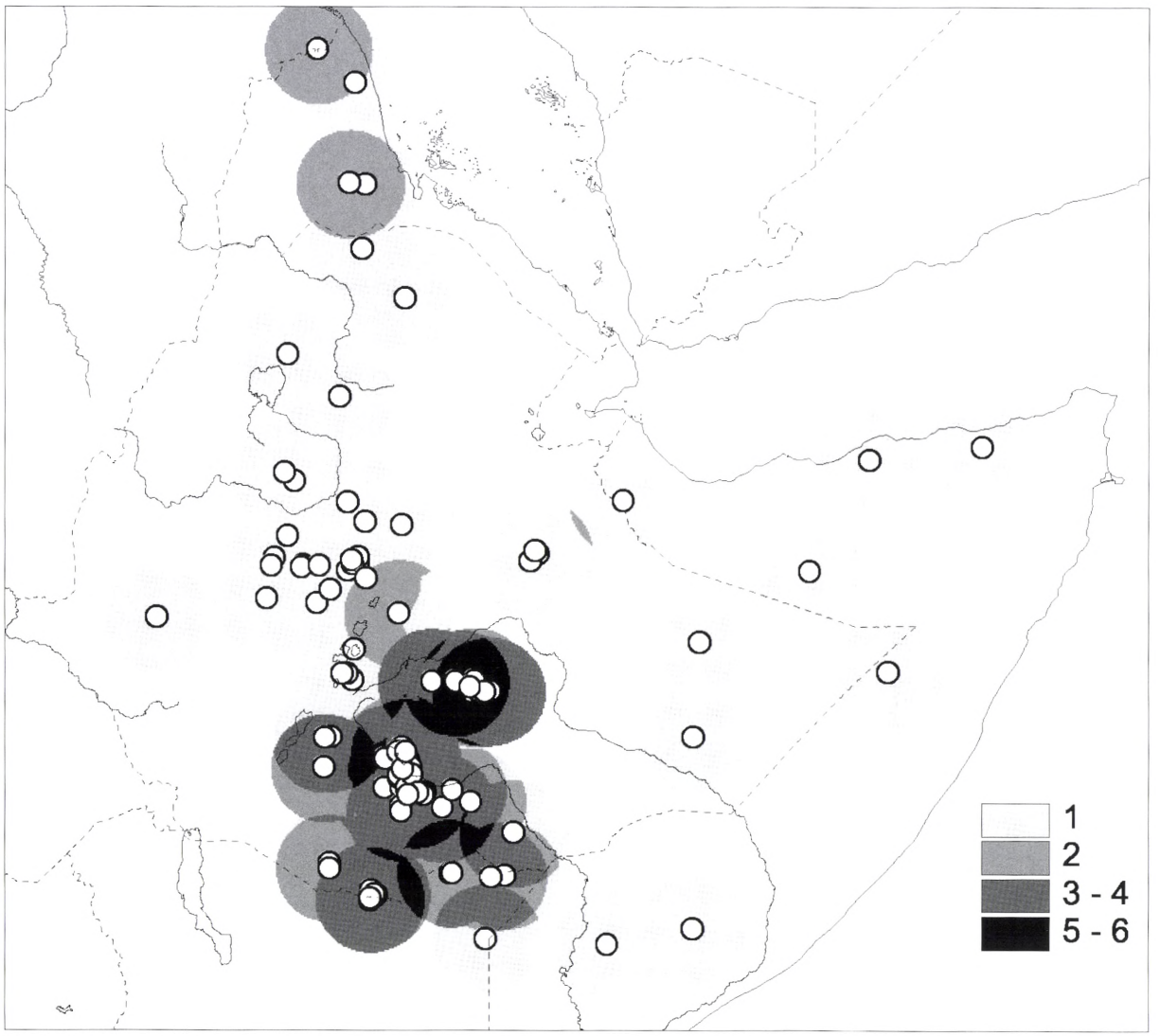

Fig. 2. The distribution of (near-)endemic taxa of Anthericaceae in Ethiopia. The shaded areas represent zones of overlapping species (see text).

fee plantation (6° 50' N, 35° 15' E, 1050 m a. s. l.) certainly belongs to *C. filipendulum*, a species with an otherwise wide distribution in the Guineo-Congolian rain forests. *C. macrophyllum*, on the other hand, belongs in woodland and forest fringes and is mainly a Sudano-Zambesian taxon.

The number of species within Anthericaceae in the Ethiopia and Eritrea has, accordingly, increased from 26 to 28 species (3 *Anthericum* and 25 *Chlorophytum*). There are three strict endemics and six near-endemics, giving a frequency of (near-) endemics of 36%.

The (near-)endemic taxa of the family Anthericaceae can be divided into three geo-

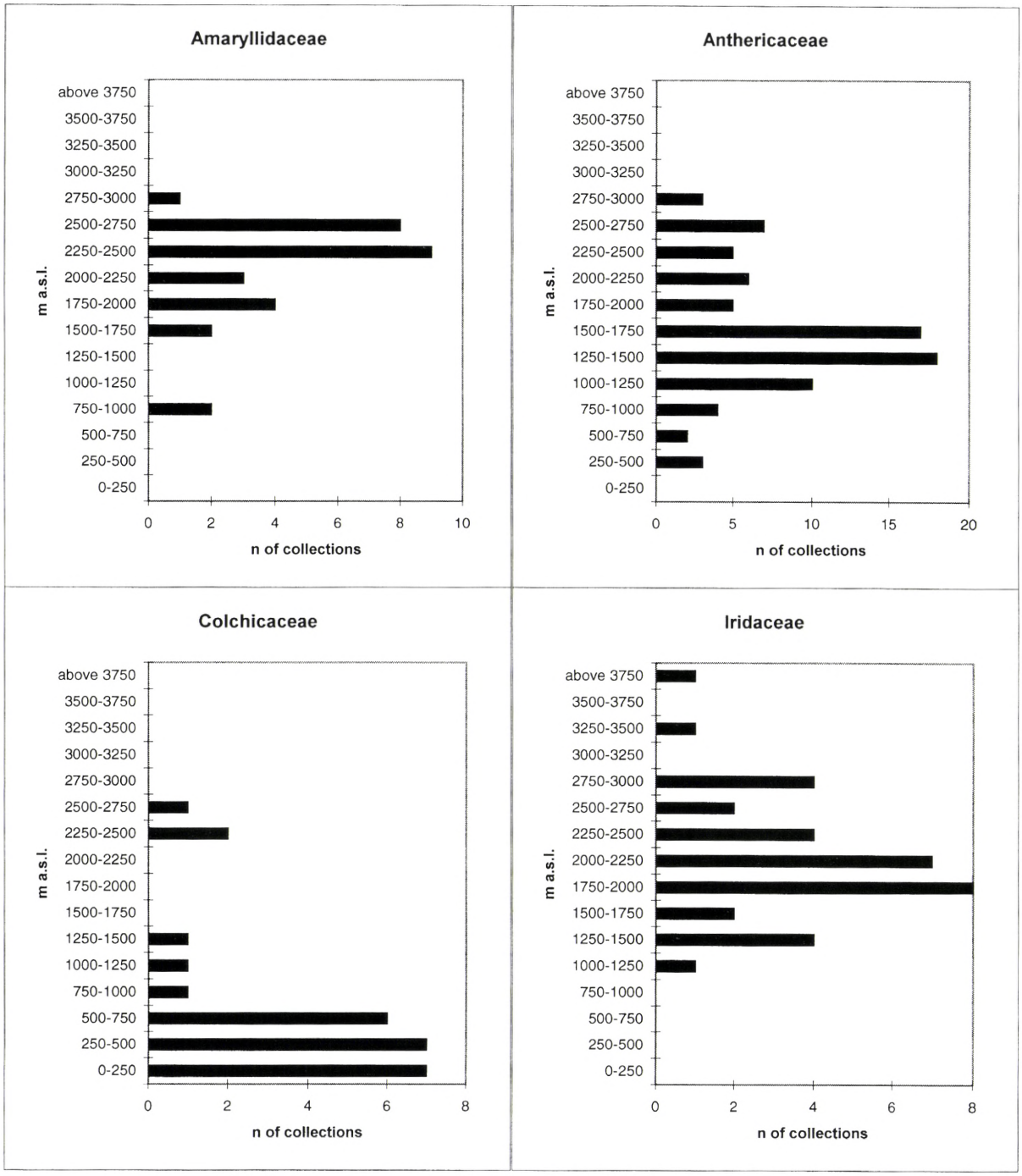

Fig. 3. The altitudinal ranges of endemic species within the families exhibiting a considerable degree of endemicity.

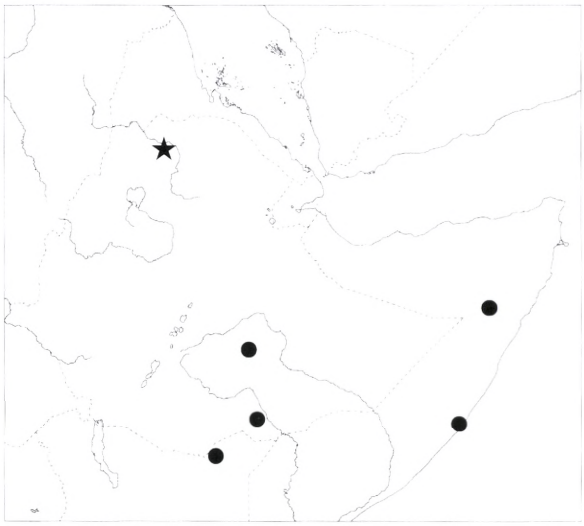

Fig. 4. The distribution of the genus *Jodrellia* on the Horn of Africa.

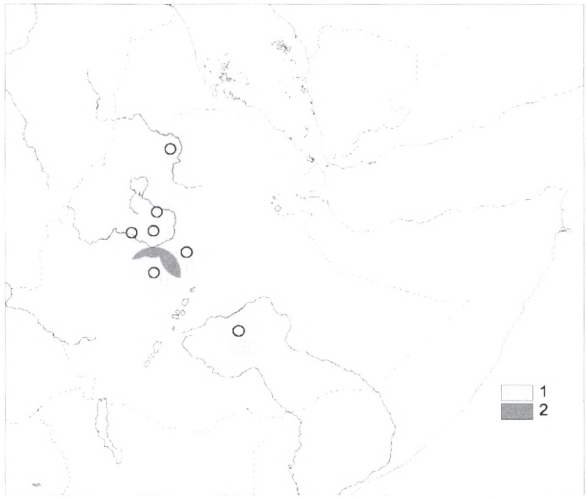

Fig. 5. The distribution of endemic taxa of Hyacinthaceae in Ethiopia. The shaded areas represent zones of overlapping species (see text).

graphical groups based on their distribution in Ethiopia. The first group, exemplified by *C. neghellensis* (Fig. 1A), has its centre in southern Ethiopia (Bale and Sidamo). This group also includes *C. pterocarpum*, *C. zavattarii*, *C. humifusum*, and *C. pendulum*. The second group, exemplified by *C. tetraphyllum* (Fig. 1B), has a wider north/south distribution in Eritrea and Ethiopia. In addition to *C. tetraphyllum*, also *C. inconspicuum* and *C. ducis-aprutii* are included in this group. The third group, exemplified by *Anthericum jamesii* (Fig. 1C), has an eastern centre on the African Horn, and includes further *C. bifolium*.

The overall analysis of endemism in the family Anthericaceae is presented in Fig. 2. Centres with as much as 5-6 endemic species within circles of a radius of 100 km are found within southern to south-eastern Ethiopia (Sidamo and eastern Bale).

The altitudinal distribution (Fig. 3) is wide, ranging from about 500 to 3000 m, with a concentration from 1250 to 1750 m a. s. l., showing the highest frequency in the lower part of this interval.

Asphodelaceae

This family includes five genera, given the fact that the more or less woody genus *Aloe* is referred to a family of its own, the Aloaceae. The most species-rich genus, *Kniphofia* with seven species, of which five are endemic, most often grow in wetter habitats than typical geophytes and is not included here. The genus is at the moment being thoroughly analysed within Ethiopia by Tilahun Teklehaymanot (unpublished Ph.D. thesis).

The other genera include species with thick short rhizomes and fairly thick roots, which might be classified as typical geophytes. *Bulbine* and *Trachyandra* are represented by one widespread species each, *B. abyssinica* A. Rich. and *T. saltii* (Baker) Oberm., both fairly common from southern tropical Africa along the eastern parts north to northern Ethiopia (Tigray). *Asphodelus fistulosus* L., widely distributed in the Mediterranean region, has its southern limit in Eritrea.

The genus *Jodrellia* includes still unsolved

taxonomic problems. All the taxa described so far are based on type material from the Horn of Africa: *J. fistulosa* (Chiov.) Baijnath from Gonder/Tigray, *J. miguirtina* (Chiov.) Baijnath from Somalia, and *J. macrocarpa* Baijnath from Bale. *Jodrellia macrocarpa* was regarded as a synonym of *J. miguirtina* in the FEE (Sebsebe Demisew & Nordal 1997), representing a taxon with inflated fruits. *Jodrellia fistulosa*, otherwise recorded from Tanzania, Zambia and Zimbabwe, is only known from the type locality (Tacazze River) in Ethiopia and an unidentified locality in Eritrea. The type specimen does not display inflated fruits, but that might, in fact, be due to the young stage of the fruits in the collected specimens. The Tacazze locality has the last years been searched several times, at different seasons, without any luck. The known distribution on the Horn of Africa of the taxa in the genus is given in Fig. 4. They may turn out to represent one near-endemic species, which in this case should be named *J. fistulosa*. If so, the southern tropical specimens of the genus (which certainly not exhibit inflated fruits) need a new name.

Eriospermaceae

This family, with a centre of diversity in South Africa, includes two widespread taxa, both rare in Ethiopia: *Eriospermum abyssinicum* Baker in Gonder and *E. triphyllum* Baker in Sidamo (Sebsebe Demissew 1997a). Both are typical geophytes with particularly prominent corms compared to the size of the plants.

Hyacinthaceae

Seven genera are represented in the FEE: *Schizobasis*, *Dipcadi*, *Drimiopsis*, *Ledebouria*, *Albuca*, *Drimia*, and *Ornithogalum* (Stedje 1997). All of them have well-developed bulbs. Only two of them, *Ledebouria* and *Drimia* include endemic species, one out of six in the former (*L. urceolata* Stedje from Gojam, Shewa and northwestern Bale) and two out of six in the

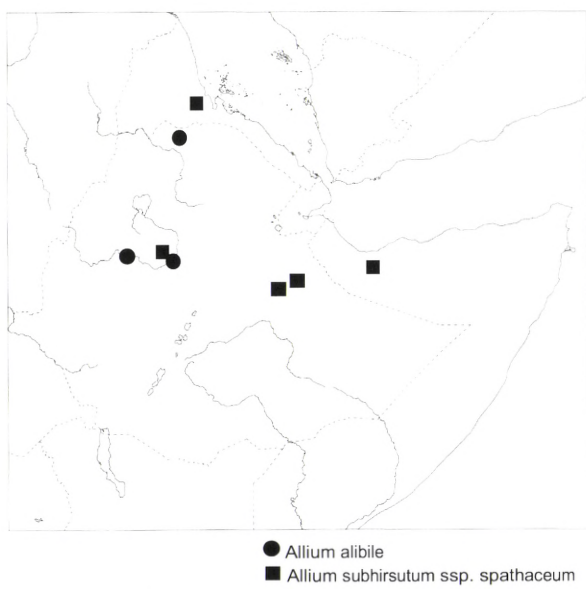

Fig. 6. The distribution of (near-)endemic taxa of Alliaceae.

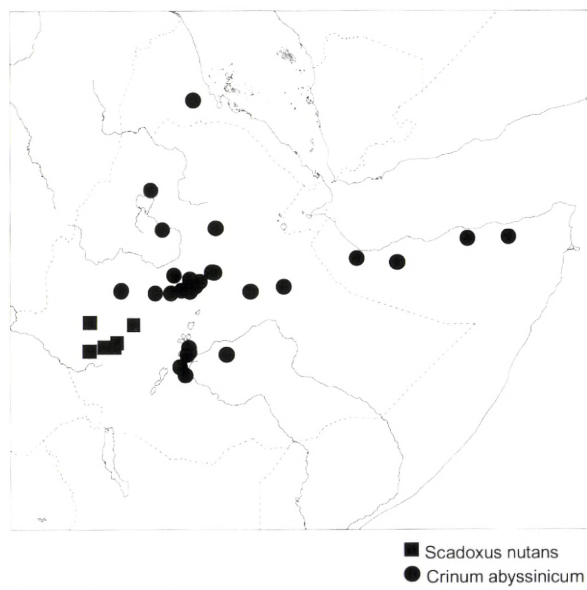

Fig. 7. The distribution of (near-)endemic taxa of Amaryllidaceae.

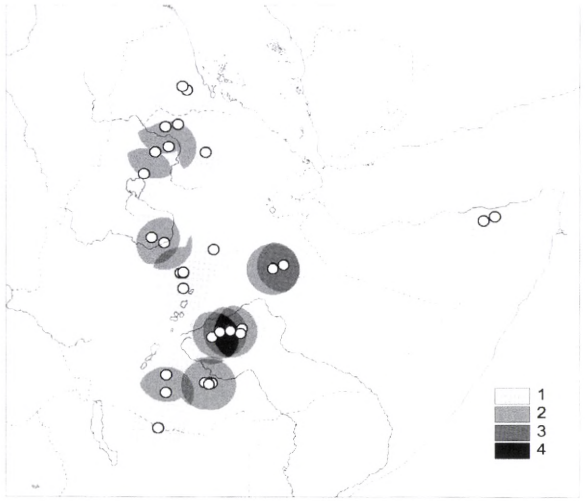

Fig. 8. The distribution of endemic taxa of Iridaceae in Ethiopia. The shaded areas represent zones of overlapping species (see text).

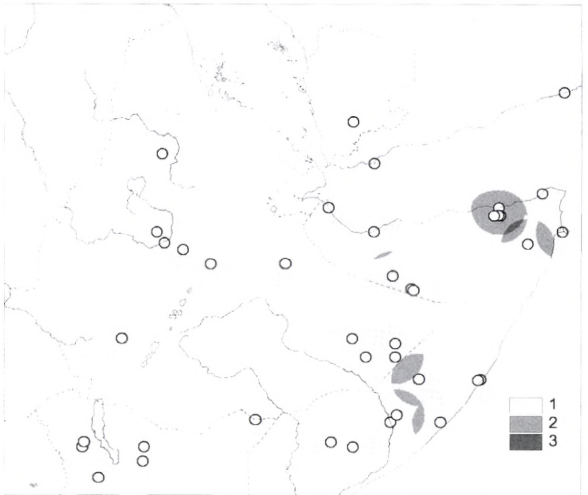

Fig. 9. The distribution of endemic taxa of Colchicaceae in Ethiopia. The shaded areas represent zones of overlopping species (see text).

latter (*D. exigua* Stedje from Kefa and Shewa, and *D. simensis* (Hochst.) Stedje from Gonder and Shewa). The distribution of the endemic taxa is given in Fig. 5. The few specimens known of the endemic taxa have altitudinal records ranging from 1000 to 3270 m.

Alliaceae

Most *Allium* species in the region are well-known cultivated taxa. One species and one subspecies appear to be near-endemic: *A. alibile* Steud. ex A. Rich., known from Tigray and Shewa, but probably also reaching the Sudan, and *A. subhirsutum* L. subsp. *spathaceum* (Steud. ex A. Rich.) Duyfjes, known from Eritrea, Gonder, and Harerge (Fig. 6), but also extending to Somalia and northern Sudan (Tewolde & Edwards 1997). The total altitudinal range is from approximately 1600 to 3500 m.

Amaryllidaceae

The Flora of Ethiopia and Eritrea includes four indigenous genera, *Scadoxus*, *Crinum*, *Ammocharis*, and *Pancratium*, with endemic taxa in the first two genera (Nordal 1997c). *Scadoxus* includes three species, of which *S. nutans* is endemic in Ilubabor and Kefa, between 1000 and 2300 m. This species belongs in an evolutionary lineage with rhizomatous rain forest taxa (Bjørnstad & Friis 1972; Nordal & Duncan 1984), which probably have developed from bulbous geophytes. Also the genus *Crinum* includes three indigenous species, of which *C. abyssinicum* is near-endemic, with a relatively wide distribution mainly in central Ethiopia, reaching the northern mountain range of Somalia (Fig. 7). This species is bulbous and belongs in seasonally waterlogged grassland from 1650 to 3300 m (Fig. 3).

Iridaceae

There are seven indigenous genera within the FEE, *Aristea*, *Moraea*, *Lapeirousia*, *Dierama*, *Hesperantha*, *Romulea* and *Gladiolus* (Goldblatt 1997). Endemic species are found in *Lapeirousia*, one species out of two, *L. abyssinica* (R. Br. ex A. Rich.) Baker. In *Gladiolous*, out of 16 species, six are narrow strict endemics: *G. balen-*

sis Goldblatt, *G. negeliensis* Goldblatt, *G. mensensis* (Schweinf.) Goldblatt, *G. colcicola* Goldblatt, *G. longispathaceus* Cufod., and five are near-endemics, *G. boranensis* Goldblatt, *G. gunnisii* (Rendle) Marais, *G. abyssinicus* (Lemaire) Goldblatt & de Vos, *G. schweinfurthii* (Baker) Goldblatt & de Vos, and *G. sudanicus* Goldblatt. The percentage of (near-) endemic taxa is, accordingly, as high as 69% in FEE. Most species are known from fairly few collections, and the high endemicity might partly be due to a rather narrow species concept utilised within this genus. The largest concentrations of endemic species are found in Bale and Sidamo (Fig. 8). The family is furthermore the one which has endemic species recorded at the highest altitudes. The main altitudinal range of the endemics ranges between 1750 and 2250 m, but collections from above 3750 m have also been recorded (Fig. 3).

Colchicaceae

The family includes 5 genera mostly with only one species each in FEE (Sebsebe Demissew 1997 b). *Androcymbium striatum* Hochst. ex A. Rich. and *Iphigenia pauciflora* Martelli represent the northernmost distribution of these widespread taxa in eastern tropical Africa. *Gloriosa* includes in addition to the widespread and extremely variable *G. superba* L., a closely related *G. baudii* (Terrac.) Chiov. Thulin (1995) regarded the latter as an arid ecotype or modification of the former. It was, however, referred to specific rank by Sebsebe Demissew (1997b). If so, this represents a near-endemic taxon, found in Bale and Harerge, but reaching also adjacent Somalia and Kenya. *Littonia revolii* Franch. is another near- endemic, mainly Somalian, but also found in Harerge. The last near-endemic taxon in the family, *Merendera schimperiana* Hochst., is widespread in Ethiopian mountains and extends to northern Somalia and the Arabian Peninsula. The endemic species are mapped in Fig. 9. The altitudinal distribution (Fig. 3) is bimodal due to the fact that the endemic *Gloriosa* and *Littonia* taxa belong in the lowlands below 1300 m and *Merendera* in the highlands above 2250 m.

Discussion

The overall frequency of (near-)endemic taxa in the lilioid geophytes in FEE is 31%, (33 taxa out of 110), but when only the strict Ethiopian endemics are included, the frequency is reduced to 12% (13 out of 110). The mean number of (near-)endemics, in the parts of the FEE published so far, is of the same order of magnitude, namely 28% for the (near-) endemic and 12,5% for the strict endemic taxa (Friis *et al.* 2001). The lilioid geophytes are thus representative of the total flora with respect to endemicity.

The endemic elements are distributed differently among the families: We find the main centre of endemic diversity for Anthericaceae at medium altitudes in Sidamo and adjacent Bale. Also when all the plant families that have so far been published in the Flora of Ethiopia and Eritrea are considered, it is Sidamo that houses the highest number of endemic taxa (Friis *et al.* 2001). The maximum number of taxa in the flora in general and in endemic taxa in particular is found between 1200 and 1500 m a. s. l. (Friis *et al.* 2001), fitting well with the maximum for the endemics in Anthericaceae.

The main centre of diversity of Iridaceae is a little further north in Bale compared to the centre of Anthericaceae. Endemic taxa occur at higher altitudes in Iridaceae than in Anthericaceae, and also at higher altitudes than the general trend in the Ethiopian flora.

For Hyacinthaceae the centre of endemism is placed even further to the north compared to the previous families, in Shewa, *i.e.* in central Ethiopia. Alliaceae, on the other hand, shows no clear centre. This family obviously has a

northern distribution in the Horn of Africa, not surprisingly regarding the temperate distribution of this family as a whole.

Amaryllidaceae and Colchicaceae include elements with very different connections and ecology, and "family centres", consequently do not show a clear pattern. Endemic taxa have mainly evolved at higher altitudes in the former, at lower (except *Merendera*) in the latter.

The region richest in lilioid geophytic endemics is an area reaching from Neghelle (in Sidamo) to Sof Omar (in Bale) which includes the Bale Mountains. The "gravitational centre" falls just southeast of the Bale Mountains, and is calculated to be found at 6° 30' N, 40° 12' E and at about 1250 m. This area is fairly inaccessible, and no collectors have probably been in the close vicinity of this spot. This centre is found where the lowlands are situated geographically fairly close to the highest parts of the Bale Mountains. One might expect that such areas might have experienced dramatic changes in vegetation and climate connected to the shifts between dry and wet periods during the Quaternary.

Based on the information indicated above, the Bale Mountain National Park is extremely important for the conservation of Ethiopian endemic taxa. But areas, surrounding the mountain, are also of great value. Parts of this range, crucial for the conservation of diversity and endemicity, are found within wildlife reserves and controlled hunting areas. Out of the 33 (near-)endemics, as much as 18 are found within this region. The remaining 15 have important centres within Harerge, Tigray, and Shewa, as indicated by the presented maps. The Harar Elephant Sanctuary and the Simen National Park may house some of this endemicity, whereas the heavily exploited Shewa region still lacks well protected areas to cover the unique endemic taxa.

The works of *e.g.* Friis (1994) and Friis *et al.* (2001) are important to elucidate the broad phytogeographic connections on the Horn of Africa, and the Flora database referred to by Friis *et al.* (2001) will, obviously, be a treasure of information. To obtain information relevant for local conservation, however, the 16 regions defined in the Flora of Ethiopia and Eritrea, might be too broad-scaled to catch the local evolutionary "hot-spots". For this purpose, the data collected by the actual authors of the different families might be very valuable. This paper, hopefully, contributes to identify more local centres of endemicity, and thus diversity. May be the Editorial Board of the flora project should encourage the collection of the (hopefully) more detailed information that is in the possession of the authors for the benefit of the conservation of the Ethiopian flora?

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Avian endemism in northeastern tropical Africa

Jon Fjeldså & Helen de Klerk

Fjeldså, J. & de Klerk, H. 2001. Avian endemism in northeastern tropical Africa. *Biol. Skr.* **54**: 259-271. ISSN 0366-3612. ISBN 87-7876-246-4.

The avian endemism of Ethiopia and the Horn of Africa was analyzed using a database where all bird distributions in Africa south of the Sahara are recorded in a one-degree grid. Applying a hierarchical classification algorithm, the tropical Northeastern Subregion of Africa stands out clearly and can be subdivided in an Ethiopian Highlands Province and the Somalia-Masai, Tana-Jubba and Turkana districts and a Danakil Province. The Horn of Africa Province is associated with the Northern Arid (Sahara) Subregion in this hierarchical classification, although this reflects the replacement of savanna with desert birds more than shared endemism. Although most of the Ethiopian Highland endemics are distributed all over the highland, a more complex pattern of local endemics can also be defined, using a complementarity algorithm. Local endemism is very pronounced among the larks, Alaudidae. The majority of endemics belongs to recently radiated groups, and is mainly related to the fauna of East Africa; however, the fauna of the Sidamo district contains relict elements, two of these of a significant evolutionary age. The pattern of endemism in the birds of northeastern tropical Africa has a number of features in common with patterns found in plants.

Jon Fjeldså, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen, Denmark. E-mail: jfjeldsaa@zmuc.ku.dk

Helen de Klerk, Cape Nature Conservation, Scientific Services Division, Private Bag X5014, Stellenbosch, 7599, South Africa. E-mail: hdeklerk@cncjnk.wcape.gov.za

Introduction

Being the largest highland area in Africa, well isolated from other Afromontane areas by the lowlands grass savannas of southern Sudan and by the desert of the Lake Turkana area (White 1983), it is not surprising that the Ethiopian highlands have a number of unique and endemic species of birds (Urban & Brown 1971; Stattersfield *et al.* 1998; BirdLife International 2000). Other smaller aggregates of endemic species have been defined in the adjacent foothills and for various parts of the Horn of Africa. However, a large proportion of the avifauna is comprised of widespread species, and other species are disjunctly distributed (Fig. 1), illustrating how endemism may arise as once-widespread species decline to form widely isolated populations.

In this paper we will analyse patterns of endemism and biogeographic relationships of birds in Ethiopia and adjacent areas using a database of bird distributions in Africa south of the Sahara. The Percy FitzPatrick Institute of Cape Town and the Zoological Museum of Copenhagen jointly developed this database. We used the Worldmap software (Williams 1998), which is a PC-based graphical tool designed for rapid and interactive digitisation

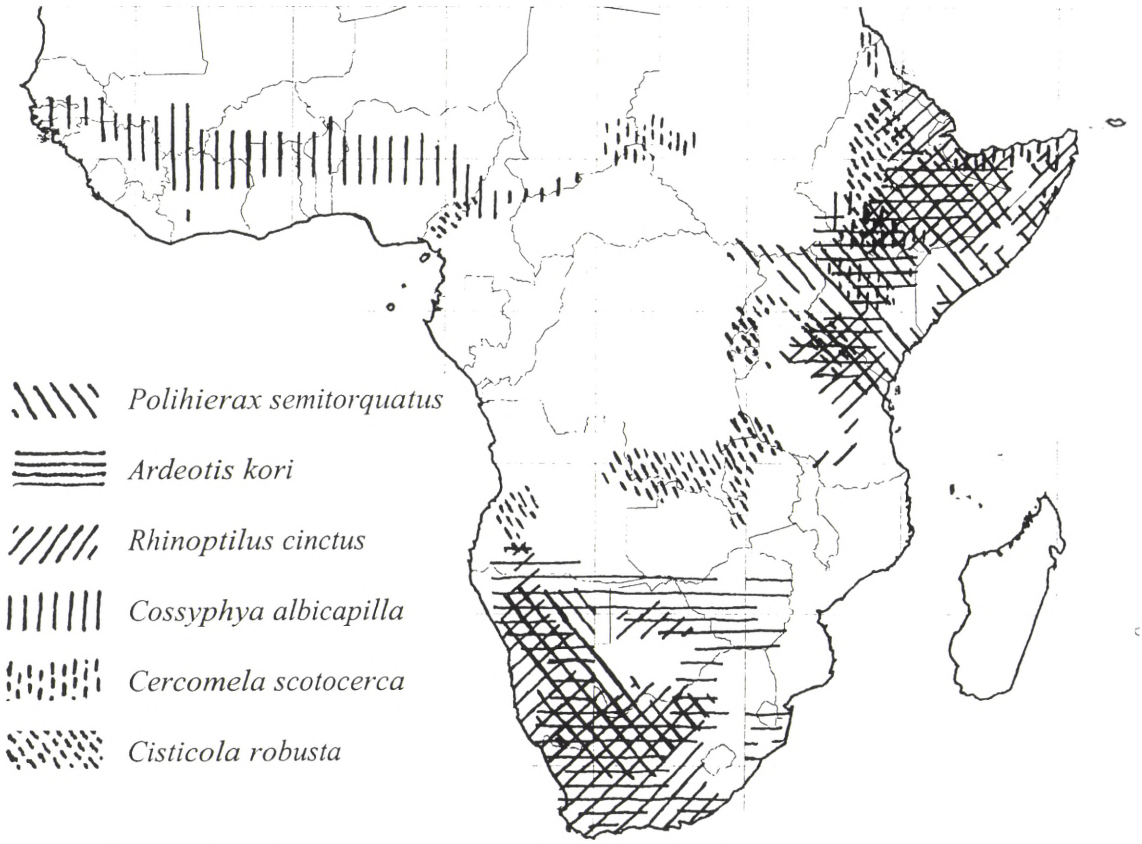


Fig. 1. Distribution of six species of non-migratory Afrotropical birds with disjunct distributions (note that some of the populations may already be recognizable as phylogenetic species).

of distributional data for large numbers of species. The records were allocated to grid cells corresponding to geographical degrees, for range-maps (made by conservative interpolation, and taking the distribution of suitable macrohabitats into account), or point localities for species that are considered genuinely rare or local. The distributional data were compiled from regional handbooks and distribution atlases (for northeastern tropical Africa especially Archer & Godman 1937; Cave & MacDonald 1955; Urban & Brown 1971; Nikolaus 1987; Solomon Tilahun *et al.* 1996; Ash & Miskell 1998) and published articles (*e.g.* Safford *et al.* 1995; Ash & Miskell 1988; Ash 1998; Ash & Gullick 1990) as well as information from a large number of persons, and from the databases of BirdLife International. Preliminary descriptions of the databases are given in Burgess *et al.* (1998, 2000) and in Brooks *et al.* (in press). The avifauna of Ethiopia and the Horn of Africa can therefore be analyzed in a continent-wide perspective.

Widespread and endemic species

The variation in species richness across Africa is illustrated in Fig. 2. This map clearly shows the importance for biodiversity of the highlands in eastern Africa, and especially of dis-

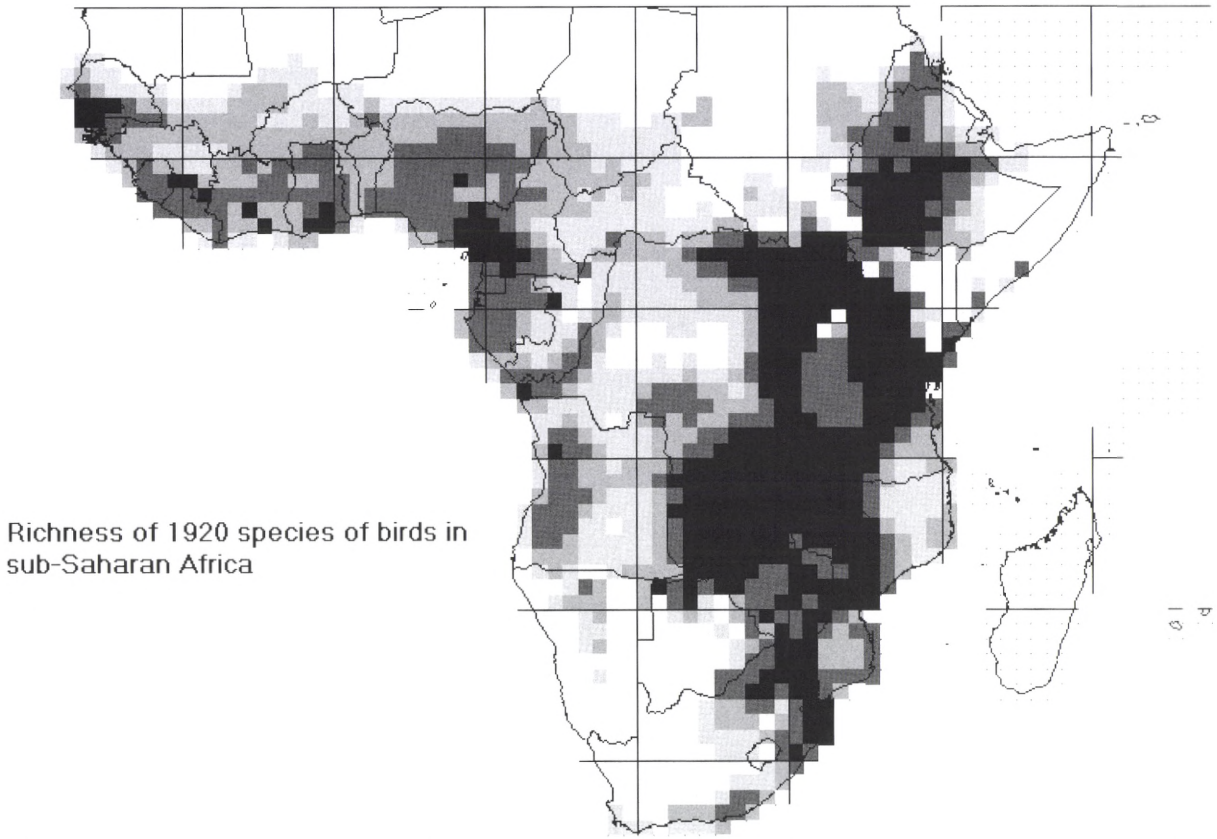


Fig. 2. Species richness of all species of birds in Africa south of the Sahara. The darkest areas have the highest relative species richness.

tricts with mosaics of savanna and forest and high topographic complexity. It also shows the relatively isolated position of the Ethiopia highland, and its somewhat impoverished fauna, compared with the highlands of Kenya and the Albertine Rift. The Ethiopia highland stands out more clearly if we consider endemism (sum of inverse range-sizes for all bird species represented in each grid-cell). Its importance is even more marked if we illustrate instead (Fig. 3) the distribution of threatened birds (critical, endangered and vulnerable categories, following the IUCN criteria, see Collar & Stuart 1985, Mace & Stuart 1994 and BirdLife International 2000). According to these criteria many species are classified as endangered because of their small distributions, so this map illustrates a combined effect of endemism and intensive human land conversion. According to Fig. 3 the entire Ethiopian mountain massif west of the Rift Valley is important from a conservation perspective, together with the Nechisar and Bale areas and foothills of the Sidamo area, and some highland sites around the Gulf of Aden.

The entire tropical northeastern region of Africa (Ethiopia, Eritrea, Somalia and the Turkana district of Kenya) has some 672 resident species of birds, of which some 80 (12%) species are endemic and near-endemic. Of

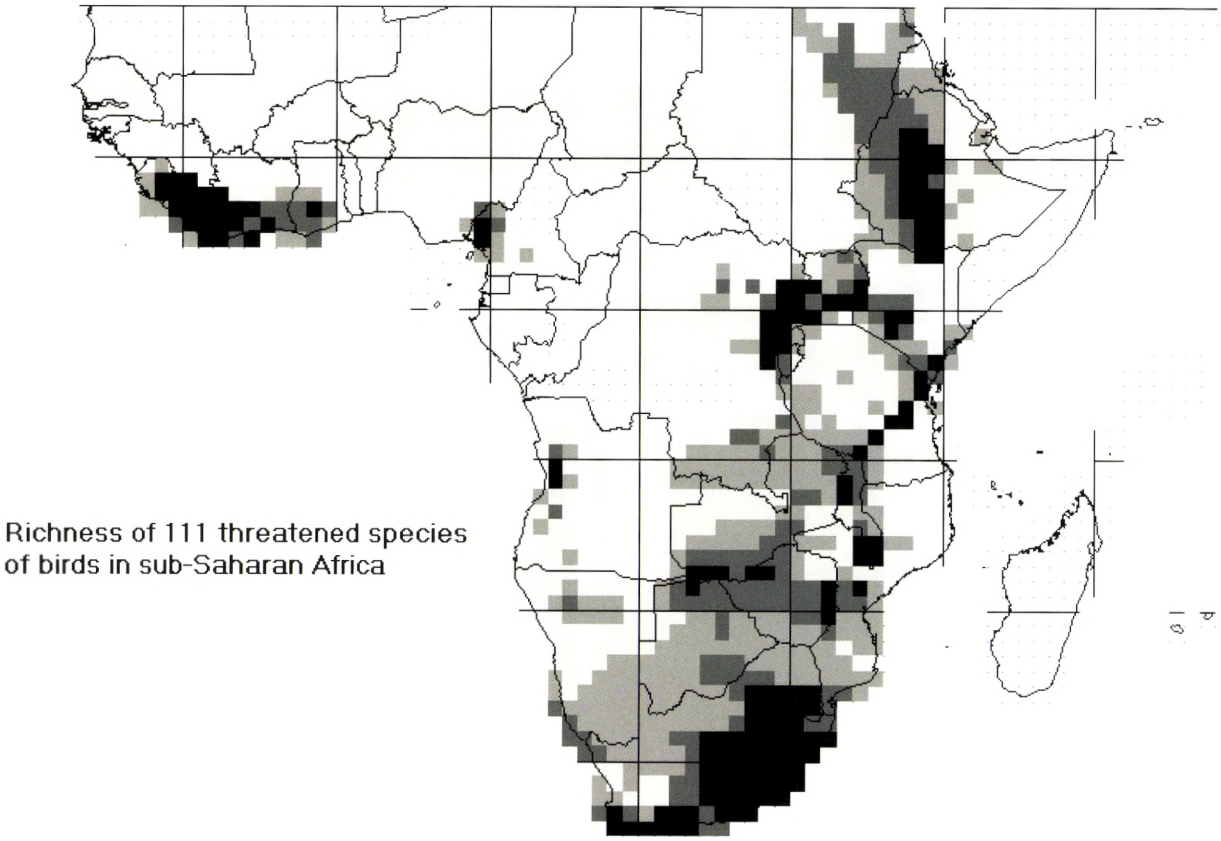


Fig. 3. Species richness of threatened species (*i.e.* critical, endangered and vulnerable categories, in this case including northern migrants). The darkest areas have the highest relative species richness.

these only 22 are forest or woodland birds. Among the remaining open-land birds, the most remarkable group is the larks (*Alaudidae*) with 31 species of which 12 are endemic. Some of these have very small ranges (single sites in some cases) and are associated with very specific kinds of semi-desert terrain, characterised by different soils (rocks to barren red soil) and specific kinds of vegetation, presumably of restricted distribution. Most African larks are resident, and recent molecular studies indicate that the pattern of differentiation may be much more complex than suggested by the currently accepted species level classification (Ryan & Bloomer 1999).

Hamilton (1989) considered Ethiopia to be a minor core area for endemism and biodiversity, while Brenan (1978) suggested the plant endemism of Ethiopia to be over 20%. Friis *et al.* (2001) judges the plant endemism of Ethiopia to be between 10 and 20 per cent, and Lye (2001) considers the endemism (of Cyperaceae) to be even higher in Somalia. Compared with plants, the avian endemism is modest, with much fewer examples of very narrow distributions, although the larks represent exceptional cases, which almost parallel the endemism in geophytes (Nordal *et al.* 2001).

Definition of avifaunistic regions

Our Africa Bird Database is well suited for objectively defining large-scale biogeographic regions, as the data are recorded in 1° cells rather than for predefined eco-regions of variable size. The ideal method for defining patterns of endemism would be to use a Parsimony Analysis of Endemism (see Morrone 1994). However, the existing software and computers unfortunately cannot handle datasets of >1700 species and 2169 area units according to this algorithm.

We therefore used a Bray-Curtis distance index (*e.g.* Everitt 1993) to measure the dissimilarity, cell by cell, for the endemic terrestrial Afrotropical birds (de Klerk, unpublished thesis, and see Williams *et al.* 1999 for Twinspan and Decorama ordination using the same dataset). We use the Bray-Curtis index here since it does not consider conjoint absences (*e.g.* Sneath & Sokal 1973; Krebs 1989). A hierarchical classification algorithm was applied to the resultant distance matrix in order to indicate groupings, or clusters, of grid cells that comprise similar avifaunas, and to indicate how these clusters relate to each other. A UPGMC (unweighted pair-group method using centroid) algorithm (Sneath & Sokal 1973) was applies using BMDP-2M software (Dixon 1990). It needs to be born in mind that this is a divisive cluster analysis, which simply represents a joining of objects into groups based on a set of rules. So the result is neither true nor false, and should be judged on the usefulness of the results (Everitt 1993) for the practical subdivision of faunas.

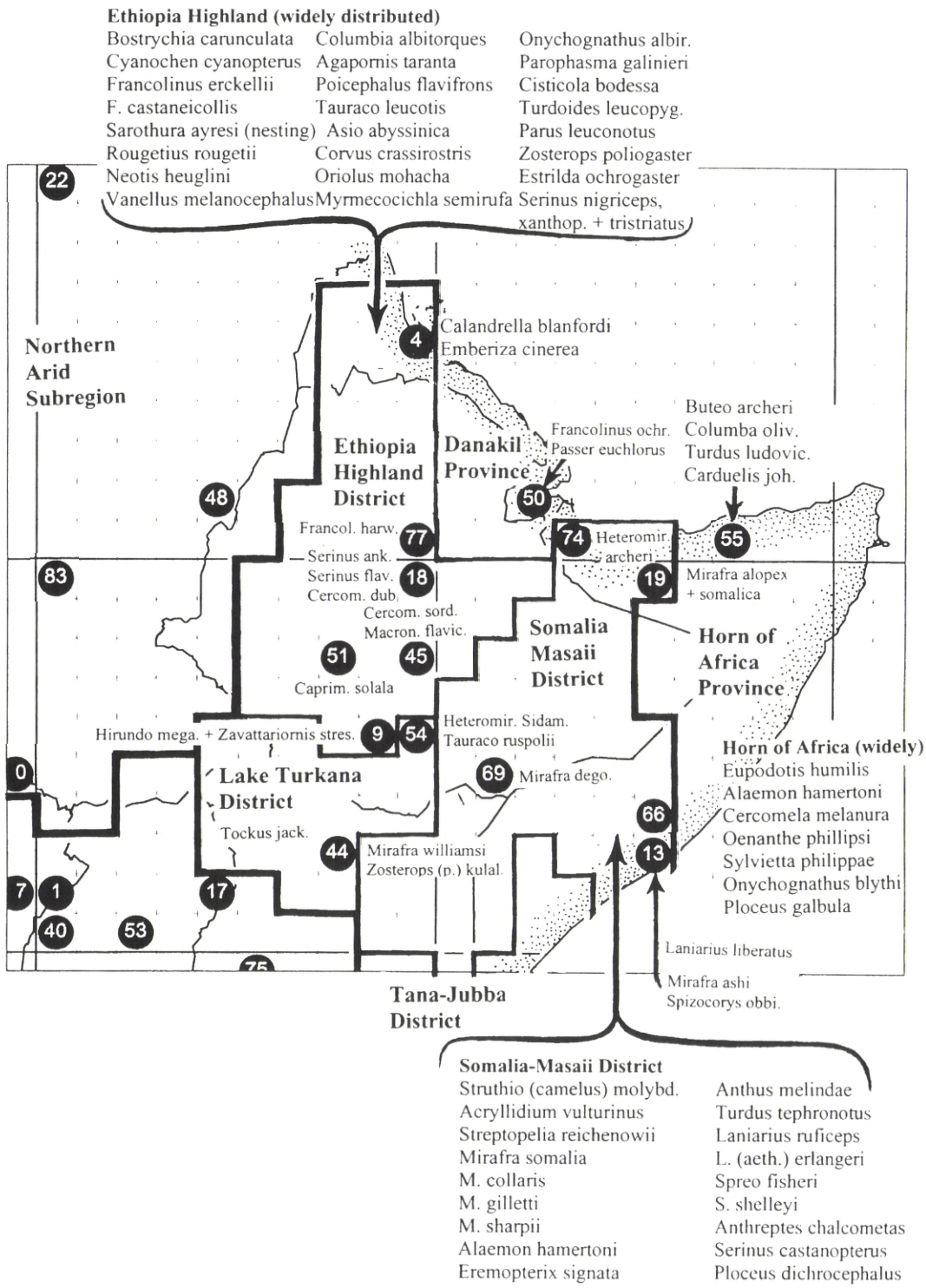
The boundaries of biogeographic provinces and districts in tropical northeastern Africa are drawn in Fig. 4. On this illustration is also listed all species which are endemic (or near-endemic) to the respective regions. For detecting the finer patterns of differentiation we used a complementarity algorithm: here all species distributions are compared and a minimum number of areas is identified which covers all endemic African birds (see legend to Fig. 4 for explanation). The software also has functions for identifying species, which are exclusively represented in the particular cells of the minimum set (as indicated in Fig. 4). It also has functions for displaying the combined (superimposed) distributions of these particular species as well as information about the total array of species represented in a particular cell (Fig. 5).

The Northeastern Subregion

In the hierarchical classification of areas, the area we deal with in this paper, the tropical *Northeastern Subregion* of Africa, stands out as a distinctive cluster with altogether 58 zone-restricted bird species. The subregion can in turn be divided into an *Ethiopian Highlands Province* and several lowland districts, namely the *Somalia-Masai*, *Tana-Jubba* and *Turkana Districts* and the *Danakil Province*. The strong affinity of the lowland districts to each other is attributable to a number of species that are distributed more or less throughout the dry and arid *Acacia-Commiphora* thorn scrub and savanna that sweeps from the Gulf of Aden to Lake Turkana. However, it should be noted that some of the narrowly endemic species (including the distinctive *Hirundo megaensis*, *Zavattariornis stresemanni* and *Tauraco ruspolii*, covered in cells 9 and 54 in Fig. 4) inhabit different habitats in the foothills of the Borana district, which span the borderline to the Ethiopian Highland Province (Syvertsen & Dellelegn 1991). This means that the data are not sufficiently fine-grained to identify minor areas of endemism and describe the pattern with precision.

The Ethiopian Highlands Province

The *Ethiopian Highlands Province* is the most important avifaunal zone in terms of numbers of endemics. However, most of the endemic


Ethiopia Highland (widely distributed)
Bostrychia carunculata
Cyanochen cyanopterus
Francolinus erckellii
F. castaneicollis
Sarothura ayresi (nesting)
Rougetius rougetii
Neotis heuglini
Vanellus melanocephalus
Columbia albitorques
Agapornis taranta
Poicephalus flavifrons
Tauraco leucotis
Asio abyssinica
Corvus crassirostris
Oriolus mohacha
Myrmecocichla semirufa
Onychognathus albir.
Parophasma galinieri
Cisticola bodessa
Turdoides leucopyg.
Parus leuconotus
Zosterops poliogaster
Estrilda ochrogaster
Serinus nigriceps, xanthop. + tristriatus
22
Northern Arid Subregion
4
Calandrella blanfordi
Emberiza cinerea
Buteo archeri
Columba oliv.
Turdus ludovic.
Carduelis joh.
Francolinus ochr.
Passer euchlorus
Ethiopia Highland District
Danakil Province
50
48
Francol. harw.
77
74
Heteromir archeri
55
Serinus ank.
Serinus flav.
18
19
Mirafra alopex + somalica
83
Cercom. dub.
Cercom. sord.
Macron. flavic.
Somalia Masaii District
Horn of Africa Province
51
45
Caprim. solala
Hirundo mega. + Zavattariornis stres.
9
54
Heteromir. Sidam.
Tauraco ruspolii
Horn of Africa (widely)
Eupodotis humilis
Alaemon hamertoni
Cercomela melanura
Oenanthe phillipsi
Sylvietta philippae
Onychognathus blythi
Ploceus galbula
0
Lake Turkana District
69
Mirafra dego.
66
Tockus jack.
44
13
Mirafra williamsi
Zosterops (p.) kulal.
7
1
17
40
53
Laniarius liberatus
Mirafra ashi
Spizocorys obbi.
Tana-Jubba District
Somalia-Masaii District
Struthio (camelus) molybd.
Acryllidium vulturinus
Streptopelia reichenowii
Mirafra somalia
M. collaris
M. gilletti
M. sharpii
Alaemon hamertoni
Eremopterix signata
Anthus melindae
Turdus tephronotus
Laniarius ruficeps
L. (aeth.) erlangeri
Spreo fisheri
S. shelleyi
Anthreptes chalcometas
Serinus castanopterus
Ploceus dichrocephalus

species occur widely distributed in the highland, although often segregated in different habitats of forest and montane grassland. The majority of the endemic highland species are associated with forest (*Francolinus castaneicollis, Tauraco leucotis, Zosterops poliogaster, Agapornis taranta*; *Poicephalus flavifrons* and *Asio abyssinicus* in *Podocarpus* forest, *Parophasma galinieri* in bamboo forest and *Cisticola bodessa, Dendropicos abyssinicus* and *Oriolus monacha* in *Juniperus procera* forest). Others occupy woodland (*Parus leuconotus*), grassland (*Cyanochen cyanopterus, Vanellus melanocephalus, Rougetius rougetii, Macronyx flavicollis, Estrilda ochrogaster*), or moor- and heathlands (*Serinus nigriceps*). *Sarothura ayresi* depends on seasonally inundated montane grassland, and its known breeding population is restricted to Berga and Weservi. Associated with cliffs are *Columba albitorques, Corvus crassirostris, Myrmecocichla melaena, Onychognathus albirostris, Passer swaynsoni* and *Serinus ankoberensis*.

The most narrowly endemic species do not show a particularly clustered (nested) pattern, but occur single or a few together. As examples, *Francolinus harwoodi* has a tiny range in thornscrub around the upper Blue Nile (cell 77 of the minimum set, with parts of the Abbai [Blue Nile] River Basin, see Robertson *et al.* 1997, and possibly in Gore). The entire distribution area of *Cercomela dubia* and *Serinus flavigula* is covered by the adjacent cell 18. In addition, *Myrmecocichla melaena* and *Serinus ankoberensis* inhabit rocky terrain in both these cells. *C. dubia* is known from scattered records also elsewhere in the province. The single specimen of *Caprimulgus solala* is from the Rift Valley at Nechisar (cell 51). No bird species is narrowly endemic to the eastern highland (unlike *Tachyoryctes macrocephalus* and *Megadendromus nikolausi* among rodents).

Lake Turkana District

A remarkable aggregate of very narrow endemics is found on the transition from the Ethiopian Highland towards the Turkana desert, in the Borana district. This includes red soil desert with *Mirafra somalica, Acacia* forests with *Zavattariornis stresemanni* and *Hirundo megaensis* near Yabello and Mega, montane grassland with *Heteromirafra sidamoensis* near Negele, and evergreen forests with *Tauraco ruspolii* near Arero and Negele). The Turkana desert is species poor, characterised by *Tockus jacksoni*, and by two narrowly endemic species in the Kenyan part (*Mirafra williamsi* at Marsabit and Isiolo, and *Zosterops (poliogaster) kulalensis* in a montane forest 'island').

The Somalia-Masai District

The *Somalia-Masai District* covers the foothills and plains east and southeast of the Ethiopian highland, as far as and including the Haud Plateau, from the Gulf of Aden to northeastern Kenya. The district is dominated by *Acacia-Commiphora* thickets, and its endemic species occur single or a few together in a quite complex pat-

← **Fig. 4.** Areas of avian endemism in northeastern tropical Africa, as determined using the distributions of endemic African landbirds. Thus we excluded for this analysis waterbirds and northern migrants and species shared with the Palearctic region. The lines separate the biogeographic regions as determined by the cluster analysis, while numbered dots represent the near-minimum set of areas needed to cover all species, using a complementary analysis. In the latter analysis the most species rich cell is first chosen (1; a cell on the Congo/Uganda border), then the cell is chosen which provides most new species which were not represented in the first cell (2; a cell on Mt. Cameroon not shown), then the cell with the second highest number of new species (3; a cell with the East Usambara Mts of Tanzania), and then the cell with the third highest number (4; a cell at the Red Sea coast of Erithrea), and so onwards untill all species are chosen; this is followed by a redundancy back-check. The endemic and near-endemic species are listed for each Province or District, with species represented only by one cell in the minimum set mentioned in connection with this cell.

tern. The endemic species inhabit riparian woodland in Somalia (*Streptopelia reichenowi, Laniarius liberatus, Anthus melindae*), riverine marshland (*Ploceus dichrocephalus*), highland grassland (*Heteromirafra archeri*), dry bush and *Acacia* scrub (*Mirafra aloplex*) and more open and rocky habitat (*Mirafra sharpii* and *M. degodensis* (the latter only at Bogol Mayo). Finally, two species are known from the coastal dune grassland, *Mirafra ashi* in one red-soil site, *Spizocorys obbiensis* more widely and up towards the Horn.

The Danakil Province

The *Danakil Province* resembles the Somalia-Masai semi-desert grassland and shrubland and regs, hamadas and wadis of the Danakil depression and the Red Sea coast and neighbouring hills, and the norhern limits of the Chercher Highlands with *Juniperus procera* forests. *Francolinus ochropectus* is the only strictly endemic species (in Djibouti), as other characteristic species are non-endemics which extent along the Red Sea coast or into adjacent parts of the Arabic peninsula. There is also a considerable overlap with the Ethiopian highland fauna.

The Horn of Africa Province

The portion of the Haud (Ogaden) Plateau of the Somali peninsula that does not fall into the Somali-Masai District is identified by the cluster analysis as the *Horn of Africa Province*. This province does not form part of the tropical Northeastern Subregion, but is rather part of the *Northern Arid Subregion*. This is not due to shared endemic species, but more accurately due to the loss of savanna species, and the fact that these savanna species are replaced with desert birds, as we pass into the Sahara and towards the Horn. The Twinspan and Decorana analysis (Williams *et al.* 1999) associates the avifauna of the Horn of Africa with that of the *Northeastern Subregion*, and demonstrates that the transition is characterised mainly by a high index for range edges and a decline in species richness.

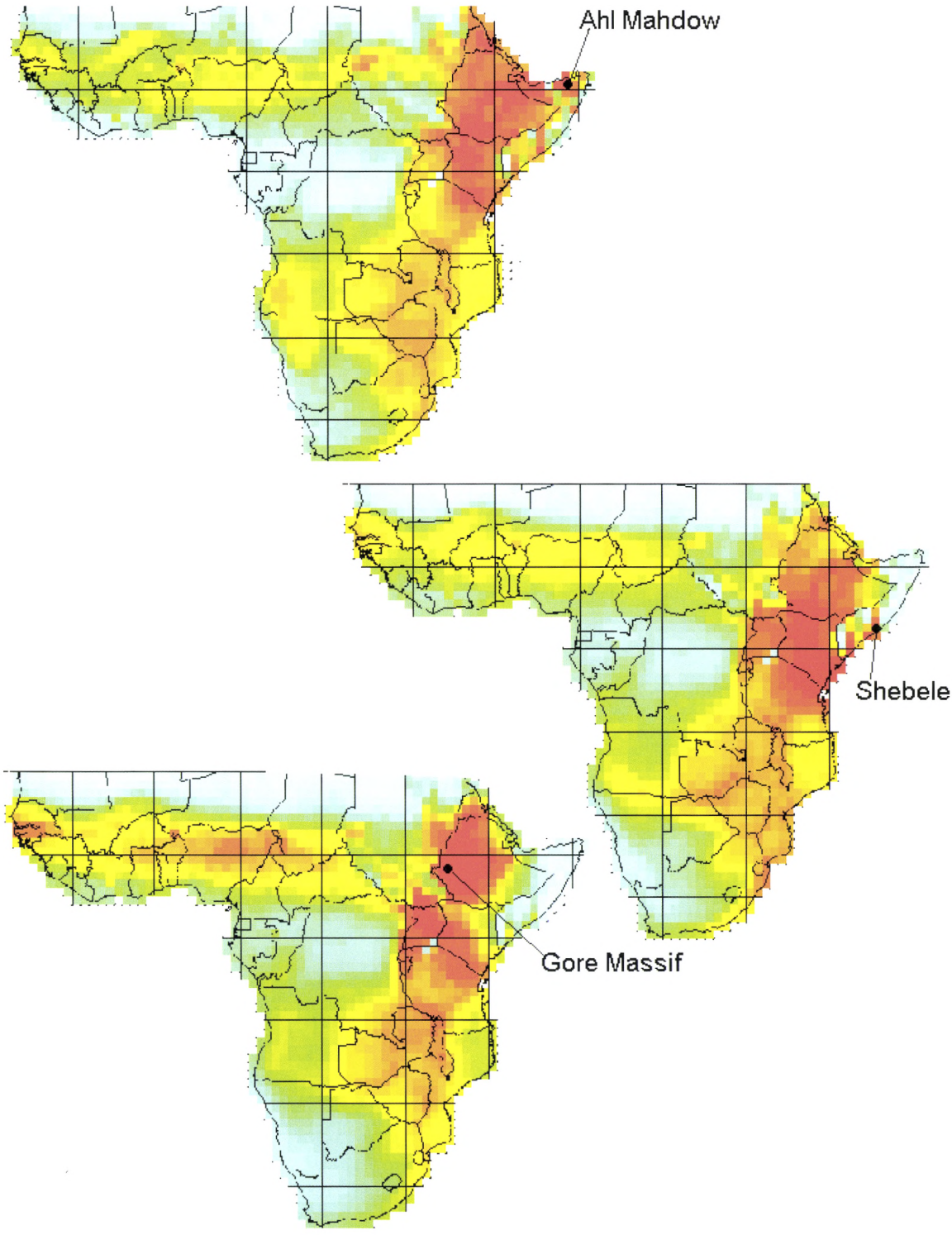
Endemic species for the Horn are *Sylvietta philippae, Eupodotis humilis and Oenanthe phillipsi*, and in the Nugal depression and Obbia coastline the larks *Mirafra somalica, Alaemon hamertoni* and *Spizocorys obbiensis*. The Warsengelia Highland and Ahl Madow scarp (previously Ahl Mado) has *Buteo archeri, Columba oliviae, Turdus (olivaceus) ludoviciae, Carduelis iohannes* (the two latter of these associated with the Daloh *Juniperus procera* forest).

Socotra Island, which has six endemic bird species, was not included in our dataset. The avifauna here is more closely associated with that of Africa than with the Arabian Peninsula. The avian endemism is quite modest compared with what is found in some other groups such as lizards.

The Tana-Jubba District

This is a mosaic area of coastal and riverine forests, evergreen and deciduous bushland and savannas, and extends southwards into Kenya, as a transition between the African Horn and the habitat mosaics of eastern Africa. The majority of species are shared with the coastal zone of Tanzania and Mozambique, but a few species are more narrowly endemic (*Tauraco fischeri, Macronyx aurantiigula, Phyllastrephus terrestris, Erythrocercus holochlorus, Cinnyris nectarinoides, Ploceus castaneiceps* and *P. boieri*).

Fig. 5. Biogeographic affinities of the bird fauna in northeastern tropical Africa, illustrated as the geographical distribution (richness) of species represented in three areas of endemism. Top: the distribution of the species of birds occurring on the northern scarp of the Horn of Africa at Ahl Madow. Right: the distribution of the species of birds occurring on the lower Shebele River in Somalia. Bottom: the distribution of the species of birds occurring at the Gore Massif, on the western slope of the Ethiopian Highlands. →


Ahl Mahdow
Shebele
Gore Massif

Evolution and biogeographic affinities

Two different approaches were used to determine the biogeographic affinities of the avifauna of tropical northeastern Africa: (1) Superimposing the current distributions of all species which are found in the different cells of the minimum set, and (2) reviewing the literature regarding relationships of the narrowly endemic species.

Superimposing distributions of widespread species
Some examples of the first approach are shown in Fig. 5. The resident birds of Gore, of the western slope of the Ethiopia Highland (Fig. 4, bottom) are well distributed all over the Ethiopia highland, with the majority of the species also present south of the Sudd and the Turkana Desert, in Kenya and Uganda. Many species are widely distributed in the savanna regions of eastern Africa, or they are found in the northern woodland savannas. However, the map illustrates a large amount of range disjunctions in southern Sudan, corresponding to the Sudd swamps and adjacent grass savannas. Birds from Addis Ababa, and those of other parts of the Ethiopia Highland, show very similar patterns, although with slightly fewer species represented in the western savannas. The birds of the lower Shebele River of Somalia (Fig. 5, right) are more uniformly distributed across Kenya to northeastern Tanzania, and are much less represented in the western savannas.

The birds of the fairly species-rich Ahl Madow scarp (on the northern edge of the Horn, Fig. 5, top) are rather locally distributed elsewhere on the Horn, but are generally well represented in the drylands and uplands of Ethiopia and East Africa, and fairly well represented along the Red Sea (many species also in Yemen). Many species are also represented in the Jebel Marrah highland of Darfur in central western Sudan and locally in the Sahel, and also locally in the southern savannas and drylands. The strong connection westwards over Darfur is also clearly demonstrated by the Danakil avifauna (Djibouti cell).

The general pattern that emerges from this is that the majority of birds in the tropical Northeastern Subregion of Africa are quite widely distributed in the African savannas, except for a poor representation in the grassland savannas of southern Sudan. This seems, overall, to be a more efficient barrier than the Turkana desert, except of course for the forest birds, where also the gap between the Boran foothills and the Kulal and Marsabit highlands represent a significant isolating barrier. In many cases, the faunal connection with the western savannas apparently was over the hills of central Sudan and Darfur, which in the past may have had a richer vegetation cover than today, maybe with some woodland.

Evolutionary relationship of endemics
The majority of endemic species of the tropical Northeastern Subregion have their closest relatives in eastern Africa south of the Turkana desert. In some cases, however, a considerable distribution gap exists (especially for some Somali endemics, some of which have their nearest relatives in southern Africa, as illustrated in Fig. 1). While the Danakil Province has a strong influence from the Palaearctic fauna, this is much less the case with the endemic fauna of the Ethiopia highland. Examples comprise populations of the northern *Tadorna ferruginea* and *Pyrrhocorax pyrrhocorax* and possibly *Aquila chrysaetos*, and two endemics: *Serinus ankoberensis*, which is related to *S. menachensis* of southwestern Arabia, and *Asio abyssinicus*, which is related to a widespread Palaearctic form. Overall, the affinities between the endemic Ethiopian avifauna and that of Arabia and Eurasia appear to be weak (in contrast to for instance mammals and plants).

Overall, speciation in birds seems to involve geographic isolation, either after chance dispersal across a habitat gap, or because of a disruption (by vicariance or relictuation) of a once-continuous range (Fig. 1). Recent analyses using DNA data suggest that, during the most recent geological past, the most intensive diversification in Africa was in the savanna regions, and mainly in mountainous areas. In contrast, the lowland rainforests seem largely to act as 'museums' retaining the species of the biologically much richer Tertiary rainforests (Fjeldså & Lovett 1997; Roy et al. 1997; contrary to earlier ideas about speciation caused by isolation in Pleistocene forest refuges, see Diamond & Hamilton 1980).

Patterns of local endemism

Within the montane areas, the narrow endemism is often locally aggregated in places with predictable ecoclimatic conditions, probably due to local orographic moderation of extreme weather conditions (Fjeldså *et al.* 1997). This implies that much of the endemism in the Afrotropical avifauna is relictual, and that the emergence of new species in the African avifauna is often related to stable local conditions.

The Ethiopia Highland seems to differ from this picture as most endemics live all over the highland, and do not show marked local aggregates. The highland is climatically unstable, with high vulnerability to drought and high inter-annual variability in the vegetation index (Fjeldså *et al.* 1997). Over a longer time perspective, the rifting and volcanism meant an enormous environmental disturbance (Sayer *et al.* 1992). In this case, the endemism seems to reflect the isolation of the highland as a whole, more than special local conditions. An exception may be the scarp near Addis Ababa, which has more stable local conditions, the foothills south of the Bale highland towards the Borana district (see below), and the Ahl Madow scarp on the north side of The Horn.

Molecular data and species ages

The distinctive appearance of many Ethiopian highland birds may reflect strong directional selection caused by the unstable and harsh climate (Dorst & Roux 1972). A molecular study of the large genus *Serinus* (Arnaiz-Villena *et al.* 1999) suggested that this group radiated since the end of the Miocene. Unfortunately the study did not include any of the endemic species of the tropical Northeastern Subregion of Africa, but judging from phenetics, all the endemic species seem to cluster fairly closely with species which were studied, and therefore seem to represent recently derived branches. However, a few highland endemics may represent much deeper branches. This applies to the distinctive highland rail *Rougetius rougetti*, which, according to preliminary DNA analysis, is a deep split (together with the East African *Crecopsis egreria*) within the cosmopolitan *Rallus* clade (B. Slikas, pers. comm). The highland goose *Cyanochen cyanopterus* is assumed to be related to the Andean and Patagonian geese of the genus *Chloephaga* (Johnsgaard 1965).

Stable local conditions, which may have allowed persistence of relict taxa, possibly exist in the Boran foothills. This area is characterised by a low inter-annual variability in ground conditions compared with most parts of the Ethiopia highland (Fjeldså *et al.* 1997). Furthermore, this area falls between the biotic influence of the ecoclimatically unstable western savannas and the Somali desert, and it is isolated towards the south by the Turkana desert. Three of the five narrowly endemic birds of this area may be relicts. The lark *Heteromirafra sidamoensis* belongs to the *H. ruddi* superspecies, which has a relict/disjunct distribution in Africa. The very aberrant 'crow' *Zavattariornis* is usually assumed to be related to the *Podoces* groundjays of the Asiatic highlands, and this is also indicated by a preliminary analysis of mitochondrial DNA data (P. Ericson, pers. com.). According to a phylogen-

etic analysis of tauracos (Veron 1999), *Tauraco ruspolii* is basal to all the typical green tauracos, which suggests that it may represent an ancient relict population, maybe of Miocene age (rather than being sister to *T. leucotis*, which inhabits adjacent geographical areas, as suggested by Borghesi 1997).

Acknowledgements

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Origin and evolution of rural homegardens in Ethiopia

ZEMEDE ASFAW

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Small-scale traditional agricultural ecosystems, commonly known as homegardens, were studied in the semi-arid central and the humid southwestern parts of Ethiopia. Hundred homegardens, with fifty in each of the two areas, but otherwise randomly sampled, were scored as being in pioneer, intermediate or climax stages. In the southwest, the percentage of climax gardens was 11% above country average, while in central Ethiopia it was 10% below average; the opposite was the case with intermediate gardens; the percentage of pioneer gardens was nearly the same in the two areas. Qualitative information recorded from observation of gardens at different stages was used to discuss general trends in the development of homegardens. In central Ethiopia homegardens are generally established outside agricultural land, often on stony or rocky ground earmarked for living quarters, while in the southwest homegardens are usually established in forest clearings where useful forest plants are deliberately retained *in situ*. Microhabitats diversify as the homegardens mature, vertical and horizontal patterns develop, and the diversity of cultivated species increases, as well as the range of variation in horticultural, physiognomic and phenological features. The vertical structure and complex intercropping is more developed in homegardens of the southwest, while there is more emphasis on the horizontal structure of the homegardens of central Ethiopia. Homegardens in southwestern Ethiopia utilise many species of the natural ecosystem and recruit promising new crops through an open-door strategy, which facilitates geneflow between spontaneous and homegarden populations of crop species, as well as with their wild relatives. Conservation can learn a lesson from traditional management of rural homegardens in southwest Ethiopia, but these homegardens will no doubt be poorer if the surrounding natural forest continues to disappear.

Zemede Asfaw, Department of Biology, Addis Ababa University, P. O. Box 3434, Addis Ababa, Ethiopia. E-mail: nat.heb@telecom.net.et

Introduction

The term homegarden is applied to a variety of small-scale farming premises attached to the living quarters. Homegardens mainly serve family needs for food, medicine and other products of domestic importance (Brownrigg 1985; Soleri & Cleveland 1989; Christanty 1990). Homegardens are known by various vernacular designations in different cultures, *viz.* backyards, compound farms, kitchen gardens, homestead farms, or mixed gardens. Homegardens constitute part of the traditional farming systems, and are charged with crop production, while they also help conserving agrobotanical biodiversity on-farm (Brownrigg 1985; Soleri & Cleveland 1989; Christanty 1990; Fer-

nandes & Nair 1990; Marten 1990; Okigbo 1990; Wojtkowski 1993; Nguyen 1995, Power & Flecker 1996; Gesseler *et al.* 1996, 1997; Godbole 1998; Wang 1998). In a broader context, homegardens are systems that include the people on the farm and the domestic animals, together with the plants maintained in the small space around the homestead. Planting patterns in homegardens often include patches, rows, or complex intercropping, or may be according to a seemingly random design. Homegardens make up a complex agro-ecosystem that simultaneously functions as a vegetable garden, an orchard, a medicinal plant garden, a spice lot, a bee yard, a garbage disposal corner, a compost heap, and much more. Homegardens serve critical functions in fulfilling community needs, which may range from basic food security to general nutrition, primary healthcare, income generation and other specialised functions, while ensuring conservation of agrobiodiversity and sustenance of a healthy environment around the living quarters.

The history of homegardening discloses that it has been an integral component of human subsistence strategies since the Neolithic Age (Soleri & Cleveland 1989). The earliest records of homegardens are from the third millennium BC in the Near East, where the homegardens we know about seem largely to have been associated with temples, palaces and elite residences (Brownrigg 1985). At present homegardens are widespread in the tropical and subtropical regions of Asia (Christanty 1990; Marten 1990; Nguyen 1995; Godbole 1998; Wang 1998), Africa (Okigbo 1990) and Central and South America (Padoch & Jong 1991; Esquivel & Hammer 1992; Hammer *et al.* 1992; Caballero 1992). In ecological terms, homegardens can be viewed as managed ecosystems with a dynamic interplay between the biotic, abiotic and socio-cultural factors (Power & Flecker 1996; Gesseler *et al.* 1997).

In Ethiopia, the antiquity of homegardens is still undocumented due to absence of palaeoethnobotanical studies, but the long history and present significance of homegardens is fully acknowledged (Westphal 1975; Okigbo 1990; Zemede Asfaw & Ayele Nigatu 1995). The frequency of homegardens, and the intensity with which they are cultivated, varies from region to region. Homegardens are well developed in the south and the south-west, where vegeculture abounds, and the eastern part of the country where diverse cropping patterns are known, but homegardens are rudimentary in the north, which is dominated by cereal culture (Zemede Asfaw 1997). Many indigenous crops of Ethiopia are cultivated in homegardens, and for some species there are both cultivated forms in the home gardens and spontaneous populations that occur wild in the natural ecosystems. Considering the long history of agriculture in Ethiopia (Harlan 1969; Westphal 1975; De Wet 1979; Brandt 1984) and the presence of ancient crops in homegardens, it can with reasonable safety be speculated that gardening was among the earliest forms of farming practised in Ethiopia.

The last couple of decades have witnessed an increasing world-wide interest in homegardens, exposing their potentials for sustained subsistence farming (Benneh 1974; Torquebiau 1992) and biodiversity conservation (Brownrigg 1985; Caballero 1992; Okigbo 1994; Godbole 1998). Homegardens contribute to diversification of the agrobiodiversity in terms of genera, species, cultivars, and ecological specialisation, which under traditional management may show regular progression towards climax structures of intensive land utilisation in space and time (Rico-Gray *et al* 1990; Wojtkowski 1993). Homegardens have preserved local knowledge of plants and skills of their cultivation and utilisation, and traditional homegardens offer opportunities for ethnobotanical and agroethnobotanical studies. Though homegardens

have been characterised in many agroecosystems of the world, the dynamic processes during their growth to maturity still await elucidation on a broader scale. Limited studies have focused on the evolution of homegardens, but it has been supposed that they arose from shifting cultivation to overcome resource constraints and to ascertain rights to land resources (Fernandes & Nair 1990; Jose & Shanmugaratnam 1993). Very little is yet known about Ethiopian homegardens, but some information can be gathered from the work of Okigbo (1990), Zemede Asfaw & Ayele Nigatu (1995), Zemede Asfaw (1997), and Zemede Asfaw & Zerihun Woldu (1997). To date, the aspects of origin and evolution have never been investigated, though from earlier observations some clues can be found on the ecological succession and the biotic, abiotic and socio-cultural factors that governs it. This paper is focused on the origin and evolution of rural homegardens in two agroecologic zones in central and southwest Ethiopia.

The study area

An initial survey of homegardens in Ethiopia (Zemede Asfaw 1997) and a study that focussed at homegarden crop associations (Zemede Asfaw & Zerihun Woldu 1997) have highlighted the poor knowledge of homegarden inception and evolution in rural Ethiopia. Consequently, two agroecologically and culturally different zones, in the semi-arid Central Rift Valley and in the humid southwest respectively, were identified and data pertaining to origin and evolution collected. Data collection and observation was undertaken during fieldwork in 1996-1998, undertaken to study land resources in the Central Ethiopian Rift Valley (Zemede Asfaw 1999), and during an ethnobotanical study (1998) conducted in southern and western Ethiopia. The former study site is located in the area of the Ziway-Shala basin at approximately 8° N and 39° E. This area is relatively dry, and the crops are mostly annuals, but some woody and perennial herbaceous species occur, including *Citrus spp., Rhamnus prinoides, Catha edulis, Coffea arabica, Ensete ventricosum*, and *Brassica carinata.*

The second study site is located in the Kefa-Sheka zone in the area adjoining Bonga town at approximately 7°03' N and 36° E. This area is located in the high rainfall zone of Ethiopia, with natural multiple canopy rain forest containing spontaneously growing forest coffee (*Coffea arabica)* (see Friis 1979) and other plants also in cultivation, including *Rhamnus prinoides, Aframomum corrorima*, and *Ensete ventricosum.*

Methods

With the progress of the documentation of the Flora of Ethiopia, which has simplified determination of plants and made it easier to trace basic literature, it is becoming more and more feasible to take up the study of ethnobotany, agroethnobotany, indigenous food plants and their use in homegardens. During the work described in this paper, voucher specimens of taxa for which identification in the field was not certain were secured and deposited at the National Herbarium (ETH); the same applies for those species of which the available herbarium collections were felt to be insufficient. The initial study was a survey of homegardens, the results of which has already been published (Zemede Asfaw & Ayele Nigatu 1995; Zemede Asfaw 1997). These initial studies were followed by a study of homegarden crop associations (Zemede Asfaw & Zerihun Woldu 1997). The present study focuses on origin and evolution of homegardens in the two study areas in central and southwestern Ethiopia. However, the observations that led to this paper were also of a more opportunistic nature, undertaken over a prolonged time. Fifty rural homegardens have been randomly sampled in each region and scored as representing

the pioneer, the intermediate and the climax stage. The scoring was made on the basis of visual assessment, taking into account soil related factors, crop diversity, proportion of annual and perennial species, age classes of the dominant perennial species, the overall horticultural mix as well as the diversification of vertical and horizontal structures. Crop arrangement inside the garden was observed during transect walks from the house to the rear end of the garden: the species in each major zone were identified and mapped, together with the horizontal crop layout. Qualitative descriptions were provided to illustrate the ongoing changes and to paint a general picture of the pioneer, intermediate and climax homegardens of the two sites. Since the variation within each stage is wide, the description was of necessity general, and emphasis was given to the climax stage, in which the differences between the agrobotanical features of homegardens of the two study areas come out most clearly.

Results

Ethiopian homegardens have diverse structures, showing variation with the agroecology and general cultural diversity of the people. Collectively, the homegardens maintain a large assemblage of useful plants. The homegardens of some rural families, apparently crop conservators, were found to maintain an amazing number of crop diversity, a feature that has also been observed elsewhere in the world (Altieri & Merrick 1987). During the survey work of Ethiopian homegardens (Zemede Asfaw & Ayele Nigatu 1995; Zemede Asfaw 1997) a list of 172 species of useful plants maintained in Ethiopian homegardens was compiled. About 74% of these species were grouped as food crops, the remaining 26% as non-food crops. A recent ethnobotanical survey in southern and western Ethiopia showed that about 90% of the crops cultivated by each of the eleven ethnic groups surveyed were recorded from homegardens, and that about 60% of the crops cultivated by these people at present are only grown in homegardens (Zemede Asfaw 1998). The plants could be allocated to a wide range of horticultural groups, including food, medicinal herbs, spices, ornamentals and many other categories and subcategories. Mostly, the families assess the agricultural output of their homegardens by the degree of continuous availability of diverse fresh products with a significant nutritional complement (Zemede Asfaw & Zerihun Woldu 1997). Homegradens should therefore to a high degree be evaluated on their role for food security, although they of course have many other roles.

Of 100 rural homegardens observed with the intention of elucidating their developmental stages, 75 were scored as climax while 20 were intermediate and 5 were pioneer types that were just initiated. In the site in central Ethiopia, 64% of the gardens scored were at the climax stage, 30% at the intermediate and 6% at the pioneer stage. In the southwest, 86% was at the climax, 10% at the intermediate and 4% at the pioneer stage. Thus, there were relatively more mature gardens in the southwest than in central Ethiopia, relatively more intermediate gardens in central Ethiopia. This observation can be related to other observations, namely that in the two areas, homegardens are brought to life under different inception patterns, and that they progress to different climax stages. Since each garden has its unique features with regard origin, dynamics and content, the descriptions has essentially to focus on the main aspects rather than on specifics.

Inception and maturity of homegardens in central Ethiopia

In central Ethiopia, farmers build their living houses outside the farming area, usually on an outcrop mainly used for grazing of farm animals, and the place is frequently covered with

bushes and grasses when the new homestead is going to be established. The families begin by carving out the area needed for the house somewhere in the centre of the identified site. The animal stall is constructed at a suitable place, often where it is practical to accumulate manure that will be used to fertilise the cropping area. The usual practice is, however, from time to time to shift the location of the stall to a new site in the neighbourhood of the house, and to convert the old site of the stall to a cropping site that would become a new main garden area. Elders may identify these future cropping-sites during the initial planning phase, before the construction work on houses and stalls begins. The fertility of the garden soil gradually builds up, and some weedy and ruderal plant species become established in the garden, following the moving in of humans and domestic animals. The most common colonising herbs, some of which may be utilised for domestic purposes, include *Amaranthus spp., Solanum nigrum, Lycopersicon esculentum, Physalis peruviana, P. micrantha, Avena sp., Nicotiana tabacum, Cucurbita spp., Lagenaria siceraria, Commelina spp.* and several others. Some indigenous invasive species (*e.g. Lippia adoensis, Ocimum lamiifolium, Rosa abyssinica, Rubus spp.* and *Carissa edulis*) are tolerated along the garden fences and around unworked spots, and may be part of the fencing. The *in situ* garden species usually establish on the rubbish heaps and on places where the domestic animals rest. The pioneering conventional garden crops usually include spices, for example garlic, basil, peppers, and shallot, and vegetables, for example tomato, kale, cabbage, cucurbits, and white potato, as well as ornamentals that are gradually being planted by members of the family. The potential space of the garden is gradually being claimed while soil conditions improve. Land preparation, organisation of nursery beds and special plots for different horticultural purposes continues in new areas, while older parts of the garden are planted with intermixed cropping. Once deliberate planting starts, family members bring seeds and seedlings from abandoned houses in the village, from neighbours, or from the market, and piece by piece the family stocks their garden with an increasing number of taxa, increase the density of plants and the number of horticultural categories that give different products. As is clear from this description, relatively young gardens contain few species, many of which are annual herbs and juvenile perennials, while seasoned gardens contain more diversity and a higher proportion of perennial species and seasoned specimens of shrubs or trees.

Farmers sometimes opt for faster garden establishment by ploughing or hand digging the new ground in order to cultivate one or several crops of legumes (*e.g. Pisum sativum*, and *Vicia faba*) or cereals (*e.g. Hordeum vulgare, Eragrostis tef*). If this is done for the first season, the soil is rendered suitable for planting the regular garden crops in the following season. Sometimes homegardens are short-lived, as in central Ethiopia where they are partly meant for improving the future farm soil. The practice not only involves periodic shifting of the stalls and the garden plots, it also means shifting the entire living quarters together with the homegarden to less fertile sections of the farm and using the more fertile garden site for cultivation of the major field crops. In this process, the house is moved to a less fertile spot and gardening is started afresh. Such itinerant homegardens will usually have a limited total number of species and fewer perennial elements.

Inception and maturity of homegardens in southwestern Ethiopia

In the high-forest areas of southwestern Ethiopia, homegardens originate amidst the forest. Suitable sites are initially prospected and approved by knowledgeable elders on visual inspection of the sites and with due consideration to cultural traditions. Through

selective clearing of the forest, the useful elements, which include *Coffea arabica, Rhamnus prinoides, Aframomum corrorima, Piper capense* and *Passiflora edulis,* and a range of shade trees with other uses (*e.g. Cordia africana, Millettia ferruginea* and *Erythrina brucei*) are protected *in situ* inside the developing garden and/or as live fence plants. After clearing, the house is constructed at a suitable site within the cleared area, and members of the family prepare the land, taking good care of the useful forest plants left behind. Step by step the introduction of the usual garden crops proceeds, either from old houses, neighbours or the market, and a homegarden begins to mature.

The local people around Bonga asserted that the standing coffee crop in that general area has largely been claimed from spontaneous stands of coffee in the forest through such selective clearing. The same is the case with the cultivated false cardamom (*Aframomum*) and *Rhamnus*. The people also explained that wild enset is not claimed from the forest because of the local belief that wild enset (locally known as the devil's kotcho) is the devil's crop and not for human consumption. However, bananas from wild enset may occasionally be eaten, but only in limited amounts, and wild enset plants may be used as fodder, and the leaves provide wrapping and roofing material, the plants may be used for a number of other purposes. It was observed that wild enset in this part of Ethiopia mainly grows in association with river valleys, in places not suitable for housing sites, which may also partly account for these plants not being claimed in the establishment of new gardens as the other forest-growing crop species.

Patterns of homegarden evolution

General trend of the changes

Some of the main changes reflecting the growing complexity of Ethiopian homegardens can be related to the general patterns and processes of vegetation changes (Burrows 1990). Mature homegardens share to varying degrees the characteristics of climax ecosystems, such as relative stability, self-sustainability and ability to maintain productivity from inputs of solar energy. For that reason they are regarded by different authors as man-made ecosystems that mimic the natural tropical forests (Power & Flecker 1996; Jose & Shanmugaratnam 1993).

As homegardens grow to maturity, the following main changes are usually observed:

1. Improvement in soil conditions
2. Better suitability for a variety of different horticultural and physiognomic classes (plants for food, medicine, fragrance, fodder, construction material, implements, crafts, ornamentals and other use-values)
3. Increase in the number of crop species or cultivars
4. Higher frequency of perennial species
5. Increasing structural complexity in the homegarden (more patches, horizons and layers, diversification in growth forms; this and the following two points lead to higher intensity of land use)
6. Increasing complexity of intercropping
7. More patches of mixed stands of physiognomic and phenologic classes
8. Higher share in relation to total crop production on the farmstead, and higher share in the cash generation of the family.

A well-developed homegarden with diverse horticultural classes and high species diversity indicates that the family has higher levels of agricultural activities and more functional roles in the local community. This results in environmental, social and economic benefits for the family. It is a general feature throughout the tropics that homegardens originate, develop gradually and undergo subtle changes towards maturity and relative stability at their climax stages (Fernandes & Nair 1990; Jose &

Shanmugaratnam 1993). When finally terminated by human action, homegardens leave traces for years even after the homes are abandoned and the houses collapsed or removed from the site. This is seen in some parts of southern Ethiopia where the patchy wild enset stands appear to be indicators of abandoned homegardens of varying age. However, as mentioned above, around Bonga wild enset is found on hilly sides of streams, and it is unlikely that these were from ancient homegardens since families never build homes on riverbanks.

Specific aspects of homegarden evolution

In the semi-arid central Ethiopia, the setting up of a stable homegarden takes longer time, as the land needs repeated working and fertilising. Some of the crops require supplementary irrigation either for raising seedlings or for establishing transplants. More species need protection from the sun and moisture stress. In these areas homegardens with more perennial species are often those that are close to streams. Homegardens in the semi-arid zone start from an initial monolayered structure, mostly mixtures of annual herbs and a few juvenile perennials, and only gradually they progress to the emergence of distinct horizontal patches and in rare cases to multilayered structures. Compared to younger stages, climax homegardens in this area have a higher proportion of perennial species and seasoned shrubs or trees. With ecological changes in the area, and the receding of natural vegetation from the inhabited areas, the role of the homegarden as a place for maintaining medicinal and other useful plants increases. This results in the acceptance around the living quarters of such weedy medicinal herbs or spicy plants that would elsewhere be collected from nature. Experimental planting of wild collected seedlings of useful plants, and raising of the same from seeds, increases with advancing land degradation. It is common for farmers to collect *Rhamnus prinoides* seedlings from spontaneous stands in nearby montane forests and transplant them in homegardens. Sometimes coffee seedlings germinated from bird droppings in the vegetation of riverbanks are uprooted and transferred to nursery beds in homegardens for later transplanting.

In the humid southwestern zone, homegardens grow to climax within a relatively short period. This happens because of the good soil condition, the favourable environment with high rainfall and the *in situ* crops retained from the original natural forest. Young and seasoned homegardens have mixtures of crops of different ages, but the density of crops, the horticultural mix, the complexity of garden structure and the diversity of species increase with age. The main garden crop of the area, enset (*Ensete ventricosum*), soon emerges as a dominant element in the homegardens. Other common species include *Colocasia esculenta, Xanthosoma sagittifolium, Dioscorea alata, D. bulbifera, Musa paradisiaca, Cyphomandra betacea, Coccinia abyssinica, Passiflora edulis, Sechium edule, Ipomoea batatas, Saccharum officinarum, Zea mays, Sorghum bicolor* (sugary sorghum) and many species of *Cucurbita*, leafy vegetables, spices, medicinal herbs and others (see Table 1 below). The cropping layout gradually develops some pattern and will remain unaltered so long as owners maintain the home sites, which they can do for generations in this area.

Normal harvesting and replanting will ensure that the vertical and the horizontal structure of the climax homegarden remain unmodified. The system survives as a kind of traditional agroforestry system. Continued harvesting of enset for food does not change the structure to any noticeable degree because of renewed planting, which is well staggered in time and ensures presence of many stages of the plant within the same garden. The frequency of useful trees in the homegarden

Table 1. Horizontal layout of crops in a typical climax homegarden in the vicinity of Bonga town, southwest Ethiopia. The crops (a total of 48 species) have been recorded in different rings (from A (species from the ring with smallest diameter nearest to the home) to D (species from the ring with the largest diameter furthest from the home)). Species may occur in more than one ring.

A (9 species)	B (20 species)	C (23 species)	D (4 species)
Ocimum basilicum	*Artemisia afra*	*Dioscorea bulbifera*	*Ensete ventricosum*
Thymus sp.	*Ruta chalepensis*	*Dioscorea alata*	*Musa paradisiaca*
Allium sativum	*Brassica spp.*	*Sechium edule*	*Citrus sinensis*
Foeniculum vulgare	*Nicotiana tabacum*	*Cucurbita pepo*	*Ricinus communis*
Solanum tuberosum	*Cymbopogon citratus*	*Lagenaria siceraria*	
Iresine herbstii	*Rumex bequaerti*	*Brassica oleracea*	
Euphorbia pulcherrima	*Phaseolus vulgare*	*Saccharum officinarum*	
Canna indica	*Allium sativum*	*Nicotiana tabacum*	
Ruta chalepensis	*Capsicum sp.*	*Capsicum annuum*	
	Allium cepa	*Aframomum corrorima*	
	Zingiber officinale	*Coccinia abyssinica*	
	Foeniculum vulgare	*Canavalia ensiformis*	
	Lippia adoensis	*Coffea arabica*	
	Curcuma domestica	*Citrus aurantifolia*	
	Aframomum corrorima	*Citrus aurantium*	
	Lycopersicon esculentum	*Citrus sinensis*	
	Solanum tuberosum	*Colocasia esculenta*	
	Iresine herbstii	*Xanthosoma sagittifolium*	
	Euphorbia pulcherrima	*Manihot esculenta*	
	Canna indica	*Carica papaya*	
		Cyphomandra betacea	
		Ensete ventricosum	
		Sorghum bicolor	

reduces as people start utilising them for wood and other uses than fruit picking, but when a critical level of utilisation is reached the owners normally start encouraging spontaneous seedlings or planting those trees that they expect they will need in the future. The people have mimicked nature and increased the capacity of the homegarden to produce the optimal amount of the materials that they needed for everyday life. Here, crop production is directly linked with diversity as the people cultivate a very diverse assemblage of crops. Continuation of this tradition will have a good future for the biodiversity of food and agriculture.

The planting pattern secures that the size of the plants, on the average, successively increase with distance from the house and the diversity of taxa is highest relatively near to the homes (but not immediately around the house), and is re-

Table 2. Species both cultivated in homegardens and wild in natural ecosystems around Bonga or naturalized (*=a new record for the flora region). The probable place of domestication is indicated according to Hill (1972), Kunkel (1983), and Hancock (1992).

Species	Family	Probable place of domestication	Place of occurrence (other than homegarden)	Remarks
Aframomum corrorima	Zingiberaceae	Ethiopia	Forest	Native
Amaranthus caudatus, A. cruentus, A. hybridus	Amaranthaceae	South /Central America	Weedy	Naturalised
Anethum graveolens	Apiaceae	Mediterranean/Eurasia	Disturbed sites	Naturalised
Arundinaria alpina	Poaceae	Africa	Forest	Native
Arundo donax	Poaceae	Mediterranean/Eurasia	Forest	Naturalised
Coccinia abyssinica	Cucurbitaceae	Ethiopia	Forest	Native
Coffea arabica	Rubiaceae	Ethiopia	Forest	Native
Colocasia esculenta	Araceae	Southeast Asia	Escape from cultivation	Naturalised
Echinops kebericho	Asteraceae	Ethiopia	Wild habitats elsewhere	Native
Ensete ventricosum	Musaceae	Ethiopia	Forest	Native
Foeniculum vulgare	Apiaceae	Mediterranean	Montane grasslands	Naturalised
Lycopersicon esculentum	Solanaceae	Central/South America	Rubbish/refuse spots	Naturalised
Ocimum lamiifolium	Lamiaceae	Ethiopia	Forest margins	Native
Passiflora edulis	Passifloraceae	South/Central America	Forests and margins	Naturalised
Physalis peruviana	Solanaceae	South America	Disturbed sites	Naturalised
Piper capense	Piperaceae	Southern Africa	Forest	Native
Psidium guajava	Myrtaceae	Tropical America	Secondary bushland	Naturalised
Rhamnus prinoides	Rhamnaceae	Ethiopia	Forests	Native
Ricinus communis	Euphorbiaceae	Ethiopia-Egypt	Disturbed sites	Native
Solanum dasyphyllum	Solanaceae	Tropical Africa	Disturbed sites	Native
*Xanthosoma sagittifolium**	Araceae	Tropical America	Escape from cultivation	Naturalising

duced further away. Through cross-sectional transects taken from the back of the houses of climax homegardens in the southwest, 48 species were recorded. The gardens were sectioned into four semi-concentric rings (circular zones). In the four rings, indicated in Table 1 as Columns A, B, C, and D, 9, 20, 23, and 4 species were recorded, respectively. In each ring, some characteristic crop combinations are maintained. Zones close to the living houses contain higher number of species used as spices, medicinal plants and vegetables (Table 1, Column A). This first circle is worked upon, harvested and restocked mainly by the women of the house, and mainly by that part of the adult generation to which the mothers belong, who thus show their gender roles in homegarden management together with a host of other collective responsibilities. Many species that are grown in the first ring are represented by only a few individuals, sometimes only a single bush (*e.g. Ruta chalepensis, Cymbopogon citratus,* and *Foeniculum vulgare).* These plants are only needed in small quantities. Plants of fragrance and ornamental value

are also grown just around the house in the first ring, and only in small numbers. Further away from the houses, the circumference of the garden increases while the number of species reduces and the number of individuals of a species increases, the plants being grown in large plots of one or two species. Hence, species number per unit area decreases from A to D, while the number of individuals of a species reduces in the reverse direction. The crop diversity in southwest Ethiopia follows similar pattern as reported for the general cultivated landscapes of tropical Africa (Okigbo 1994), that is that diversity is highest near and around the homes.

The homegarden may contain both native and exotic species, as is true elsewhere (Harlan 1969; Macioti 1992; Hancock 1992). Many of the native crops are known to have rich genepools in Ethiopia. Some native species, and some that have naturalised in forests and forest margins, are found both in homegardens and the wild in the southwestern study site. Table 2 gives a partial list of such crops, their probable status in Ethiopia, and the putative centres of domestication. It can be seen that some crops having been domesticated within Ethiopia, in the rest of Africa and outside the continent both occur in homegardens and in wild habitats. Species with spontaneous populations in southwestern Ethiopia include *Coffea arabica* (see Friis 1979), *Ensete ventricosum, Aframomum corrorima, Coccinia abyssinica, Piper capense, Rhamnus prinoides* and others. Another group of species is not indigenous, but have naturalised populations at forest margins or in suitable places with secondary growth and in otherwise disturbed sites, *e.g. Colocasia esculenta, Amaranthus spp.*, and others. The interface between homegardens and natural forests must be studied in order to learn about the gene pools and population genetic structure of such species. Natural or human interaction between homegarden and spontaneous populations may result in cross-fertilisation and seed dispersal, and ultimate gene-flow in either direction. Since the homes in a village are usually contiguous and since in many instances natural forests are not far from homegardens, it is probably plausible to invoke the metapopulation concept (Hanski & Simberloff 1997) in the interpretation of such species that are both wild and domestic.

Discussion

Since Ethiopian homegardens have been places where plants from the natural ecosystems and plants introduced from abroad are grown together, the crops demonstrate different degrees of domestication. The farming system has intensified by adopting the strategy of mixing compatible crops, the application of organic manuring, and intensified labour input, all organised in space and time. The dynamic processes are propelled by the combined effects of biotic, abiotic and socio-cultural factors that govern the overall changes in plant assemblages of the garden (Rico-Gray *et al.* 1990; Zemede Asfaw & Zerihun Woldu 1997). However, not all homegardens are intensively cultivated, and in fact many are under-utilised. The homegarden agrosystem is yet to develop to its full potentials, and domestication is still on the move with regard to some indigenous species which apparently fairly recently have been introduced into cultivation (*e.g. Echinops kebericho, Solanum dasyphyllum*).

Traditional tropical African agriculture is characterised by co-existence of forests with crops. The area around homes is planted with crops without removing all the trees, and therefore with minimum environmental interference. As time has gone by, and some areas have become more densely populated, more trees have been cut down, and more land converted to crop fields. The typical crop fields in Ethiopia dotted with trees on margins or in little used parts of the farmland are reminiscent of

this past environment. Forest trees that have positive associations with garden crops are retained, and may have significant use values to the community. One of the virtues of traditional rural homegardens is that it delays the process of deforestation and land degradation, partially preserving a range of forest species.

Soil conditions of homegardens may continue to improve with time, and manuring, crop rotation, recycling of crop residue, domestic wastes and litter from trees all contribute towards improving soil conditions. Even when there is no significant crop rotation involving leguminous crops and trees, soil fertility may improve because of inflow of domestic wastes in the agrosystem. Much organic material originating in crop fields, forests, grasslands and markets finally end up in the garden soils through decomposition and mineralisation. Mineral recycling in homegardens is shown to be particularly high in the cultivation of *Ensete ventricosum* (Asnaketch Woldetensae 1997).

Through years of experimentation, the owners of Ethiopian homegardens have developed a general garden design with considerable diversity and flexibility that allows them to fit in and produce a wide range of crops of their own choice. As archetype agricultural "engineers" and "breeders", farmers have managed to select crops that are co-adapted and give aggregated benefits, including multipurpose trees for adding soil fertility, serving as shade and material for construction, crafts and household and farm implements. These "engineers" and "breeders" have designed the homegardens to allow optimal harvest of solar energy through the strategy of manipulating physiognomic forms, phenological classes and other growth forms for a rich niche diversification. A plethora of indigenous agricultural knowledge survives in the practices around the homegarden, and this is being increasingly called upon to establish and strength the scientific basic of *in situ* conservation of the agricultural biodiversity (Mooney 1992). The homegarden is a living archive of agroethnobotanic knowledge and natural cultural history. Considering only dietary criteria, each well managed rural homegarden vows a nutritional calculus in its making, as it maintains crops that are sources of starch, legumes, oils, leaves and other categories proportionately mixed to best serve its primary home use function (Marten 1990; Zemede Asfaw & Zerihun Woldu 1997). This is a cultural heritage passed from generation to generation through action and word of mouth. While there is a general pattern, as described above, each garden is unique in its design and crop mix.

Traditional rural homegardens are meant for bio-production, but as already pointed out above they also maintain agrobiodiversity *in situ* in association with the wild flora (Power & Flecker 1996; Gesseler *et al.* 1996, 1997; Godbole 1998). Among the main determinants of the evolution of homegardens given by these authors are ecological factors (soil, altitude, water, *etc*), personal factors (preferences, interest, knowledge, *etc.*), socio-cultural and economic factors (household-needs, gender interests, preferences of social groups, market conditions, general wealth status, *etc.*) and political factors (land-use systems, general marketing and conservation policies, and agricultural support systems). The view of Harlan (1975) that differences between wild, tolerated, encouraged and cultivated plants are less clear in the tropics is well illustrated in the homegardens of southwest Ethiopia. Plants are transplanted from the wild, brought into the garden and escape again and escape again into the naturalized state. The movement of useful plants from the wild condition to the cultivated and back again can be easily observed. The indigenous management system of Ethiopian homegardens employs time and space based multiple strategies to maintain the biological and environmental heterogeneity and meet economic, social, cultural and ecological needs, as has

been described for traditional crop fields (Melaku Werede 1992).

People have responded to scarcity of arable land created by population growth by intensification of homegardens, and studies undertaken elsewhere have shown that homegardens have reached high levels of development in terms of plant diversity, labour input and income derived in regions where the human population density has reached high levels, 750 persons per square kilometre in Java for example (Padoch & Jong 1991). In parts of Ethiopia, intensification of homegardening has helped to avert some of the adverse effect of high human population density. Changes in homegardens are brought about by a number of natural and human factors, including the deliberate activities of the plot managers, non-intentional human actions, accidental occurrences, predictable successional changes and combinations. Where the intensification of Ethiopian agriculture has gone to the limits, homegardens have already become regular places for obtaining woody materials like the indigenous mountain bamboo (*Arundinaria alpina*), a common element in homegardens of southern and southwestern Ethiopia, where it is needed for construction purposes.

The strategy of the homegarden owners to adopt plant material from wild habitats, sometimes referred to as an "open-door strategy", provides opportunities for embracing novel plants of alleged use from any source (this may be from the wild flora or improved types from elsewhere). In the past this has contributed significantly to the increase of the agrobiodiversity and helped to maintain it on a high level. There is no reason to assume that this rich tradition can not continue, and Ethiopian homegardens should be able to persist through further intensification in a continuing tradition, even though modern agriculture has not as yet developed a positive attitude towards it. In fact, most attempts of organised modernisation have so far not succeded in changing this highly polycultural system to a monoculture.

Along with the growing socio-economic challenges to develop homegardens, halting the ecological degradation of the environment to maintain the rich reservoir of biodiversity is an important and promising issue (Nations 1988). In addition to its regular provision of household necessities, the homegarden preserves relics of the natural ecosystem and of a rich cultural heritage. The challenge is to understand and adapt the indigenous practices and knowledge systems so as to enhance sustainable gardening with the desired input from modern agriculture (Boef *et al.* 1996).

Conclusion

Globally, there has been a growing interest in homegardens during the last couple of decades, both with regard to the taxonomy of the species cultivated and in the possibility for further development of the techniques. The completion of the work on the Ethiopian flora is crucial for the study of Ethiopian homegardens, agroethnobotany and ethnobotany. The ecological significance of the traditional rural homegardens, especially those complicated ones of the Bonga area, demonstrate how important such studies are, if the homegardens of tropical environments are to continue to play significant roles in the provision of food, medicine, fodder, construction materials, firewood and other necessities mainly for home use.

One way to combat the ecological crisis of Ethiopia is to study the traditional homegarden agrosystem, and to develop it further. Completely new, but probably technically feasible possibilities are for example incorporation of biogas generation, the development of fishponds and mushroom cultivation. By such initiatives, the traditional Ethiopian homegarden can be developed into a self-contained future agroforestry complex with multiple functions

expanding into the realms of energy and home industry. This would lead to a polyfunctional production system, which would be in keeping with the mainstream of homegarden evolution, as we have seen it up to now. The future development of homegardens promises to be a dialectic link between bio-production and bio-conservation if we develop it according to the principles practised since long time ago. However, the positive effects of homegardens have developed in balance with a healthy environment. Maintenance of a healthy ecological balance between homegardens and the natural forests is therefore in the best interest of homegarden perpetuation and development. The challenge of the future will be how to obtain such a balance. We do not yet know, but I fully agree with the statement of Jose & Shanmugaratnam (1993) that a good strategy is to direct the development of homegardens, rather than to try and control it in minute detail.

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Morphological characterization of domestic vs. forest-growing Ensete ventricosum (Welw.) Cheesman, Musaceae, in Sheko district, Bench-Maji Zone, southwest Ethiopia

ELISABETH HILDEBRAND

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The morphological differences between domestic and forest-growing enset (*Ensete ventricosum*) have been studied in Sheko woreda (district) of Bench-Maji Zone (southwest Ethiopia). Presence of a waxy bloom on the ventral leaf blade, tendency to discolour upon cutting, basal swelling of the pseudostem, reproductive capability, and palatability were characters pointed out by Sheko enset-growers as the characteristic differences between forest-growing and domestic enset. These differences were evaluated through measurement and observation of relevant morphological characters of 247 domestic, naturalised and forest-growing individuals in seven localities. It was found that domestic, cloned enset was distinct from seed-propagated forest enset and from naturalised enset in several important ways that loosely correspond to differences identified by Sheko and Bench farmers. Many characteristic traits of forest-growing enset reappear within five generations of naturalisation. The differences documented here reflect ongoing, ever-changing selection practices on the part of the Sheko farmers, and thus may not all be characteristic of enset throughout Ethiopia.

Elisabeth Hildebrand, Department of Anthropology, Campus Box 1114, Washington University in St. Louis, One Brookings Drive, St. Louis, MO 63130 USA. E-mail: eahildeb@artsci.wustl.edu

Introduction

Comparisons of indigenous crops and their wild progenitors have shed light on processes of plant domestication and the advent of food production in many parts of the world (De Wet *et al.* 1976; Kaplan 1981; Nabhan *et al.* 1981; Nabhan & De Wet 1984; Smith 1992). Although the Horn of Africa is one of the world's primary centres of plant domestication (Vavilov 1951; Harlan 1969, 1971; Phillipson 1993), such comparisons have only recently been attempted in Ethiopia (D'Andrea *et al.* 1998). For indigenous Ethiopian crops grown for their underground storage organs, such as yams (*Dioscorea* spp., Dioscoreaceae) and enset (*Ensete ventricosum* (Welw.) Cheesman (1947), Musaceae), present-day comparative studies may be our sole and disappearing avenue to understand domestication processes: poor preservation of vegetative tissue makes demonstration of domestication through archaeological data an unlikely prospect, and forested habitats that harbour uncultivated relatives as analogs to wild progenitors are endangered. In this study, I characterise morphological differences between domestic and forest-growing

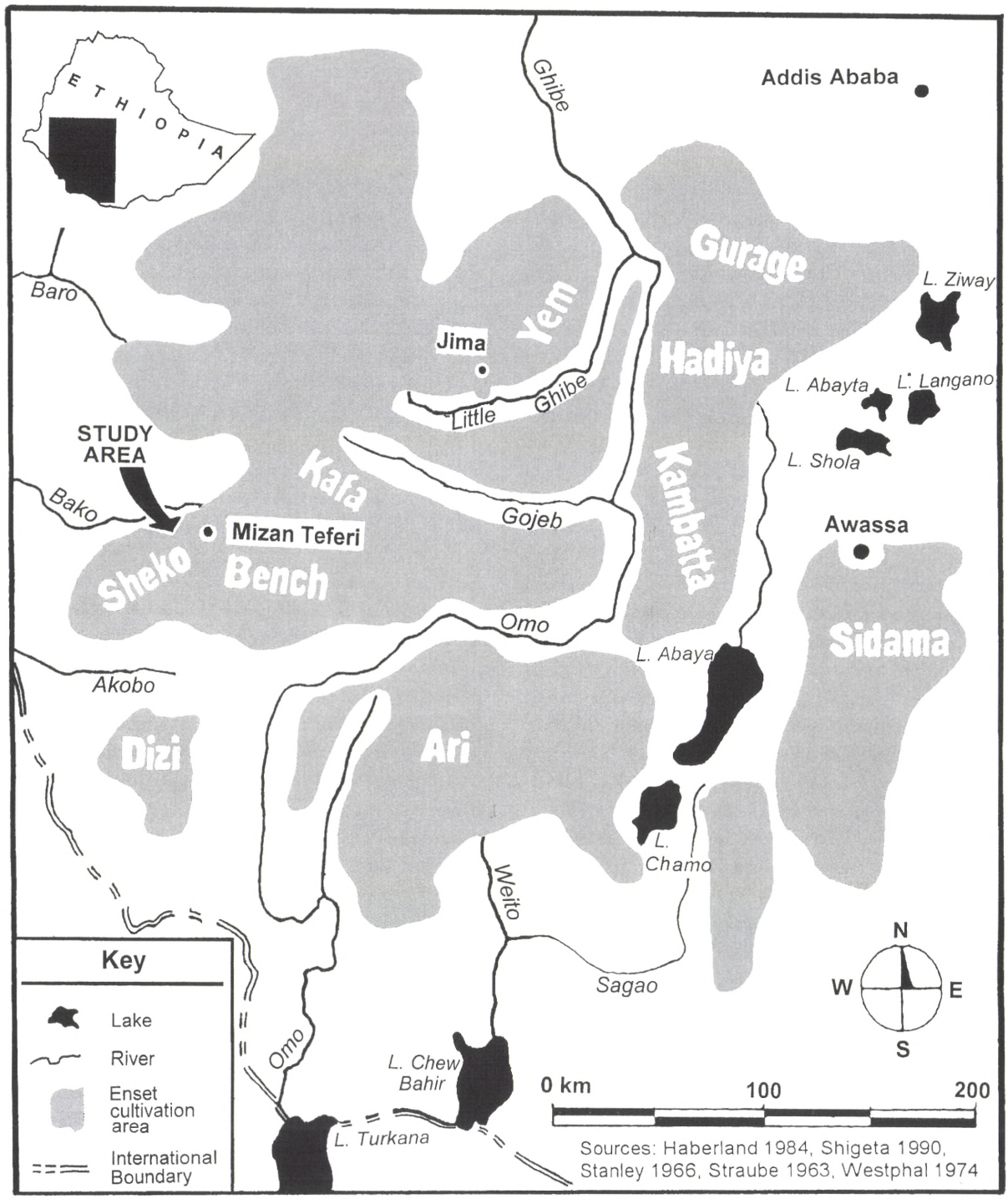


Fig. 1. Geographic regions of enset cultivation in southern Ethiopia, and major enset-cultivating ethnic groups.

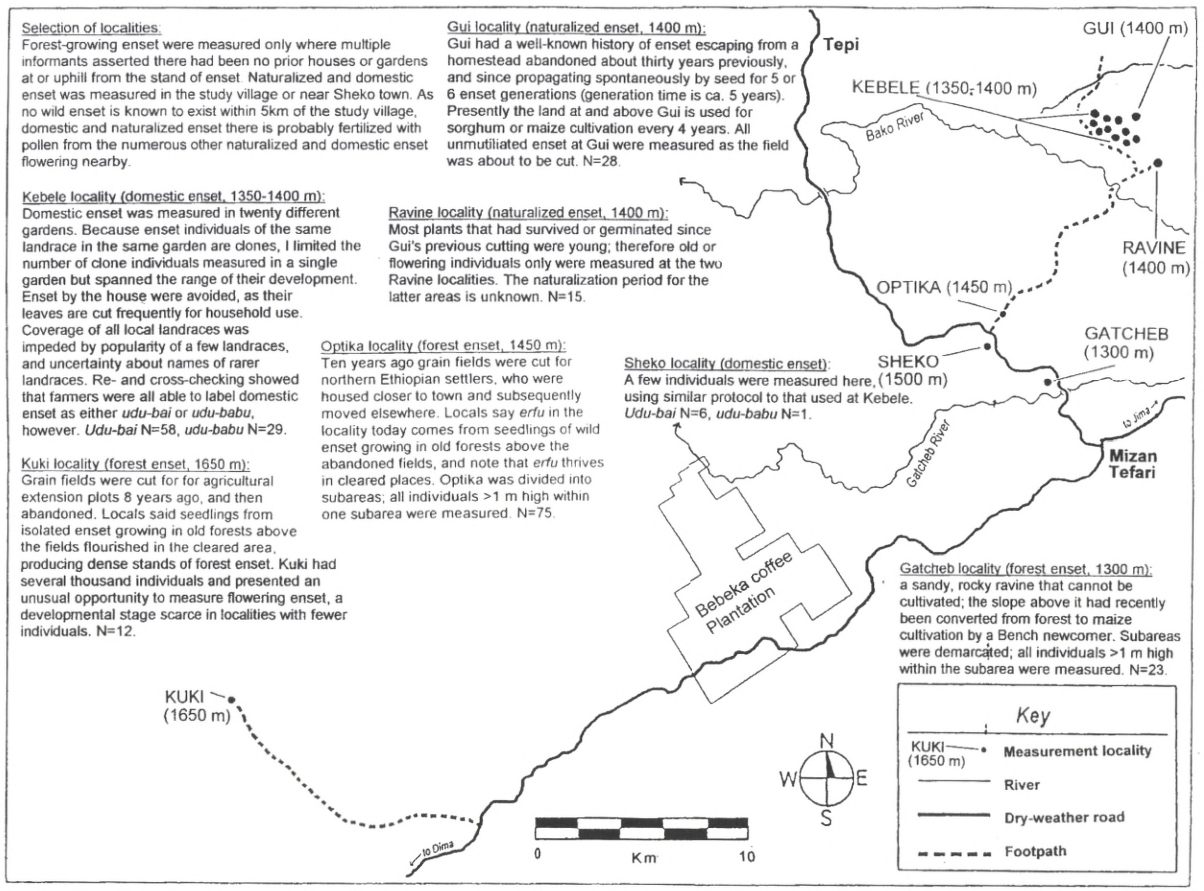


Fig. 2. Map of Sheko Woreda (District) showing enset measurement localities.

enset. (Of the many vernacular names for *E. ventricosum*, the Amharic word *enset* is used here because it is recognised throughout Ethiopia.)

Distributed across tropical and southern Africa, *E. ventricosum* is the only member of its paleotropical genus of about seven species (Lock 1993) to be domesticated and to constitute a staple food. Interactions between humans and enset span nearly the entire continuum of intensity modelled by Harris (1989), from wild procurement to full domestication. *E. ventricosum* is self-propagated via seeds and used casually through much of its range (Rossel 1998), but is cultivated intensively and dependent on humans for vegetative propagation only in southern Ethiopia (Fig. 1). As a domesticate, enset is remarkable for its large size, multitude of uses, drought resistance, year-round availability, long maturation period, and the limited geographic spread of its cultivation. Although Shigeta (1990, 1991) has outlined general differences between wild and domestic enset in Gamo-Gofa, detailed, quantitative morphological studies of differences between wild and domestic enset have not been done. In the absence of such studies, attempts by archaeologists to model the origins of enset cultivation, enset domestication

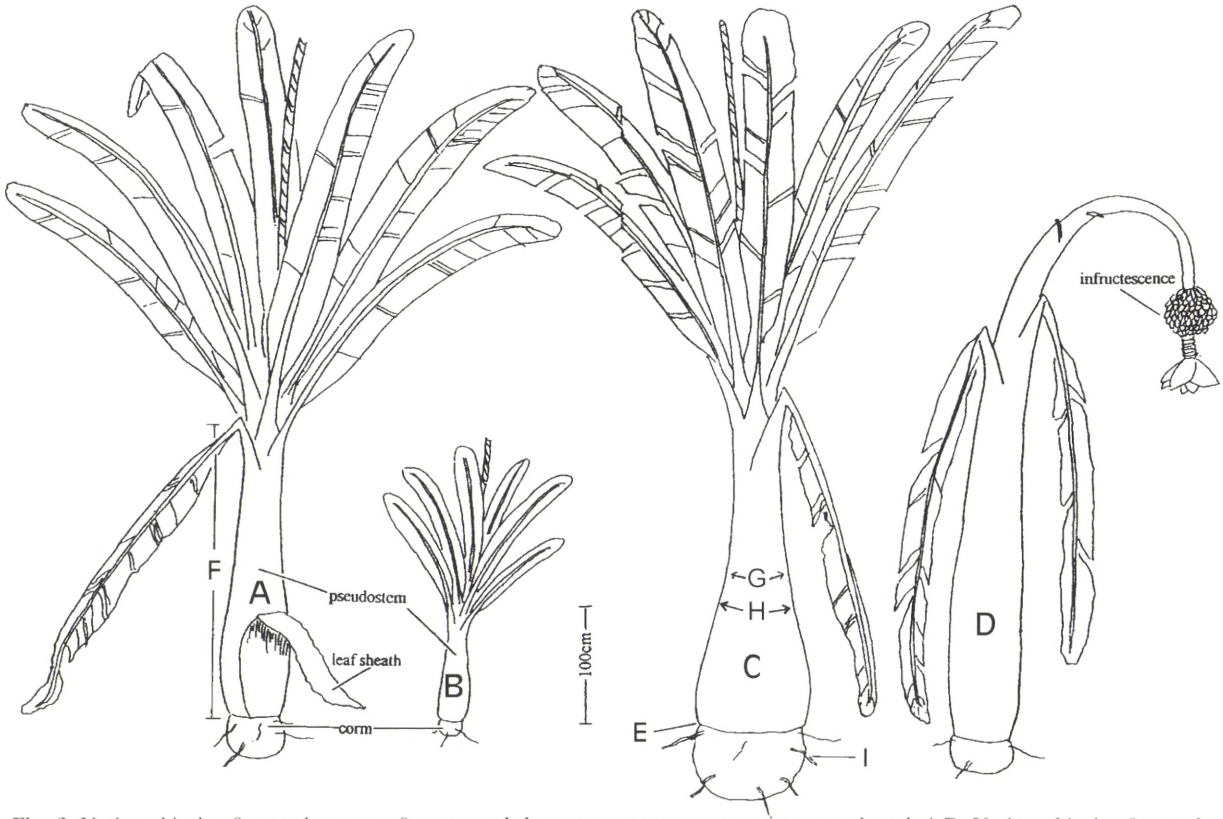


Fig. 3. Various kinds of growth stages of enset and the measurement parameters employed. **A-D:** Various kinds of growth. **A:** Full-size Sheko domestic enset c. 3 years old, non-flowering. Basal area of pseudostem almost unswollen. **B:** Young domestic enset c. 1.5 years old. **C:** Full-sized forest enset, age unknown, non-flowering. Basal area of pseudostem swollen. **D**: Enset with infructescence, c. 5 years old. The drawn individual would have a basal girth of c. 150 cm. **E-G**: Useful measurements and scaling parameters included. **E:** Basal girth measured around the pseudostem/corm junction. **F:** Height measured from the pseudostem/corm junction to the first bent-down leaf. **G**: Girth of pseudostem at halfheight measured halfway between the pseudostem/corm junction to the first bent-dawn leaf. **H-I**: Problematic measurements taken but not reported in this paper because they are inconsistent between individuals included: **H:** Girth of pseudostem 100 cm above the pseudostem/corm junction. This measurement could not be done on younger plants (such as B), and was still within the swollen basal area in large forest individuals (such as C). Measuring girth at an arbitrary height above the pseudostem/corm junction in a population with such a large range in height is inappropriate for scaling purposes. **I**: Root width. Some enset individuals have an entirely subterranean corm, making only upper, slender roots accessible to measurement. In other individuals, the corm protrudes above ground; deeper, robust roots are accessible but upper root wither and cannot be measured.

processes, and related social and environmental phenomena remain pure conjecture.

This study tests the hypothesis that morphological differences exist between wild and domestic enset by comparing domestic and forest-growing enset in Sheko woreda (district) of southwest Ethiopia's Bench-Maji Zone. Sheko experts described several differences between wild and domestic enset: the presence of a wax bloom on the ventral leaf blade, tendency to discolour upon cutting, basal swelling of the pseudostem, reproductive capability, and

palatability. These were evaluated through measurement and observation of morphological characters of 247 individuals in seven localities (Fig. 2). In this paper I present primary field data supporting some of these distinctions.

Economic significance of enset

Enset is a major dietary constituent or food security resource for at least ten million southern Ethiopians (Pankhurst 1996), who grow enset for its edible corm, a squat, rounded underground stem up to 1 m in diameter (Fig. 3). The starch of corm and pseudostem of domestic enset is a palatable source of carbohydrates. Throughout much of southern Ethiopia enset is eaten as *kocho* bread: starch for *kocho* is obtained by pulverising the corm, and by ripping the fibrous exterior off of one side of each leaf sheath of the pseudostem and then scraping soft starch out of the interior of each leaf sheath. Corm and pseudostem starch is mixed, fermented in leaf-lined pits for at least a week, and baked. Scraping enset and making *kocho* were historically taboo among the Sheko, who simply steam pieces of the corm. This is common food at Sheko funerals. Sheko do not favour steamed enset and often complain after a funeral that it has caused a bloated stomach. Nevertheless, the plant is easy to prepare quickly, available all year, and an important hedge against failure of sorghum and maize crops, which Sheko prefer but are more vulnerable to drought.

Leaf blades and petioles of cultivated and uncultivated enset are used in southwest Ethiopia for housing, clothing, bedding, cordage, wrappers, serving dishes, and many other impromptu purposes. Leaf blade and petiole use has also been observed in northern regions where enset is casually encouraged or planted but not propagated vegetatively, and local people are unaware of or choose not to make use of the food potential of the corm (Brandt *et al.* 1998). Thus, although the need for food would seem the most likely reason for domestication of enset, non-food uses also may have motivated its initial cultivation by humans.

Terms employed in this study

When one sets out to compare domestic enset in gardens, and "wild" enset growing in forest far from human settlement, one necessarily

Table 1. Categories of enset and their interactions with humans in Sheko district.

Designation	**Domestic enset**	**Naturalised**	**Forest enset**
Relation to humans	Cultivated	Uncultivated	Uncultivated
Sheko name	*Udu* (*Udu-bai* and *udu-babu*)	*Erfu*	*Erfu*
Sheko use	Food; fibres, building materials, coverings	Famine food; building material, coverings, fibre	Famine food; building material, coverings, fibre
Mode of propagation	Depends on humans for vegetative propagation	Self-propagates by seed; spontaneous.	Self-propagates by seed; spontaneous.
Probable ancestry	Cloned by humans for Generations	Descended from domestic enset by sexual reproduction.	Descended from wild enset via sexual reproduction.
Context	Gardens	Old gardens, abandoned gardens, village stream-banks, areas downhill from abandoned gardens	Deep forests, areas away from villages, areas with no known history of enset gardening

envisages a dichotomy between the two kinds. In fact, this strict division is blurred by self-propagating naturalised enset growing near many villages. Table 1 designates the resulting three categories of enset, and their relations to humans. To forestall confusion, the terms "domestic," "naturalised" and "forest" will be used wherever possible in this paper. In some situations, both naturalised and forest categories are lumped together and termed "uncultivated" or "seed-propagated" enset.

The term "forest enset" is more appropriate than "wild enset" because one cannot prove that any spontaneous individual, however remote from settlements, is not distantly descended from a domestic individual. Inability to equate forest enset with a wild progenitor raises a serious question: Are differences between today's domestic and forest enset necessarily indicative of differences between domestic enset and its wild progenitor? One cannot be sure. Opportunities to compare domestic and forest enset in proximate, environmentally similar contexts are scarce and decreasing rapidly, however; they should be taken while they still exist. The Bench-Maji zone is a good place to do so, because some old-growth forests remain, with uncultivated enset thought by locals to be truly wild, rather than recently naturalised. Moreover, as pointed out by Zemede Asfaw (2001), there are interesting examples of domestication and naturalization in the homegardens of southwestern Ethiopia.

Deriving hypothetical differences between forest and domestic enset from indigenous observations

Shigeta's (1990, 1991) descriptions of wild and domestic enset touch on some morphological traits; differences between the two kinds have not been evaluated, however, and formal taxonomic classification of domestic vs. wild enset has not been done. Given the dearth of published information, indigenous knowledge and categories of enset were useful starting points in hypothesising differences between domestic and forest-growing enset. During twenty months of fieldwork in Bench-Maji zone, I had several semi-structured interviews with five adult or elder Sheko, two Bench, and one Kefa, all of whom were especially knowledgeable about enset. Interviews were repeated with most experts after several weeks or months, and the information was cross-checked with neighbours and family members.

Sheko and Bench farmers recognise two gross categories of enset. *Erfu* is any enset that has come from seed. It includes enset known to have germinated from seeds dropped from domestic enset in gardens, stands of enset in long-abandoned homesteads or the ravines below them, and enset growing deep in the forest with no known history of human interference. Sheko subcategories of *erfu* refer to midrib colour (red or white) rather than to habitat or history. Opposed to *erfu* is *udu*, the Sheko name for all cultivated enset grown from shoots produced by notching the basal pseudostem, digging out the central pith, and smearing the crevices with soil. Differences between *erfu* and *udu* as perceived by Sheko experts are presented in Table 2.

Sheko farmers subdivide domestic enset (*udu*) into two general categories, woman-enset (*udu-bai*) and man-enset (*udu-babu*), which they identify with near-universal certainty and agreement. These categories pertain to the issue of enset domestication and forest/domestic comparisons in that *udu-babu* is said to have been domesticated quite recently for use of its leaves, whereas *udu-bai* has been cultivated since ancient times for food and general use. Although Sheko recount little oral history about the origin of enset cultivation, Bench elders say that both *udu-bai* and *udu-babu* were originally *erfu* that was brought from

Table 2. Differences between forest and cultivated enset as characterised by Sheko farmers.

Trait	Domestic enset (*udu*)	Uncultivated enset (*erfu*)
White, dusty coating ("wax bloom") on ventral leaf blade and midrib, and upper pseudostem	Present	Absent
Darkening of liquid and tissue in pseudostem shortly after cutting	Absent	Present
Adventitious roots emanating from corm	Thin	Thick
Pseudostem basal width (compared to width of upper pseudostem)	Base is same width as upper parts	Base is fat or swollen compared to upper parts
Number of seedlings under fruiting parent	None or few	Many
Colour and palatability of corm after cooking	White, soft, tasty	Black, hard, bad

the forests and planted in gardens. *Udu-bai* was domesticated in the distant past, whereas *udu-babu* was brought from forest to garden much more recently (but not within memory) to spare *udu-bai* from constant leaf-cutting. Today, the two categories have disparate uses, preparation methods, size, and timing to maturity.

Udu-bai is cultivated primarily for its edible corm, which is sweet and tender and is prepared simply by cutting into small chunks and steaming in a pot for 1.5 hours. *Udu-babu* is cultivated primarily for its leaves, which are used for many household tasks. *Udu-bai* is said to be smaller and useable after two years, flowering after three; Sheko women prefer younger, pre-flowering individuals for plain steam cooking, as the corm becomes tougher after the inflorescence emerges. *Udu-babu* is known to attain a larger size, and to flower after four or five years. Until recently Sheko ate *udu-babu* only in times of scarcity or social emergency such as a sudden funeral with few kin to provide or prepare food. Compared to *udu-bai*, its steamed corm is hard, tough, and not sweet.

Today, Sheko are learning *kocho*-making from their Bench neighbours as they discard a taboo against scraping the pseudostem. Previously, *udu-babu* and flowering *udu-bai* had little perceived comestible value due to the toughness of the corm. Now such plants are often called *kocho* regardless of their original landrace name, because *kocho* is usually made from hard-cormed *udu-babu*, or newly flowering *udu-bai* whose corm is beginning to shrink and toughen. In either case, fermentation, pounding, and slicing mitigate the toughness of the corm to produce a tasty bread, and a palatable food is gained from the plant before its death.

From the above ethnographic and ethnohistorical data, I have constructed the following working hypotheses: (1) that domestic and forest-growing enset may differ in the ways described by the Sheko and summarised in Table 2; (2) that non-cloned, naturalised enset may be morphologically intermediate between domestic and forest-growing enset or have some traits associated with each category; and (3) that *udu-babu* may retain some similarities to forest enset (*erfu*) due to its alleged recent domestication for non-comestible purposes.

Methods

To test these hypotheses, morphological data was collected from 247 enset plants in Sheko district, where domestic, naturalised, and forest enset all grow in similar altitude and rainfall

conditions. Domestic enset is well-known to vary according to altitude and/or associated factors in its growth speed and ability to send forth vegetative shoots (K. Zippel, pers. comm.), and in adult size and age of flowering individuals. In a single location, domestic landraces may differ in colour of midrib, leaf axis, and sheath, as well as in size and uses; forest enset also varies in colour and dimensional attributes in a single locale. To avoid confusing environmentally-caused or intra-category variation for genuine differences between domestic, naturalised, and forest enset, research design called for large sample sizes in a geographically circumscribed area of roughly consistent altitude and rainfall, and sampling of as many domestic landraces as possible. Enset was measured at seven localities in five kebeles or townships (Fig. 2), which were all 1350-1650 m a.s.l., and all received roughly comparable rainfall.

Morphological study of enset can be difficult because of its large size (pseudostems reach 5 m in height), the ill-defined boundary between pseudostem leaf sheaths and free petioles, retention of dead tissue on the plant's exterior, and its tendency to grow in wet ravines and garden areas of rubbish, manure, and night soil accumulation. Baker & Simmonds (1953), Cheesman (1947), Simmonds (1960), and IPGRI (1996) delineate few measurement conventions pertaining to traits noted by the Sheko. Study methods were therefore devised during fieldwork and are briefly summarised below and in Fig. 3.

The white coating (wax bloom) on the ventral leaf axis was evaluated visually: it was either heavy, sparse, or absent. Discoloration of pseudostem tissue was tested by cutting off a still-living leaf sheath c. 1 m above the ground and checking its colour after five minutes and again after half an hour. A range of leaf axis tissue darkening to grey, purple, or brown was recorded, but is reported here simply as none, light, and dark. Also observed during data collection, but not described by the Sheko, was a rapid darkening of the watery liquid in the pseudostem to a bright orange, noted during data collection on a presence/absence basis. Root width measurements proved inconclusive due to inconsistent measurement parameters: some enset individuals have an entirely subterranean corm, leaving only the uppermost, slender roots accessible to measurement. In other individuals, the corm protrudes above the soil surface, rendering the deeper, most robust roots accessible to measurement; upper roots wither and cannot be measured.

Evaluating the nature and degree of basal pseudostem swelling required choosing a location to measure the base, and appropriate scaling variables. These are illustrated and explained in Fig. 3. Sheko descriptions referred to the widest portion of the pseudostem. This location was impossible to measure consistently because of numerous dead leaf sheaths clinging to pseudostems, sometimes swollen and dripping, sometimes thin, dry, and brittle. The circumference of the pseudostem-corm junction (c. 40 cm below the widest point) was chosen because it was easy to define, clean, and measure consistently.

Fertility was evaluated by dissections of infructescences from one forest, one escaped, and two domestic individuals, and by observing infructescence and seedling development. Infructescences were obtained for dissection as the fruit began to turn orange, so that seeds were fairly mature but monkeys had not yet taken fruit away, as is common among uncultivated enset. Colour and palatability of the corm were tested during two cooking experiments performed in October 1998 and July 1999. During each experiment, forest enset from Optika locality and domestic enset from the nearest village were steamed simultaneously for 1.75 hours.

Results

Wax bloom

The Sheko characterisation of forest enset as lacking in the white dusty coating (wax bloom) on the ventral lamina and midrib is accurate (Table 3). Enset naturalised over a 30-year period (5 or 6 generations of spontaneous seed propagation after probable fertilisation with pollen of nearby domestic and naturalised enset) resembles forest enset in this regard: of 42 individuals, only four have wax blooms, which are much less marked than those on domestic enset. All domestic individuals have a wax bloom of some sort except an old, withering individual that was difficult to evaluate. Among domestic enset, the frequency of weak wax blooms is greater among *udu-babu*; most *udu-bai* plants have obvious wax blooms.

Discoloration of tissue after cutting

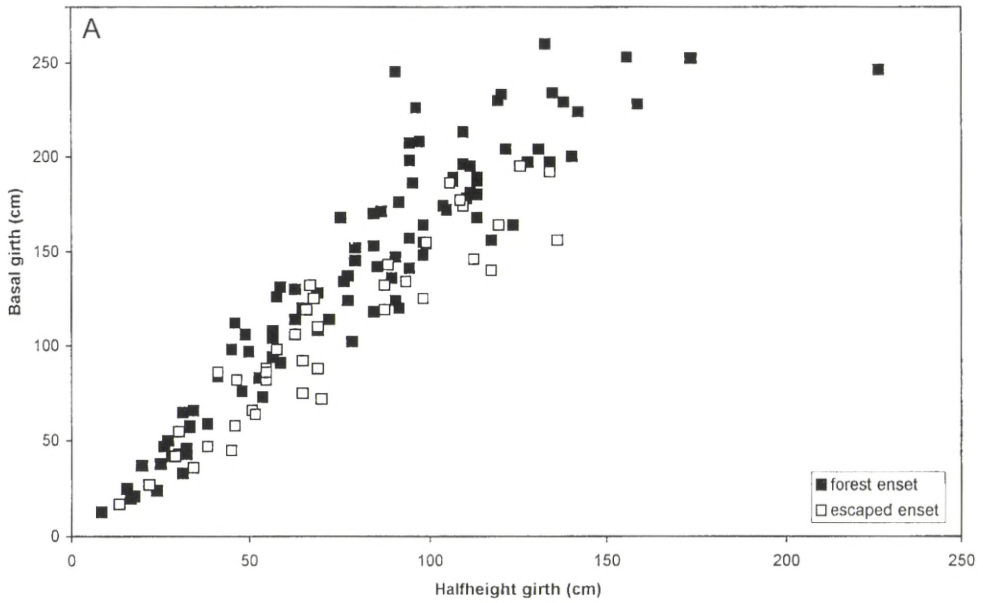
Tissue discoloration data do not bear out a dichotomous characterisation of domestic enset as white and seed-propagated enset as dark (Table 4). Although forest enset has universal discoloration after cutting, several domestic landraces also show significant tissue darkening. Heavy discoloration is uncommon among even these landraces, however. Enset escaped from cultivation 30 years before shows universal discoloration. Among both forest and escaped enset, the final colour and speed of discoloration varies.

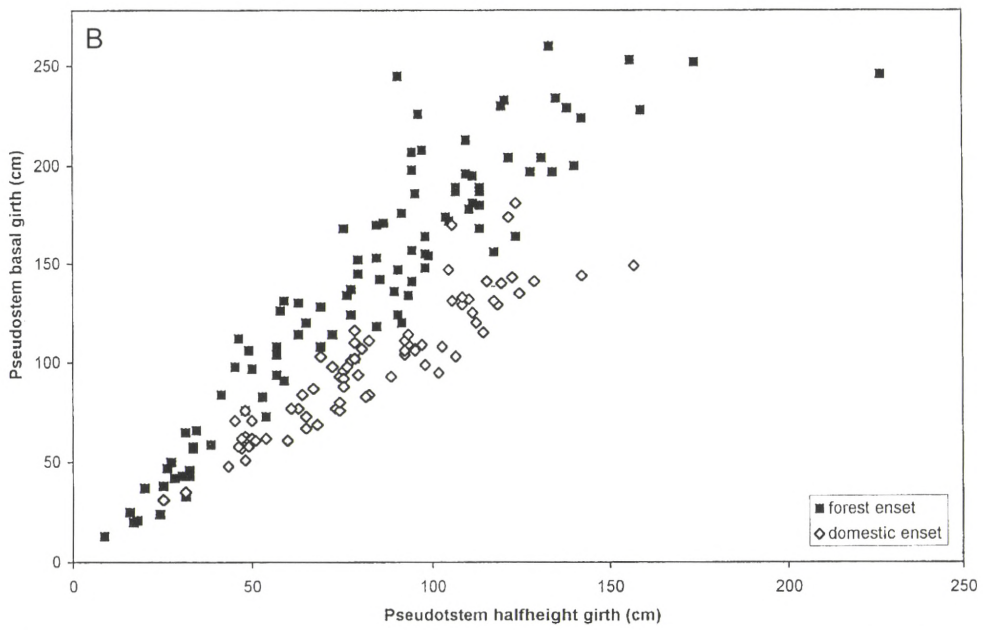
Table 3. Presence/absence of white coating (wax bloom) on ventral leaf blade and leaf axis. Note that the wax bloom trait was not evaluated for a few individuals at the beginning of the study, and for some individuals that were old or withering, because it would have been difficult to see on dead tissue.

Enset category (local name)	Heavy wax bloom	Slight wax bloom	No visible wax bloom	No. of plants evaluated
Forest (*erfu*)	0 (0%)	0 (0%)	83 (100%)	83
Escaped (*erfu*)	0 (0%)	4 (10%)	38 (90%)	42
Domestic total (*udu*)	70 (85%)	11 (13%)	1 (1%)	82
Domestic (*udu-babu*)	21 (72%)	7 (24%)	1 (4%)	29
Domestic (*udu-bai*)	49 (92%)	4 (8%)	0 (0%)	53

Table 4. Discoloration of pseudostem tissue and liquid after cutting. Not all individuals were evaluated for this trait because cutting enset to check discoloration initially seemed potentially intrusive enough to jeopardise permission to conduct the measurements, especially among domestic enset and one stand of naturalised enset. Later, as people became accustomed to the procedures, leaf sheath cutting was integrated into the study.

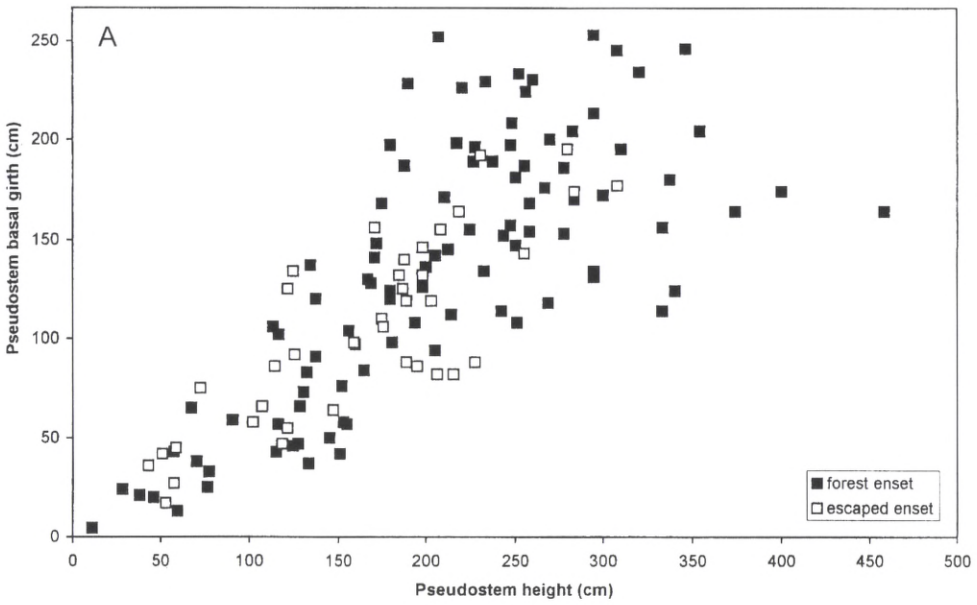
Enset category (*local name*)	Tissue discoloration 30 min. after cutting			No. of plants evaluated	Liquid orange 5 min after cutting
	Heavy	Slight	Absent		
Forest (*erfu*)	74 (90%)	8 (10%)	0 (0%)	82	58 (71%)
Escaped (*erfu*)	31 (82%)	7 (18%)	0 (0%)	38	11 (29%)
Domestic total (*udu*)	11 (16%)	25 (36%)	33 (48%)	69	13 (19%)
Domestic (*udu-babu*)	4 (15%)	9 (33%)	14 (52%)	27	7 (26%)
Domestic (*udu-bai*)	7 (17%)	16 (38%)	19 (45%)	42	6 (14%)

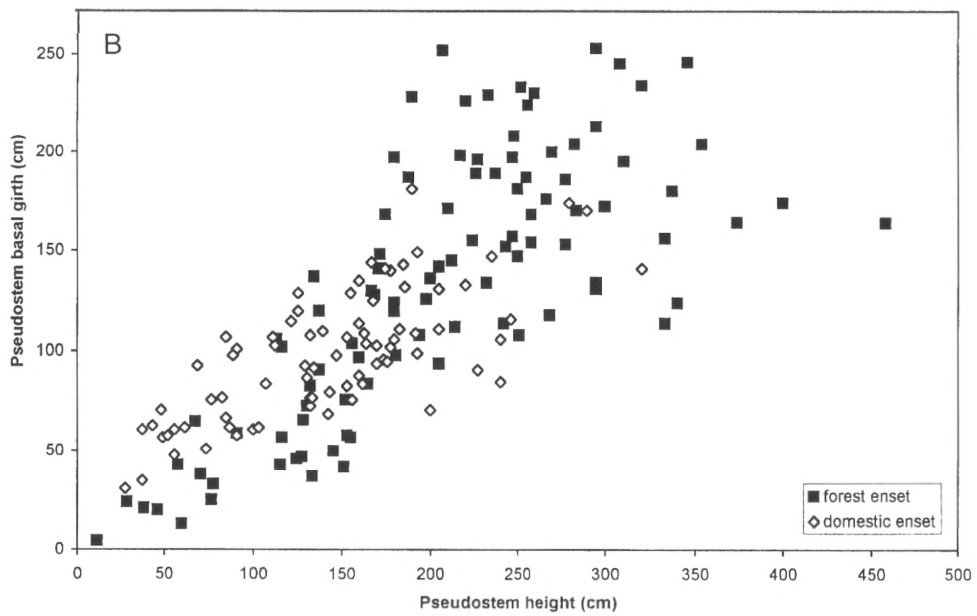




Regression equations:	Significance:
Figure 4a. Mean basal girth controlling for halfheight girth: $X_{FOREST-XNATURALIZED} = 18.3$	Yes; $p<0.01$
$Y = 17.6 + 1.5HALFHEIGHT - 12.4FOR.NAT - 0.008FOR.NATXHALFHEIGHT$	No
Figure 4b. Mean basal girth controlling for halfheight girth: $X_{FOREST-XDOMESTIC} = 40.6$	Yes; $p<0.01$
$Y = 17.6 + 1.5HALFHEIGHT - 7.0FOR.NAT + 0.4FOR.DOMXHALFHEIGHT$	Yes; $p<0.01$

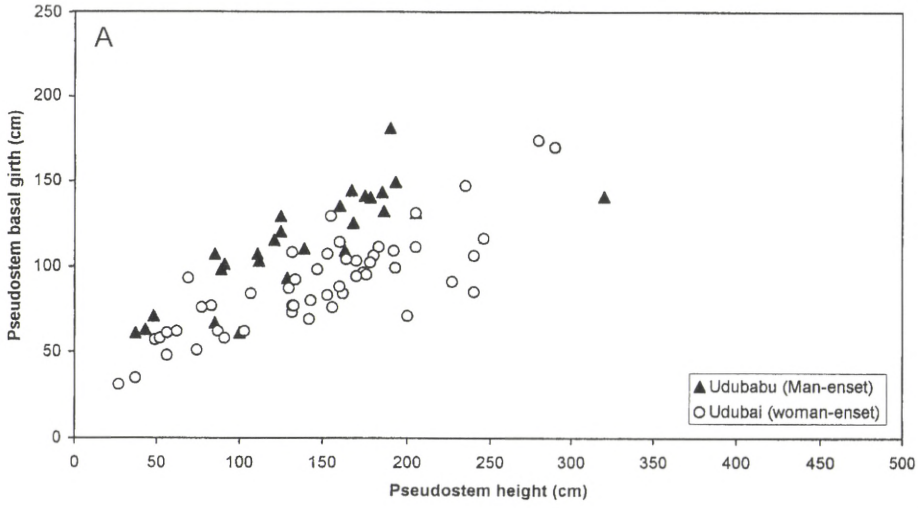
Fig. 4. Two scatter plots showing basal girth of pseudostem (vertical axis) and halfheight girth of pseudostem (horizontal axis) in a number of individuals of: **above:** forest enset and escaped enset. **below:** forest enset and domestic enset.

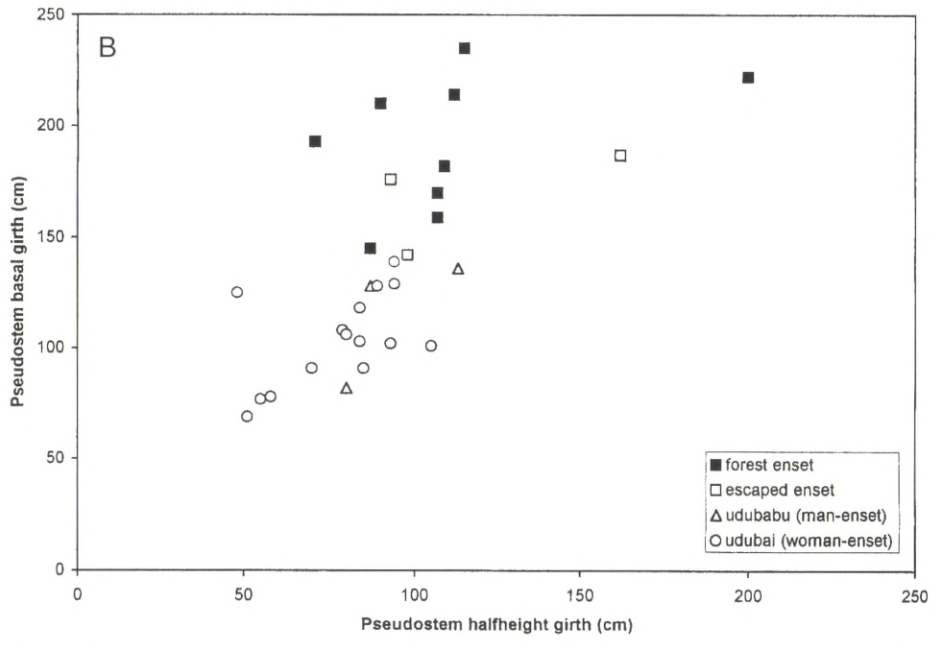




Regression equations:	Significance
Figure 5a. Mean basal girth controlling for height: XFOREST-XNATURALIZED = 6.34	No
Y = 10.87 + 0.55HEIGHT + 9.44FOR.NAT + 0.02FOR.NATxHEIGHT	No
Figure 5b. Mean basal girth controlling for height: XFOREST-XDOMESTIC = 4.85	No
Y = 44.64 + 0.37HEIGHT - 24.16FOR.DOM + 0.18FOR.DOMxHEIGHT	Yes; p<0.05

Fig. 5. Two scatter plots showing basal girth of pseudostem (vertical axis) and height of pseudostem (horizontal axis) in a number of individuals of: **above:** forest enset and escaped enset. **below:** forest enset and domestic enset.





Regression equations:	Significance
Figure 6a. Mean basal girth controlling for height: XUDUBABU-XUDUBAI = 27.66	Yes
Y = 58.62 + 0.40HEIGHT - 24.70BABU.BAI + 0.02BABU.BAIxHEIGHT	No
Not illustrated: Mean basal girth controlling for halfheight girth: XUDUBABU-XUDUBAI = 2.3	No
Y = 18.4 + 1.0HALFHEIGHT + 15.1BABU.BAI + 0.2BABU.BAIXHALFHEIGHT	No

Fig. 6. Two scatter plots showing: **above:** basal girth of pseudostem (vertical axis) and height of pseudostem (horizontal axis) in a number of individuals of man-enset and woman-enset. **below**: basal girth of pseudostem (vertical axis) and. halfheight girth of pseudostem (horizontal axis) in a number of individuals of flowering enset.

Dimensional differences in the pseudostem base

Dimensional measurements generate an ontogenetic picture of basal pseudostem girth in comparison to halfheight girth (Fig. 4a, 4b, 6b) and height (Fig. 5a, 5b, 6a); differences in the regression slopes can also indicate differences in the rates of expansion in the pseudostem base *vs.* other scaling factors. Forest enset's basal and halfheight girths correlate well throughout its development. Naturalised enset's basal girths are significantly less than those of forest enset, but the two regression slopes do not differ significantly (Fig. 4a). Domestic enset (*udu*) has a consistently smaller basal/midheight girth ratio and shallower regression slope than does seed-propagating enset (Fig. 4b). Basal/halfheight circumference scaling corroborates the Sheko characterisation of forest enset (*erfu*) as basally swollen compared to domestic enset, and suggests that basal girth of domestic enset increases more slowly throughout development than that of forest enset.

Scaling pseudostem basal circumference against pseudostem height reveals a more complicated situation. Forest enset's basal girth/height ratio varies greatly throughout its development. The girth/height ratio for naturalised enset has a similar range and distribution and follows a similar regression slope (Fig. 5a): domestic enset has a larger base/height ratio than seed-propagated enset early in its development, but after attaining a maximum basal circumference of c. 140 cm, domestic enset grows only vertically, whereas forest enset continues gaining in both height and girth (Fig. 5b).

At all stages, *udu-babu* has a greater basal girth/height ratio than that of *udu-bai* and a steeper regression slope as well (Fig. 6a); no significant difference is found in either the basal girth/halfheight girth ratio or the regression slope of *udu-bai* vs. *udu-babu*, however (not illustrated; regression equation follows Fig. 6a and its equation). Flowering individuals show a clear disjunction between the maximum dimensions attained by domestic *vs.* seed-propagated enset: basal girths of domestic flowering individuals are less than 140 cm (mean=106, n=18) while those of forest enset all exceed 142 cm (mean=186, n=12) (Fig. 6b).

Fertility: seed development in forest and domestic enset infructescences

Dissection and observation both verify Sheko assertions that forest enset is extremely prolific but domestic enset is not, even when allowed to flower. Dissection of infructescences from two domestic, one escaped, and one forest enset shows a marked difference in the number of well-formed, seemingly viable seeds per fruit, and per infructescence (Figs. 7, 8). Infructescences of forest and naturalised enset have thousands of seeds, while domestic enset infructescences have few fruits with full-sized seeds, and low numbers of seemingly viable seeds in each such fruit. Forest enset infructescences have plump fruits like squat bananas; hundreds of heavy, hard, black seeds c. 12 mm in diameter drop from a single individual, germinate, and seem hindered in their growth only by excessive crowding. The thumb-sized fruits of domestic enset bear mostly seeds c. 3 mm in diameter that are obviously incompletely developed. Some domestic fruits contain seeds that are full-sized (c. 12 mm) but pale and soft. Black, hard, full-sized seeds indistinguishable from those of forest enset are present but infrequent in domestic infructescences.

Dissection-based assessments of potential seed viability should be ideally tested by experiments, but are supported by observations of forest and garden enset seeds throughout the study. Although garden enset seeds fall into disturbed, rich soil with plenty of sunlight and moisture, on most occasions few or none from *udu* germinate. No seedlings developed from

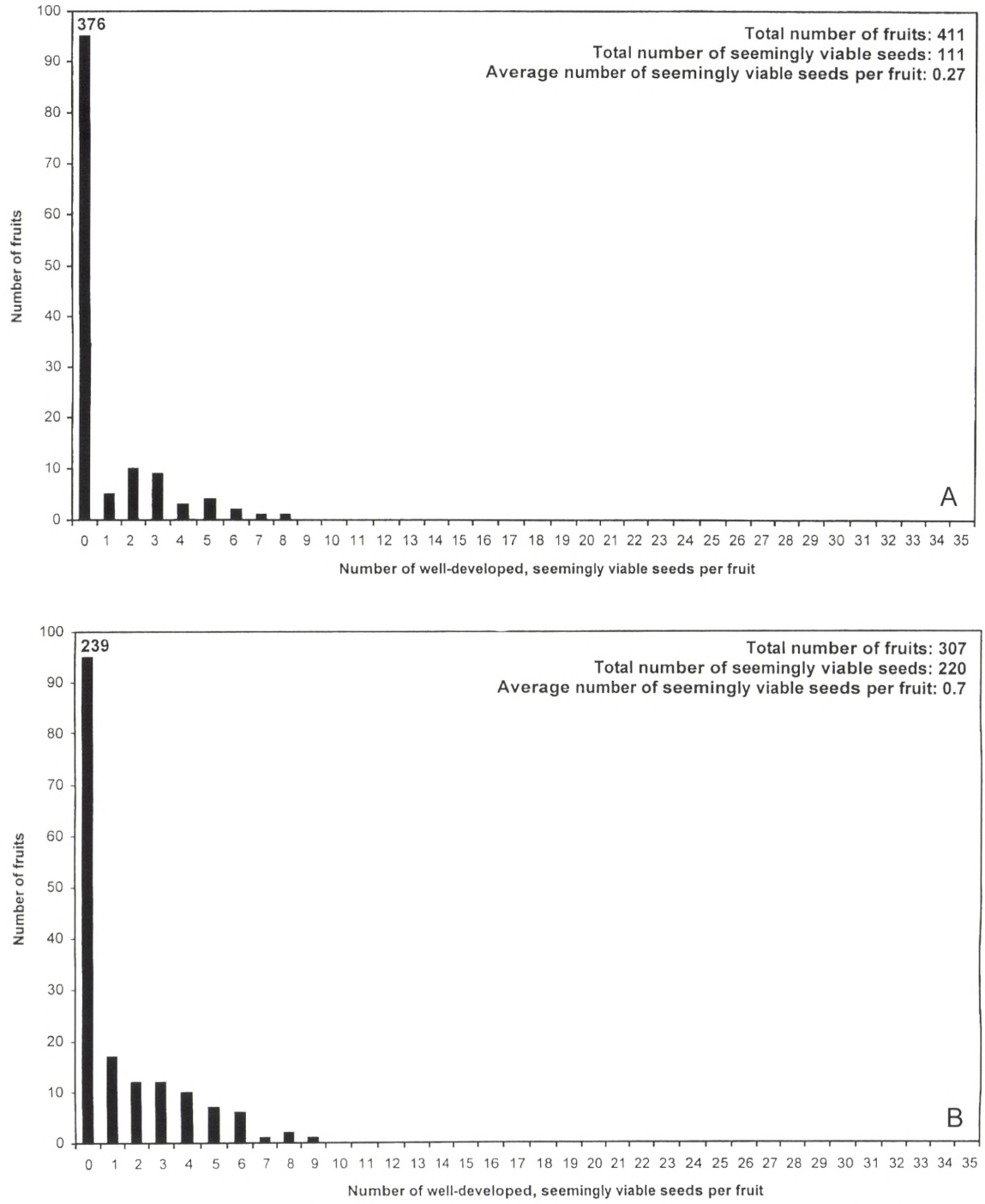


Fig. 7. Two bar charts showing the number of well-developed and seemingly viable seeds per fruit in two different infructescences of domestic enset from the Kebele locality. **above**: Infructescence 1. **below**: Infructescence 2.

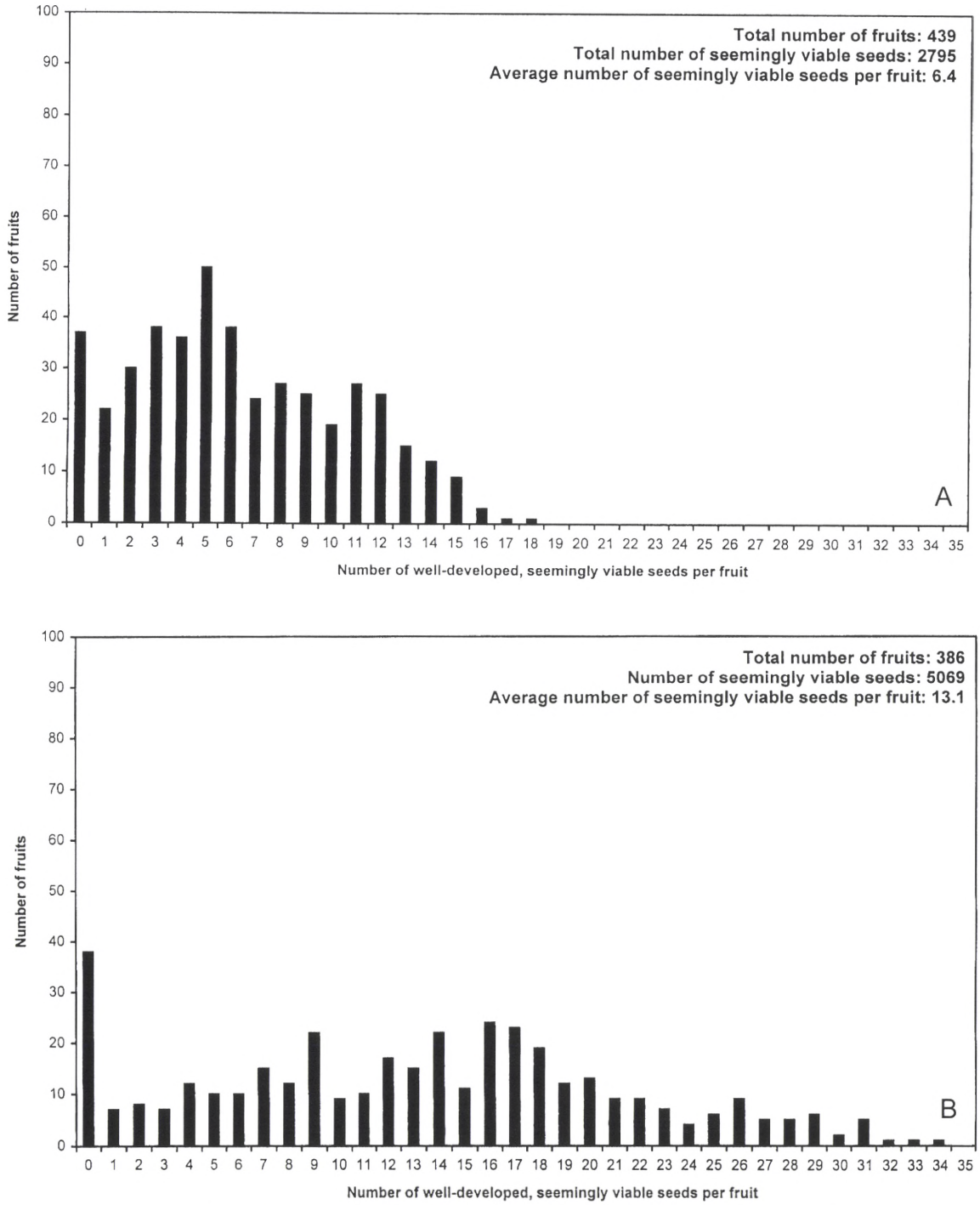


Fig. 8. Two bar charts showing the number of well-developed and seemingly viable seeds per fruit in infructescences of naturalised enset and forest enset. **above**: naturalised enset from Gui locality. **below**: forest enset from Optika locality.

eight domestic infructescences flowering in separate gardens and ten individuals in a single garden without human interference. One domestic infructescence yielded three small seedlings that grew for a month but then disappeared. In another garden, however, one seedling had grown to adulthood and was referred to as *erfu*. It bore an infructescence that resembled those of forest enset: at the time of discovery half of the fruits had fallen and 355 seedlings had germinated in a 30 x 30 cm area beneath the drooping infructescence; remaining fruits were fat and each contained 14-17 seeds. The first-generation *erfu* and the dissected naturalised infructescence show that sexual reproduction quickly restores fertility.

Palatability of the enset corm: oral history and cooking experiments

The first cooking experiment at Optika corroborated claims by northeastern Sheko that *erfu* is not palatable. Corm chunks from a large *erfu* steamed for 2 hours failed to attain the white, fluffy, soft, starchy consistency (similar to a well-baked potato) of *udu* steamed for the same period on a similar fire. *Erfu* stayed hard, grey, solid, and tough; when squeezed, the hot corm chunk dripped water. Extending the steaming overnight achieved only a more rubbery consistency. *Erfu* consumption did not cause any unusual digestive disturbances, however. The first experiment suggested that *erfu*, while probably not poisonous, was certainly a tough, undesirable food source.

Subsequently, southwestern Sheko elders reluctantly recalled a period when inter-tribal hostilities had forced them to flee their farms. They lived in the forests for a year, and ate *erfu* after other resources ran out. Elders advised me that smaller individuals, with pseudostems about 2 m tall, were better than large ones. A second set of cooking experiments at Optika bore out these statements: steamed corm from a 2 m tall *erfu* attained a starchy consistency no worse than domestic *udu-babu* served during an exceptionally sudden and difficult funeral two weeks previously. Optika Sheko, though still unenthusiastic about eating it, were surprised by its cooked appearance and said it was "like *udu-babu*." The two cooking experiments show that full-grown *erfu* with a large corm is unpalatable, but younger *erfu* with a smaller corm is tender and quite edible.

Discussion

Although field data appear to substantiate many Sheko folk distinctions between forest and garden enset, their pertinence to deliberate or inadvertent selection on the part of farmers remains unexplored. A few preliminary ideas are offered here.

Wax bloom

The white coating on the abaxial leaf blade, midrib, axis, and upper sheath is a wax bloom. A wax bloom occurs only if the length or width of a plant's epicuticular wax projections approximates the wavelength of light; the projections scatter the light and produce the visual effect of the wax bloom, which exists on a wide range of plant taxa including leaves of *Eucalyptus* sp. and *Brassica* sp., and the fruits of plums (*Prunus domestica*) (Martin & Juniper 1970). Rubbing the surface disturbs the configuration of wax projections and eliminates the scattering effect. As well as on cultivated enset, wax blooms appear on abaxial leaf surfaces of its close relatives *Heliconia* sp. and cultivated *Musa* (Personal observations during fieldwork (*Musa* sp.) and at the Missouri Botanical Gardens' Climatron (*Heliconia sp.*)). Systematic SEM studies of epicuticular wax ultrastructure have shown that *Ensete ventricosum*, *Musa* spp., and *Heliconia* spp. all have the "*Strelitzia*-type" of epicuticular wax, consisting of compound rodlets, shared by many farinaceous monocots (Fröhlich & Barthlott 1988). Those listed by Frölich &

Barthlott (1988: 106-107) are *Musa acuminata, M. rosacea,* and *M. sapientum; Heliconia aurantiaca, H. marginata, H. collinsiana, H. mariae, H. wagneria,* and *H. swartziana.* The enset specimen is listed as *Ensete ventricosum*; the authors do not state whether it is wild or cultivated, nor name its country of origin.

The lack of a wax bloom on forest and most naturalised enset does not signify a lack of epicuticular wax, however. Rather, it indicates that light scattering is minimised because dimensions of wax bodies on uncultivated enset differ from the wavelength of light. This could be due to a slight dimensional disparity, or to gross differences in wax body configuration or composition, as the ultrastructure of wax bodies is often linked to their chemical constituents (Jeffree 1986; Jeffree *et al.* 1976). Documenting a tendency for many "*Strelitzia*-type" waxes to be made up mainly of wax esters, Meusel *et al.* (1994) note that although *Musa paradisica* follows this trend, wax of *M. acuminata* and *M. balbisiana* consist less of wax esters than hydrocarbons, primary alcohols and fatty acids. The consequences of these compositional differences for configuration of *M. acuminata* and *M. balbisiana* waxes are not yet certain, but it is clear that wax constituents and, presumably, configuration can vary considerably even within a genus. Understanding variation in wax ultrastructure between domestic and uncultivated *Ensete ventricosum* will require examination of wax configuration via SEM, and molecular characterisation of wax constituents.

Pending such research, the possible functional significance of epicuticular wax ultrastructure deserves mention. Certain configurations of wax bodies can inhibit gas exchange, reducing water loss via transpiration in hot or dry environments (Martin & Juniper 1970). Epicuticular wax can serve many other functions, however (Baker 1982, Riederer & Markstadtler 1996). In this study, observations of heavy wax blooms on domestic enset in hot, sunny gardens compared with bloomless forest enset in cooler, shady habitats would suggest that the domestic-type wax configurations might be more effective in limiting water loss. Bloomless naturalised enset growing in hot, uncanopied abandoned gardens and sunny streambanks are inconsistent with the above trend, however: sexual reproduction appears to restore forest-type (bloomless) wax in naturalised enset, despite hot conditions in which limits on transpiration would be advantageous. This raises questions as to 1) how naturalised enset reverts to forest-type traits in so few generations of sexual reproduction (discussed later), and 2) whether bloom-producing domestic-type wax configurations have any functional significance. The latter question should be evaluated in future studies documenting rates of water loss in enset plants with each kind of wax.

Discoloration of enset tissue after cutting

Distinctions in tissue discoloration between domestic and forest enset, although not so consistent as Sheko farmers suggest, might indicate the presence of polyphenols in pseudostem tissue (J.M. Lock, pers. comm.). Tannins have been found previously in *Musa* leaves (Gibbs 1974; Tomlinson 1969). Tomlinson (1959) also reports tannins in undifferentiated *Musa* tissue and describes "articulate laticifers associated with the vascular bundles of all organs except the root, the mucilaginous contents of these elements exuding at cut surfaces and darkening on exposure to air" (p. 794). Polyphenols in *Musa* spp. and uncultivated enset probably discourage their consumption by insects and other animals (D. Milanowski, pers. comm.). They did not deter elephants formerly present in the region from eating forest enset, however.

Sheko lumped dark colour and bad taste as universal traits of forest enset. One might con-

clude that polyphenols have been selected against during or after domestication due to their harsh flavour. The domestic landrace *arka*, however, had prompt, obvious tissue discoloration, and was popular both in terms of the number of gardens it appeared in and in terms of the number of individuals per garden. *Arka*'s tissue discoloration did not signal poor taste to Sheko farmers. It may be that the polyphenols causing discoloration of the degree observed in *arka* are sufficiently diminished in intensity as to not affect comestibility. Testing for tannins among corms of all domestic landraces, and quantitative comparisons of tannin concentrations between various landraces and forest enset would be useful starting points for biochemical study of the differences between domestic and forest enset.

Sheko did not seem to be aware that orange discoloration of pseudostem liquid was a common trait among forest enset. One domestic landrace was named *yerbm-udu* ("blood-enset") for its tendency to "bleed" orange or pink liquid if the pseudostem was cut. On one occasion that Sheko witnessed an *erfu* "bleeding," they said it was "like *yerbm-udu*," rather than the converse: they related the forest individual to the one domestic landrace that bleeds, rather than recognising that the *yerbm-udu* landrace has a trait that is widespread in *erfu*. The exact nature of compounds causing both kinds of discoloration will require biochemical investigation.

Dimensional differences in the pseudostem base, and motivations for selection

Pseudostem basal girth/height ratios do not differ significantly between *udu* and *erfu*, which may reflect the great variation in basal girth/height among forest enset. Their regression slopes do differ significantly, however: domestic enset tends to attain a large base earlier in development, and its base increases more slowly later, as the plant gains height (Fig. 5b). Growth of forest enset's basal area appears to be steadier throughout its development. Domestic enset flowers and dies while the plant is smaller in all respects, whereas forest enset attains much greater overall size before flowering (Fig. 5b, 6b). Forest and domestic enset have quite disparate basal girths at the time of flowering, regardless of height (Fig. 6b). Domestic enset's basal girth is significantly smaller, and grows significantly slower than that of forest enset using halfheight girth as a size control (Fig. 4b). The basal/midheight girth ratios for domestic enset lie mostly outside the range of variation for forest enset, indicating that even after bringing enset individuals from forest to domestic contexts, humans have continued to select (consciously or unconsciously) for a smaller basal area among their cultivated enset.

Cooking experiments have provided one possible impetus for selective reduction in basal girth: a narrower base corresponds to a smaller corm that is more likely to be tender and palatable. They also suggest that selection has been done in the absence of *kocho* technology, which renders large, tough enset more palatable and lessens incentives to select for narrower bases or smaller corms. But the cooking experiments have raised another question: if immature forest enset can yield tender individuals, why initiate cultivation? There are three possibilities: first, enset may have reproduced poorly in a heavily forested preagricultural landscape and not been sufficiently abundant, so that people may have viewed intervention as necessary simply to sustain it. Second, people may have sought to expand the distribution of enset beyond its natural range to more convenient locations in their seasonal round. In either of these cases, selection of narrower-based, more palatable individuals for propagation may have been deliberate or incidental. Third, people may have had plenty of enset but

consciously sought to enhance palatability through deliberate selection.

Comparisons between *udu-bai* and *udu-babu* are interesting in view of their different histories and uses. Pseudostem bases (scaled against height) are significantly wider in *udu-babu*, which also has a significantly steeper regression slope than *udu-bai* (Fig. 6a). Tissue discoloration was similar between the two, and obvious wax blooms are slightly less prevalent among *udu-babu*. The fact that one scaling factor (height) produces significant differences between the two kinds but the other (halfheight) does not makes interpretation difficult, however. It is possible that *udu-babu*'s corm size has not been reduced as much as that of *udu-bai* due to a shorter period of human selection, or to palatability concerns being less important due to its use for leaves or *kocho*. *Udu-babu*'s other traits may have been subjected to similar selective forces as those of *udu-bai* or responded to these forces more quickly. Such conclusions are premature considering the limited number of individuals and landraces sampled, however; additional measurements and interviews are called for.

Naturalisation of garden enset

In comparison to forest enset, naturalised enset has significantly smaller basal/halfheight girth ratios (Fig. 4a) but similar regression slope for growth of basal girth (Fig. 4a, 5a). Naturalised enset's observed range of viable seeds per fruit (0-18) falls short of that reported by Baker & Simmonds (1953) for wild *E. ventricosum* throughout East Africa (0-35), with which this study's dissections of forest enset (0-34 seeds per fruit) concur. Such differences tend to support the premises that forest enset, even if naturalised in the distant past, has at least regained full fertility relative to that of truly wild enset, and that forest and naturalised enset in Bench-Maji zone are indeed distinct from one another.

On the other hand, naturalised enset's reversion to forest forms of several traits (partial restoration of fertility, increased tissue discoloration, and loss of epicuticular wax bloom), within five or six generations and in a habitat similar to a domestic garden, is also interesting. One possible explanation for this would be hybridisation between naturalised enset and forest enset, whereby genetic material from the latter would cause the reappearance of forest-enset traits. The difficulty with this explanation is that forest enset is rare around the study village (Kebele locality) and naturalised enset localities (Ravine and Gui). When I sought *erfu* near the study village, farmers said elephants had eaten all of the local forest enset in times past, and could only direct me to "*erfu*" in or below extant or abandoned gardens, which was probably naturalised. During 18 months of residence and frequent foot trips through the forest to several nearby settlements and market towns, Optika locality proved to be the nearest known substantial, longstanding population of forest enset to the study village. Because Optika lies 8 km and over a 1700 m ridge from the Gui and Ravine localities (Fig. 2), a more likely pollen source for enset in the study village would be other local domestic or naturalised enset. At least twenty domestic and ten naturalised enset were flowering in the study village during 1998-1999, all less than 2 km from the Gui and Ravine localities.

How could sexual reproduction between domestic and/or naturalised enset individuals result in the observed reversion to so-called forest enset traits? Each domestic landrace has been cloned for countless generations and may also have been highly inbred in the past; any hybridisation between different landraces, or between domestic and naturalised enset, might generate offspring of F1 hybrid genotype with increased fertility, that phenotypically resemble other non-inbred, sexually reproducing forest enset. If this is indeed true, landraces

can best be maintained via somatic reproduction and the Sheko differentiation between *udu* (shoot-propagated) and *erfu* (seed-propagated) is in fact the most salient distinction among the enset of Bench-Maji Zone.

Differences between forest and domestic enset in other regions of Ethiopia

Observations by fieldworkers in other zones of Ethiopia are at odds with at least one of the distinctions documented in this study (Shigeta 1991; Fekele Woldeyas 2000; Zemede Asfaw pers. comm.). Although most of these reports are not yet published and do not rely on quantitative morphological data such as that gathered in this study, they indicate that in areas of Ari (Gamo-Gofa Zone) and Kefa (Kefa-Sheka Zone), domestic enset actually has a fatter pseudostem base than spontaneous enset growing in nearby forests (Table 5). In all of these areas, *kocho*-making or other methods of enset processing are done routinely, mitigating large-based enset's palatability problems. Under these circumstances, farmers might deliberately select for large-based enset because of its higher yield. The preference and selection for small-based enset documented in this study may be unique to the Sheko and other peoples who do not scrape or ferment enset.

Shigeta's research also reveals that Ari define "wild" and "domestic" enset in a different way than Sheko do. Ari definitions are based on spatial context and use: seed-propagated enset appearing spontaneously in gardens may be adopted by a farmer as domestic, and may be re-cloned and incorporated into the agricultural system. Sheko definitions are based on mode of propagation and much more rigid: clones are "domestic," and seedlings are "wild" and not to be eaten or re-cloned, though they may be used opportunistically for non-comestible purposes. Ari appear to have a mechanism in place for "wild" genetic material to enter the agricultural sphere via cloning of seedlings, but the Sheko do not. Ari practices of cloning seedlings blur distinctions between "wild" and "domestic" enset and could hinder strict morphological comparison. Contrasts between the Ari and Sheko systems may however, yield fascinating insights about domestication and selection processes in both prehistoric and recent times. They also indicate that for-

Table 5. Differences between wild and domestic enset in areas inhabited by the Ari, southwest Ethiopia. Most information in this table comes directly from M. Shigeta's unpublished doctoral thesis, page 129. For additional published descriptions see also Shigeta 1990, 1996; Ari enset cultivation practices clearly differ in many important respects from those of the Sheko.

Shigeta's category/Ari name	**Domestic enset/*Agemi***	**Wild enset/*Gela***
Relation to humans	Cultivated	Uncultivated
Use by Ari	Food, other multipurpose uses	Not utilised
Context	Gardens near houses, 1200-2800 m	Swamp, riverbank, ritually taboo areas, 1200-1600 m
Base of pseudostem	Enlarged	Not enlarged
Corm size, taste	Big, not bitter	Small, bitter
How Shigeta's categories of "domestic" and "wild" enset may both contain naturalised enset (from Shigeta 1991 text, passim)	Category includes enset grown from seeds and tolerated or encouraged in Ari gardens; farmers may later re-clone a seedling with traits they desire.	Category includes spontaneous enset appearing near agricultural settlements; this enset may be naturalised rather than wild.

est/domestic morphological comparisons and ethnobotanical interviews among several other enset-cultivating peoples are needed, and generalisations regarding enset domestication processes across southern Ethiopia may prove elusive.

Conclusions

Domestic, cloned enset in Sheko district is distinct from seed-propagated forest and naturalised enset in several important ways that loosely correspond to differences identified by Sheko and Bench farmers. It possesses a visible epicuticular wax bloom and has a reduced tendency to discolour upon cutting. Its base is narrower (scaled against circumference at half-height) than that of seed-propagated enset, and it flowers and dies at much smaller dimensions than forest enset. Perhaps linked to smaller size is a tendency for domestic enset's corm to be more tender and palatable. Fertility of domestic enset is severely reduced, but if sexual reproduction is allowed and generates any viable offspring, then forest traits and partially restored fertility appear within five generations. Differences in basal pseudostem girth suggest that human selection for smaller corms continued well after enset was brought into gardens, and that *udu-bai* has been subjected to longer or more extreme selection than *udu-babu*. Maintenance of sufficient enset populations, expansion of enset distribution, and increased corm palatability are among possible motives of the prehistoric hunter-gatherers who first undertook enset husbandry. Diverse enset processing practices of other ethnic groups in southern Ethiopia may have led their farmers to have different priorities in selecting for corm size *vs.* palatability, however. The differences between domestic and forest enset documented in Sheko district through interviews and morphological study cannot be generalised throughout Ethiopia; rather, they reflect ongoing, ever-changing relations between the Sheko people, their enset cooking technology and ideology, and the traits they favour in an enset plant. Understanding such relations among a number of enset-cultivating ethnic groups may well reveal other patterns of people-enset interactions, as the domestication process continues.

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Ethiopian artefacts made with plant materials: Vanishing wonders

SALLY BIDGOOD

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The artefacts listed in this paper were collected during field trips to many parts of Ethiopia from 1995 to 1999. The collection gives an idea of the range of plants and plant materials used for the production of everyday articles in Ethiopia. A wide range of materials and objects, from spices, foodstuff and incense, beautiful traditional cotton clothing and elegant carvings to colourful furniture and other household objects made of grass or palm leaves, has been collected. The new and imaginative use of plant materials can indeed be surprising, such as a car seat made from palm leaves and grass. Unfortunately, today many traditional crafts are under threat from the global economy, and artefacts produced from plant materials are replaced with imported products made of plastic.

Sally Bidgood, The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, England, UK. Email: s.bidgood@rbgkew.org.uk.

Introduction

During field work, which the author has undertaken in Ethiopia since 1995 together with Prof. Ib Friis, c. 65 objects, including samples of spices, etc., made from plant materials by the local people have been collected. The main objective of the field work was to collect herbarium material to document vegetation studies and floristic distributions for the Flora of Ethiopia and Eritrea, but to collect objects made from plant materials by local people was considered an important side issue.

The field work was supported financially and otherwise by the Carlsberg Foundation and the Royal Botanic Gardens, Kew, and received great help from the Ethiopian Flora Project. The objects were bought in markets, from roadside vendors and from farmers or nomads, when we observed objects made of plant material during our travels. Before sending the collections out of the country, the artefacts were inspected by the National Herbarium of Ethiopia and the National Museums of Ethiopia. This was done in order to obtain the necessary clearance for export.

It was thus certified that the artefacts were produced with material of plants that were not threatened, and that the artefacts were not antiques. These artefacts and products are now deposited in the Economic Botany Collections of the Royal Botanic Gardens, Kew, UK, together with plant-based handiwork from all around the world.

The purpose of making these collections has been to record the range of artefacts produced in various parts of Ethiopia, and to identify the

plants used. This must now be considered urgent because plastic and man-made fibres are replacing many traditional materials, even in remote areas. The fundamental idea of the collections is to serve education and conservation.

At the Royal Botanic Gardens, Kew, the general public has access to information about these collections. They are partly exhibited as part of the economic botany exhibitions called *Plants & People* in the Kew Museum (No. 1), the purpose of which is to show an international audience the range of skills and materials used, as well as the beauty of the artefacts produced from plant materials.

Many countries now want to re-establish their cultural identities. Even if the art of producing artefacts from plant materials is lost among some ethnic groups in Ethiopia, collections within local and international museums can at least show what was previously achieved. The collections may also assist future generations to resurrect lost skills. Another purpose is to support plant and habitat conservation. When woodlands, wetlands and forests are used by local people to collect materials for artefacts, food and medicine there is an inherent interest in conserving these areas. At the present time cultures are changing, even disappearing, through globalisation and with them the habitats people traditionally relied upon. If wetlands, woodland and forests with rare species are lost, they cannot be recovered because the rare species are gone. If the skills of producing artefacts are lost, they may never be recovered either. Increasing reliance on man-made materials will mean the economy of many self-sustaining peoples will be adversely affected because most man-made materials are imported, and some of the new materials may be less suited to local conditions than were the traditional materials.

An example of this was observed during our field work in the Borana region: the Borana people have always used wooden milk churns that have been fumigated with the smoke from burning twigs of *Ocimum americanum*. These wooded churns are now being replaced by plastic buckets, which cannot be fumigated in the same manner. Instead the buckets are washed with often dirty water, which creates potential health problems.

It is therefore hoped that this collecting activity in Ethiopia can be continued to cover an even wider selection of ethnic groups and materials, and that the plants and the skills may be recorded and conserved for future generations.

List of objects, arranged according to region

The objects are arranged according to the traditional administrative regions of Ethiopia, and are listed in the way they are depicted and grouped in Fig. 1. The entries should otherwise be self-explanatory.

Tigray

Floor brush. Object made of *Phoenix reclinata* Jacq. (Arecaceae). Local name: ***Meteregiya*** (Amharic: broom).

Notes: Made from leaves.

Cotton dress and shawl. Object made of *Gossypium sp.* (Malvaceae). Local name: Not recorded.

Notes: Dress and shawl are worn by women for religious days and other special occasions.

Fig. 1. Map of Ethiopia and Eritrea overlaid with pictures showing groups of artefacts. The artefacts are grouped as in the list. →

KHARTOUM
TIGRAY
GONDER
GOJAM
WELEGA
SHEWA
ILUBABOR
KEFA
ARSI
GAMO GOFA
SIDAMO
REPUBLIC

Spools for cotton spinning. Objects made of *Arundo donax* L. (Poaceae). Local name: ***Qesem*** (Amharic: spool).

Notes: Made from stem sections.

Fan (shaped as dish). Object made of *Cyperus involucratus* Rottb. (Cyperaceae). Local name: ***Maragebya*** (Amharic: fan).

Notes: Made from stems. Used for fanning charcoal stove during coffee ceremony.

Tubers (in small dish). *Cyperus esculentus* L. (Cyperaceae). Local name: ***Quni*** (Amharic: meaning unknown).

Notes: Used as incense during coffee ceremony.

Tubers used for cosmetic purposes. *Impatiens tinctoria* A. Rich. (Balsaminaceae). Local name: ***Enselale*** (Amharic: name of a dye).

Notes: Tubers cooked and mashed. Used for dying hands, feet and vagina of women a very dark red colour. The effect is to tan the skin making it more pliable and protecting it from cracking. It is done for beauty particularly for special festivals. The use as a cosmetic dye is also mentioned by Cufodontis (1957) who among others records the Amharic name *esosila*.

Gonder 1

Dish/Tray. Object made of *Cyperus involucratus* Rottb. (Cyperaceae). Local name: ***Sefade*** (Amharic: pan, tray).

Notes: Made from woven leaves. Used for putting Injera on when it comes out of the oven. The dish to the left (mottled light and dark). Next to the other dish is a bundle of the species of *Cyperus*.

Shopping basket. Object made of Cyperus involucratus Rottb. (Cyperaceae). Local name: **Thenbel** (Amharic: meaning unknown).

Notes: Made from woven leaves.

Large basket with lid. Object made of *Cyperus involucratus* Rottb. (Cyperaceae). Local name: ***Lamat*** (Amharic: basket).

Notes: Made from stems. Used for holding Injera. Will take up to 50 pieces, which stay fresh in the basket for up to 4 days.

Dish. Object made of various grasses, including *Pennisetum sphacelatum* (Nees) Th. Dur. & Schinz and *Eleusine floccifolia* (Forssk.) Spreng. Local name: ***Sefade*** (Amharic: pan, tray), ***Gundo*** (Oromigna: meaning unknown).

Notes: Made from woven leaves. Used for winnowing and cleaning grain, carrying Injera and as a lid when baking Injera. The dish to the right (uniformly light).

Small coloured basket with lid. Object made of *Eleusine floccifolia* (Forssk.) Spreng. (Poaceae; determination uncertain). Local name: ***Mudiy*** (Amharic: type of small basket)

Notes: Made from stems. Used for keeping precious items.

Bundle of grass stems. *Eleusine floccifolia* (Forssk.) Spreng. (Poaceae). Local name: ***Sebeze*** (Amharic: meaning unknown).

Notes: Made from stems. Painted in different colours and used for baskets like the preceding item. Bundle to the right in Fig. 1.

Bundle of grass stems. *Pennisetum sphacelatum* (Nees) Th. Dur. & Schinz (Poaceae). Local name: ***Sendedo*** (Amharic: name of the plant).

Notes: Made from stems. Used as strengthening when making baskets.

Gonder 2: A selection of spices bought in Gonder market.

Roots. *Curcuma domestica* Valeton (Zingiberaceae). Local name: ***Erd*** (Amharic: name of this kind of spice).

Notes: Roots used as a spice. Now grown in Ethiopia, formerly imported from India.

Seeds. *Trigonella foenum-graecum* L. (Fabaceae subfam. Papilionoideae). Local name: ***Abesh*** (Amharic: name of this kind of spice).

Notes: Seed used as a spice in boiled milk and in Injera. Seed used to make a non-fermented beverage. Used medicinally as a cleanser and strenghthener.

Seeds. *Brassica nigra* (L.) Koch var. *abyssinica* A. Braun (Brassicaceae). Local name: ***Senafech*** (Amharic: name of this particular kind of seed).

Notes: Seed used as a purgative (strongly cathartic) by man. Seed used as a spice for special foods during fasting and also to make a dip for raw meat. Cufodontis (1957) mentions the use of the leaves as vegetables, but claimed that in Wolamo the seeds were only used as a medicine. This does not agree with our information from Gonder.

Seeds. *Brassica carinata* A. Br. or *Erucastrum abyssinicum* (A. Rich.) R. E. Fries (both Brassicaceae). Local name: ***Gomen Zer*** (Amharic: cabbage seeds).

Notes: Seed crushed and used to oil the baking plate for making Injera. Seeds used as cleansing agent (cathartic) by man. Cufodontis (1957) mentions the use of both *Brassica carinata* and *Erucastrum abyssinicum* as cabbage.

Seeds. *Nigella sativa* L. (Ranunculaceae). Local name: ***Tekur Azemud*** (Amharic: black spice seeds).

Notes: Seed used as a food flavouring, particularly whole in some types of bread. Pounded with garlic and ginger as a spice in meat dishes. See also under Anuak Tobacco (Gamo-Gofa).

Seeds. *Coriandrum sativum* L. (Apiaceae). Local name: ***Demblale*** (Amharic: name of this kind of spice).

Notes: Seed pounded with chillies into Berberi powder.

Seeds. *Trachyspermum ammi* (L.) Turrill (Apiaceae). Local name: ***Nech azmud*** (Amharic: white spice seeds).

Notes: leaves used as spice.

Gojam and Welega

Rope. Object made of *Hyphaene sp.* (Arecaceae). Local name: Not recorded.

Notes: Made from fibres of palm leaves.

Car seat of palm leaves and grass. Object made of *Phoenix reclinata* Jacq. (Arecaceae). Grass not identified. Local name: Not recorded.

Notes: Made from interwoven palm and grass leaves.

Pouffe. Object made of Poaceae sp. indet. Local name: ***Ketema*** (Amharic: leaves of grass traditionally spread on floor during holidays).

Notes: Made from woven grass leaves.

Shopping basket. Object made of *Arundinaria alpina* K. Schum. (Poaceae). Local name: ***Zembil*** (Amharic: kind of basket).

Notes: Made from stems only.

Shewa

Straw hat. Object made of *Pennisetum thunbergii* Kunth (Poaceae). Local name: Not recorded.

Notes: Made from woven stems.

Inflorescences and seeds. *Eragrostis tef* (Zucc.) Trotter (Poaceae). Local name: ***Teff*** (Amharic: name for this kind of cereal).

Notes: Cereal crop.

Bread rolls and flat bread. Object made of *Eragrostis tef* (Zucc.) Trotter (Poaceae). Local name: ***Injera*** (Amharic: name for the kind of pancake-like bread made from *teff*).

Notes: Bread made from Teff.

Leaves. *Ocimum americanum* L. (Lamiaceae). Local name: ***Zeka-keba*** (Amharic: spice used to give taste to butter).

Notes: Leaves used as food flavouring.

Cotton and spinning equipment. Object made of *Gossypium sp.* (Malvaceae). Local name: ***Yetendefe Tete*** (Amharic: cotton from which the seeds have been cleaned).

Notes: Clean cotton. Stick made from bamboo, circular part from gourd.

Model of Ethiopian Orthodox church. Object made of *Zea mays* L. (Poaceae). Local name: not recorded.

Notes: Made from the pith of stems.

Seven toothbrushes. Object made of *Stereospermum kunthianum* Cham. (Bignoniaceae) ***Butore***, *Olea africana* Mill. (Oleaceae) ***Weyra***, *Pittosporum sp.* (Pittosporaceae) ***Ambelby***, *Myrsine africana* L. (Myrsinaceae) ***Kechemo***, *Sideroxylon oxyacanthum* Baill. (Sapotaceae) ***Tefa***, *Olea sp.* (Oleaceae) ***Gerse***, *Rytigynia neglecta* (Hiern) Robyns (Rubiaceae) ***Mito***. Local name: Local names above all Amharic. They refer to the names of the trees, rather than to the product.

Notes: Made from twigs.

Ilubabor

Anuak tobacco pipe. Object made of *Lagenaria siceraria* (Molina) Standl. (Cucurbitaceae). The pipe tubes are made of plastic. Local name: Not recorded.

Notes: In the past the tubes would have been made of bamboo or a similar hollow stem.

Lunch Box. Object made of *Pennisetum sphacelatum* (Nees) Th. Dur. & Schinz (Poaceae). Local name: ***Ageligil*** (Amharic: kind of food container).

Notes: Box of cowhide lined with grass.

Boat-shaped basket. Object made of *Grewia mollis* A. Juss. (Tiliaceae), the grasses used are *Panicum maximum* or *Echinochloa colona*. Local name: Not recorded.

Notes: Basket woven from strips of *Grewia* bark and *Panicum/Echinochloa* leaves.

Prepared wrapped tobacco. *Nicotiana tabacum* L. (Solanaceae) and *Nigella sativa* L. (Ranunculaceae). Local name: Anuak tobacco.

Notes: Tobacco leaf is collected, mixed with *Nigella sativa* and crushed. Then packed into a leaf and buried for 15 days after which it is ready for use. Used for chewing as much as for smoking.

Food container. Object made of *Pennisetum sphacelatum* (Nees) Th. Dur. & Schinz or *P. thunbergii* Kunth (Poaceae). Local name: ***Ageligil*** (Amharic: kind of food container).

Notes: Made from stems.

Kefa

Dining table. Object made of *Pennisetum sphacelatum* (Nees) Th. Dur. & Schinz (Poaceae). Local name: ***Misob*** (Amharic: basket table made of grass for eating *injera*).

Notes: Made from leaves.

Sieve. Object made of *Pennisetum sphacelatum* (Nees) Th. Dur. & Schinz (Poaceae). Local name: ***Genigisha*** (Oromigna: meaning not known).

Notes: Woven from stems.

Rope. Object made of *Ensete ventricosum* (Welw.) Cheesman (Musaceae). Local name: ***Enset*** (Amharic: name of the plant).

Notes: Said to be very waterproof, including having resistance to salt water.

Drinking vessel. Object made of *Cordia africana* Lam. (Boraginaceae). Local name: ***Malakia*** (Amharic: container for liquid).

Notes: Also used as a measure for liquid.

House paint brush. Object made of Cyperaceae sp. indet. Local name: Not recorded.

Notes: Made from leaf fibres.

Gamo-Gofa 1 (Konso area)

Female doll. Object made of *Commiphora sp.* (Burseraceae). Local name: ***Gahato*** (Amharic: name of the tree).

Notes: Figures like these (but larger) are placed over burial grounds as totems. One of a pair with the following doll.

Male doll. Object made of *Eucalyptus sp.* (Myrtaceae). Local name: ***Bahr Zaf*** (Amharic: tree from abroad, the commonly used name for all species of *Eucalyptus*).

Notes: Model of a wooden totem placed over the graves in burial grounds.

Toothbrush. Object made of *Olea sp.* (Oleaceae). Local name: ***Hade*** (Amharic: name of the tree).

Notes: Made from twigs.

Frankincense. Object made of *Boswellia neglecta* S. Moore (Burseraceae). Local name: ***Qundi*** (Amharic: name of the tree).

Notes: Exudate from trunk used as incense. Widely used in homes during the coffee ceremony, and where a dead body is lying before burial. Also used in various religious ceremonies in the Ethiopian Orthodox Church.

Musical instruments. Objects made of *Capparis sp.* (Capparidaceae). Local name: Not recorded.

Notes: Four fruits and two fruits tied together used as whistles.

Musical instrument. Object made of *Gerrardanthus lobatus* (Cogn.) C. Jeffrey (Cucurbitaceae). Local name: Not recorded.

Notes: Blown across the top like a flute.

Musical instrument. Object made of *Phragmites karka* (Retz.) Steud. (Poaceae). Local name: Not recorded.

Notes: Made from hollow grass stems, blown as a Pan's pipe.

Toy. Object made of *Ricinus communis* L. (Euphorbiaceae). Local name: ***Gulo*** (Amharic: name of the plant).

Notes: Made from wood. Squeeze at base and man vaults over bar.

Gamo-Gofa 2 (other ethnic groups)

Sieve. Object made of *Hyphaene sp.* (Arecaceae). Local name: ***Wonfit*** (Amharic: sieve).

Notes: Woven from palm leaves.

Food basket, oval with lid. Object made of *Hyphaene sp.* (Arecaceae). Locan name: not known.

Notes: Woven from palm leaves.

Alcohol distiller. Object made of *Ensete ventricosum* (Welw.) Cheesman (Musaceae). Local name: ***Yearegen mawcha*** (Amharic: distilling equipment).

Notes: String and loop made from leaves wrapped around bamboo stem.

Egg basket with small handle. Object made of *Arundinaria alpina* K. Schum. (Poaceae). Local name: ***Fundura*** (Amharic: meaning unknown).

Notes: Made from stems.

Basket for cereal crops. Object made of *Eleusine floccifolia* (Forssk.) Spreng. (Poaceae). Local name: Not recorded.

Notes: Often used by small children when selling *colo* (roasted cereals) and peanuts.

Sidamo 1

Comb. Object made of *Podocarpus falcatus* (Thunb.) Mirb. (Podocarpaceae). Local name: Not recorded.

Notes: Made from wood by Borana men.

Walking stick. Object made of *Acacia sp.* (Fabaceae subfam. Mimosoideae). Local name: ***Ororo*** (language unknown).

Notes: Made from wood by Borana men. For use by men, partly as a sign of social status.

Sweeping brush. Object made of *Ehretia cymosa* Thonn. (Boraginaceae) and *Phoenix reclinata* Jacq. (Arecaceae). Local name: ***Ulaga*** (handle only) (Oromigna: meaning unknown).

Notes: Made from wood (handle) and palm leaves.

NB! This artefact is from Kefa but has been placed in this group for ease of arranging pictures.

Sidamo 2

Clothing. Object made of *Gossypium sp.* (Malvaceae). Local name: ***Shamma*** or ***Shemma*** (Amharic: outer garment for men).

Notes: Clothing worn by Borana men.

Ornament. Object made of *Podocarpus falcatus* (Thunb.) Mirb. (Podocarpaceae). Local name: Not recorded.

Notes: Carved patterned ornament from Yavello.

Stool and headrest. Object made of *Acacia sp.* (Fabaceae subfam. Mimosoideae). Local name: Not recorded.

Notes: Made from wood. Yavello Market.

Milk container. Object made of *Acacia sp.* (Fabaceae subfam. Mimosoideae). Local name: ***Sorora*** (Amharic: meaning unknown).

Notes: Made from wood. From near Yavello.

Fruit basket. Object made of *Arundinaria alpina* K.Schum. (Poaceae). Local name: Not recorded.

Notes: Made from stems. Can also be used to protect domestic birds and small animals.

Camel bell. Object made of *Delonix elata* (L.) Gamble (Fabaceae subfam. Caesalpinoideae). Local name: ***Kokegala*** (Amharic: meaning unknown).

Notes: Made from wood. Allows herder to hear where animal is and what it is doing. The sound indicates whether the animal is grazing or moving, as well as the speed with which it moves.

Rope. Object made of *Erythrina abyssinica* DC. (Fabaceae subfam. Papilionoideae). Local name: ***Qereri*** (Amharic: meaning unknown).

Notes: Bark from roots (dark) and branches (light) used as rope.

Milking bucket. Object made of *Erythrina abyssinica* DC. (Fabaceae subfam. Papilionoideae). Local name: Not recorded.

Notes: Made from wood. From near Yavello.

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The shrubland vegetation of Adwa, northern Ethiopia

ZERIHUN WOLDU & ENRICO FEOLI

ZERIHUN WOLDU & FEOLI, E. 2001. The shrubland vegetation of Adwa, northern Ethiopia. *Biol. Skr.* **54**: 319-333. ISSN 0366-3612. ISBN 87-7876-246-4.

A study of the vegetation of Adwa, Northern Ethiopia, was made to identify vegetation types and to relate the types identified to time of protection, physical and biological environmental factors, and to collect information for the decision support system. The vegetation data include binary and cover of the plant species encountered in 26 relevés collected according to the Braun-Blanquet approach. Multivariate numerical analyses of the data gave four vegetation types and 21 species groups. The vegetation types followed the altitudinal gradient ranging from 1500 m in river valleys to 2030 m on mountain ridges. The binary data set was found to be more informative than the cover data set. There is a direct correlation between length of protection time and species richness. The length of protection time has the same effects on the vegetation structure of different vegetation types. The recovery process of the vegetation begins with the increment in richness and cover of grass species. Then, after some years (3-5) shrubs and trees take over by depressing the grass component.

Zerihun Woldu, Department of Biology, Addis Ababa University, P.O. Box 3434, Addis Ababa, Ethiopia. E-mail zerihun.herbarium@telecom.net.et, zerihunw@hotmail.com

Enrico Feoli, Dipartimento di Biologia, Universita degli studi di Trieste, Via Licio Giorgieri 10, I-34127 Trieste, Italy. E-mail ecoqua@univ.trieste.it

Introduction

A long history of land clearing and sedentary agriculture has changed the vegetation cover in the highlands of Ethiopia. The natural vegetation of the northern and central Plateau of Ethiopia for example, may have been dry evergreen montane forest with *Juniperus procera* and *Olea europaea* subsp. *cuspidata* as the dominant species (Pichi-Sermolli 1957). It has disappeared from most parts except a few remnant patches around holy places and in inaccessible areas. Records of early European travellers in the fifteenth and sixteenth century (Almeida 1954; Alvarez 1970) indicate that the agro-climatic conditions were similar to those of the present day. The landscape then seems to have looked much like the present-day landscape, with the exception of the density of the trees in the crop fields; the number of trees was higher then than it is now.

The northern and central plateau of Ethiopia is characterised by mixed cereal and livestock agriculture. Nutrient deficient soils, high stocking rates and shortage of animal feeds are common features. As more land is cultivated to compensate for the diminishing

soil fertility, and to meet the ever-increasing food demands, grazing is being pushed to very steep slopes and marginal lands.

In northern Ethiopia in general, and in Tigray in particular, government attempts mobilising the population to combat soil erosion and nutrient depletion. The activities to achieve these goals include adopting traditional indigenous methods of raising the fertility of the soil and terracing agricultural fields following contour lines and closing hill sides through participatory approach. These local improvements have created a suitable situation for estimating rates of recovery of the vegetation in the area. Some places have been protected for 15 years and have attained good vegetation cover, while others were protected for a quarter of a year. However, the majority of the sites visited have not been protected at all.

The objectives of the study were (1) to identify vegetation types, (2) to estimate the rate of recovery, and (3) to understand relation of the vegetation to environmental factors and anthropogenic influences.

Data collection

Sampling

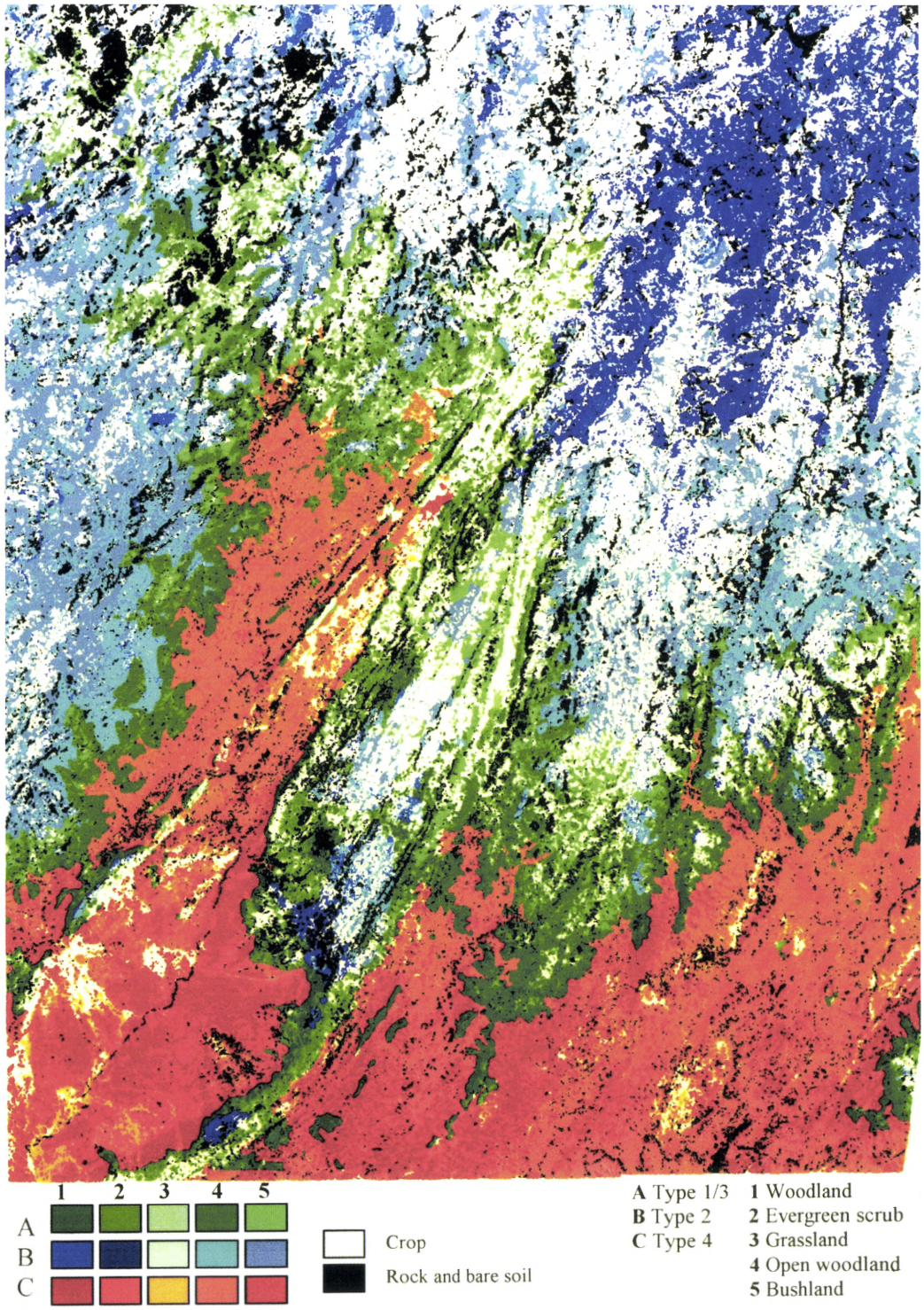
A reconnaissance survey was made in Adwa zone of Tigray Administrative Region in 1992 to select sampling points. This survey was conducted as the first phase of the Braun-Blanquet approach (Westhoff & Van der Maarel 1978). The activities during the survey included a visual inspection of the general vegetation pattern and an attempt to establish the apparent relations between vegetation and the environment. Sampling in this context would be essentially preferential (Orloci 1978). The preferential sampling approach was considered since it is believed to give the relevant information on several aspects of the vegetation in relation to management and physical environmental conditions. Moreover, the approach presumes to avoid redundancy and loss of time. Twenty-six relevés were sampled along the main road to the south from Adwa towards Weri River, which the road crosses approximately 40 km south of the town on the way to Abbi Adi. The Weri River is part of the Tacazze River system. The landscape is characterised by rounded mountain ridges (Fig. 1).

Environmental data

The following categories of environmental data were observed during the study:

GPS (Geographic Positioning System): The position of the relevé on the surface of the earth was observed. The observations were expressed both in degrees (geographic latitude and longitude) and in UTM kilometric co-ordinates. Every relevé has been georeferred with a 12 meters precision by using a GPS receiver that calculates a position based on data coming from at least 3 of several orbiting satellites.

Fig. 1. Floristic-physiognomic vegetation types of the study area as analysed from a Landsat TM (1989) satellite image of the area south of the town of Adwa, towards the Weri River and Addi Abi, in part of the Adwa zone of Tigray Administrative Region. The ridges in the upper right corner, made up mainly of volcanic rocks, are characterised by vegetation type B (= type 2, with evergreen bushes, especially *Euclea* and sometimes *Dodonaea*). The middle level has the majority of the farmland in the area (indicated by white, signifying crops) and vegetation type B (= types 1 and 3; mainly vegetation with many weedy species). The river valleys, predominantly in the lower left corner, have cut into the rocks of the metamorphic basement complex and are characterised by vegetation type C (= type 4, dominated by short-lived grasses and annuals, whereas trees and shrubs, such as *Albizia amara* and *Becium filamentosum*, are not so common). Certain species, *e.g. Acacia etbaica* and *Becium filamentosum*, are freqent in all the vegetation types. Rocks, indicated by black, are common on the ridges and at the upper, steep edges of the river valleys. →


1 2 3 4 5
A
B
C
Crop
Rock and bare soil
A Type 1/3
B Type 2
C Type 4
1 Woodland
2 Evergreen scrub
3 Grassland
4 Open woodland
5 Bushland

Altitudes: This information was collected using a pressure altimeter and GPS. Altitudes in meters above sea level were scored.

Aspect and inclination: These measurements were made using a compass. The aspect was scored on a scale from 1 to 9. Inclination was degrees deviating from horizontal.

Parent material: this is the rock from which the soil or the colluvial deposits has been formed. The presence or absence of volcanic, metamorphic or sedimentary rocks were scored as 1 or 0.

Soil type: the morphologic description (form and colour). Further soil data of horizon A were also collected, but are not given in this paper; they are only utilised in a comparison in Table 4.

Erosion: the main erosive processes, like sheet wash (superficial elemental water flowing without a precise direction), rill-wash (water flows following precise directions, excavating furrows in the ground). Seepage and gullies were expressed by an ordinal scale (1 to 6) of erosion intensity that has been established by combining the different erosion characteristics.

Vegetation physiognomy: This refers to a description of the vegetation morphology such as: size of trees, shrubs, herbs and grasses, spatial distribution, cover of vegetation as projection on the soil. Cover of grasses and shrubs has been scored in percent; the height of the vegetation in cm.

Management: various land uses were identified: cultivated, grazed, enclosed, afforested; interviews with peasants were conducted to get an overview of the land use history in the past such as the age terraces and enclosed areas. Terracing was scored on a scale from 1 to 3; particularly important was the duration of protection, if any (scored as number of years protected.

The environmental data are given in Table 1.

Vegetation data

The vegetation relevés consists of the species list compiled on homogeneous surfaces of about 400 m^2. To each species a percentage of cover value was assigned by visual estimation. The relevés are shown in Table 2. This table is structures according to the results of clustering analysis of the binary data (presence =1; absence =0).

Analyses of the vegetation data

Multivariate methods of data analysis were applied to define vegetation types and to evaluate the correlation between vegetation types and environmental variables.

Classification of vegetation

The agglomerative method, complete linkage (Anderberg 1973) with similarity ratio (Westhoff & Van der Maarel 1978) as index of resemblance was applied both on the binary (presence-absence) and cover data. The species were classified by complete linkage clustering with correlation coefficient as index of resemblance applied on the cover data (Feoli *et al.* 1982). The original table was restructured based on the classification of the relevés and the species. The structured tables of species-groups and relevé-groups were subjected to analysis of concentration (AOC; Feoli & Orloci 1979). This technique gives the relationships between species groups and relevé-groups in a reduced multidimensional space by decomposing the total chi-square (χ^2) of a table in canonical variates.

Ordination of the vegetation

The relevés were ordered using the principal component analysis (PCA) and eigenvectors of the similarity ratio matrix (Feoli 1977) applied on the soil and other environmental data, and on the binary and cover vegetation data (EOB = Eigenvector Ordination of the Binary data, EOC = Eigenvector Ordination of Cover data)

Table 1. Environmental data of the 26 relevés (excluding soil data of A horizons).

Sedimentary rocks	Metamorphic rocks	Volcanic rocks	Aspect	Terracing	Erosion	Protection (yr)	Inclination	Stoniness	Vegetation height	Grass cover	Shrub cover	Irradiation	Altitude
0	0	1	3	1	2	0	25	50	200	10	35	298	1795
0	0	1	1	1	2	0	26	70	200	40	1	252	1805
0	1	0	3	2	2	1	25	20	300	100	5	298	1500
0	1	0	2	1	2	3	25	20	70	100	1	298	1500
0	1	0	3	3	2	0.25	4	25	80	90	40	312	1750
0	1	0	3	3	2	0.25	12	50	70	50	50	309	1755
0	1	0	3	1	2	3	25	80	100	40	15	298	1950
0	0	1	1	1	2	3	40	80	100	100	20	199	1950
0	0	1	2	2	2	0	25	50	70	20	5	271	1970
0	0	1	3	2	2	0	31	50	100	30	20	291	1990
0	1	0	5	3	2	0	22	80	100	5	15	317	1950
0	1	0	2	3	2	15	24	40	200	100	50	274	2030
0	1	0	7	3	2	0	33	20	200	5	5	288	1786
0	1	0	7	3	2	0	30	100	200	1	1	302	1810
1	1	0	7	1	2	0	25	100	100	5	35	298	1800
0	1	0	1	3	2	1	30	25	50	100	1	243	1790
1	1	0	3	1	2	0	32	50	300	50	1	290	1720
1	1	0	7	1	2	1.5	32	30	300	65	1	290	1700
1	1	0	3	1	2	1.5	30	20	300	100	1	302	1655
1	0	0	7	1	2	0	5	50	200	10	5	312	1870
1	0	0	8	1	2	2	8	80	30	60	10	303	1865
1	1	1	5	1	2	0	25	50	150	20	35	314	1950
1	1	0	3	1	2	3	20	80	250	50	5	303	1790
0	1	1	3	2	2	0	24	70	150	5	50	289	1750
0	1	1	1	1	2	0	25	50	150	40	0	259	1773
0	1	1	3	1	2	0	40	50	200	10	10	260	1780

respectively. This is expected to give the pattern of variation of the vegetation in the multidimensional ecological space (Feoli & Orloci 1991).

Correlation between vegetation and environment

Both the binary and cover data were considered in order to evaluate which of the two data sets is more correlated to environmental data. Predictivity was measured by *indirect* and by *direct* approaches (Feoli 1983).

The indirect approach

1. Mutual information and its decomposition in rows and columns (Feoli *et al.* 1982) of the table obtained by the centroids of vegetation clusters described by environmental data (Table 1) and those of the soil data of horizon A (not given here). The data were normalised by rows before the application of mutual information.
2. Autocorrelation following Feoli & Ganis (1989) for each of the environmental variable superimposed on EOB and EOC ordinations.

Table 2. Species/Relevé matrix arranged according to the sequence of the complete linkage clustering Veg type: The four vegetation types. Spg.: The twenty-one species groups.

	Veg.type.	1						2						3						4								
Spg	Species/Relevés	20	23	19	25	10	14	6	7	8	9	11	15	21	24	1	2	12	13	4	5	22	3	3b	17	18	16	
1	*Abutilon bidentatum*																							1				
	Aristida keniensis																							10				
	Aristida triticoides																							20				
	Tagetes minuta												1										1	50				
	Dichrostachys cinerea						1																	5				
	Commicarpus grandiflorus						1									1		1		2		2		10		1	1	
	Becium filamentosum	1	1		1			2		1	1	1	2			1				2	1		2	10				
	Dicoma tomentosa								1								1			1			1	5				
	Flueggea virosa								1							1	1			2				5			1	
	Chloris virgata			1									2				1					5	20	60	5	5	1	
	Commiphora africana																						2	5				
	Cyathula orthacantha																						1	2				
	Digitaria velutina																2	1			2	2	20	30	10	1	1	
	Striga hermontheca																						1	1			1	
2	*Phyllanthus maderaspatensis*		1	1								1	1							1			1	1				
	Albizia amara																1						10	1	1	5		
	Cadaba farinosa																						1					
	Desmodium ospriostreblum																						1					
	Grewia villosa																						1					
	Hibiscus trionum																						1					
	Ipomoea sinensis																						1					
	Lannea schimperi																						1					
	Rhynchosia nyasica																						1					
	Guizotia schimperi														1						1		5					
	Senna italica																						2	1				
	Vernonia popeana											1											1					
3	*Setaria acromelaena*		1	1												1							2		1		1
	Achyranthes aspera											1	1			1					1	1	1		2	1		
	Bidens biternata																			1	1			20				
	Rhus natalensis																							1				
	Commicarpus ambiguus								2				1				1				1		1		5	1		
4	*Pennisetum nubicum*																			20		30			40			
	Bidens pilosa	2		2			1	2	1					1		5	2	1	1	1			5		20	60	1	
	Boswellia papyrifera																									10		
	Combretum adenogonium																									1		
	Delphinium dasycaulon																									1		
	Terminalia brownii																									1		
	Gardenia lutea																									10	1	
5	*Sida alba*		1													1				1					1	1	1	
	Bidens macroptera		1			1				1	1	1	1		1						1	10					20	
	Otostegia integrifolia																										1	
	Ozoroa insignis																										1	

	Veg.type.	1						2						3						4								
Spg	Species/Relevés	20	23	19	25	10	14	6	7	8	9	11	15	21	24	1	2	12	13	4	5	22	3	3b	17	18	16
6	*Cistanche phelipaea*																								1		1
	Grewia ferruginea																					1					
	Pennisetum pedicellatum																					1					
	Indigofera spicata																	1				5				1	
	Crotalaria plowdenii																					1	1				
7	*Zizyphus spina-christi*															1			1			1					
	Acacia etbaica	40	30	40	30		1	2		1	1	2	1	10	2	5	1	10	1	30	2	30	1	2	1		5
	Andrachne aspera	1	1																	1							1
	Bothriochloa insculpta	10							5			2	5							10	1						
	Heteropogon contortus	5	1						2			5	2							5	1	5					
	Leptochloa panicea	1																		1		1		1			
	Crotalaria spinosa	2															1										
	Gloriosa simplex	1															1										
	Cynodon dactylon	5		1		1	1		1							1	1	1									
	Monsonia angustifolia	1																									
	Periploca linearifolia	1																									
	Aloe sp.	1		5	1				1	1		1		1													
8	*Medicago polymorpha*	1		1		1			1			1				1	1	1				1					
	Brachiaria comata	5	1	1	1			1			1										15	1	1				
	Flaveria trinervia																				1						
	Indigofera brevicalyx																				1						
	Satureja simensis																				1						
	Rumex nervosus					1		1	5		1					1	1				50						1
	Cometes abyssinica																			1	1						
	Chenopodium ambrosioides																			1	1						
	Exotheca abyssinica																			1	1			1			
	Maytenus senegalensis																			1	1	1					
9	*Solanum nigrum*																1			1	1	1					
	Cynoglossum lanceolatum	1	1					1	1	1						1	1	1		10							5
	Justicia cordata																			1							
	Pseudognaphalium oligandra																			1							
	Xanthium spinosum																			1							
	Oxygonum sinuatum		1	1			1		1			1			1	1	1		1	10	1		1	2	1		
	Eragrostis tenuifolia	1						1	2	1	1					1				3	1						
10	*Eragrostis cilianensis*			1		1	1				1					1		1		2	1				1		
	Acacia oerfota																1										
	Chloris gayana																1										
	Galinsoga parviflora																1										
	Oxalis corniculata																1										
	Senna obtusifolia			1												2	10						1				
	Commicarpus helenae																1				1						
	Guizotia villosa										1						1										
	Croton machrostachyus						1		1								1								1		

	Veg.type.	1						2						3						4							
Spg	Species/Relevés	20	23	19	25	10	14	6	7	8	9	11	15	21	24	1	2	12	13	4	5	22	3	3b	17	18	16
11	*Oxalis obliquifolia*								1								1										
	Acacia seyal						1						1	1		1				1							
	Spermacoce chaetocephala	1	1	1	1		1						1	1	1	2	1			1	1		1				
	Acanthospermum hispidum															1											
	Cissus jatrophoides															1											
	Conyza tigrensis															1											
	Euphorbia indica															1											
	Hackelochloa granularis															1											
	Salvia merjamie															1											
	Thunbergia alata															1											
	Tribulus terrestris															1											
	Barleria acanthoides															5	1						2				
	Barleria eranthemoides		1		1	1	1	2				1				5							1	5			
	Tetrapogon cenchriformis	2	1							1	1		1		1	5	1	1		2	1		1				
	Polycarpaea eriantha					1										1											
	Commelina subulata															1	1										
	Trichodesma physaloides															1	1										
12	*Commicarpus pedunculosus*															1	1			1							
	Brachiaria deflexa		1			1	1				1					1					1					1	
	Galinsoga quadriradiata					1	1				1					1		1					1				
13	*Leucas martinicensis*					1	1				1	1		1		1	1	1	1	1			1		1	1	
	Dactyloctenium aegyptium		1								1			1	1	1	1	1		1		1	1		1		
	Senna occidentalis		1				1								20												
14	*Tragus berteronianus*	1	1	1	2		1				1		1		2	2	1	1		1		1			1	1	1
	Acokanthera schimperi						1																				
	Commelina velutina						1																				
	Sansevieria .sp						1																				
	Teclea nobilis						1																				
	Solanum schimperianum						5									1								1			1
	Cyphostemma molle					1	2				1											1					
	Kalanchoe lanceolata	1					1				1																
	Hypoestes forskolei	5	5	10	10	5	20		1		5		2	10	5			20		5	2				1	1	1
	Capparis tomentosa		1				1	1																			
	Evolvulus alisinoides		1				1									1	1		1								
15	*Oxalis radicosa*		1				1					1			1				1								
	Aerva javanica																	1	1	1	1						
	Argemone mexicana															1		1	1								
	Cerastium octandrum																	1	1								
	Geranium arabicum																	1	1								
	Plantago afra						1											1	1								
	Sonchus sp.						1						1					1	1								
	Plantago lanceolata												1				1	1	1								
	Anagalis arvensis														1			1									
	Eragrostis papposa																	1									
	Panicum atrosanguineum																	1									
	Tridax procumbens																	1									
	Zehneria scabra																	1									

	Veg.type.	1						2						3						4								
Spg	Species/Relevés	20	23	19	25	10	14	6	7	8	9	11	15	21	24	1	2	12	13	4	5	22	3	3b	17	18	16	
16	*Sida ovata*									1								1										
	Anthemis tigreensis					1				1																		
	Arthraxon lancifolius					1																						
	Centella asiatica					1																						
	Ctenium concinnum					1																						
17	*Crassula alba*					1																						
	Actiniopteris radiata										1																	
	Adhatoda schimperi										20																	
18	*Sporobolus festivus*									1	1																	
	Antopetitia abyssinica							2																				
	Boscia salicifolia							1																				
	Scleranthus annuus							2																				
	Echinops. sp							10	1					1		1	1		5									
	Argyrolobium arabicum							1	1																			
	Vermifrux abyssinica							2	2																			
	Otostegia fruticosa							1	1				1															
	Aristida adoensis	10	2	1	2	1	1	30	10	1	5		1		1	5	1	2	1	25	10	1	20	20		5	1	
19	*Verbascum sinaiticum*							1	1							1				1							1	
	Calpurnia aurea								10					5														
	Vigna membranacea								1					1														
	Cissus quadrangularis								2													1						
	Cyanotis barbata								1																			
	Hypoestes triflora								5																			
	Ruellia patula								5						1													
	Harpachne schimperi					1		1	5	1	2	1	1															
	Cymbopogon nardus								30	1	1	20	1	1														
	Rhynchelytrum repens							1	5			2	1											1	1		1	
	Peristrophe paniculata			1					3			1				1	1											
	Indigofera costata								1			1	1									1						
	Conyza stricta							1	1		1	1								1								
	Plectranthus barbatus								1		1	1																
	Satureja punctata								1	1	1	1																
	Dyschoriste radicans	1	5			1	1		5		1							4										
	Maytenus arbutifolia	1	1		1	1	1		1	1		1		1		1						1						
	Senna singueana	5	5	5	10	5	5	5	15	5	2	2		5		5	2	1		1		1	1		1	1	1	
	Cordia africana													1														
20	*Euclea schimperi*					10	10	10	20	10	20	20	5	40														
	Andropogon abyssinicus											2																
	Asparagus africanus											1																
	Cicer cuneatum											1																
	Clutia abyssinica											1																
	Gladiolus psittacinus											1																
	Osyris abyssinica											2																
	Pterolobium stellatum											2										1						
	Sporobolus africanus											1																
	Themeda triandra											2																
	Trifolium tembense											1																

	Veg.type.	1						2						3						4								
Spg	Species/Relevés	20	23	19	25	10	14	6	7	8	9	11	15	21	24	1	2	12	13	4	5	22	3	3b	17	18	16
20	*Eucalyptus camaldulensis*											5															
	Rhus retinorrhoea											5															
	Dodonea angustifolia								2		1	40	1														
	Ormocarpum trichocarpum				1					1		5	1	1		1											
	Clerodendrum myricoides										1	2	1														
	Clematis simensis											2										1					1
	Plumbago zeylanica								1			2								1	1						
	Helictotrichon elongatum											1						1									
	Satureja abyssinica							1	1		2							1	1								
	Pimpinella hirtella					1						1												1			
	Tragia brevipes								1			1												1			
	Polygala albida											1	1	1	1						1						
21	*Sida rhombifolia*										1	1	1					1			1			1			
	Aeschynomene abyssinica	1							1				2								1						
	Alysicarpus quartinianus												5								1						
	Eragrostis cylindriflora												1														
	Hyparrhenia anthistirioides												1														
	Lactuca.sp												1														
	Snowdenia minima												1														
	Vigna vexilata												1														
	Hyparrhenia polystachya							2					60								1	5					
	Zornia glochidiata												1							1							
	Tephrosia pumila			1						1		1	2		1	1		1									1
	Corchorus trilocularis							1		1			1										1				

The direct approach

1. Canonical correlation analysis (CCA) using the ordination axes of PCA as independent set of variables and EOC and EOB axes as dependent sets.
2. Autocorrelation of the position of vegetation types in the spaces given by PCA of environmental and soil data.

Computer packages

Ordinations, CCA, classifications and mutual information was done using the program packages FIVEPA (Feoli *et al.* 1991) and ARCVEG (Burba *et al.* 1992), chi-square (χ^2) was computed using program ACTUS (Estabrook & Estabrook 1989).

Results

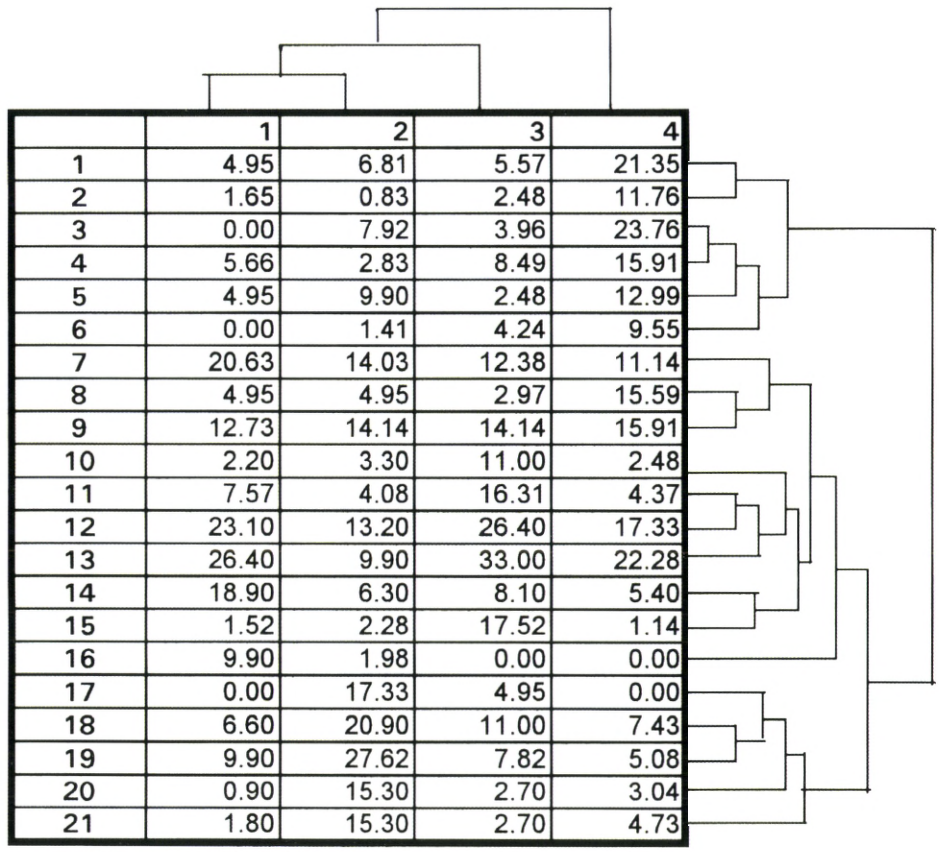
Classification of the vegetation

The overall floristic similarity between the relevés of both the binary and cover data is high. In the first case the last level of dendrogram fusion (similarity ratio) was 0.02, while within the groups the last level ranged between 0.11 to 0.16. In the second case it was less than 0.001 and the last level within the groups ranged between 0.02 and 0.07. This result indicates that the relevés represent different environmental situations. Eighteen eigenvalues were necessary to get more than 80% of the total variation showing the heterogeneity of both the binary and the cover data.

Table 3. Analysis of concentration of the species groups and relevé groups of the binary data matrix

The clusters of relevés (the four vegetation types) are indicated above the table.

The clusters of the twenty-one species groups are indicated to the right of the table.



	1	2	3	4
1	4.95	6.81	5.57	21.35
2	1.65	0.83	2.48	11.76
3	0.00	7.92	3.96	23.76
4	5.66	2.83	8.49	15.91
5	4.95	9.90	2.48	12.99
6	0.00	1.41	4.24	9.55
7	20.63	14.03	12.38	11.14
8	4.95	4.95	2.97	15.59
9	12.73	14.14	14.14	15.91
10	2.20	3.30	11.00	2.48
11	7.57	4.08	16.31	4.37
12	23.10	13.20	26.40	17.33
13	26.40	9.90	33.00	22.28
14	18.90	6.30	8.10	5.40
15	1.52	2.28	17.52	1.14
16	9.90	1.98	0.00	0.00
17	0.00	17.33	4.95	0.00
18	6.60	20.90	11.00	7.43
19	9.90	27.62	7.82	5.08
20	0.90	15.30	2.70	3.04
21	1.80	15.30	2.70	4.73

The classification of the relevés of both the binary and the cover data gave four main clusters, indicated as columns in Table 2, while the classification of species gave 21 species groups, indicated as rows separated by double lines in Table 2.

The analysis of concentration (for binary data, Table 3) shows the concentration of species groups and the rank of species groups according to the decomposition of the total mutual information. The results of mutual information and AOC suggest that the classification of the vegetation based on binary data has a higher internal predictivity than the classification based on cover data (Feoli 1983). The relevé-groups obtained by binary data and cover data show good correspondence since almost 70% of the relevés reflect the same classification.

These groups of relevés represent four vegetation types as follows (see also Table 2):

Vegetation type 1: characterised by *Acacia etbaica, Cynodon dactylon, Hypoestes forskaoli,* and *Barleria eranthemoides.* It had a high concentration of species groups 7, 14 and 16. This vegetation type is similar to vegetation type 3, as clearly depicted in Figs. 1 and 2. The type occurs at the middle level of the study area at an altitudinal range between 1750 and 1850 m, mainly on sedimentary and metamorphic parent materials.

Vegetation type 2: characterised by *Euclea*

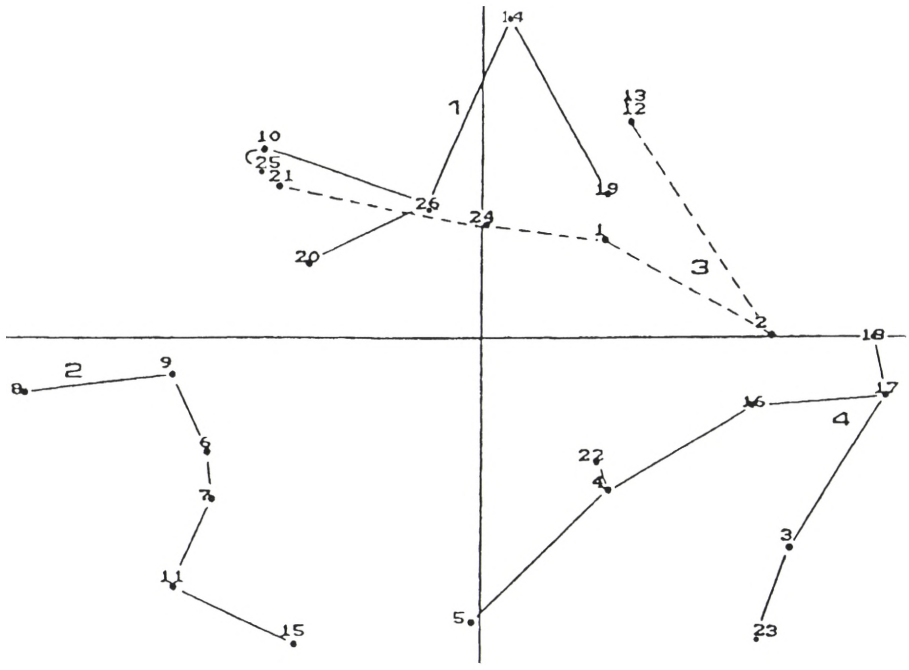


Fig. 2. The four vegetation types (indicated by the larger sized numbers 1-4) given by the binary data for the relevés (indicated by smaller numbers 1-26) superimposed on the 2nd and 3rd axes of the same data for the 26 relevés.

schimperi, Harpachne schimperi, Cymbopogon nardus, Dodonea angustifolia, and *Clerodendrum myricoides.* It had a high concentration of species groups 17, 18, 19, 20 and 21. This vegetation type occurs on the mountain ridges of the study area in the altitudinal range between 1850 and 2200 m, mainly on volcanic parent materials.

Vegetation type 3: characterised by *Senna obtusifolia* and *Dactyloctinium aegyptium.* The species groups with high concentration are 10, 11, 13 and 15. This vegetation type, like vegetation type 1, occurs at the middle level in the altitudinal range between 1750 and 1850 but mainly on volcanic and metamorphic parent materials.

Vegetation type 4: characterised by mani grasses, *e.g. Chloris virgata, Digitaria velutina, Pennisetum nubicum.* Trees, *e.g. Albizia amara* and occasionally *Acacia etbaica,* and shrubs, *e.g. Becium filamentosum,* are not prominent. It has a high concentration of species groups 1, 2, 3, 4, 5, 6 and 8. This vegetation type occurs where watercourses have cut down to the basement complex, and hence mainly on soils derived from metamorphic parent material, in the altitudinal range between 1500 and 1750 m.

Certain species, *e.g. Acacia etbaica,* is prominent in all the vegetation types. Each of these four vegetation types are divided into four physiognomic types each, as can be seen in unsupervised classification of the Landsat TM (1989) image (Fig. 1). The image also clearly shows how the vegetation types are associated with different types of landscapes in the area.

Ordination of the vegetation

The EOB and EOC (2^{nd} and 3^{rd} axes) show a rather well separated dispersion of the 4 vegetation types. However the ordination based on binary data shows a more clear separation between vegetation types (Fig. 2). The first two

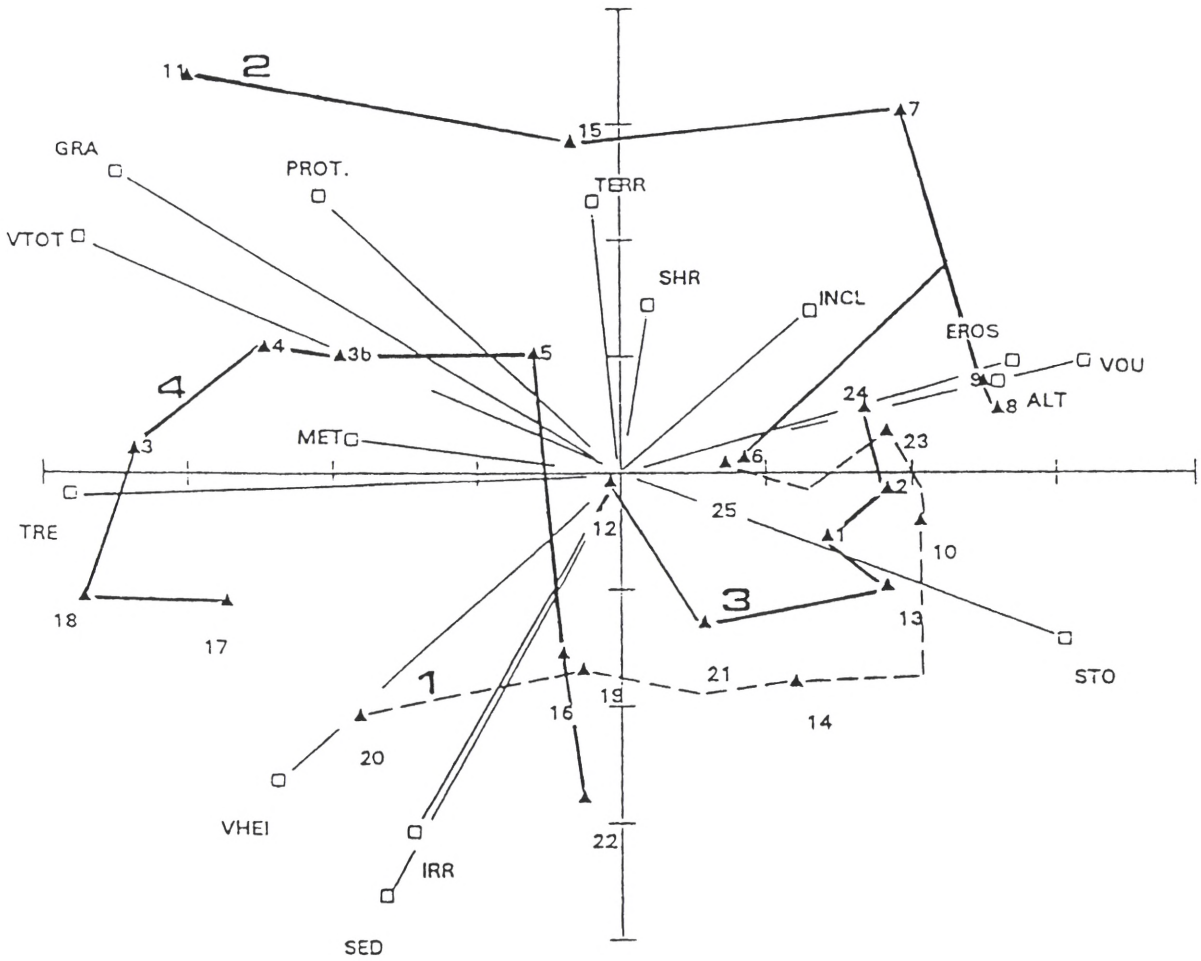


Fig. 3. The four vegetation types (indicated by the larger sized numbers 1-4) given by the classification of the binary data superimposed on the ordination of the 1st and 2nd axes of the environmental data (abbreviations in agreement with the data set in Table 1).

axes of PCA ordinations of the environmental data (Fig. 3) show the relevés of four vegetation types as being distinct. However within each vegetation type there are evident trends of variation mainly owing to erosion, stoniness, altitude, years of protection. The same applies for the further soil data (only horizon A) which were gathered during the study.

Correlation between vegetation and environment

From the decomposition of total mutual information of the groups, it appears that the predictivity of classification based on binary data (2I=354) is higher than the one based on cover data (2I=119). In both cases the most discriminating environmental variable is the length of time of protection, which is correlated with

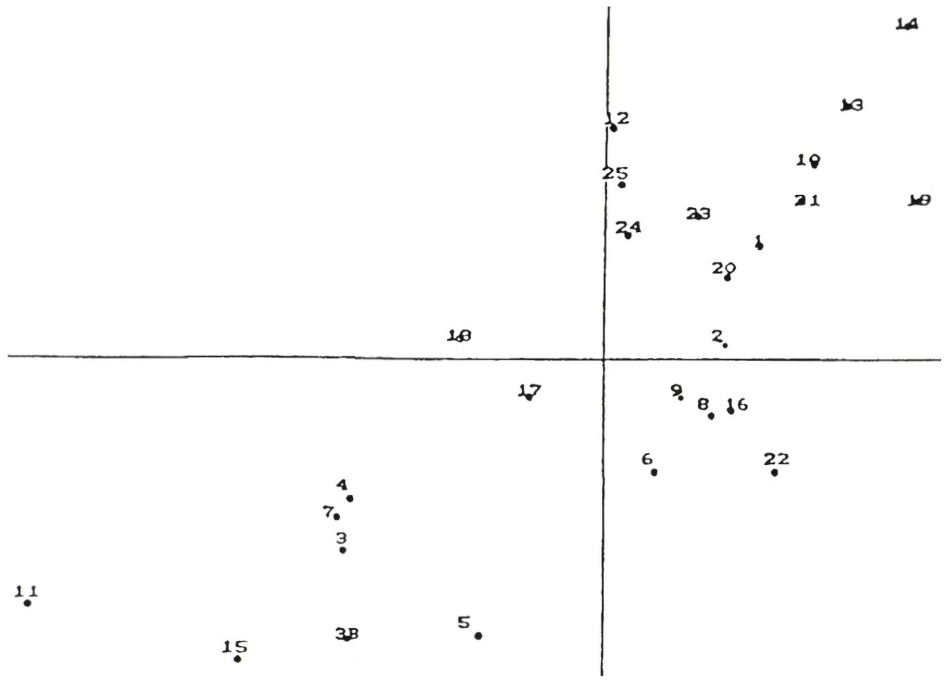


Fig. 4. Canonical correlation analysis of the environmental and the binary vegetation data for the 26 relevés.

the herb cover. The 2nd eigenvectors of the similarity matrices in EOB and EOC ordination show a gradient of protection decreasing from left to right. This separation is mainly due to altitude with type 2 having an average altitude of 1950 m and type 4 having 1670 m. The autocorrelation of environmental variables for EOB confirms the importance of altitude. In fact the autocorrelation shows significant aggregation for clay, altitude, pH, sand and protection (z=1.3). The autocorrelation of environmental variables for EOC shows significant aggregation only for altitude, sand, clay and grass-herb cover (z=1.2). This corroborates that EOB is more predictive than EOC.

The results of canonical correlation analysis (CCA, Fig. 4) also confirms that the predictivity of binary data is higher than that of cover data. In both cases the test of Bartlett (Feoli *et al.* 1991) is significant, however the one corresponding to EOB is higher than the one of EOC. The autocorrelation of the distribution vegetation types in the PCA ordinations based on environmental data and the soil data (only horizon A) mentioned above has shown that the aggregation is significant only for vegetation types 4 and 2 (Table 4a, b).

Conclusion

The vegetation of the study area is classified into four main vegetation types. These types are mainly influenced by altitude. There is a direct correlation between length of protection time and species richness. The length of protection time has the same effects on the vegetation structure of different vegetation types. However the grass species recovering at low altitude are different from those recovering at a higher altitude. The recovery process of the vegetation starts always with the increment in richness and cover of grass species. Then, after some years (3-5) shrubs and trees take over by depressing the grass component.

Table 4. Autocorrelation of the four vegetation types with environmental data and soil data. Spatial Autocorrelation for 26 relevés, 3 axes and Random H0 hypothesis.

Significance level		0.100	0.050	0.010	0.005	0.002
One tail Z test		1.282	1.645	2.326	2.576	3.090
Two tail Z test		1.645	1.960	2.576	2.813	3.291

(a) Environmental data		**Sum**	**Average**	**Observed values**	**Expected values**	**Z TEST**
Vegetation type 2		5.00	0.19	0.1331	-0.0400	3.1195
Vegetation type 4		5.00	0.19	0.1184	-0.0400	2.8546
Vegetation type 3		3.00	0.12	-0.0069	-0.0400	0.6145
Vegetation type 1		5.00	0.19	-0.0482	-0.0400	-0.1400
(b) Soil data						
Vegetation type 3		3.00	0.12	0.0281	-0.0400	1.4427
Vegetation type 2		5.00	0.19	0.0158	-0.0400	1.1664
Vegetation type 4		5.00	0.19	-0.0086	-0.0400	1.0161
Vegetation type 1		5.00	0.19	-0.0224	-0.0400	0.3692

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Flora and Vegetation of the Simen Mountains National Park, Ethiopia

Sileshi Nemomissa & Christian Puff

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The Simen Mountains National Park, a UN World Heritage site, known for its spectacular scenery, the endemic Walia Ibex, and endemic plant species such as *Rosularia semiensis* (Crassulaceae), comprises a high plateau area (usually above 3200 m, to over 4000 m), steep escarpments, and a "lowland area" (usually less than 3000 m, down to less than 2000 m, where it is dissected by river valleys). Flora and vegetation of all parts of the park were studied during three expeditions (December 1996-January 1997, September-October 1998, and May 1999). While the afroalpine area, with its large and common stands of *Lobelia rhynchopetalum* in *Festuca*-dominated grassland, is the most spectacular part of the park, the "lowland" (*i.e.* afromontane) area of the park is far more interesting botanically, and also much richer in species. As this part of the park is rather densely populated, only patches of relatively undisturbed afromontane vegetation remain. They comprise, depending on their exposition and location, "wet" types of forest (rather species rich), "dry" forest patches (dominated by *Olea europaea* subsp. *cuspidata*, but usually not *Juniperus procera* which is rather uncommon in the park), and intermediate vegetation types. The escarpments between the "low" and "high" areas of the park have dense stands of *Erica* forest, with *E. arborea* locally replaced by *E. trimera* at higher altitudes. Steep and shady gorges with extensive, often vertical cliffs harbour interesting and rare plants such as *Dianthus longiglumis*, *Saxifraga hederifolia*, *Primula verticillata* subsp. *simensis*, and *Rosularia semiensis*.

Sileshi Nemomissa, National Herbarium of Ethiopia, Addis Ababa University, P.O. Box 3434, Addis Ababa, Ethiopia. E-mail: nat.heb@telecom.net.et

Christian Puff, Institute of Botany and Botanical Garden, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. E-mail: christian.puff@univie.ac.at

Introduction

The characteristic vegetation types and zonation of the East African high mountains were extensively investigated by Hedberg (1951, 1957, 1964). One clear topographic difference between the Ethiopian and East African mountains is that the latter mountains are clearly separated by extensive lowland areas, while the former are connected by a high plateau with extensive farming. In Ethiopia, the ericaceous and afroalpine belts *sensu* Hedberg (1951) have been intensely degraded through burning, firewood collection, grazing, and agriculture (Scott 1958; Hedberg 1971, 1978).

The northern highland areas of Ethiopia were the first to be explored, more than a century ago, by various European botanists *viz.* G. W. Schimper, R. Quartin-Dillon, A. Petit, E.

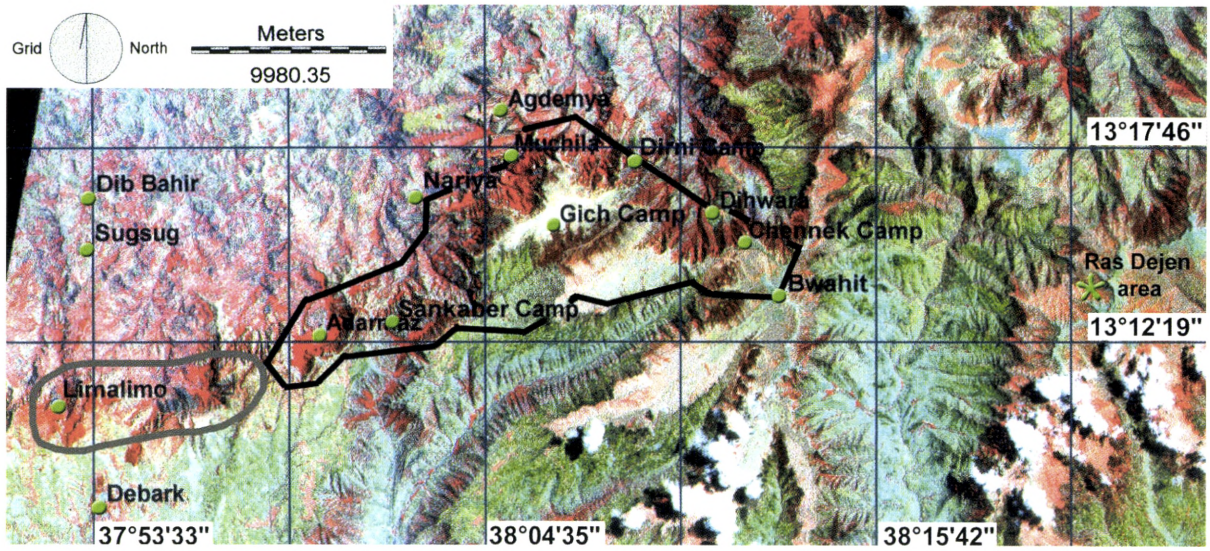


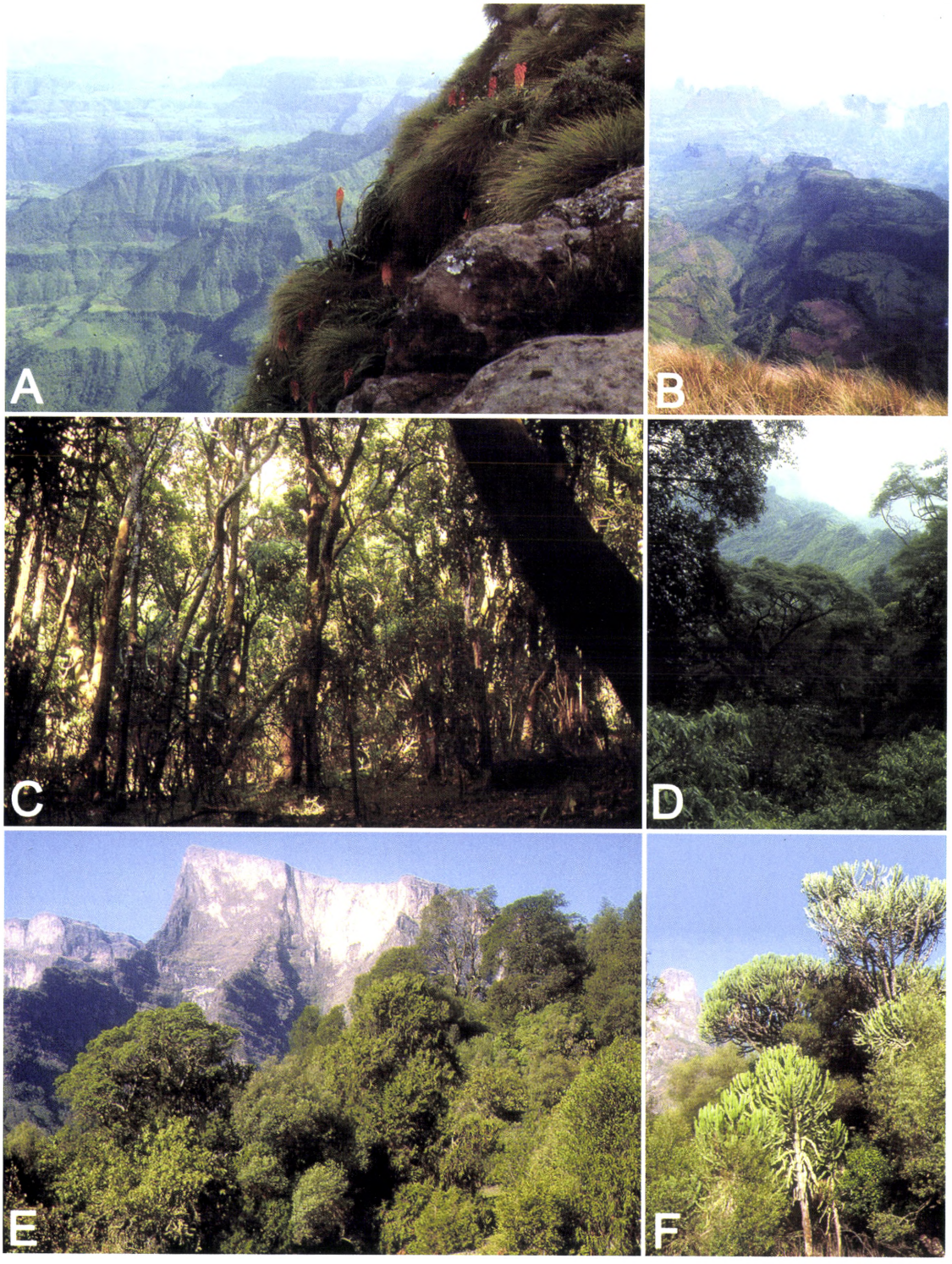
Fig. 1. LandSat image of the Simen Mountains National Park (border delimited by black line), the adjacent Lemalimo (= Limalimo) escarpment and surrounding areas. Solid plant cover (forested areas, etc.) show up in red. A white haze obscures the core area of the afroalpine belt (around Gich Camp).

Rüppell, and H. Steudner, laying the ground work for A. Richards' *Tentamen Florae Abyssinicae* and G. Cufodontis' *Enumeratio plantarum Aethiopiae Spermatophyta*. More recently, Scott (1958) and Sebald (1968) explored Simen (sometimes also spelled Semien or Simien) and made extensive collections. Some of the species found by these collectors have not been encountered since.

Simen Mountains National Park (SMNP; Fig. 1) is listed as one of the world heritages with an area of 22,000 ha (in the year 1978) and situated approximately at 13° 14' N, 38° 04' E. The park occupies a broad undulating plateau of open grassy plains and includes a wide altitudinal range at 1900-4624 m (World Bank 1993). The plateau is bounded on the south and northeast by the deep valleys of the Tekeze River and its tributaries, and is dissected from north to south by the Meshah River (which is the principal catchment area). The SMNP is a delineated sanctuary for threatened fauna such as the Walia Ibex (*Capra walie*), the Geleda Baboon (*Theropithecus gelada*), and the Ethiopian Wolf (formerly known as the Semien Fox; *Canis simensis*). The Walia Ibex has always had a restricted distribution range in Ethiopia, and the Simen Mountains are the southernmost limit of all species of ibex (Curry-Lindahl 1968). The SMNP does not include the nearby Ras Dejen, the highest peak in Ethiopia.

The climate of Simen Mountains is characterised by frequent frost, occasional snow at high elevation, and frequent hailstorms

Fig. 2. A-B. View of "lowlands." **A**. From around Sankaber Camp (c. 3200 m). **B**. From Gidir Got area (c. 3400 m). Note patches of Afromontane forest (at c. 2400 m) around fields. **C-F.** Afromontane forest in the "lowlands." **C-D**. "Wet" types. **C**. Interior of Adarmaz forest (c. 2400-2700 m; see text). **D**. *Albizia schimperiana* dominated forest in the Adarmaz T/Himanot R. valley (c. 2060 m). **E-F.** "Dry" types (near Tiya village; c. 2800 m). **E.** A type with *Juniperus* and *Olea*. F. A type with also *Euphorbia ampliphylla* dominant. Reproduced from colour slides by C. Puff. →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(Hurni *et al.* 1987; Sebald 1968). Changes between clear days and night hailstorms have frequently been reported. During September/October (almost end of the rainy season) we observed clear mornings that were frequently followed by a strong build-up of fog, which instantly may cover the mountains, and heavy rain and hailstorms at night. Under these conditions, it was practically impossible to see the mountains and sceneries of the Simen Mountains in the afternoon. It is very cold at night and relatively warm with clear skies in the day, especially in the mornings during the rainy season. We observed frequent snow in December/January (dry season). The more accessible (*i.e.* less steep and ± flat) parts of the Simen Mountains are favourable for barley cultivation, which is practised up to *c.* 3600 m. Hurni *et al.* (1987) characterised the climate of Simen and divided it into two categories, namely the upper (above 3500 m) and the lower (1500-3200 m) climatic types.

Gillett (1955) described the differences between the plateaux of Ethiopia and the East African Mountains, while Beals (1968) pointed out that the Simen Mountains are floristically different from the high southern and south-eastern mountains of Ethiopia. Hedberg (1971) pointed out that such differences might be due to insufficient collection of the Ethiopian flora.

Since the time of G.W. Schimper, the flora of Simen Mountains has been relatively little investigated by botanists, partly due to recent socio-political problems. The SMNP and the surrounding high mountains are type localities for *c.* 220 taxa. Many of the type collections (especially G.W. Schimper's) for these taxa were destroyed during the Second World War in Berlin. The National Herbarium, Addis Ababa University, has relatively few representative collections from Simen Mountains. The present study was designed to (1) provide new collections to facilitate the writing of the Flora of Ethiopia and Eritrea, (2) provide data on the endemic plants in the park to help the SMNP management, and (3) provide an overview of the tree species of the afromontane forests inside the park.

Terminology

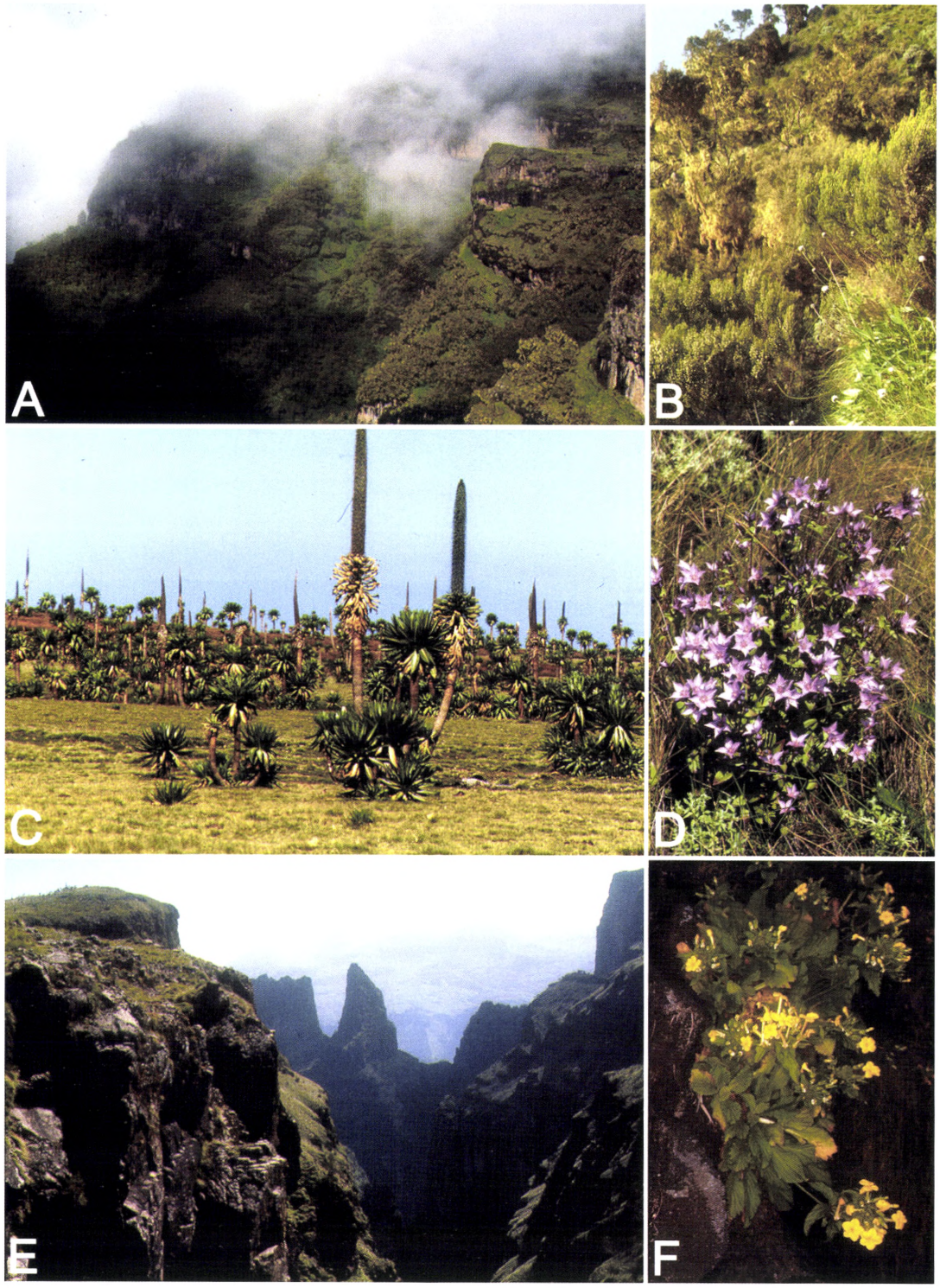
The terms afroalpine, ericaceous, and afromontane are used according to Hedberg (1951), and assuming that these terms are also applicable to Ethiopian vegetation.

Study areas and itinerary

This study presents information and observations on Mt. Bwahit, Ras Dejen, and the Lemalimo Wildlife Reserve. Both Bwahit and Lemalimo are bordering the park, and there are plans to add these areas in the future. For the importance of the former area as type locality for many species, see Edwards (1996). Ras Dejen is further away from the SMNP in a northeasterly direction.

Three expeditions were made to the study area. The first expedition took place in December/January 1996-1997 (dry season). Collections of specimens around Sankaber, Gich, Emet Gogo, Saha and Muchilla Afaf, and investigation of the afromontane forest along Wazla

Fig. 3. A-B. Ericaceous belt. **A**. Escarpment below Chennek Camp (c. 3600 m); in this area, *Erica trimera* is more common than *E. arborea*. **B**. Around Chennek Camp; both *Erica trimera* and *E. arborea* (foreground, left) are visible (*Dipsacus pinnatifidus* in the foreground, right). **C-D**. Afroalpine belt around Saha (c. 3700 m). **C**. *Lobelia rhynchopetalum*, with *Carex monostachya*, brown, in the background. **D**. *Swertia fimbriarta* in *Festuca abyssinica* grassland. **E**. Entrance to Dirni gorge (c. 3700 m); *Primula verticillata* subsp. *simensis* (seen in **F**) is common in the shady, vertical cliffs. Reproduced from colour slides by C. Puff. →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Wenz were undertaken. The second expedition was made in September/October 1998, almost at the end of the rainy season. This expedition was organised into three phases.

1. Phase 1: Activities around the Sankaber Camp (see landscape on Fig. 2A).
2. Phase 2: Activities around the Gich Camp; collection around the camp, day trips to Saha (see landscape in Fig. 3C-D), Emet Gogo and Muchilla Afaf.
3. Phase 3: Activities around the Chennek Camp (see landscape in Fig. 3A-B) and work in the "lowland" (locally called *Kolla*). The trip to Kolla was organised with mules and mule drivers hired at Chennek Camp (3600 m). The expedition team camped at sites between Chennek and Adarmaz Camps (2400 m). We climbed up to Sankaber Camp (3100 m) from Adarmaz via Chilkiwanit, using wire ropes fixed on the cliffs. These wire ropes have been fixed by mountaineers of the Nature Oriented Tourism Development Project, Austria. The route from Adarmaz Camp (2400 m) to Chilkiwanit (slightly over 3000 m) was previously only accessible to local people because of the very steep cliffs.

The third expedition was made in May 1999 at the beginning of the rainy season. The expedition team left the Sug Sug area (*c.* 2150 m), a few kilometres above Dip Bahr village, for the Chennek Camp, passing through the "lowland" areas (See Fig. 2A-B). It took the team two days to reach Adarmaz Camp and 6 additional days to reach Chennek Camp. The trip to Ras Dejen was organised from a base at Chennek Camp.

Geographical positions, using GPS readings, were established at each camp, and botanically interesting sites were localised with a Magellan GPS Pro 5000. Altitude was measured with a Thommen altimeter with a range to 6000 m.

Vegetation

The vegetation of Simen Mountains can be divided into 3 distinct types ("belts" sensu Hedberg 1951), namely (1) the afromontane forest, (2) the ericaceous belt, and (3) the afroalpine zone. There is a clear transition from one belt to the other, although the upper and lower altitudinal limits of indicator species such as *Erica arborea* may vary with microclimatic conditions. *Lobelia rhynchopetalum* (which is the characteristic species of the afroalpine belt) also grows in wet sites at lower altitudes, *e.g.* near streams in ericaceous forest, which is sometimes dotted with *Hypericum revolutum*. The vegetation types are sometimes not clear because one or more types are strongly modified by human impact, such as cutting and clearing, or completely replaced by cultivation. This impact is very strong around Amba Ras, Argen, and Gich village where both the ericaceous and afromontane forests are cleared and replaced by cultivation.

1. Afromontane forests

There are two types of afromontane forest encountered in this study: the dry and the wet types. Various environments such as exposed slopes, rock outcrops, open areas, and gullies are found in the afromontane forest belt of the Simen Mountains. These varied environments support different species.

1A. Wet afromontane forest patches

These patches are often found on the moist North- or Northwest-facing slopes, and in steep and shady gullies. The characteristics and species composition of these wet afromontane forest patches are presented below.

i. Adarmaz forest – This forest (see Fig. 2C) is found at 2400-2700 m. Large and prominent tree species are *Prunus africana, Apodytes dimidiata* var. *acutifolia, Bersama abyssinica, Schefflera abyssinica, Olea capensis* subsp. *hochstetteri,*

Euphorbia ampliphylla, and *Pittosporum viridiflorum*. Epiphytic plants such as ferns and *Peperomia* species are common on tree trunks and large branches, and mosses are also present. The herbaceous layer is very poor because of the limited amount of light that penetrates the canopy. *Brucea antidysenterica* reaches in this forest the rather unusual height of about 10 meters. The forest is also characterised by the presence of woody lianas, such as *Embelia schimperi* and *Phytolacca dodocandra*, and a shrub layer with *Pavetta oliveriana* and the pauchycaul *Lobelia giberroa*.

Olea europaea subsp. *cuspidata* occurs in the drier, more exposed part of the forest patch. *Dombeya torrida* subsp. *torrrida*, on the other hand, is only found at the upper limit of the forest. Other characteristic species are enumerated in Table 1.

The Adarmaz forest is comparable to the forest patch along the valley of Wazla Wenz (restricted to gully) with regard to species composition, presence of epiphytic *Peperomia*, and the niche preference of *Olea europaea* subsp. *cuspidata*. These two forest patches differ, however, in the composition of canopy species. *Olea capensis* subsp. *hochstetteri* and *Apodytes dimidiata* var. *acutifolia* are absent as canopy trees from the Wazla Wenz forest patch. On the other hand, *Myrsine melanophloeos* (syn. *Rapanea simensis*) and *Myrsine africana*, common in the Wazla Wenz area, are absent from Adarmaz forest. Furthermore, the canopy of Adarmaz forest is more closed.

ii. Albizia schimperiana dominated forest – This forest patch occurs at *c.* 2060 m in the valley of Adarmaz T/ Himanot River (see Fig. 2D). The canopy of this forest includes *Albizia schimperiana, Millettia ferruginea* subsp. *ferruginea, Croton macrostachyus, Olea capensis* subsp. *hochstetteri, Euphorbia ampliphylla*, and *Schefflera abyssinica*. *Olea europaea* subsp. *cuspidata* is mostly restricted to the drier and exposed portions of this forest. The herbaceous layer is poor in species composition. There is a pure stand of *Debregeasia saeneb* along the river bank. One species characteristic of riverine forest, *Mimusops kummel*, is also recorded. Characteristic species are enumerated in Table 2.

iii. Muchila – Neznazit afromontane forest patch – This patch is restricted to slopes facing North and Northwest and in shady gullies. The forest is characterized by the presence of *Hagenia abyssinica*, *Dombeya torrida* subsp. *torrida*, *Myrica salicifolia*, and *Schefflera abyssinica*. *Olea europaea* subsp. *cuspidata* mostly occupies drier part of this forest. Woody lianas such as *Rubus steudneri* and *Pterolobium stellatum*, form impenetrable thickets. Species recorded are listed in Table 3.

1B. Dry afromontane forest patches

These forest patches are generally located on South- or Southeast-facing slopes and are rather poor in species. Characteristic taxa are *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, and *Euphorbia ampliphylla*. *Juniperus procera* is rather uncommon in the SMNP. More extensive stands were observed between Antola, Tiya, and Truwata villages. There was also a remnant *Juniperus-Olea-Euphorbia* forest at the graveyard near Tiya village (see Fig 2E-F). The typical *Juniperus-Olea* dry forest common elsewhere in the northern highlands of Ethiopia is otherwise not present in the park.

The dry afromontane forest patches typically contain the species listed in Table 4. Some afromontane forest remnants are intermediate in that both „wet“ and „dry“ elements occur in it.

1C. Farmland and secondary scrub

In many places, natural afromontane vegetation is replaced by farmland and secondary scrub. The most common and prominent solitary, large trees (10 m to > 20 m) found in such areas are listed in Table 5.

Appendix to 1. Afromontane forests: The Lemalimo Wildlife Reserve (LWR) and its vegetation

The LWR is not part of the SMNP, but it is located immediately adjacent to it. It includes the area that is the continuation of the SMNP escarpment to the West. The LWR thus encompasses altitudes from over 3000 to less than 2300 m. The main road leading from Debark northwards, taking one down the escarpment (this is the famous "Wolkefit pass" collecting locality of older collectors!), divides the LWR into two parts.

Two areas of the LWR were surveyed:

i. afromontane forest areas both to the left and right of the road, at 2600-2700 m, and
ii. the steep, wooded slopes along the road (Wolkefit pass) from the Spring (2610 m) down to 2550 m.

i. Afromontane forest – The forest shows a species composition that, as far as woody plants are concerned, is essentially comparable to Adarmaz forest (Table 6; compare with Table 1). The major difference, however, is that the general canopy height is low, mostly under 10 m; only few solitary large (*i.e.* 20-25 m) trees are left. The latter is an indication that the forest has been – and is – selectively logged (see also below!).

There is a swampy area at the middle of the forest lined by a nice stand of *Salix subserrata* trees.

ii. The steep, wooded slopes along the road below the spring (Wolkefit) – These sites are also of considerable botanical interest because the steep to vertical, permanently wet rocks and their immediate surroundings harbour a number of plants which are otherwise only found in the high Simen, at altitudes well above 3300 m (Table 7).

2. Ericaceous belt

This belt is situated above the afromontane forest belt *sensu* Hedberg (1951). However, the altitudinal range of this belt on Simen Mountains does not correspond to it altitudinal range on the mountains of tropical East Africa. The ericaceous belt on the Simen Mountains is characterized by the occurrence of *Hebenstreitia dentata, Scabiosa columbaria, Arabis alpina, Swertia engleri* var. *engleri, S. lugardae, S. fimbriata* (see Fig. 3D), *Haplosciadium abyssinicum, Arabis thaliana, Saxifraga hederifolia*, and *Satureia simensis*. Of the ericaceous shrubs or trees, only *Erica arborea* was previously recorded from the SMNP (Klötzli 1986; Hurni *et al.* 1987), but we found that *E. trimera* is also present, locally replacing *E. arborea* at higher altitudes.

The ericaceous formations are different from site to site because of differences in the intensity of grazing and anthropogenic disturbances. In some little disturbed sites *E. arborea* has a well-developed bole, a feature rarely seen elsewhere. On the northern or northwest sides, *e.g.* facing Hawuza or Dirni (see Fig. 3E), the ericaceous forest is highly affected by human encroachment such as clearing for cultivation. These sides are more humid than the east or southeast-facing cliffs, which are exposed to a longer period of direct sun. However, patches of pure ericaceous forests still cover the inaccessible cliffs and rocky outcrops. Furthermore, the inaccessible cliffs and steep slopes provide a good habitat for Walia Ibex. The accessible *Erica*-dominated forests have few herbs due to overgrazing and human impacts such as cutting *Erica* for construction and fuel and clearing for cultivation. These forests are dotted with *Hypericum revolutum*. There are notable differences in disturbance of the ericaceous forests on the north/northwest and eastern/south-east facing slopes. Unfortunately, there is no sign of regeneration of *E. arborea* in any of the studied sites. The grass-dominated undergrowth of the open ericaceous forest is

dotted with beautiful flowers of *Gladiolus abyssinicus*, *Dipsacus pinnatifidus*, *Kniphofia foliosa*, and *Hebenstretia dentata*. The ericaceous belt at Chilkwanit harbours a rare Simen endemic species, *Ceropegia sobolifera* (Asclepiadaceae), that was encountered in small populations only twice during the field trip.

3. Afroalpine belt

The afroalpine region is dominated by various grass and herbaceous species, but the really magnificent landmark species is *Lobelia rhynchopetalum*. *Helichrysum* scrub, *Carex monostachya* bog, and *Festuca* grasslands are the most important plant communities. Different plant communities also occur along streams and on rocky outcrops. Characteristic species of this area include *Trifolium* and *Alchemilla* species, *Ranunculus oreophytus*, *Arabis alpina*, *Swertia engeri*, *S. fimbriata*, *Dipsacus pinnatifidus*, etc. Some of the herbaceous species of the area are characterised by the development of a thick, deep tap root system and short internodes (*e.g. Haplosciadium abyssinicum*). The afroalpine belt on Mt. Bwahit is mainly rocky and relatively species poor in comparison to a comparable area at Saha and Emet Gogo. This area is roughly above 3500 m and is mainly grassland with different plant communities. The communities are presented separately below:

3A. Long Festuca abyssinica-Lobelia rhynchopetalum community at Saha

This community is not affected by grazing because of the unpalatable *Festuca abyssinica*. The soil is as disturbed as on the Bale Mountains, where mole rats play an important role for the establishment of pioneer plant species. The herbaceous species of this community are *Swertia fimbriata, Dipsacus pinnatifidus,* and *Trifolium* species. The community is poor in species.

3B. Carex monostachya bog with scattered Lobelia rynchopetalum at Saha

This community has a very restricted distribution in the Simen Mountains.

3C. Rocky outcrops

This habitat harbours succulent plants such as *Rosularia semiensis*, *Aeonium leucoblepharum* and other afroalpine species such as *Arabis thaliana*, *Primula verticillata* subsp. *simensis* (see Fig. 3F). This habitat is mainly found on steep, inaccessible cliffs.

Conservation of the natural resources and threat to biodiversity of the park

The accessible ericaceous and afromontane forest belts are increasingly being cleared for cultivation. Overgrazing and human encroachment for new agricultural fields, logging for charcoal, timber, and firewood limit the regeneration of the vegetation in the ericaceous and afroalpine belts. The herb layer of the *Erica* forests is very open or almost non-existing, consisting merely of short grasses. The afroalpine belt suffers from overgrazing, which has facilitated erosion, especially along cattle trails. The characteristics of intensive overgrazing are seen above Gich (above 3600 m) and around Chennek and Amba Ras, where the vegetation consists of extremely short grasses and lacks the regeneration of *e.g. Kniphofia foliosa, Lobelia rhynchopetalum* and other species, which normally occur at this altitude in undisturbed areas. Herds of different grazing capacity (sheep, cattle, mules, horses, and donkeys) usually graze in the park, and the trampling of these herds is believed to be the major cause for the failure of the establishment of seedlings. We compared a relatively inaccessible and well-protected pocket of ericaceous vegetation at Chenneck with the same formation at roughly the same altitude at Gich, which is severely affected by overgrazing. The comparison showed that the number of small,

herbaceous species at Gich is only 25% of the number of species at Chennek, thus documenting the dramatic impact of overgrazing and trampling on the biodiversity of the park. Similarly, there is a significant difference between disturbed and undisturbed afroalpine environments with regard to biodiversity. An exception is the afroalpine areas of Mt. Bwahit (c. above 4000 m) which is rocky and naturally species poor.

We therefore recommend that

1. the remaining environments of the park be effectively protected as quickly as possible (to ensure recovery and regeneration), and
2. the Lemalimo area be added to the SMNP.
3. Grazing, selective logging and human encroachment be strictly forbidden in the park for the reclamation of the degraded environments of the park and conservation of its natural resources. In our opinion, *immediate action* is needed, as during our preliminary exploration, disturbing signs of illegal exploitation were observed: trees (and mostly the largest ones still left) are apparently felled at a regular basis, as can be concluded from tree stumps with cut-marks of varying ages. During a single afternoon, smoke from illegal charcoal making was observed from three different, more remote areas of the Lemalimo Wildlife Reserve. Moreover, far too many cattle from neighbouring farms are driven into the forest each day. There are distinct signs of overgrazing. The many cattle trails seriously hamper natural regeneration of forest elements.
4. the park boundaries are to be redelimited.

Acknowledgements

We would like to thank the Simen Mountains National Park Management Office and the Austrian Government funded SMNP Nature Oriented Tourism Development Project (Gondar) for helping us in arranging the field trips and general logistics. Many people from and outside the park were involved in this project; we are very much indebted to all of them. Mrs. Doris Brunner of the Nature Oriented Tourism Development deserves our special thanks for her enthusiasm in the realisation of this project. Financial support by the SMNP Nature Oriented Tourism Development Project and the Austrian Development Corporation (Addis Ababa) is very much appreciated.

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Table 1. The most common woody and herbaceous plants found in Adarmaz forest.

Taxon	Family
Prominent large trees	
Apodytes dimidiata var. *acutifolia*	Icacinaceae
Bersama abyssinica subsp. *abyssinica*	Melianthaceae
Dombeya torrida	Sterculiaceae
Ekebergia capensis	Meliaceae
Euphorbia ampliphylla	Euphorbiaceae
Olea capensis subsp. *hochstetteri*	Oleaceae
Olea europaea subsp. *cuspidata*	Oleaceae
Pittosporum viridiflorum	Pittosporaceae
Prunus africana	Rosaceae
Schefflera abyssinica	Araliaceae
Less prominent trees	
Brucea antidysenterica	Simaroubaceae
Cassipourea malosana	Rhizophoraceae
Clausena anisata	Rutaceae
Croton macrostachyus	Euphorbiaceae
Discopodium penninervium	Solanaceae
Erica arborea	Ericaceae
Galiniera saxifraga	Rubiaceae
Hypericum revolutum	Guttiferae
Woody lianas	
Embelia schimperi	Myrsinaceae
Phytolacca dodecandra	Phytolaccaceae
Shrubs	
Maytenus arbutifolia	Celastraceae
Pavetta oliveriana	Rubiaceae
Rhus glutinosa subsp. *glutinosa*	Anacardiaceae
Ritchiea albersii	Capparaceae
Rosa abyssinica	Rosaceae
Herbs and pachycauls	
Girardinia bullosa	Urticaceae
Lobelia giberroa	Lobeliaceae
Thalictrum rhynchocarpum	Ranunculaceae

Table 2. The most common woody plants of the *Albizia* dominated forest in the valley of Adarmaz T/Himanot River.

Taxon	Family
Prominent large trees	
Albizia schimperiana	Mimosaceae
Croton macrostachyus	Euphorbiaceae
Euphorbia ampliphylla	Euphorbiaceae
Millettia ferruginea subsp. *ferruginea*	Fabaceae
Olea capensis subsp. *hochstetteri*	Oleaceae
Olea europaea subsp. *cuspidata*	Oleaceae
Prunus africana	Rosaceae
Schefflera abyssinica	Araliaceae
Smaller trees	
Bersama abyssinica subsp. *abyssinica*	Melianthaceae
Brucea antidysenterica	Simaroubaceae
Debregeasia saeneb	Urticaceae
Erica arborea	Ericaceae
Mimusops kummel	Sapotaceae
Phoenix reclinata	Arecaceae
Richtiea albersii	Capparaceae
Teclea nobilis	Rutaceae
Woody lianas	
Phytolacca dodecandra	Phytolaccaceae
Pterolobium stellatum	Caesalpiniaceae

Table 3. The most common woody and herbaceous plants of Muchila-Neznazit forest.

Taxon	Family
Prominent large trees	
Dombeya torrida subsp. *torrida*	Sterculiaceae
Hagenia abyssinca	Rosaceae
Myrica salicifolia	Myricaceae
Olea europaea subsp. *cuspidata*	Oleaceae
Schefflera abyssinica	Araliaceae
Smaller trees or shrubs	
Bersama abyssinica subsp. *abyssinica*	Melianthaceae
Carissa edulis	Apocynaceae
Clausena anisata	Rutaceae
Galiniera saxifraga	Rubiaceae
Myrsine africana	Myrsinaceae
Nuxia congesta	Loganiaceae
Osyris quadripartita	Santalaceae
Pittosporum virdiflorum	Pittosporaceae
Salix subserrata	Salicaceae
Lianas	
Pterolobium stellatum	Caesalpiniaceae
Asparagus africanus	Asparagaceae
Clematis simensis	Ranunculaceae
Rubus steudneri	Rosaceae
Stephania abyssinica	Menispermaceae
Herbs and pachycauls	
Epilobium stereophyllum	Onagaraceae
Eulophia streptopetala var. *streptopetala*	Orchidiaceae
Lobelia giberroa	Lobeliaceae
Pelargonium multibracteatum	Geraniaceae
Rubia cordifolia subsp. *conotricha*	Rubiaceae
Thalictrum rhychocarpum	Ranunculaceae
Epiphytes	
Peperomia abyssinica	Piperaceae

Table 4. The most common woody plants found in dry afromontane forest remnants.

Taxon	Family
Prominent large trees	
Euphorbia ampliphylla	Euphorbiaceae
Juniperus procera	Cupressaceae
Olea europaea subsp. *cuspidata*	Oleaceae
Smaller trees and shrubs	
Clerodendrum myricoides	Verbenaceae
Dodonaea angustifolia	Sapindaceae
Erica arborea	Ericaceae
Hypericum quartinianum	Guttiferae
Hypericum revolutum	Guttiferae
Myrsine africana	Myrsinaceae
Nuxia congesta	Loganiaceae
Osyris quadripartita	Santalaceae
Protea gaguedi	Proteaceae
Rosa abyssinica	Rosaceae

Table 5. Solitary, large trees found in farmland and cultivated fields.

Taxon	Family
Apodytes dimidiata var. *acutifolia*	Icacinaceae
Bersama abyssinica subsp. *abyssinica*	Melianthaceae
Ekebergia capensis	Meliaceae
Olea europaea subsp. *cuspidata*	Oleaceae
Prunus africana	Rosaceae
Schrebera alata	Oleaceae
Syzygium guineense	Myrtaceae

Table 6. Woody plants (trees, shrubs, and woody climbers) observed in the Lemalimo Forest (2600-2700 m).

Taxon	Family
Prominent large trees	
Apodytes dimidiata var. *acutifolia*	Icacinaceae
Dombeya torrida	Sterculiaceae
Myrica salicifolia	Myricaceae
Olea capensis subsp. *hochstetteri*	Oleaceae
Prunus africana	Rosaceae
Smaller trees, shrubs or lianas	
Bersama abyssinica subsp. *abyssinica*	Melianthaceae
Brucea antidysenterica	Simaroubaceae
Buddleja polystachya	Loganiaceae
Cassipourea malosana	Rhizophoraceae
Clausena anisata	Rutaceae
Croton macrostachyus	Euphorbiaceae
Debregeasia saeneb	Urticaceae
Discopodium penninervium	Solanaceae
Dovyalis abyssinica	Flacourtiaceae
Ekebergia capensis	Meliaceae
Erica arborea	Ericaceae
Galiniera saxifraga	Rubiaceae
Hypericum quartinianum	Guttiferae
Hypericum revolutum	Guttiferae
Jasminum abyssinicum	Oleaceae
Maesa lanceolata	Myrsinaceae
Maytenus arbutifolia	Celastraceae
Myrsine africana	Myrsinaceae
Nuxia congesta	Loganiaceae
Olea europaea subsp. *cuspidata*	Oleaceae
Osyris quadripartita	Santalaceae
Pavetta oliveriana	Rubiaceae
Phytolacca dodecandra	Phytolaccaceae
Pittosporum viridiflorum	Pittosporaceae
Protea gaguedi	Proteaceae
Psychotria orophila	Rubiaceae
Myrsine melanophloeos	Myrsinaceae
Rhus glutinosa subsp. *glutinosa*	Anacardiaceae
Rosa abyssinica	Rosaceae
Salix subserrata	Salicaceae
Schefflera abyssinica	Araliaceae
Urera hypselodendron	Urticaceae
Vernonia conyzoides	Asteraceae

Table 7. Common plants recorded on wet rocky cliffs at and below the spring (Wolkefit pass).

Taxon	Family
Bartsia kilimandscharica	Scrophulariaceae
Epilobium stenophyllum	Onagaraceae
Erica arborea	Ericaceae
Galium thunbergianum	Rubiaceae
Myrica salicifolia	Myricaceae
Primula verticillata subsp. *simensis*	Primulaceae
Swertia kilimandscharica	Gentianaceae
Wahlenbergia edulis	Campanulaceae

Fire regimes, floristics, diversity, life forms and biomass in wooded grassland, woodland and dry forest at Gambella, western Ethiopia

Michael Jensen & Ib Friis

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The Gambella Region contains examples of most Sudanian vegetation types found in Ethiopia. Five sites up to 85 km from Gambella town and subject to different fire regimes in wooded grassland, deciduous woodland and dry forest were investigated with regard to the floristic composition, diversity, life forms and biomass of the vascular plants. Exact quantification of the fire pressure is difficult, but it seems likely that fires occur at least once a year in nearly all vegetation, dry forest excepted. Severe fires are found to be associated with low plant diversity. A total of 50 plant families, 94 genera and 135 species were observed in the studied sites (14000 m^2); families represented with more than 2 species are Gramineae (Poaceae), Fabaceae (Papilionaceae), Acanthaceae, Combretaceae, Tiliaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Rubiaceae, Verbenaceae, Vitaceae, Capparaceae, Malvaceae, Mimosaceae, Asteraceae, and Rhamnaceae. The life form spectra of woodlands and wooded grasslands have high frequencies of phanerophytes, hemicryptophytes and geophytes; the frequency of hemicryptophytes, geophytes and therophytes seems to increase with decreasing severity of burning, but low frequencies of all life forms except phanerophytes are found in dry forest. The biomass of the tree and shrub strata seems to be inversely related to the severity of the burning, which is positively correlated with the grass biomass. Size class studies show that large-size trees are almost entirely absent from the most severely burnt sites. Differences in soil conditions, apart from the marked distinction between vertisols and ferralsols, do not seem to play a major role in the determination of the vegetation types. Total protection from fire seems to lead to the development of dry forest and shading out of almost all the grasses, and most of the herbs are replaced with a low number of shade tolerant forest species.

Michael Jensen, Botanical Institute, Dept. of Plant Ecology, Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark. E-mail: micjen@vip.cybercity.dk

Ib Friis, Botanical Museum and Library, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark. E-mail: Ibf@bot.ku.dk

Introduction

This paper is part of a series dealing with studies of fire susceptible ecosystems across Africa from Senegal to Ethiopia. The field and laboratory work behind these papers has been carried out during 1996-1999. The project was part of a collaborative research programme involving scientists at a number of institutes at the Faculty of Science, University of Copenhagen (the Geographical Institute, the Botanical Institute, the

Botanical Museum and Library, the Institute of Molecular Biology, and the Zoological Institute), biologists and geographers at the Centre de Suivi Écologique (CSE), Dakar, Senegal, the University of Ouagadougu, Burkina Faso, the University of Ghana, Legon, Ghana, and the Addis Ababa University, Ethiopia. This collaborative programme, called FITES (Fire in Tropical Ecosystems) has been supported by a joint grant for all the groups from the Danish Council for Development Research. The present paper reports on our studies of fire susceptible vegetation in the western Ethiopian lowlands, and the results are seen in a wider African context wherever available material for comparison makes this possible. Other related papers deal with the soil seed bank and above-ground cover of a dominant grass, *Hyparrhenia confinis*, in the area (Menassie Gashaw & Michelsen 2001), and with the effects of experimental fire on plant, soil and microbial biomass and nutrient pools (Jensen *et al.* 2001).

Wooded grasslands, woodlands and forests in the Sudanian Region: definitions

The study sites, situated between 10 and 85 km from Gambella town in the western Ethiopian lowlands fall within the eastern part of the Sudanian phytogeographical region, and the vegetation can be referred to as dry forest, woodland, wooded grassland and various kinds of thicket (White 1983: 102-109). These vegetation types experience pronounced drought for more than three months in each year. In reviews, Menaut (1983) and Menaut *et al.* (1995) have distinguished three principal vegetation types within the Sudanian and Zambezian regions: (1) savanna (in the present paper termed wooded grassland in agreement with White 1983), which has a very open canopy of scattered trees (<70% canopy cover) and large biomass in the stratum of suffrutices, herbs and grasses, enough to allow annual burning during the dry season; (2) woodland, which has an upper stratum of small or medium sized deciduous trees with a relatively species-poor canopy that covers 70-90% of a sparse woody understorey, a ground cover of grasses, herbs and suffrutescent plants in sufficient density to allow for annual burning; and (3) dry forest, which has a closed or almost closed canopy (cover 90-100%) with several woody strata of more numerous deciduous species and a weak, discontinuous and species-poor grass- and herb-stratum only allowing accidental and rare fires. The trees of the upper stratum of the dry forest proper are typically deciduous (although a facies with predominantly evergreen trees has also been described from other parts of lowland Africa by Menaut (1983)), while the lower woody strata may contain a mixture of evergreen and deciduous species. The canopy of the dry forest proper is often devoid of the dominant canopy species of the woodlands, and the species of the upper and the lower strata of dry forest are often different.

Menaut *et al.* (1995) do not discuss in detail savanna-like vegetation types with very low percentage of canopy cover (savanna grasslands), or types dominated by shrubs (thickets), but such vegetation types almost devoid of trees are described from parts of lowland Africa in Menaut's review of African savannas (Menaut 1983). They exist as edaphic vegetation types in the lowlands, and are also prominent in Afromontane vegetation (White 1983). However, our studies in the Gambella Region do not include these vegetation types, and in the following account we will therefore apply the combined definitions of Menaut *et al.* (1995) and White (1983) for the three terms of the vegetation we have studied: wooded grassland, woodland and dry forest.

Previous descriptions of vegetation types in the western Ethiopian lowlands

On the vegetation map of Ethiopia by Pichi-Sermolli (1957) the vegetation of western

Ethiopia on and below the western escarpment of the Ethiopian highlands consists of "deciduous woodland," with a mosaic of patches of "bamboo thicket (*Oxytenanthera*)" scattered in the woodland. The areas in the lowlands north and south of the Gambella Region are characterised as "savanna (various types)," while approximately the whole of the Gambella Region is referred to as "xerophilous open woodland." According to Pichi-Sermolli, the latter is a vegetation type with its main distribution on the eastern side of the Ethiopian highlands, where it refers to a fairly dense type of *Acacia-Commiphora* bushland, especially in Sidamo, Bale, Harar, Somalia and eastern Kenya. In Breitenbach's elaborate system of Ethiopian vegetation types (Breitenbach 1963), discussed by Friis *et al.* (1982) and Friis & Sebsebe Demissew (2001), the dominant vegetation in the western part of the Ethiopian highlands is referred to as "Lowland-Woodlands"; in the western lowlands north of the town of Asosa (Gonder and Gojam regions) and south-west of the town of Maji (Kefa region) as "Lowland-Savannahs", while in western Welega, Ilubabor (incl. the Gambella Region), and in western Kefa south west of Maji, as "Lowland Steppe." We do not find that either of these two systems described the Gambella vegetation adequately.

Friis *et al.* (1982) followed the system for descriptive classification of African vegetation by Greenway (1973) when they referred to the vegetation of the western Ethiopian escarpment and the deep river valleys in Kefa and Ilubabor as "deciduous woodland," a characterisation also used by White (1983), although the trees in some of these sites are rather widely spaced in relation to the strict definition of woodland. Some of White's vegetation types are grasslands, which occupy only very small and marginal areas along the border with the Sudan, such as his no. 61, "Edaphic grasslands in the Upper Nile basin", or his no. 62, "Edaphic grassland mosaics with *Acacia* wooded grassland", and his no. 64, "Edaphic grassland mosaics with semi-aquatic vegetation." The western escarpments and lowlands of Ethiopia on White's vegetation map are referred to as a fairly uniform 100-200 km broad zone of (no. 29a) "Undifferentiated woodland (Ethiopian type)" which borders almost the whole of the western Ethiopian escarpment from Eritrea in the north to the Boma Plateau south west of the town of Maji, penetrating into the highlands along the major rivers. This zone is widest in the Gambella Region. The westernmost part of the Gambella Region is considered a transition zone indicated as White's no. 35b "Transition from undifferentiated woodland to *Acacia* deciduous bushland (Ethiopian type)". The "Undifferentiated woodland (Ethiopian type)" contains according to the descriptive memoir (White 1983: 107) *Anogeissus leiocarpus, Balanites aegyptiaca, Boswellia papyrifera, Combretum collinum, C. hartmannianum, Commiphora africana, Dalbergia melanoxylon, Erythrina abyssinica, Gardenia ternifolia (lutea), Lannea schimperi, Lonchocarpus laxiflorus, Piliostigma thonningii, Stereospermum kunthianum* and *Terminalia brownii*. A note (White 1983: 62) describes the "Transition from undifferentiated woodland to *Acacia* deciduous bushland (Ethiopian type)" as "transition from the edaphic grasslands of the Flood Region of the Nile to the *Anogeissus-Combretum hartmannianum* woodland flanking the Ethiopian Highlands to the east. *Acacia seyal* and *Balanites aegyptiaca* occur throughout except for patches of thornless woodland dominated by *Combretum hartmannianum, Sterculia setigera, Stereospermum kunthianum* and *Adansonia digitata*." The few marginal vegetation types (White's no. 61, 62 & 64) mentioned above are in Ethiopia, as far as we have been able to see, basically only localised vegetation patches, not extensive habitats. But it is quite possible that more extensive areas with such grassland or mosaics

exist further away from Gambella town towards the Nile plains.

Sebsebe Demissew *et al.* (1996) has published a vegetation map of Ethiopia and Eritrea on a small scale. This map attempts to show formations, of which 8 are recognised on the map and described in the text (see Friis & Sebsebe Demissew 2001). The map shows a zone of *Combretum-Terminalia* deciduous woodland throughout the western Ethiopian escarpments and lowlands from approximately the Boma Plateau in the south through the Gambella Region to the western escarpment of Eritrea in the north. Sebsebe Demissew *et al.* (1996) also mentions the dense semi-deciduous lowland forest south of Gambella town, particularly between Abobo and Gog, and refers to the description by Friis (1992).

The broad outline of White's and Sebsebe Demissew *et al.*'s characterisations of the Ilubabor lowland agree well with observations from field trips to areas near the Ethiopia-Sudan border, partly undertaken with Sally Bidgood, Royal Botanic Gardens, Kew, Menassie Gashaw and staff members from the Ethiopian National Herbarium of Addis Ababa from 1973 and onwards. These trips went to the Humera area (northwestern Gonder), the Galabat-Matemma area (western Gonder), the Guba region (western Gojam), the Asosa-Kurmuk-Gizen area (western Welega), and the Dima area (southwestern Kefa), and the Gambella area (western Ilubabor). Indeed, these observations form a small part of the background material for both White's and Edward's maps and descriptions, as appears from acknowledgements in the two works.

Own observations on vegetation in western Ethiopian sites

According to the observations made on these field trips, a mosaic of various types of evergreen and deciduous forest, riverine forest, deciduous woodland, wooded grassland and grassland covers the western lowlands of Ethiopia. These vegetation types, especially the deciduous woodlands and wooded grasslands, penetrate deeply into the Ethiopian highlands along the deep river gorges. The physiognomy of the vegetation and the floristic composition vary considerably within the lowlands, but patches of vegetation which are floristically very similar can be found on comparable sites throughout the area from the border with Eritrea to the Boma Plateau south west of the town of Maji in south western Kefa. The variation seems to be caused by differences in altitude, local edaphic variation, drainage conditions and fire regimes, rather than a south-north gradient, which runs parallel with increasing latitude, as in West Africa. A complex study of wooded grasslands on rocky slopes and adjacent lowlands in Sudanian vegetation in Northern Nigeria was carried out by Ramsay & de Leeuw (1964, 1965a, 1965b). They found *Combretum*-dominated woodland and wooded grassland on basaltic rocky slopes, together with the following species also found in our area: *Acacia hockii*, *Annona senegalensis*, *Balanites aegyptiaca*, *Crossopteryx febrifuga*, *Zizyphus mauritiana*, *Terminalia laxiflora*, *Anogeissus leiocarpus*, *Maytenus senegalensis*, *Stereospermum kunthianum*, and *Entada africana*. In some cases vicariant species were found in Nigeria and Ethiopia, *e.g. Boswellia dalzielii* (*B. papyrifera* further to the north on the western Ethiopian escarpment, but not in our site), and *Sterculia setigera* (*S. africana* in our site, but *S. setigera* also occurs on the western Ethiopian escarpment). Furthermore, the following species were both found in the Nigerian plots and occur on the western Ethiopian escarpment, but were not found in our sites: *Securidaca longipedunculata*, *Sclerocaria birrea*, and *Pseudocedrela kotschyi*. *Afzelia africana* was found in the Nigerian plots and occurs in southern Sudan, but is not known from Ethiopia. On the alluvia clays and sands, Ramsay & de Leeuw (*l.c.*) found the fol-

lowing species also found in our sites: *Acacia senegal, Annona senegalensis, Anogeissus leiocarpus, Balanites aegyptiaca, Combretum molle, Crossopteryx febrifuga, Grewia mollis, Lonchocarpus laxiflora, Terminalia laxiflora,* and *Zizyphus mauritiana.* Thus, there is great floristic and ecological similarity between the two study areas.

The chief variation in the vegetation of the western Ethiopian lowland is between rocky sites, sites with sandy soils, and sites with impeded drainage and dark vertisols. These major types are covered in the analyses from the Gambella Region in the parts of this paper termed "Description of the five study sites ..." and "Analysis of vegetation data."

There seems to be no striking difference between regularly burned woodland on basaltic rocks and regularly burnt woodland on rocks formed by the basement complex. Dominant in these woodlands are all the trees mentioned above by White (1983: 107) as characteristic of the "Undifferentiated woodland (Ethiopian type):" Open *Balanites aegyptiaca* or *Acacia seyal* wooded grassland is characteristic of large areas in the lowlands along the Barka River (western Eritrea) and in the northern part of the lowlands around the Anghrib River (western Gonder), both areas with seasonal water-logging and the development of vertisols. In Uganda and eastern Sudan such woodlands are typically found in seasonally waterlogged sites (White 1983). Throughout Africa, seasonal waterlogging tends to reduce tree growth and promote the development of grasslands (Michelmore 1939). The Baro Lowlands, which cover the whole of the Gambella Region, carry a mosaic of broad-leaved Sudanian woodlands and wooded grassland with *Terminalia spp.*, local patches of dry semi-evergreen or deciduous forest, and along the rivers narrow bands or patches of riverine forest, riparian scrub and areas of seasonally flooded grassland which locally may be treeless. Thus, a classification of the western Ethiopian lowlands in the broad categories (29b and 35b) of White (1983), leaving no. 61, 62 and 64 as local variants not shown on the vegetation maps, as Sebsebe Demissew *et al.* (1996) has done, seems to agree best with our observations.

The area around Gambella town studied in more detail in this paper was chosen because it contains a large mosaic of the most extensive examples of fire-prone woodlands and wooded grasslands in western Ethiopia. It is, according to our surveys, typical of comparable lowland vegetation from the Eritrean border to the Boma Plateau south west of the town of Maji, that is the whole of the Ethiopian lowlands within the Sudanian phytogeographical region.

Fire as an ecological factor

For thousands of years, fire has been an important factor in vegetation development in many dry tropical areas, including the Sudanian vegetation zone of Africa. Natural fires have probably always existed. It is likely that natural phenomena like lightning and volcanic activity were the cause of fires in the past, and the general fire frequency was probably considerably lower than now. Lock (1998) has assumed that "... it seems a reasonable hypothesis that the frequency of fire increased when man first began to use fire in Africa (probably 1.0-1.5 Myr BP ...), again when fire could be made, and yet again with the introduction of the safety match." It has been shown that the African wooded grassland flora has characteristic adaptations to burning, for example that awned grass propagules like those of *Themeda triandra*, capable of burying themselves in the soil and hence perhaps an adaptation to grass fires, are a distinctive feature of African grasslands and wooded grasslands (Lock & Milburn 1971). In fact, it can be demonstrated that the frequency of awned species of grasses in the African grassland is higher than in the grassland flora of South America (Lock 1998). It is tempting to

see the effect of increased fire frequency during the evolution of the African grasslands and wooded grasslands in such trends, but much more work is of course still needed to illustrate the fire adaptation in the African savanna flora. Today increasing population pressure and human activity are no doubt the main reasons why fires have become much more frequent, often being an annual occurrence in many places.

Also in the wooded grasslands and woodlands of south-western Ethiopia there has apparently been a general trend towards more frequent fires, presumably causing a more open canopy in the woody vegetation and a more lush ground cover, but this information is only obtained from local informants and our personal general observations and judgement of the development of the area. There are no exact records of fire frequency and extent available, even from recent years. In the years from 1996 to 1999 when this project has been in operation, the tall grass was burnt annually at all study sites situated around the regional capital Gambella, except the dry forest inside the Airport area. However, it was not always 100% of the surface that was burnt in a single fire. According to observations from residents as well as researchers visiting the area on earlier occasions, this pattern has probably been in existence for some time before the beginning of the study period. The following analysis will attempt to point out the effect of fire as one of several factors causing the variation between the sites selected for study in different habitats around Gambella town.

Study sites and methods

Five sites were selected for detailed study in the Gambella Region (Fig. 1). The sites were selected in such a way that they sampled a cline from almost closed dry lowland forests with fine loamy soil through vegetation on the floodplains near the Alwero and Baro Rivers with a mosaic of finer and coarser loams to open woodland on flat ground far away from the western Ethiopian escarpment with dark brown vertisols to a somewhat sloping woodlands near the western Ethiopian escarpment with a very stony fine loam. The observations of the sites were carried out from October 1996 until December 1998.

The location of the sites was determined with a GARMIN 45 GPS navigator. At each of the five different sites (situated 10 to 85 km from Gambella town), which we believed to have differing severity of fire, 3 replicate plots were established, except at site X where it was only possible to establish two replicates. This location, situated within the area of the local airport, was used as control site for a number of other studies mentioned in the introduction to this paper, since this area was found to the only one that had enjoyed some protection from fire. This protection was estimated to have lasted for at least 10 years and probably much longer, as suggested by $^{13}C/^{12}C$ measurements, because C-3- (mainly trees) and C-4-plants (mainly grasses) discriminate differently against these two isotopes during carbon assimilation. The analysis is further described by Michelsen, Friis, Jensen & Andersson (in prep.). The other 4 sites were judged from a number of subjective indicators (fire scars on trees, charcoal remains, etc.) to suffer increasing fire severity in terms of intensity and/or frequency in the following order: B, A, D and C. Each plot measured 20 by 50 meters. In each plot, all trees and shrubs were identified, mapped and DBH and stem and total height were measured. All grasses and herbs were identified either in the field or collected as voucher specimens and subsequently identified at the National Herbarium in Addis Ababa or at the Royal Botanic Gardens at Kew, England. Plant collection was carried out continuously over the three fire seasons covered by the

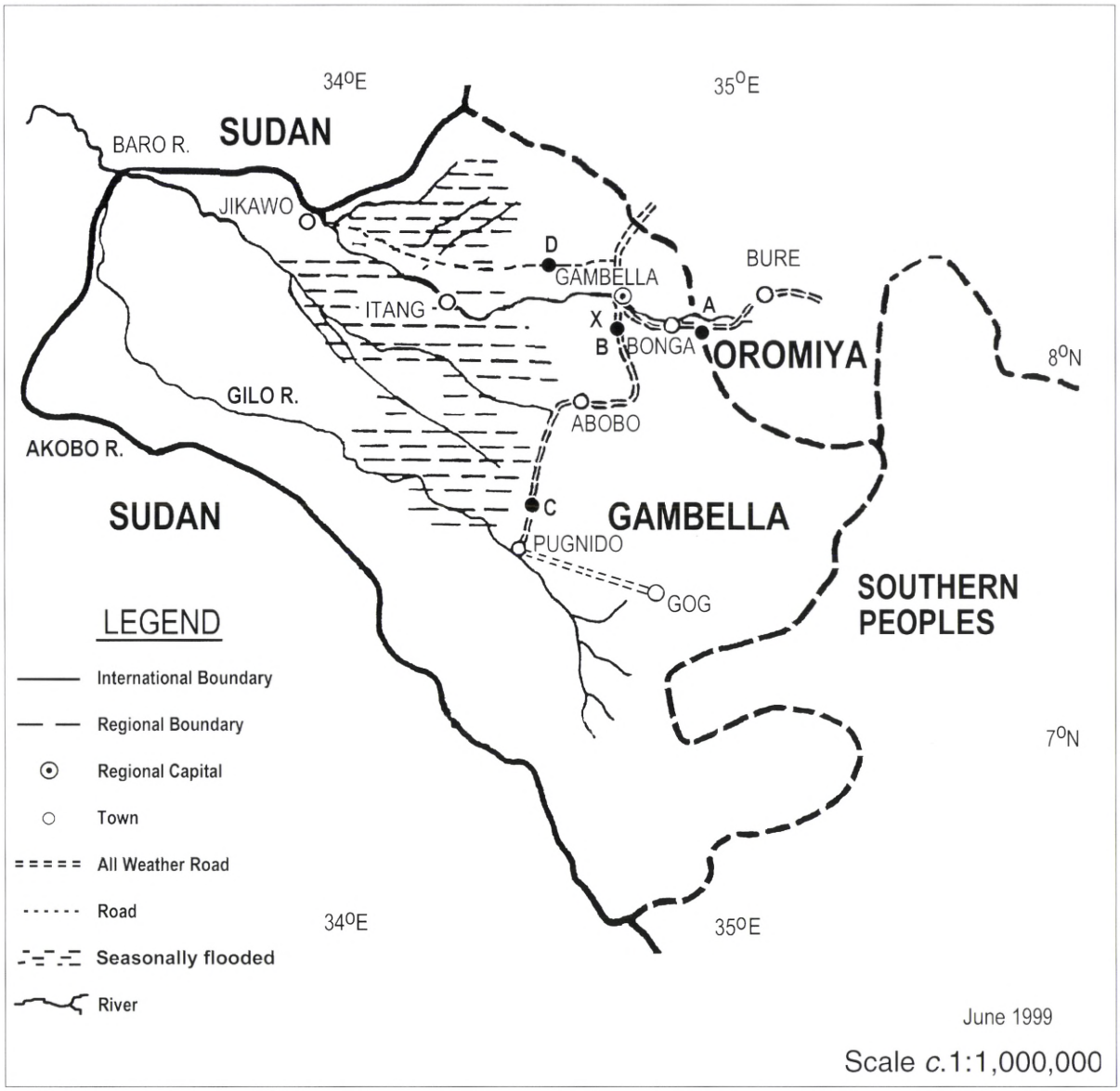


Fig. 1. Map of the Gambella Region. The region borders to the Sudan (west), the Oromiya Region (north-east) and the Southern Nation, Nationalities and Peoples' Region (south east). Redrawn and modified from Solomon Tilahun et al. (eds.), Ethiopian Wildlife and Natural History Society: Important Bird Areas of Ethiopia. A first inventory. Addis Ababa. (1996).

project, and at different times of year, since there was a number of species only occurring during distinct seasons, especially among the geophytes and therophytes.

At the end of the wet season, tree canopy cover was estimated and at the same time plus in the dry season as well as at the beginning of the rainy season, the grass and broad-leaved

herb cover was estimated. In both cases a method of pinpointing with a long stick along 4 lines in the plot was used. The lines and 100 points were applied in a "stratified random" manner. If plants touched the stick when this was put down vertically in the vegetation, this was recorded as one hit. Multiple hits were not recorded. Canopy cover was estimated by recording whether the vertical projection of the stick hit the canopy above. Initial testing of this modified standard method gave very good replicability with variations as low as 1-2%.

Grass and herb biomass was sampled in November 1997 at the end of the rainy season at peak biomass. In each plot 8 randomly located squares measuring 1 x 1 m were harvested, and biomass divided into grasses and broad-leaved herbs. All herb biomass was kept, and the grass biomass harvested was weighed in the field. After finely cutting and mixing of the grass biomass 5 subsamples were taken, weighed and pooled into one. Samples were then air- and sun-dried in the field and later in the oven at 80° C, and the dry weight determined. From these findings, the original total dry weight of the grass samples could be calculated.

Processed satellite data on fire densities were obtained from the archive files of the Global Vegetation Monitoring Unit's FIRE project at Space Application Institute, Ispra. Input data came from AVHRR-sensors on-board the NOAA-11 polar orbiting satellite. This satellite performs 14 complete orbits per day, and maps the entire globe in five visible and infrared bands at a resolution of about 1.1 km at nadir. Data was collected and archived, and image segments from different receiving stations are "stitched" together to produce 14 separate images per day. The fire detection took place during a total of 21 months from April 1992 to December 1993. The product files were produced with the application of a contextual algorithm used for the fire detection, because such an algorithm can be applied to a global data set without having to be adjusted for different geographical regions. The algorithm chosen is based on work by Prins & Menzel (1992) and Flasse & Ceccato (1996), as reported in Justice & Dowty (1993). The product gives a global picture of vegetation fire densities at a relative scale. The fire data set from Ispra was interpreted in the GIS-programmes ARC-Info and ARC-view at the Institute of Geography, University of Copenhagen.

Data on temperature and rainfall in the study area was obtained from the Ethiopian National Meteorological Institute in Addis Ababa.

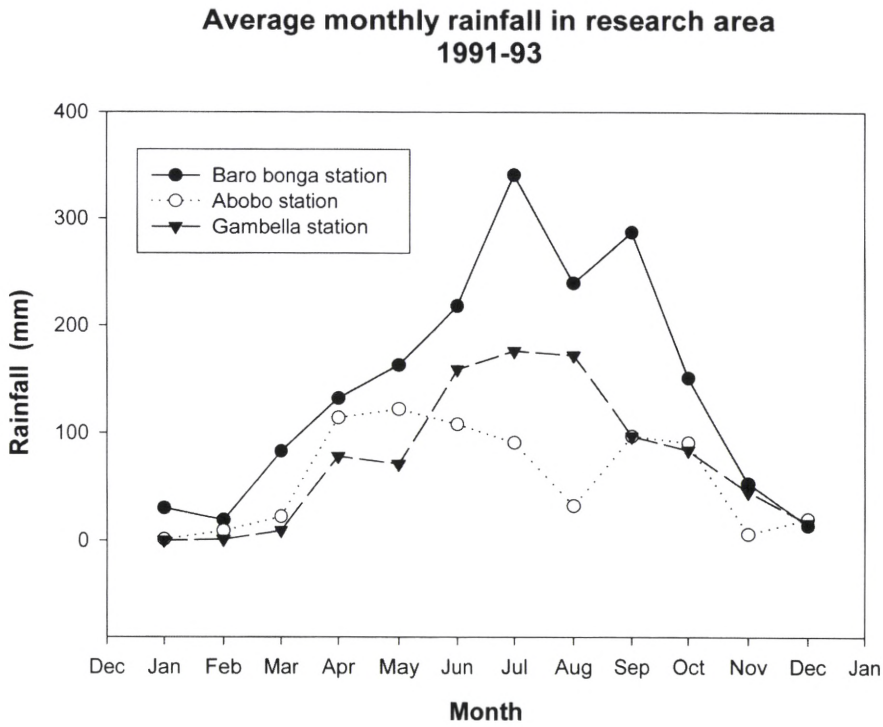
The nomenclature and classification of genera and species follow as far as possible the published volumes of the *Flora of Ethiopia and Eritrea* (Edwards & Hedberg 1989; Edwards, Mesfin Tadesse & Hedberg 1995; Hedberg & Edwards 1995; Edwards, Sebsebe Demissew & Hedberg 1997).

Description of the five study sites: climate, soil and fire

This section of the paper presents an overview of the general observations we have made in the study area, including both our own data and data on climate and fire obtained from elsewhere and analysed here. It also presents descriptions and some general observations on each of the five study sites.

Climate

The altitude of the study area varies between 550 and 650 m a.s.l. It receives an approximate average of 1100 mm rain annually, concentrated in the main rainy season from late May to October, but the variation between sites is considerable (see below). The average monthly rainfall at Gambella town (between site B and X and site D), at Abobo (between site B and site C) and at Baro Bonga (near site A) during the years 1991-1993 is shown in Fig.



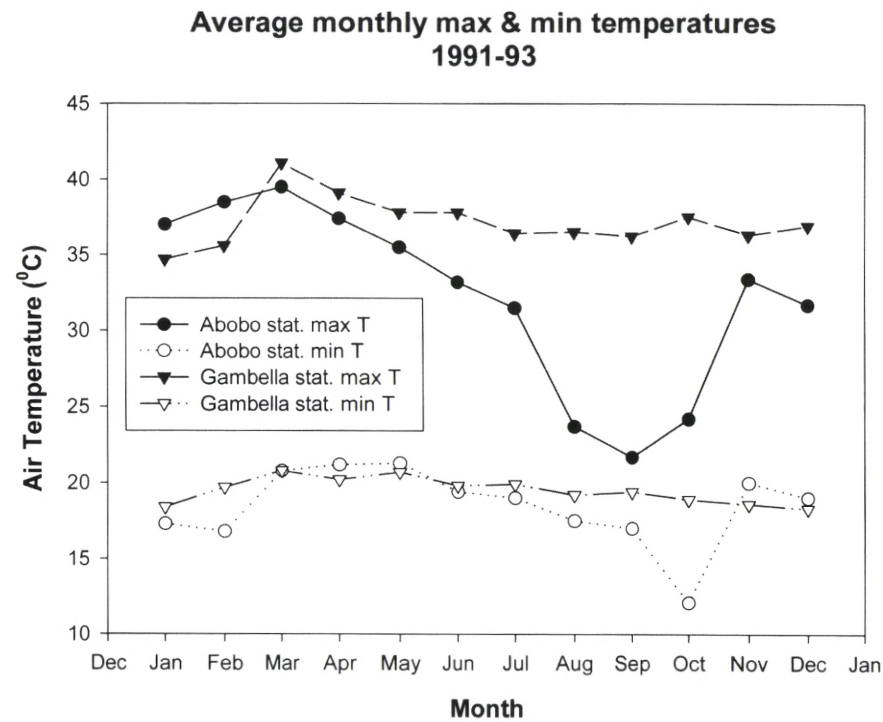


Fig. 2. Annual monthly rainfall and maximum and minimum temperatures in the research area 1991-1993. The diagram is based on results from the Ethiopian Meteorological Office in Addis Ababa. Data from the period of our studies was not available.

2, which also demonstrates the considerable variation between the sites. The lowest annual rainfall is recorded at Abobo with approximately 700 mm. The rainfall here shows a tendency to be bimodal, with the highest rainfall in April-June and in September-October. The dry season lasts approximately for 5 months, from November to March. This rainfall distribution is reminiscent of the bimodal rainfall of southern Ethiopia within the Somalia-Masai region (Ethiopian Mapping Agency 1988, map 16). The Gambella station has an annual rainfall of approximately 900 mm. The rainfall is unimodal, with early rain in April and May, high rainfall in June to August, and late rain in September-October. The dry season lasts approximately 5 months, from November to March. By far the highest rainfall is found at Baro Bonga at the foot of the southwestern escarpment of the Ethiopian highlands, with an average annual rainfall of 1730 mm. The rain starts in March-April, reaches its highest values in July-September, and is low again from November. The dry season is therefore approximately 4 months, from November to February. The high rainfall here agrees well with the rainfall higher on the western escarpment, where the highest rainfall in Ethiopia, raising to figures between 2400 and 2600 mm/year, is found in the zone from Gore to Gecha and Mezan Tefari (Ethiopian Mapping Agency 1981, map 21). The latter area at the top of the escarpment also has a different rainfall distribution, with rain in nearly all months of the year.

Observations of monthly minimum and maximum temperatures from the same period exist only from the stations at Gambella town and Abobo, also shown in Fig. 2. The recordings from the Gambella station are very constant throughout the year. The average annual maximum is 37° C, and the average monthly figures vary between 35° and 40° C. The average annual minimum is 19° C, and the average monthly figures vary between 18° and 21° C. At Abobo the average annual maximum is 32° C, but there is a very notable drop in the average monthly maximum during August, September and October, where the average maximum is below 25° C. The average annual minimum is 18° C, but also here there is a seasonal drop which reach down to 12° C in October.

Geology and soils

The soils are ultimately derived from parental material in the highlands to the east, or from underlying rocks. The tertiary volcanic rocks are restricted to the highlands east of Bure. The western escarpment of the highlands consists of Precambrian granitoids (the basement complex). These rocks can be seen as outcrops (inselbergs) in the lowlands as far west as Gambella town, or even a few isolated hills between Gambella town and Itang (Ethiopian Mapping Agency 1981, Map 6 & 1988, Map 7; personal observations). At altitudes below the escarpment and the inselbergs, the surface geology is indicated as Quaternary or Pleistocene sediments on all the geological maps we have consulted.

The published soil maps of Ethiopia indicate the soil types near the western escarpment in different ways. According to Ethiopian Mapping Agency (1981, Map 13) the soils in the Baro Valley as far as Gambella town are humic cambisols (including site A), while the soils of the plains to the west and south-west are chromic vertisols (including site B, C, D and X). Also according to the Ethiopian Mapping Agency (1988, Map 8) the soils of the sites B, C, D and X are vertisols, while the soil of site A is an orthic acrisol. We think that this part of the map may be overly simplified, and based on our field observations of soil profiles combined with the chemical analysis recorded in Table 1 we characterise the sites X, A, B and C as more or less similar weathered ferralsols, while the soils of the plains at site D are in fact a vertisol.

Table 1. The soil profile characteristics of the 5 study sites (SOM: soil organic matter)

	X	**B**	**A**	**C**	**D**
Classification (FAO/UNESCO)	Ferralsol. Surface brown, deeper strata yellowish brown to red	Ferralsol. Brown red to yellow	Ferralsol. Brown to yellowish red	Ferralsol. Yellowish brown	Vertisol. Dark brown to reddish brown
Texture group	Fine/coarse loamy	Fine/coarse loamy	Fine loamy (stony)	Coarse loamy	Fine clayey
Density (g/cm^3)	–				
Top		1.42	1.38	1.56	1.34
Medium		1.56	1.56	1.65	1.74
Deep		1.66	1.69	1.58	1.74
pH (H_2O)					
Top	7.0	6.5 ±0.4	6.9 ±0.2	6.8 ±0.3	7.0 ±0.5
SOM (%)					
Top	5.1	3.5 ±0.8	6.2 ±0.9	2.7 ±0.3	16.5 ±0.9
Medium	1.9 ±0.11	1.8	5.8	3.1	16.0
Deep	2.4 ±0.07	2.5	5.4	5.2	15.3
Carbon (%)	–	1.3 ±0.4	1.9 ±0.5	0.9 ±0.2	4.6 ±0.9
Total N (%)					
Top	0.16	0.11	0.16	0.04	0.20
Medium		0.02	0.05	0.02	0.05
Deep		0.02	0.03	0.03	0.06
Total P (%)	0.02	0.01	0.01	0.09	0.09

The latter has the characteristic dark colour of vertisols and is shrinking and cracking during the dry season, as well as being relatively more fertile than the soils at the remaining sites. All the ferralsols are rather sandy, poor in nutrients, and neutral to weakly acid. The soil at site A does not have the very acid reaction characteristic of acrisols. The total nitrogen varies from 0.04% in site C up to 0.2% in the vertisol in site D, and the phosphorus varies from 0.01% in site A and B up to 0.09% in site C and D shortly after fires. The latter two sites are those assumed to have the most severe fires, and the higher P-values here are derived from the ash input, and are seasonal (Jensen, Michelsen & Menassie, in prep.). These N- and P-figures are comparable to those indicated from Zambian woodlands (Trapnell *et al.* 1976). The soil organic matter (SOM) contents varies from 2.7% in the poorest ferralsol in site C to 16.5% in the vertisol of site D. The high organic content here is probably due to the periodic flooding inhibiting decomposition. The annual variation in the soil nutrients is dealt with in further detail by Jensen *et al.* (2001). The field experiments in the area have shown that fire plays a major role in redistributing nutrients between standing dead biomass, soil, soil microbes and plants emerging after fire (Jensen *et al.* 2001).

Fire

In the beginning of the dry season, most of the grass biomass in the vegetation around Gambella town is burned by the local population in a non-systematic way in order to gain access to

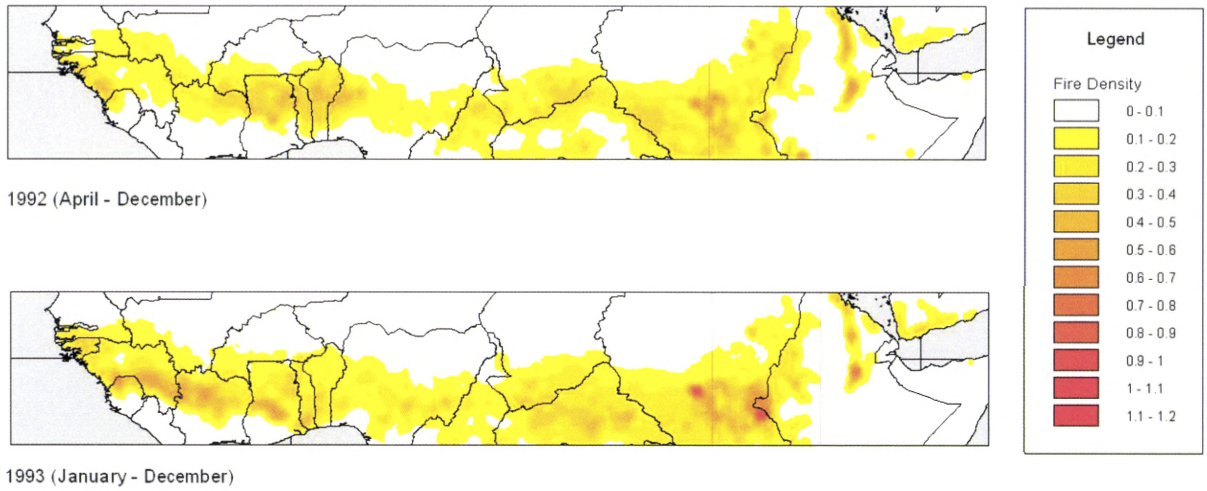


Fig. 3. Fire density across Africa in April-December 1992 and January-December 1993. Fires have been recorded within an area 50 km across; the scores have been marked on the map with a grid size of 0.1 degree. Based on data from the archive files of the Global Vegetation Monitoring Unit's FIRE project at Space Application Institute, Ispra. Produced by Thomas Theis Nielsen, Institute of Geography, University of Copenhagen, under the FITES project. The density scale is relative, and not necessarily comparable between the subsets of data represented in Fig. 3-6.

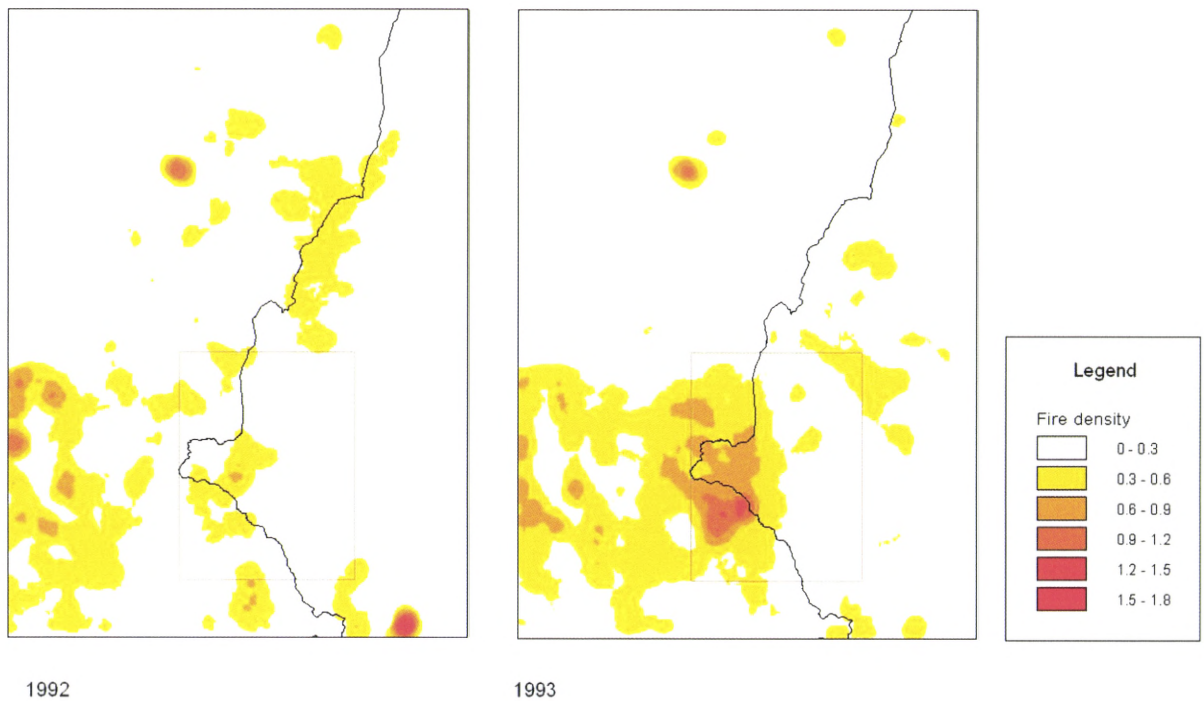


Fig. 4. Fire density of western Ethiopia in April-December 1992 and January-December 1993. Fires have been recorded within an area 25 km across; the scores have been marked on the map with a grid size of 0.01 degree. (Source etc. as for Fig. 3).

the woodland for hunting and for honey and firewood collection. Burning, which can be induced for a wide range of reasons, is done right across Africa from the Atlantic coast to Ethiopia; Fig. 3 shows that the density of fires in various areas in the fire zone across Africa may change somewhat from year to year, but generally the continental pattern is very constant, and the extent of this pattern agrees well with the Sudanian region of White (1983), especially when allowance is made for some overlap with the transition zone between the Guineo-Congolian and the Sudanian regions. This is the zone where the grass biomass is large enough and dries out well enough to produce fierce fires. Fig. 3 also demonstrates that the whole of the western lowlands of Ethiopia have fire densities comparable to the general situation across Africa, and that the areas with intense fires agree with the areas referred to the vegetation types no. 29b and 35b of White (1983), but that the highest densities in Western Ethiopia are found in the Gambella Region. Fig. 4 shows that there is high fire density in the Gambella Region in both the observed years, whereas in the lowlands to the north in the Oromia and Beni-Shangul Regions densities are lower, and it is not necessarily the same areas which burn every year. Fig. 5 has zoomed in on the Gambella Region with increasing resolution of the recording of fire density. Even within the Gambella Region, there seems to be marked variation in distribution and density of fires, although areas along major roads and around towns seem to burn annually. This is particularly notable from the figure to the left, showing the fires recorded from April to December, 1992, in a pattern that is strikingly similar to the location of roads and towns shown on Fig. 1.

Fig. 6 shows the yearly variation in fire density from April 1992 to December 1993. There are already fires in December, both in the Gambella Region and in the deep river valleys of the adjacent Ethiopian Highlands. The number and density of fires increase during January, February, March and April, whereas the density of fires in May is probably highly dependent on the onset of the rainy season. From July to October, no fires in the Gambella Region have been detected in the data shown in Fig. 6. Also in this illustration of the yearly variation, we can note that fires are most frequent along major transport routes, stressing the anthropogenic nature of most fires. In March and April fires seem to be most frequent along the rivers, probably reflecting a high frequency of people travelling by river in those months.

Description of edaphic conditions and vegetation of the sites

Dry forest: Site X

The densest and most developed vegetation was studied in site X, used as a control site with no signs of recent burning, and located inside the fence surrounding the Gambella Airport (*c.* 8° 08' N, 34° 34' E; *c.* 600 m altitude). The two replica plots were established about 500 m apart. The vegetation formed a dense woody cover with an almost continuous canopy covering 92% or more. The site had, at least according to local verbal reports from the airport staff, not been burnt recently, and it did not burn during the three years of the study; there was rotten wood on the forest floor, and no signs of charcoal or ashes were found during our studies. The soil type was a fine to coarse loamy, brown or yellowish brown to red ferralsol. The highest trees in the canopy were 20-25 m high, with one or two tree strata below and a fairly dense shrub stratum. The canopy contained *Anogeissus leiocarpus*, *Diospyros mespiliformis*, *Tamarindus indica*, and *Vangueria apiculata*. *Allophylus rubifolius*, *Erythroxylum fischeri*, *Maerua triphylla*, *Meyna tetraphylla*, and *Zizyphus*

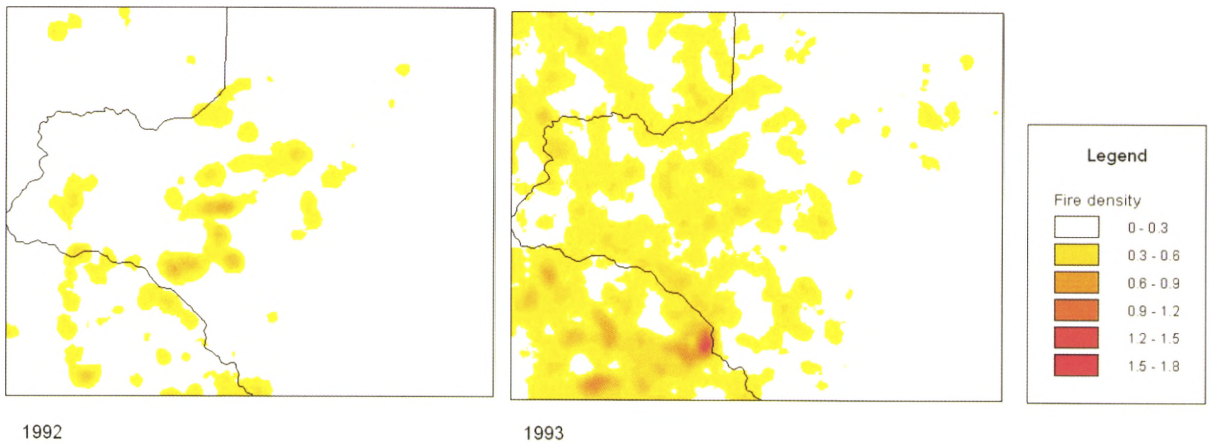


Fig. 5. Fire density of Gambella Region in April-December 1992 and January-December 1993. Fires have been recorded within an area 5 km across; the scores have been marked on the map with a grid size of 0.0025 degree. (Source etc. as for Fig. 3). For position of roads and rivers, compare with Fig. 1.

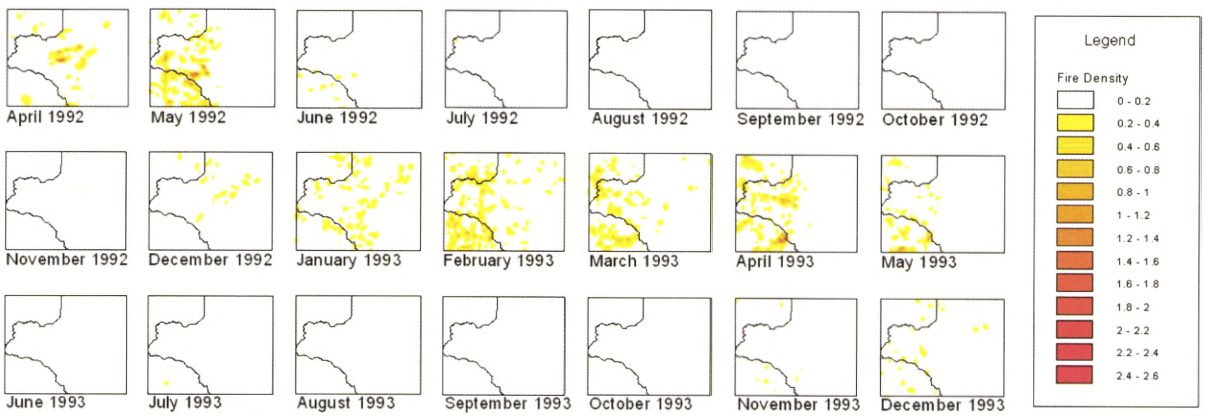


Fig. 6. Monthly fire density of Gambella Region from April 1992 to December 1993. (Source *etc.* Fig. 3). For position of roads and rivers, compare with Fig. 1.

pubescens occurred in the lower strata. Common shrubs were *Flueggea virosa* and *Harrisonia abyssinica*. Climbers were fairly prominent: *Abrus precatorius*, *Ampelocissus schimperianus*, *Periploca linearifolia*, *Plumbago zeylanica*, *Pyrenacantha kaurabassana*, *Opilia amentacea* and *Dioscorea prehensilis*. There were a number of herbs, but hardly any grasses on the forest floor (the grasses that are present have prostrate rhizomes and are not tufted as in the open vegetation): *Psilotrichum sp.* cf. *P. elliotii*, *Barleria sp.* cf. *B. ventricosa*, *Justicia diclipteroides*, *Blepharis maderaspatensis*, *Cyperus subumbellatus* and *Panicum comorense*. The standing volume of the tree trunks and other woody stems was on average 185 m^3/ha. The tree stem density was on average 329 stems/ha. The biomass of the ground cover was negligible. The vegetation can be characterised as dry deciduous forest.

Physiognomically, the forest in site X resembles the *Baphia abyssinica*-dominated semi-deciduous forest described by Friis (1992: 28-

29) from the area between Abobo and Gog, but *Baphia* and the emergent, very tall trees are absent from site X. Floristically, the forest in site X is poorer than the *Baphia abyssinica* forest, and would appear to be a transition type between the *Baphia* forest and the dense *Anogeissus* woodland.

Woodland: Site B

The second densest vegetation was studied in site B between 10 and 12 km south of the bridge across the Baro River at Gambella town on the road to Akobo and Pugnido (*c.* 8° 10' N, 34° 35' E; *c.* 550 m altitude). Three replica plots were established with two next to each other, one to the east and one to the west of the road, and the last one two kilometres to the south on the east side of the road. The landscape is slightly undulating, with faint shifts between low ridges with coarser sandy soils and lower ground with finer soils in between. The soils can be generally characterised as coarse to fine loamy, brown to red yellow ferralsols. The vegetation forms a fairly dense canopy with approximately 60% canopy cover or occasionally more, with poorly defined and very discontinuous lower woody strata. The grass cover of the site burnt in patches between late November 1996 and the end of January 1997, burnt very early during August-September 1997 and again in November-December 1997. The highest trees in the canopy were 17-20 m high. The tree stratum consisted of *Anogeissus leiocarpus, Bridelia scleroneura, Combretum collinum* subsp. *binderianum, Combretum molle, Pterocarpus lucens, Terminalia laxiflora, Strychnos innocua*, and *Zizyphus abyssinica*. A shrub stratum contained: *Grewia mollis, Maytenus senegalensis, Acacia senegal, Flueggea virosa, Gardenia ternata* subsp. *jovistonantis*, and on termite mounds *Harrisonia abyssinica*. The climbers included: *Jasminum streptopus* (which did not develop much beyond a low, climbing shrub in the plots), *Tylosema fassoglensis, Vigna ambacensis, Ampelocissus schimperianus, Cyphostemma adenocaule* and *Neorautanenia mitis*. More than 15 species of herbs, partly with woody base, were observed. The grasses were *Pennisetum polystachia, Sporobolus pyramidalis, Loudetia spp.* and *Hyparrhenia spp.*, especially *Hyparrhenia confinis* var. *nudiglumis*. All these grass species appeared to be tufted perennials, but *Hyparrhenia confinis* var. *nudiglumis* is according to Phillips (1995) a tufted annual. The standing volume of the tree trunks and other woody stems was on average 93 m^3/ha. The tree stem density was on average 240 stems/ha. The biomass of the grasses was 4.8 t/ha and of the herbs *c.* 150 kg/ha. The vegetation can be characterised as woodland.

Woodland and wooded grassland intermediate: Site A

The third densest vegetation was studied in site A located near the western Ethiopian escarpment just west of the foothills (8° 12' N, 34° 57' E; *c.* 650 m altitude) along the road from Bure to Gambella town about 8 km east of Baro Bonga. Three replica plots were established less than 500 m apart, two north of the road, and one south of the road. The landscape is gently sloping, with much loose coarse gravel or stones on the surface and in between a fine loamy brown to yellowish red ferralsol. The woody vegetation forms an open canopy with 29% cover or more, very variable from place to place. The grass cover of the site burnt before November 1996, and again before January 1997. It burnt again very early during August-September 1997, and again between December 1997 and February 1998. The tree stratum consisted of *Lonchocarpus laxiflorus, Pterocarpus lucens, Balanites aegyptiaca, Combretum collinum* subsp. *binderianum, Entada africana, Lannea barteri, Lannea fruticosa, Stereospermum kunthianum, Acacia senegal*, and *Zizyphus abyssinica*. The highest trees in the canopy were 10-15 m high. Among these, large individuals of *Sterculia africana* stood out as very large, isolated trees

with a very broad crown which locally could increase the canopy cover well above average. A shrub stratum contained: *Cadaba farinosa, Ximenia americana, Acacia senegal* and *Flueggea virosa,* and in somewhat protected sites *Harrisonia abyssinica.* The climbers included: *Tylosema fassoglensis, Cyphostemma adenocaule, Pyrenacantha kaurabassana,* and *Asparagus scaberulus.* About 5 species of herbs, partly with woody base, were observed. The grasses were *Sporobolus festivus, Loudetia spp.* and *Hyparrhenia spp.*, especially *Hyparrhenia confinis* var. *nudiglumis.* The standing volume of the tree trunks and other woody stems was on average (a single large individual of *Sterculia africana* excepted) 24 m^3/ha; if the single, large *Sterculia* is included, the figure is raised to 56 m^3/ha. The tree stem density was on average 160 stems/ha. The biomass of the grasses was 7.0 t/ha and of the herbs *c.* 30 kg/ha. The vegetation can be characterised as intermediate between woodland and wooded grassland, as the canopy cover is comparatively low for woodland vegetation, and the biomass of the ground cover is comparatively low for wooded grassland.

Wooded grassland: Site C

The fourth densest vegetation was studied in site C located *c.* 85 km south of the bridge across the Baro River at Gambella town on the road from Akobo towards Pugnido (*c.* 7° 48' N, 34° 17' E; *c.* 550 m altitude). All three replica plots were established less than 200 m from each other to the west of the road. The landscape is slightly undulating, with shifts between low ridges with coarser and lower ground with finer loams. The soils can be generally characterised as coarse loamy yellowish brown ferralsol. The vegetation forms a rather open canopy with less than 30% cover. The grass cover of the site was partly burnt between November 1996 and early February 1997, it burnt again more completely in early February 1997, and again between December 1997 and February 1998, but many of the culms of the grasses remained unburned. The highest trees in the canopy were 8-11 m high. The discontinuous tree stratum consisted of *Annona senegalensis, Lonchocarpus laxiflorus, Bridelia scleroneura, Combretum collinum* subsp. *collinum, C. adenogonum, Crossopteryx febrifuga, Lannea barteri, Maytenus senegalensis, Ochna leucophloeos, Strychnos innocua* and *Terminalia laxiflora.* Shrubs were not prominent, noted were *Grewia mollis, G. cfr. velutina* and *Harrisonia abyssinica.* Among the herbs were noted *Clerodendrum alatum, C. cordifolium, Hoslundia opposita* and *Indigofera garckeana.* Climbers were *Ipomoea blepharophylla, I. heterotricha, Jasminum streptopus* (which did not develop much beyond a low, climbing shrub in the plots) and *Neorautanenia mitis.* The most important grasses were *Hyparrhenia confinis* var. *nudiglumis, Andropogon gayanus, Hyperthelia dissoluta, Loudetia arundinacea* and *L. simplex.* The standing volume of the tree trunks and other woody stems was on average 15 m^3/ha. The tree stem density was on average 160 stems/ha. The biomass of the grasses was 14.9 t/ha and of the herbs 230 kg/ha. (In this figure is included young herbaceous parts of plants that might later develop a shrubby habit). The vegetation can be characterised as wooded grassland.

Wooded grassland: Site D

Similarly open vegetation was studied in site D located *c.* 22 km west of Gambella town along the road to Itang and Jicawo (*c.* 8° 17' N, 34° 28' E; *c.* 550 m altitude). Three replica plots were established less than 500 m from each other, two south of the road, and one north of the road. The landscape is very flat, and the soil is a rather uniform dark brown to reddish brown fine clayey vertisol. The site is probably occasionally flooded during the rainy season. The vegetation forms a very open canopy with an average of 25% cover, which varies because of the local presence of large specimens of *Ficus sycomorus.* The grass cover of the site was

burnt between November 1996 and early February 1997, and again before mid November 1997, probably most of it during an unusual, short dry spell in August-September where some burning did occur (local informant). The highest trees in the canopy were 12-15 m high. The tree stratum consisted of *Annona senegalensis, Bridelia scleroneura, Terminalia laxiflora, Ficus sycomorus, Lannea fruticosa, Lonchocarpus laxiflorus,* and *Stereospermum kunthianum.* In the shrub stratum was: *Maytenus senegalensis, Harrisonia abyssinica, Flueggea virosa, Grewia sp.* There were a few mainly herbaceous climbers: *Asparagus sp., Cissus petiolata* (or *C. populnea), Coccinia grandis, Teramnus labialis.* The herbs were: *Astripomoea malvacea, Echinops longifolius, Lippia* sp., *Indigofera sp.* cf. *I. spicata, Vernonia turbinata.* The grasses were *Andropogon gayanus, Loudetia spp.* and *Hyparrhenia spp.*, especially *Hyparrhenia filipendula.* The standing volume of the tree trunks and other woody stems was on average 36 m^3/ha. The tree stem density was on average 250 stems/ha. The biomass of the grasses was 16.9 t/ha and that of the herbs negligible. The vegetation can be characterised as wooded grassland.

Analyses of vegetation data

A number of analyses of diversity, life forms, size class distribution of woody species and biomass and annual growth of the herbaceous stratum were made on the vegetation data from the five sites. Although there now exist several studies of the Sudanian woodlands between Senegal and Ethiopia there is no comparable study recorded in the literature from other sites in the Sudanian region emphasising

Table 2. Number of species per family ranked according to size. No. of sp. = number of species.

Family	No. of sp.
Gramineae	12
Fabaceae	11
Acanthaceae	7
Combretaceae	7
Tiliaceae	6
Convolvulaceae	5
Cucurbitaceae	5
Euphorbiaceae	5
Rubiaceae	5
Verbenaceae	5
Vitaceae	5
Capparaceae	4
Malvaceae	4
Mimosaceae	4
Compositae	3
Rhamnaceae	3
Amaranthaceae	2

Family	No. of sp.
Anacardiaceae	2
Asparagaceae	2
Commelinaceae	2
Hyacinthaceae	2
Nyctaginaceae	2
Zingiberaceae	2
Agavaceae	1
Annonaceae	1
Anthericaceae	1
Araceae	1
Asclepiadaceae	1
Balanitaceae	1
Bignoniaceae	1
Caesalpiniaceae	1
Celastraceae	1
Cyperaceae	1
Dioscoreaceae	1

Family	No. of sp.
Ebenaceae	1
Erythroxylaceae	1
Icacinaceae	1
Lamiaceae	1
Loganiaceae	1
Meliaceae	1
Moraceae	1
Ochnaceae	1
Oleaceae	1
Opiliaceae	1
Oxalidaceae	1
Plumbaginaceae	1
Sapindaceae	1
Simaroubaceae	1
Solanaceae	1
Sterculiaceae	1
Taccaceae	1

the same details and using the same methods. The presentation of the observations is therefore divided into a number of themes, each of which is then compared with other available observations, which vary from subject to subject.

Family, genus and species diversity

A total of 50 families, 94 genera and 135 species were observed from the sites during our field work; see the list of species in the Appendix, the list of families in Table 2, and the list of genera in Table 3. Each plot was 20 x 50 m (1000 m^2), so our 4 sites with 3 replicate plots cover 3000 m^2 each, and the fifth site with two replicate plots covers 2000 m^2, giving a total coverage of 14,000 m^2.

A list of the number of species in each family is shown here as Table 2. The distribution of species on families is shown an graphic form in Fig. 7, where a curve expressing a inverse second order polynomial curve has been fitted, using the statistic functions of Sigma-Plot Version 4.0 Curve Fitting function (r = 0.967). A list of the number of species in each genus represented in our plots is shown here as Table 3, and the distribution of species on genera is shown an graphic form in Fig. 8, where an

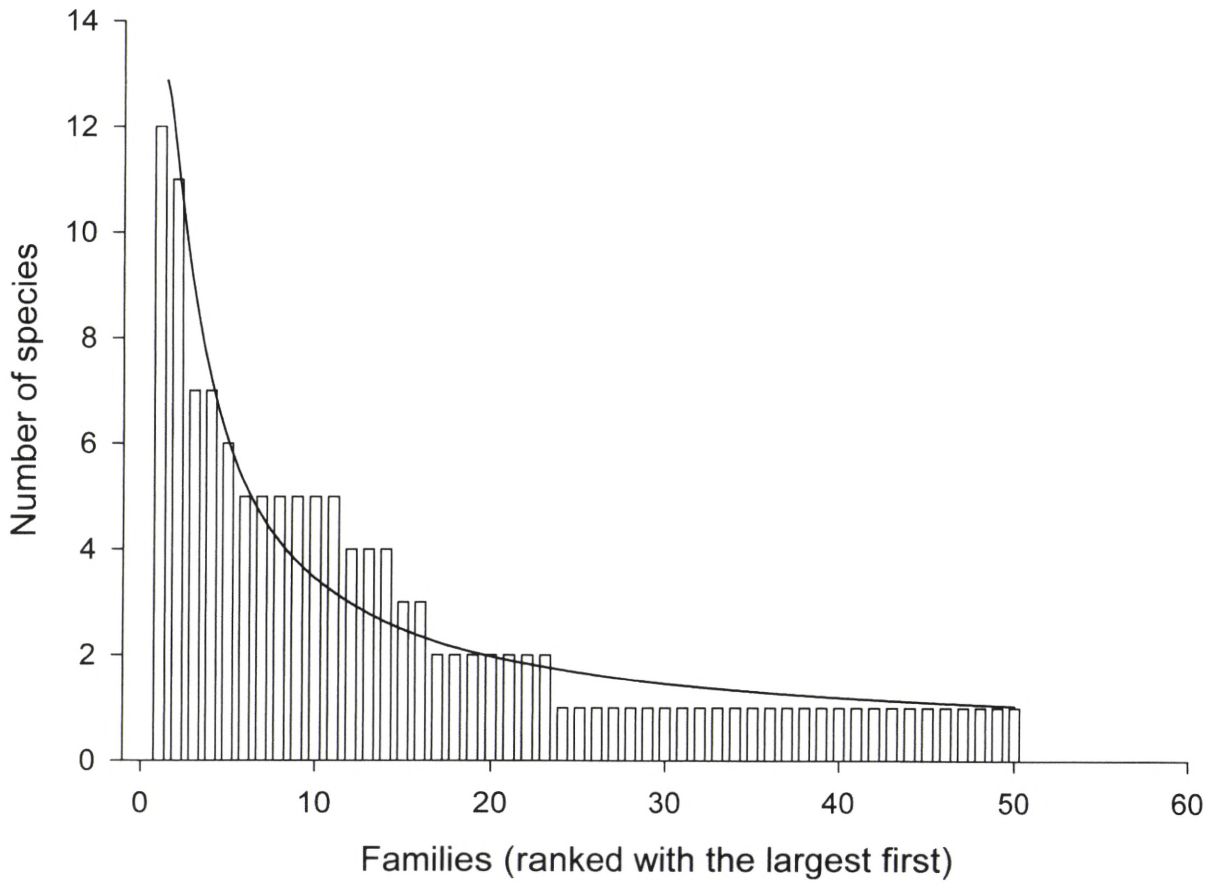


Fig. 7. Species distribution on families. The fitted inverse second order polynomial curve has the formula $y = 0.389 + 32.74/x - 21.37/x^2$. (x = number of family in ranking). r = 0.967.

Table 3. Number of species and subspecies per genus ranked according to size. (*gen. indet.*) = unidentified genus.

Genus	No. sp.
Combretum	5
Clerodendrum	4
Ipomoea	4
Grewia	4
Coccinia	3
Hibiscus	3
Hyparrhenia	3
Indigofera	3
Loudetia	3
Zizyphus	3
Abrus	2
Acacia	2
Acalypha	2
Ampelocissus	2
Asparagus	2
Barleria	2
Boerhavia	2
Cadaba	2
Cissus	2
Commelina	2
Justicia	2
Lannea	2
Ledebouria	2
Maerua	2
Sporobolus	2
Vigna	2
Abutilon	1
Acanthaceae (gen. indet.)	1
Achyranthes	1
Aframomum	1
Allophylus	1
Amorphophallus	1

Genus	No. sp.
Andropogon	1
Annona	1
Anogeissus	1
Aspilia	1
Astripomoea	1
Azadirachta	1
Balanites	1
Biophytum	1
Blepharis	1
Bridelia	1
Chlorophytum	1
Corchorus	1
Crossopteryx	1
Cucumis	1
Cucurbitaceae (gen. indet.)	1
Cyperus	1
Cyphostemma	1
Dichrostachys	1
Dioscorea	1
Diospyros	1
Echinops	1
Entada	1
Erythrococca	1
Erythroxylum	1
Ficus	1
Flueggea	1
Gardenia	1
Harrisonia	1
Hoslundia	1
Hyperthelia	1
Hypoestes	1

Genus	No. sp.
Jasminum	1
Lippia	1
Lonchocarpus	1
Maytenus	1
Meyna	1
Neorautanenia	1
Ochna	1
Opilia	1
Panicum	1
Pennisetum	1
Periploca	1
Plumbago	1
Psilotrichum	1
Pterocarpus	1
Pyrenacantha	1
Sansevieria	1
Siphonochilus	1
Solanum	1
Spermacoce	1
Sterculia	1
Stereospermum	1
Strychnos	1
Tacca	1
Tamarindus	1
Teramnus	1
Terminalia	1
Triumfetta	1
Tylosema	1
Vangueria	1
Vernonia	1
Ximenia	1

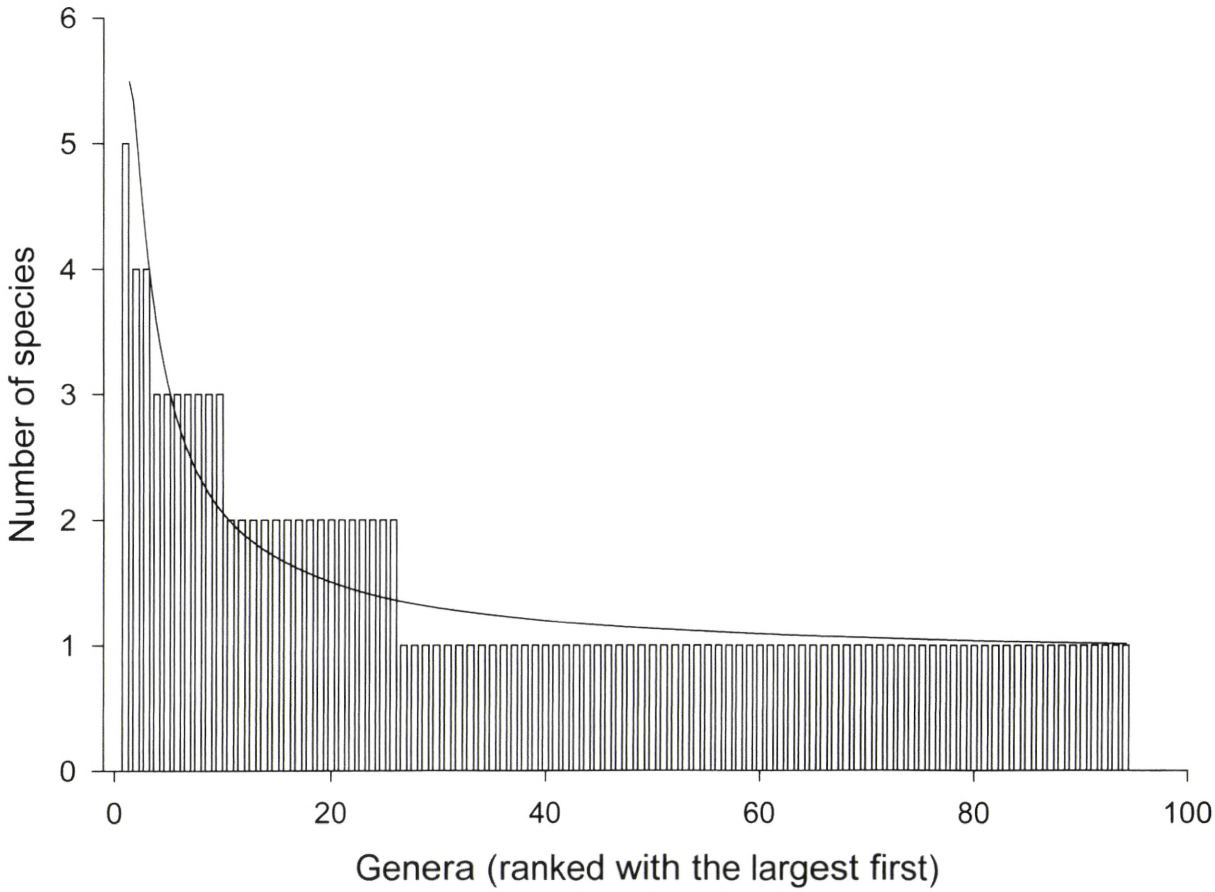


Fig. 8. Species distributions on genera. The fitted inverse second order polynomial curve has the formula $y = 0{,}874 + 13.04/x - 9.19/x^2$. (x = number of genus in ranking). r = 0.929.

inverse second order polynomial has again been fitted (r = 0.929).

The distribution of family- and genus-sizes agree with established knowledge about the size-distribution of families and genera on a world scale, and the fit with an inverse second order polynomium is acceptable for both families and genera (r > 0.9). The fact that few families have a high number of species and strikingly many families have only a few species is well known from the total flora of the world. This has for example been described by Clayton (1974) for the distribution of genera on families and species on genera on a global basis. This characteristic frequency distribution has been summed up in the colloquial sentence: *It is rare to be common and common to be rare.*

However, an excess of families represented by one or two species only, and a deficiency of families represented by a large number of species here modify the general pattern. Our sample does therefore not represent a completely random selection of the world flora. It has been suggested that disturbance at some intermediate level acts to maintain high divers-

ity (Connell 1978), and patterns like this are often found where the flora has been subjected to fluctuations over comparatively short time. In such cases, many families are represented by a single or a few widespread species each, and very few families have formed local species in the area. Also the distribution of genera size agrees with this deviation from the world pattern. However, the number of large genera is even more restricted in relation to the number of genera represented by one species only; the explanation may be as mentioned above for the family level.

The variation between the species richness in the plots is shown in Table 4. It is seen that the highest species diversity (average 32.7) is found in site B, the dense *Anogeissus* woodland south of Gambella town. The second highest value (average 26.0) is found in the dry forest (site X) at the airport south of Gambella. Slightly lower diversity (total 19.7) is found in site C, the open grass-rich site between Abobo and Pugnido. This is followed by a lower value (average 16.7) in the vegetation intermediate between woodland and wooded grassland at Baro Bonga near the western Ethiopian escarpment. The lowest diversity value (average 14.0) was found in the vegetation characterised as wooded grassland on vertisol between Gambella town and Itang (site D).

The number of studies available for comparison from other localities in the Sudanian zone is limited. Oteng-Yeboah (1985) studied 8 plots of 2500 m^2, or a total of 20000 m^2 in the savanna region of Sokoto State, Northern Nigeria. The area studied is thus comparable to our total study site, but our sites cover a somewhat wider range of habitats. In Oteng-Yeboah's sites were observed a total of 30 families, 50 genera and 66 species, or 62.5% of the number of families we have observed, 54% of genera, and 52% of the species. Without more detailed knowledge of the variation between Oteng-Yeboah's study sites it is difficult to draw conclusions from these figures about differences in the influence of fire. Oteng-Yeboah found that the most diverse families with regard to species in his sites were Mimosaceae and Combretaceae, while Caesalpiniaceae had the highest number of genera. Hence, Combretaceae scores high on both Oteng-Yeboah's list and our Table 2, whereas both Mimosaceae and particularly Caesalpiniaceae come lower down in our results. This agrees well with the known floristic composition of the "Undifferentiated woodland (Ethiopian type)" which has a very low component of Caesalpiniaceae in comparison with the Sudanian woodlands in West Africa (White 1983).

Floristic similarity between the sites

The species composition of the sites has been compared by the use of the software NTSYSpc Version 2.0 (Rohlf 1998). Species lists from the sites have been extracted from the appendix and compared. Similarity coefficients between the species lists were calculated by the use of Jaccard's coefficient, using the procedure SIMQUAL (SIMQUAL – Similarity for qualitative data). The resulting similarity matrix was analysed by the use of the module SAHN (Sequential, Agglomerative, Hierarchical, and Nested clustering methods), using the clustering procedure UPGMA (SAHN – Sequential agglomerative hierarical nested cluster analysis). The resulting cluster is shown in Fig. 9. It can be seen that the dry forest (site X) is floristically the most isolated, joining the cluster of the other four sites at the level of similarity less than 0.1. The four fire prone clusters all group together, but are divided into two groups, consisting of site A and D and site B and C respectively. A and D are located far apart and on different soil types, although both have high organic content; we must also assume that rainfall is different, certainly high at A, and probably much lower at D. B and C are also far

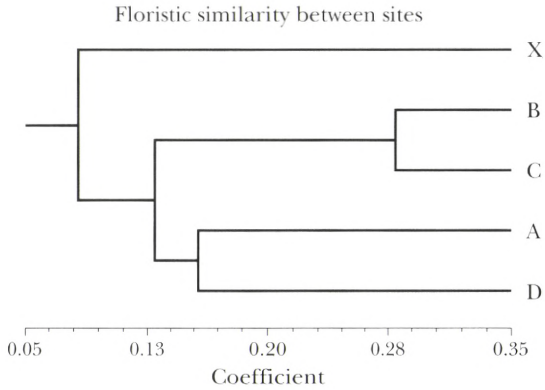


Fig. 9. Cluster showing floristic similarity between the sites. (Jaccard's coefficient of similarity and UPGM has been used). There is clear distinction between dry forest in site X and the woodlands and wooded grasslands in the othe sites (B, C, A, D).

Table 4. Number of species of trees, shrubs and herbs (grasses shown separately) in the plots (each plot was 20 x 50 m). *Av* = average. st.dev = standard deviation.

	trees	shrubs	tree+shrub	herbs	grasses	total
X1	10	3	13	14	2	29
X2	8	1	9	13	1	23
Av.	***9.0***	***2.0***	***11.0***	***13.5***	***1.5***	***26.0***
st.dev.	1.4	1.4	2.8	0.7	0.7	4.2
B1	10	4	14	24	2	40
B2	8	4	12	22	2	36
B3	4	8	12	8	2	22
Av.	***7.3***	***5.3***	***12.7***	***18.0***	***2.0***	***32.7***
st.dev.	3.1	2.3	1.2	8.7	0.0	9.5
A1	8	4	12	6	2	20
A2	9	2	11	2	2	15
A3	6	3	9	3	3	15
Av.	***7.7***	***3.0***	***10.7***	***3.7***	***2.3***	***16.7***
st.dev.	1.5	1.0	1.5	2.1	0.6	2.9
C1	12	2	14	11	4	29
C2	5	1	6	7	3	16
C3	7	1	8	4	2	14
Av.	***8.0***	***1.3***	***9.3***	***7.3***	***3.0***	***19.7***
st.dev.	3.6	0.6	4.2	3.5	1.0	8.1
D1	6	0	6	1	3	10
D2	6	1	7	9	2	18
D3	7	2	9	3	2	14
Av.	***6.3***	***1.0***	***7.3***	***4.3***	***2.3***	***14.0***
st.dev.	0.6	1.0	1.5	4.2	0.6	4.0

apart, but share rather similar edaphic conditions, and probably also very similar rainfall. The floristic similarities between the sites A, B, C, and D can thus probably be explained without invoking explanations from fire intensity. In contrast, the great differences between these sites on one hand and the dry forest in site X on the other, must be assumed to be due to the protection of site X from burning, as the edaphic and climatic conditions in site X and B are very similar.

Life forms

In this paper, two evaluations of life forms have been made. One that compares the number of species of three basic life forms (trees, shrubs, and herbs) in all plots analysed in this study and calculating the interplot variation (Table 4). Another evaluation applied here attempts at a more sophisticated subdivision of the species in the life form system of Raunkiaer (1934) (Table 5). Some comments are necessary on the problems encountered when the species are classified into life forms. The distinction between the three basic life forms (trees, shrubs, herbs) is only apparently simple; there is no clear distinction between trees and shrubs, and the border between shrubs and what is often colloquially referred to as "woody herbs" is not easily determined: many species are woody at the base and herbaceous in the younger parts of the stems. The classification does also force us to place lianas either into the shrub or the herb life form; we chose to classify lianas with woody stems as shrubs in Table 4, and as phanerophytes in Table 5, and lianas that shoot from underground tubers as herbs in Table 4, and as geophytes (geophytic lianas) in Table 5. The problem was not a large one in

Table 5. The frequency of Raunkiaer life forms in the sites. G = grass-habit. L = liana-habit.

Life form	All sites	Site X	Site B	Site A	Site C	Site D
Mesophanerophytes (MEP)	16	5	8	4	8	3
Microphanerophytes (MIP)	35	14	11	11	12	8
(Of which lianas (MIP(L))	(6)	(4)	(0)	0	(2)	(1)
Nanophanerophytes (NAP)	15	3	7	3	4	3
Of which lianas (NAP(L))	(3)	(0)	(1)	(1)	(1)	(1)
Chamaephytes (CHP)	2	1	0	0	0	1
Hemicryptophytes (HEC)	23	9	8	3	6	7
HEC that are grasses (HEC(G))	(9)	(1)	(3)	(3)	(5)	(5)
HEC that are lianas (HEC(L))	(2)	(2)	(0)	(0)	(0)	(0)
Geophytes (GEP)	23	6	14	6	5	4
Of which geophytic lianas (GEP(L))	(13)	(3)	(10)	(4)	(2)	(2)
Therophytes (THP)	16	1	13	3	4	0
Of which annual lianas (THP(L))	(1)	(0)	(1)	(0)	(0)	(0)
Succulents (SUC)	1	1	0	0	0	0
Life form not ascertainable	5	1	2	0	2	
Total no. of species (all life forms)	136	41	63	30	41	26

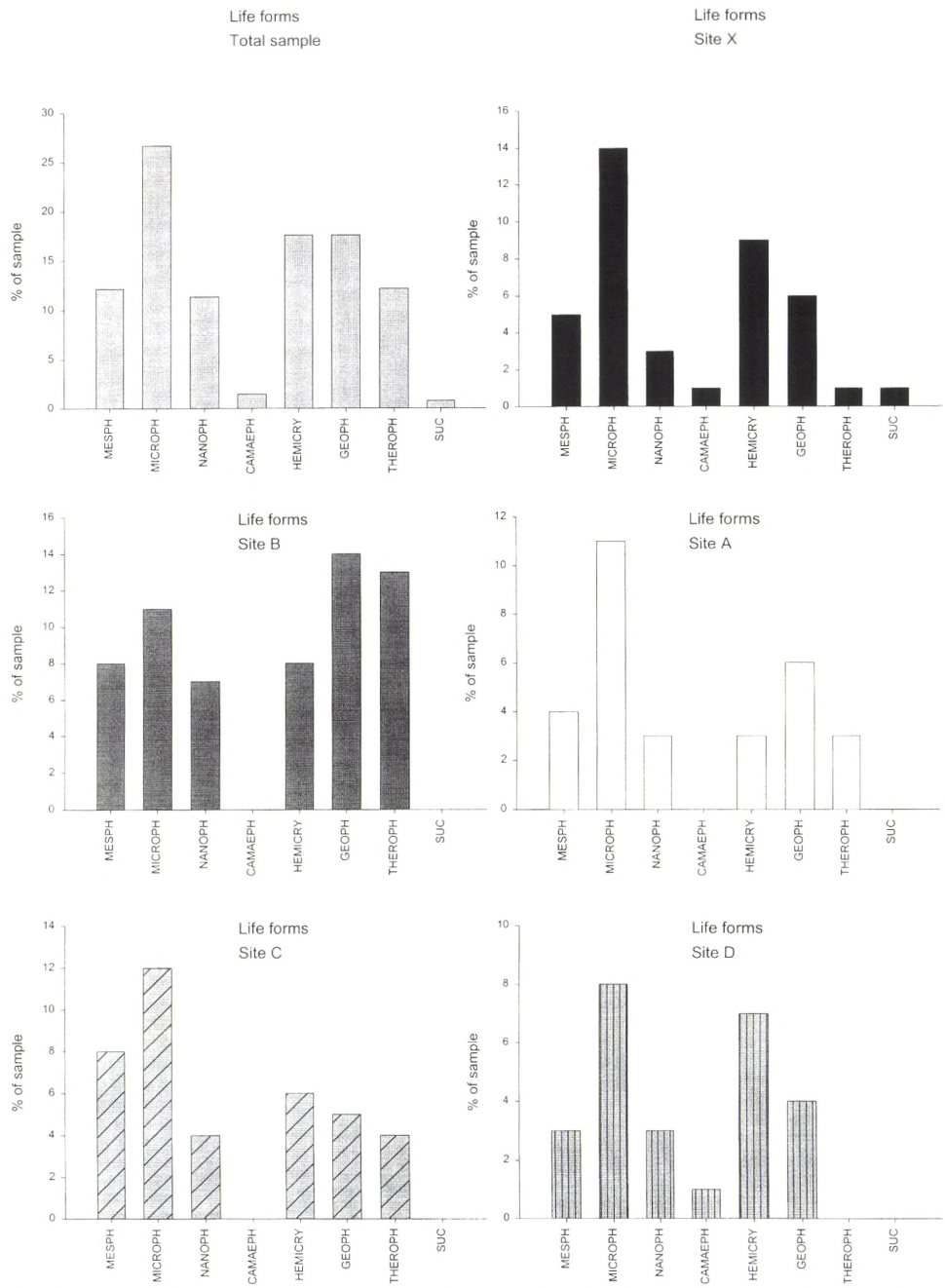


Fig. 10. Distribution on Raunkiaer's life forms shown as the accumulated figures in percent of samples from all sites, and for the individual sites. MESPH: Mesophanerophytes. MICROPH: Microphanerophytes. NANOPH: Nanophanerophytes. CHAMAEPH: Chamaephytes. HEMICRY: Hemicryptophytes. GEOPH: Geophytes. THEROPH: Therophytes. SUC: Succulents. While all sites have a rather similar pattern with regard to the classes Meso-, Micro- and Nanophanerophytes, there is considerable variation in frequencies of the other life form classes. However, Hemicryptophytes and Geophytes remain frequent in all sites.

our case, as only very few phanerophytic lianas existed in the sites.

The categories of trees and shrubs are according to Raunkiaer's system classified by the height above ground where the buds are found that shoot after the unfavourable season. This height is fairly easy to establish with the accuracy required. There were no megaphanerophytes in the plots. Mesophanerophytes have buds up to 8 to 30 m above ground; microphanerophytes have buds up to 2 to 8 m above ground; nanophanerophytes have buds up to 0.25 to 2 m above ground; all these are, as could be expected, reasonably well represented in our sites, but with a declining frequency as the buds become more and more exposed to fire in woody plants of small stature. Chamaephytes have buds between 0 and 0.25 m above ground, but only two species in this category were found in the plots, and one of those occurred in closed forest. The hemicryptophytes were nearly all grasses, where the buds are placed in the dense grass tufts, which act as protection against fire. Species have been considered geophytes if they have large, tuberous underground rootstocks from which they sprout after fire. Usually these tubers are located completely underground. The geoxylic suffrutices so characteristic of wooded grassland elsewhere in Africa, especially in the Zambezian region (Lock 1998), were not noted in our plots; they would have been classified as hemicryptophytes. Very thin and semi-woody stems of perennials are assumed to burn, and these plants must shoot from buds near the surface of the soil; such plants are rather frequent in our sites and are considered as hemicryptophytes, rather than chamaephytes. Therophytes are annual and reproduce from seeds. True stem-succulents were not recorded, but one species of *Sansevieria* was scored as a leaf succulent.

Fig. 10 shows the distribution on life forms as the accumulated percentages of life forms for all sites, and for the individual sites (A-D and X). It can be seen that the figures for phanerophytes are more stable than the figures for geophytes and therophytes, where especially site B, the woodland stands out because of high numbers of geophytes and therophytes. This is surprising, as one would expect the site with severe fires to have the highest number of these life forms, but the high numbers in site B must be seen in relation to the fact that that site has the highest species diversity of all in the study.

Comparison with other areas

We have been able to trace only relatively few studies of life forms in vegetation types comparable to those of the Gambella Region. One of the comparisons possible is with data from dry savanna in Botswana (Cole & Brown 1976). An additional number of possibilities for comparison is a summary table (Table 6.2) in Menaut (1983). Table 6 shows a compilation of all these results, most of which are found in rare publications, which we have not been able to trace, and they are therefore here cited from Menaut (1983).

Menaut (1983) points out that the Raunkiaer life form system has been widely used by botanists studying African savannas, but that it has also been criticised for not being very suitable for that purpose. He further mentions that the variability between sites of the life form "typical" of a given species is one of the characteristics of savanna plants; the life form for the same species may change from a site with regular burning to a protected site, *etc.* Tchoumé (1966) describes how species of *Cissus* may in protected forest sites be classified as lianescent phanerophytes and as geophytes in frequently burnt savanna. As pointed out by Sarmiento & Monasterio (1983), the savanna ecosystem in its many modifications probably provides the most marked example of a tropical seasonal ecosystem, and yet there seems to

Table 6. Comparison of life forms at Gambella with life forms in other savanna or woodland sites

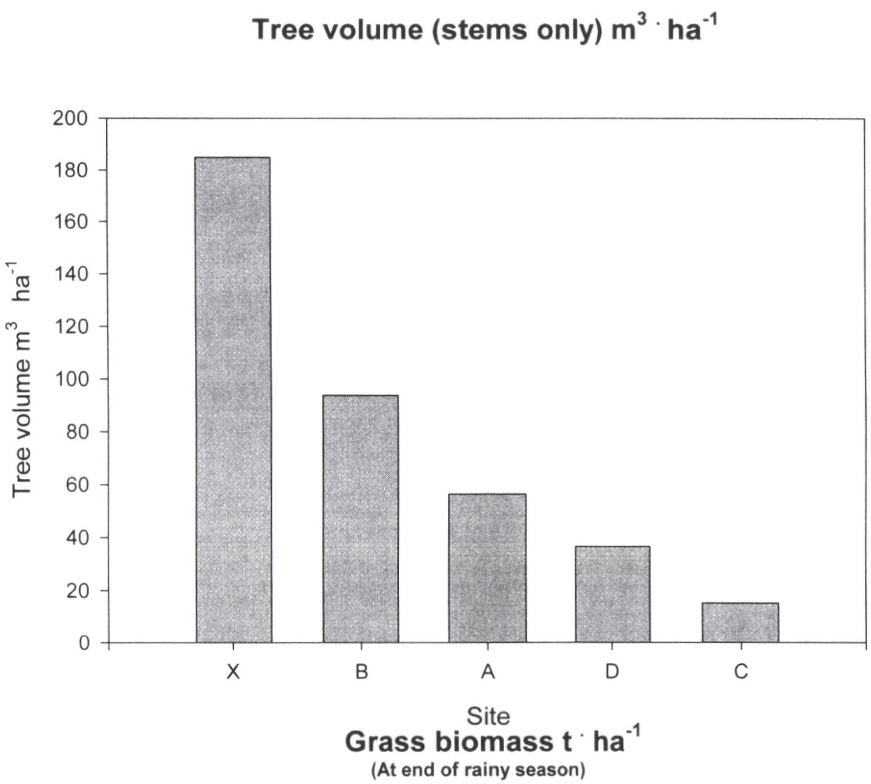
Other authors did not record succulents, of which we had a frequency of 1%.

	Oteng-Yeboah (1985)	Our data: All sites	Our data: Savanna and woodland sites	César (1971) Humid savanna Ivory Coast	Makany (1976) Humid savanna Congo	Hopkins (1962) Humid savanna Nigeria	Sillans (1958) Mesic savanna Central African Republic	Troupin (1966) Mesic savanna Rwanda	Lebrun (1947) Mesic savanna Zaire	Boudet & Duverger (1961) Dry savanna South Mauritania	Cornet & Poupon (1977) Dry savanna Northern Senegal	Gillet (1961) Dry savanna Northern Chad	Cole & Brown (1976) Dry savanna Botswana
Phanerophytes	50-77%	50%	51%	28%	14%	30%	13%	29%	38.2%	24%	19%	14%	18.0%
Chamaephytes		2%	1%	–	25%	–	24%	30%	43.6%	–	2%	2%	16.5%
Hemicryptophytes		18%	14%	42%	26%	23%	8%	12%	9.1%	6%	2%	12%	28.2%
Geophytes		18%	18%	6%	16%	21%	11%	7%	3.6%	2%	2%	5%	7.6%
Therophytes		12%	12%	24%	19%	25%	40%	20%	5.4%	61%	75%	67%	1.7%

be no characteristic life form spectrum in common for it. This is quite different from the temperate deciduous forest and the typical tropical lowland rain forest (Richards 1964: 9, Fig. 1), for which it is possible to establish generalised life form spectra. The reasons for the considerable variation in savanna life form spectra are, as pointed out by Menaut (1983) and Sarmiento & Monasterio (1983), that the types of environmental stress on the species in tropical savanna vary considerably and have allowed a wider spectrum of individual or evolutionary responses to the characteristic stress factors: seasonal drought, flood, and periodic burning. Resource allocation in all species except the tall trees may be compatible with the periodic consumption of almost the whole aerial standing crop by fire, but it is not a priori dictated by this consumption by fire whether the herbaceous plants should be annuals, geophytes or hemicryptophytes. It is therefore hardly surprising that the comparison of the representation of Raunkiaer's life forms in seven African, Malagasy and South American savannas by Sarmiento & Monasterio (1983, Table 5.1) shows at least as strongly fluctuating spectra as those shown by Menaut (1983) for African savannas.

Biomass

The biomass of trees and grasses at the end of the rainy season in November 1997 is shown in Fig. 11. As illustrated, there is a clear inverse relationship between tree trunk volume and grass biomass. No tree biomass regressions for this type of vegetation exist in the literature, and it is therefore not possible to give a more precise estimate of the total tree biomass. However, assuming an average wood density of 0.6 t/m^3 and that trunks constitute about 50% of total tree biomass one would get a very rough estimate of the total tree biomass at site X, B, A, D and C, respectively, of: 222, 112, 67, 43 and 18 t/ha, which is probably an under-estimate for all sites, since the below-ground biomass can be considerable in these habitats (Menaut *et al.* 1995). Our values agree reasonably well



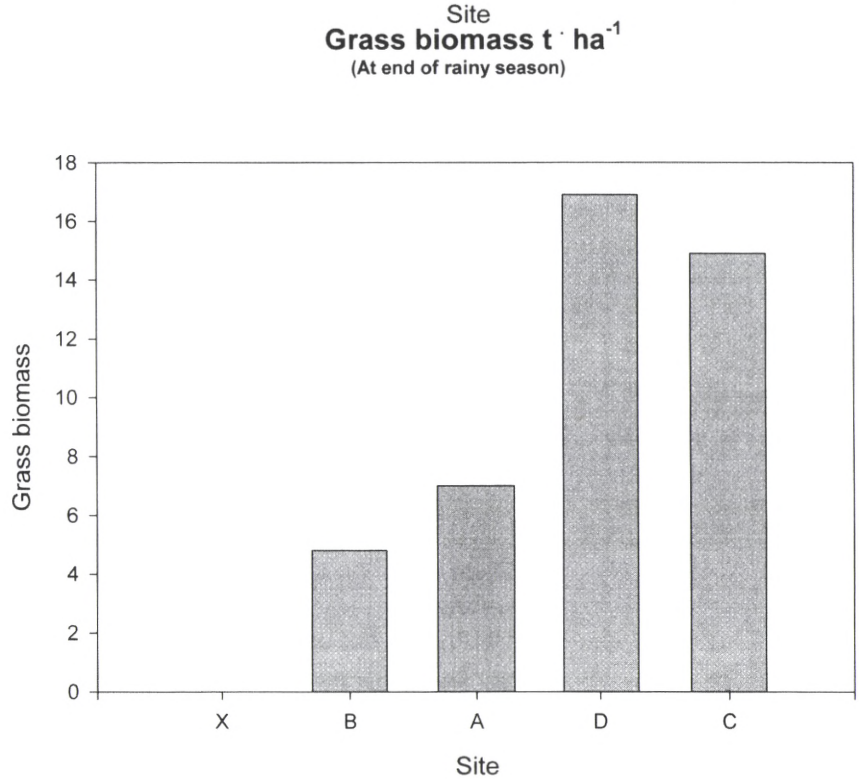


Fig. 11. The biomass of trees and grasses at the end of the rainy season in November 1997 in the sites X, B, A, D and C. The values of tree stem volume for each site represent an average of three plots (two for site X). The values of grass biomass for each site represent the average of the unburned plots at time of measurement.

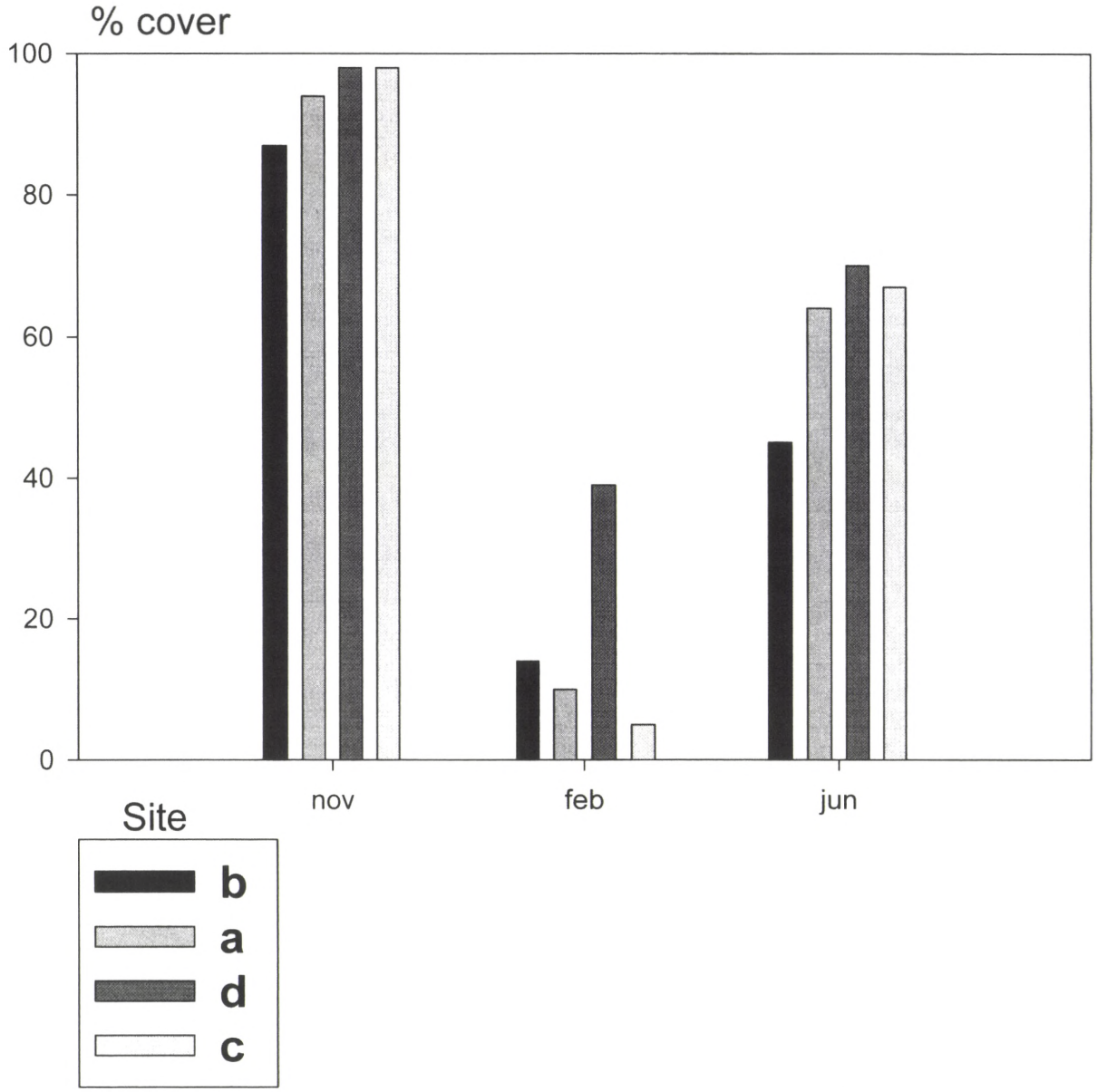


Fig. 12. Seasonal ground cover by grass, in November (end of rainy season), February (peak of dry season) and June (beginning of rainy season), in site B, A, D and C (the values for each site represent an average of three plots). Site X contained negligible to no grass cover.

with those reported from SE Zaire of 10, 150 and 320 t ha^{-1} for savanna, woodland and dry forest respectively except that our estimate of the dry forest is lower than that in Zaire (Menaut *et al.* 1995). But, according to these authors dry forests of northern Africa has con-

siderable lower biomass than southern dry forests. The northern dry forest has according to Menaut *et al.* (1995) characteristically a biomass around 140 t ha^{-1}, which in fact is lower than our estimate.

The canopy cover ranged from 25-29% in the wooded grassland and open woodland in site A, C and D, over 60% in the woodland in site B, and reached 92 % in the dry forest. Menaut *et al.* (1995) listed slightly lower ranges for savanna and higher for woodland and dry forest.

We measured a peak aboveground grass biomass of 4.8 t ha^{-1} in the woodland site (site B), whereas the wooded grassland sites (site A, C and D) ranged from 7 to 16.9 t ha^{-1}. Our values are considerably larger than those reported from SE Zaire, but falls fairly close to or a little higher than the general range for Africa of 4-10 t ha^{-1}. We can assume an additional belowground biomass of at least the same size, as this has been demonstrated in several other studies (Menaut *et al.* 1995; Kinyamario & Imbamba 1992).

Seasonal ground cover by (green) grass in woodland and woodland savanna varied considerably at all sites, as shown in Fig. 12. Values peaked at the end of the rainy season in November, dropped dramatically from above 90% cover at the end of the rainy season to around 10% or less at the height of the dry season in February, following drying and burning. Values were intermediate in June after the rains had started again in May, stimulating new growth. The seasonal pattern was more or less similar at all sites. For more details of the seasonal changes of the above-ground cover of the dominant grass, *Hyparrhenia confinis*, see Menassie & Michelsen (2001).

Although we have not aimed directly at measurements of productivity of the grass and herb layer, it is reasonable to assume that our figures for peak biomass of herbs and grasses give a very close estimate of the annual productivity in this stratum. Because of the annual burning there is an almost complete replacement of the above-ground grass and herb biomass. Our figures vary from nearly nil in dry forest (site X) to the sites with wooded grassland (site C: 1513 g/m^2, and site D: 1690 g/m^2). These latter figures are high compared with measured annual productivity in a range of African woodlands, wooded grasslands and grasslands, which according to Kinyamario & Imbamba (1992) range from 220 to 1880 g/m^2 (the latter including root production).

Size class distribution of trees

Our observations of the dimensions of trees have for all sites been divided into size classes of 10 cm DBH each (5-15 cm, 15-25 cm, etc.). We have then scored the number of individuals/ha in each size class (Fig. 13), and the sites have been arranged in order of increasing fire severity. Not all individuals could be identified to species level, especially the *Combretum* species, and size class diagrams are therefore not made for individual species. In all cases there are approximations to the logarithmic decreasing curve, which should be expected in vegetation with regular or natural turnover. However, there are deviations from this distribution, most prominently in the sites X, B and A.

The relative peak in the size classes 25-35 cm DBH in Site A (transition between woodland and wooded grassland) makes the size class distribution of this site resemble that of the forest and woodland vegetation in Site X and B. This perhaps indicates that the number of trees in site A is in the process of declining. The variation in the $^{13}C/^{12}C$ isotope ratio with soil depth also suggests that site A has experienced a change from a vegetation cover with a high frequency of C-3-plants (trees and shrubs) to a more open one dominated by C-4-plants, mainly grasses (see further in the coming work

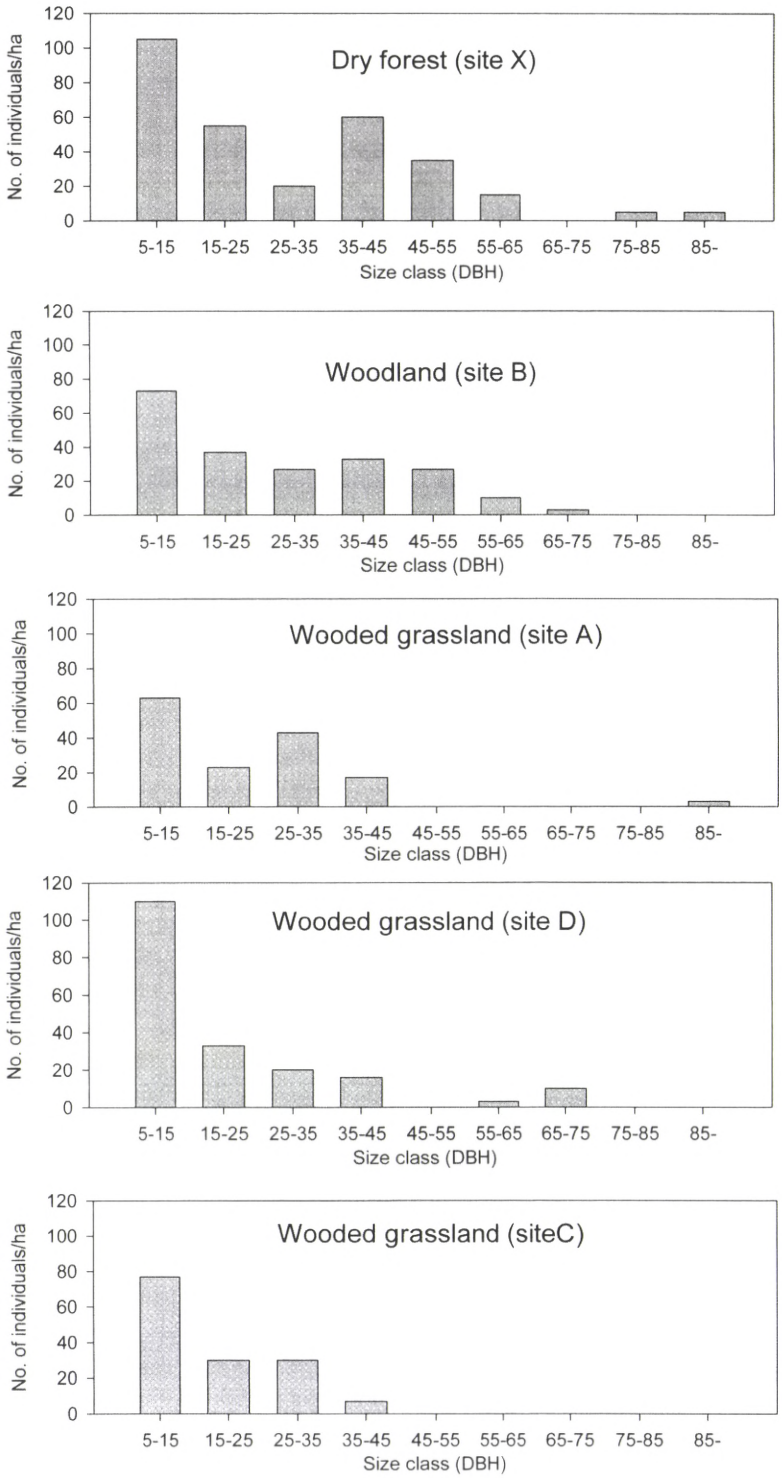


Fig. 13. Size class distribution of trees per ha in the study sites. The sites are arranged according to increasing fire severity from site X (no fires) to site C.

by Michelsen, Friis, Jensen & Andersson, in prep.). The time scale of this change is not known. The improved road conditions between the Ethiopian highlands and Gambella have much improved the access to the area in which site A is located, and there is an increasing number of Sudanian refugees in camps below the escarpment where site A is located; both of these two human factors may have some influence on this change. The tendency to a secondary peak between 35-55 cm DBH in the histograms for site X and B are not correlated with a similar change in the C isotope ratio in the soil, so it is difficult to explain this pattern. However, we noted that fuel wood cutting around Gambella town mainly affected trees in our lowest size class (5-15 cm DBH). A fairly recent increase in removal of trees in this size class could disrupt the usual size class distribution in a way similar to what we see in site X and B.

Greig-Smith (1991) has pointed out the high mortality of small woody stems in a fire-influenced derived savanna in Nigeria, resulting in a certain shift in the size structure from the usual distribution with the highest number in the smallest size-classes (< 10 cm DBH); his size class curve also shows the odd very large trees. Our examples do not show the shift away from the very small size classes clearly, partly because we have not included trees under 5 cm DBH (Greig-Smith's intervals are also smaller than ours). The largest size classes in site X and A are above 85 cm DBH, while in site B it is one individual in the class 65-75 cm DBH. Although the sites D and C also have the highest number of individuals in the smallest size class, the secondary peak found in X, B and A is not prominent, and large trees in size classes above 45 cm DBH are rare or absent, in fact restricted to 3 specimens of *Ficus sycomorus* in site D.

The high number of individuals in the small size classes may have different explanations in different sites. In the infrequently burnt sites, such as site X and B, these size classes consist partly of young individuals of species which grow to a larger size, and partly of shade-tolerant, but not fire-resistant understorey trees (*e.g. Allophylus rubifolius, Erythroxylum fischeri, Vangueria madagascariensis*, and *Meyna tetraphylla*) that do not grow to a large size. In contrast, the small size classes in the frequently burnt sites (A, C and D) consist chiefly of small, fire-adapted species such as *Grewia mollis, G. bicolor* and *Bridelia scleroneura*, which all have thick bark which do not grow to large size, whereas young individuals of the large trees were comparatively rare or absent. The presence of very large trees in two of the wooded grassland-sites (A and D) can partly be explained by their special adaptations to fire, *e.g.* through thick and peeling bark, as seemed to be the case with the isolated individual of *Sterculia africana* in site A, partly by clumped distribution, as was probably the case with the three large specimens of *Ficus sycomorus* in site D. The fire resistance of *Ficus sycomorus* is further enhanced by the fact that the shade of the broad canopy of this species reduces the growth of grasses beneath it and thus also the effect of fire. A similar phenomenon is seen on the termite mounds, where the shade of evergreen shrubs partly excludes the growth of grass. The large individuals of trees, such as *Ficus sycomorus*, can develop on termite mounds. In contrast, the large trees in site X and B (2 individuals in size classes above 75 cm DBH in site X, one in site B) are all *Anogeissus leiocarpus* that have grown beyond the common size due to the absence or low severity of fire in these sites.

Conclusion

Our study of the distribution of fires as shown by remote sensing shows that there is good agreement between high fire density and the distribution of Sudanian woodlands as defined

by White (1983), especially when allowance is made for White's transition zone between the Sudanian and the Guineo-Congolian region in West Africa. Within this broadly defined Sudanian zone fire seems to affect nearly all vegetation types, except closed forest. This is also clearly the case in western Ethiopia, from the border region with western Eritrea in the north to the Boma Plateau south west of the town of Maji in the south. Unlike what has been shown on early vegetation maps of Ethiopia, this western zone of Ethiopia has many features in common, and all parts are affected by high fire density. Within this part of Ethiopia, especially in the Gambella Region, we have noted that there is a clear association between towns and routes of transportation on one hand and density of fires on the other, indicating that man starts most fires. Within the fire-prone zone, there is a mosaic of areas with high and low fire severity, but the location of this mosaic seems to vary from year to year. There is also a mosaic of vegetation types, but this may be as much influenced by edaphic and climatic factors as by burning. Flooding is an important factor in Gambella, influencing both soil and vegetation. The effect of severe flooding and development of vertisols may influence the floristic composition as much as severe fires. There seems to be no sharp boundaries between these types with regard to floristic characteristics, again with exception of the fairly sharp distinction between forest on one hand and woodland, wooded grassland and grassland on the other. A cluster analysis of the floras of the sites showed a sharp distinction between dry forest flora on one side and all fire-influenced sites on the other. The sites have comparatively many families and genera, but a low number of species per family and genus, which is believed to be indicating disturbance.

Increasing fire severity seems to be somewhat negatively correlated with species richness, but the number of species also declines in the shaded situation of the dry forest. A clear association has been observed between severe fires and high grass biomass, whereas the tree biomass, and the number of large trees, was negatively correlated to increasing fire severity. The life forms of savanna and woodland species have evolved under the influence of fire, and apparently fire-adapted hemicryptophytes, geophytes and therophytes were prominent in the burned sites, but we found no marked difference with regard to frequency of life forms between sites in our study area.

The current situation seems to indicate a decline in the extent of dry forest, which near Gambella town only persists in protected sites. With the current population pressure and fire intensity the process of change from dry forest and dense woodland to open woodland and wooded grassland is likely to continue, and this process may ultimately lead to the destruction of dry forest and dense woodland in the region. The time scale of this process will undoubtedly be largely dependent on the demographic development in the region. Where dry forest or dense woodland has been replaced with wooded grassland, as it may probably have happened in sites C and D in our study area, the vegetation and soil seems to have reached a somewhat stable level of fertility, structure and floristics, characterised by an impoverished tree flora and a very tall and abundant grass stratum which has its peak biomass at the end of the rainy season. The burning of this very large biomass is critical. Too late, and hence very severe fires will result in a further degradation of the tree stratum.

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Appendix

Species list of the Gambella woodland savanna research sites

Includes species encountered and identified between Nov 1996 and Dec 1998. The following life forms have been recorded: MEP: Mesophanerophyte (8-30 m). MIP: Microphanerophyte (2-8 m). NAP: Nanophaneropytes (0.25-2 m). CHP: Chamaephytes (0-0.25 m). HEC: Hemicryptophytes (including the tufted grass-life form [HEC(G)]). GEP: Geophytes. THP: Therophytes. SUC: Succulent. Where the life form of a species represents lianas or vines, this has been separately indicated with "(L)".

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
Abrus schimperi Hochst. ex Bak.	Fabaceae	NAP	•	•		•	
Abrus praecatorius Linn.	Fabaceae	MIP(L)	•				
Abutilon sp.	Malvaceae	NAP	•				
Acalypha ciliata Forssk.	Euphorbiaceae	THP		•			
Acalypha villicaulis Hochst. ex A. Rich.	Euphorbiaceae	NAP		•			
Achyranthes sp.	Amaranthaceae	?	•				
Acacia senegal Willd.	Mimosaceae	MIP		•	•	•	
Acacia sp.	Mimosaceae	MIP			•		
Acanthaceae (gen et sp. indet.)	Acanthaceae	HEC	•				
Aframomum sp.	Zingiberaceae	GEP		•		•	
Allophylus rubifolius Engl.	Sapindaceae	MIP	•	•			
Amorphophallus abyssinicus (A. Rich.) N.E. Br.	Araceae	GEP	•				
Ampelocissus abyssinica (A. Rich.) Planch.	Vitaceae	GEP(L)		•			
Ampelocissus schimperiana Planch.	Vitaceae	GEP(L)	•	•			
Andropogon gayanus Kunth	Gramineae	HEC(G)				•	•
Annona senegalensis Pers.	Annonaceae	MIP					•
Anogeissus leiocarpa Guill. & Perr.	Combretaceae	MEP	•	•		•	
Asparagus scaberulus A. Rich.	Asparagaceae	NAP(L)			•		
Asparagus sp.	Asparagaceae	NAP(L)					•
Aspilia kotschyi (Sch. Bip ex Hochst.) Oliv.	Compositae	THP		•		•	
Astripomoea malvacea A. Meeuse	Convolvulaceae	NAP (?)					•
Azadirachta indica A. Juss.	Meliaceae	MIP				•	
Balanites aegyptiaca Wall.	Balanitaceae	MIP			•		
Barleria grandicalyx Lindau	Acanthaceae	HEC(?)		•			
Barleria ventricosa Hochst. ex Nees	Acanthaceae	HEC(?)	•				
Biophytum umbraculum Welw.	Oxalidaceae	THP		•			
Blepharis maderaspatensis Heyne ex Roth.	Acanthaceae	HEC	•				
Boerhavia coccinia Mill.	Nyctaginaceae	THP		•	•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
Boerhavia repens Rojas	Nyctaginaceae	THP			•		
Bridelia scleuroneura Muell. Arg.	Euphorbiaceae	MIP		•		•	•
Cadaba farinosa Forssk.	Capparaceae	NAP		•			
Cadaba sp.	Capparaceae	NAP			•		•
Chlorophytum tordense Chiov.	Anthericaceae	GEP		•		•	
Cissus petiolata Hook. f. (or C. *populnea* Guill. & Perr.)	Vitaceae	MIP(L)/ MEP(L)					•
Cissus sp.	Vitaceae	MIP(L)	•			•	
Clerodendrum alatum Gürke	Verbenaceae	GEP		•		•	
Clerodendrum capitatum Hook.	Verbenaceae	MIP(L)	•				
Clerodendrum cordifolium A. Rich	Verbenaceae	MIP(L)				•	
Clerodendrum sp.	Verbenaceae	?		•			
Coccinia adoensis (Hochst. ex A. Rich.) Cogn.	Cucurbitaceae	GEP(L)		•			
Coccinia grandis Voigt.	Cucurbitaceae	GEP(L)			•		•
Coccinia megarrhiza C. Jeffrey	Cucurbitaceae	GEP(L)					•
Combretum adenogonium Steud. ex A. Rich.	Combretaceae	MEP				•	
Combretum collinum Fresen. subsp. *binderianum* (Kotschy) Okafor	Combretaceae	MEP		•	•		
Combretum collinum Fresen. subsp. *collinum*	Combretaceae	MEP				•	
Combretum molle Engl. & Diels.	Combretaceae	MEP		•			
Combretum sp	Combretaceae	MEP		•		•	•
Commelina benghalensis Linn.	Commelinaceae	HEC		•			
Commelina sp.	Commelinaceae	HEC	•			•	
Corchorus tridens Linn.	Tiliaceae	THP		•			
Crossopteryx febrifuga Benth.	Rubiaceae	MIP				•	
Cucumis metuliferus E. Mey. ex Naud.	Cucurbitaceae	THP(L)		•			
Cucurbitaceae	Cucurbitaceae	?				•	
Cyperus subumbellatus Kukenth.	Cyperaceae	HEC	•				
Cyphostemma adenocaule (A. Rich) Wild & R.B. Drumm.	Vitaceae	GEP(L)/ HEC(L)		•	•		
Dichrostachys cinerea (Linn.) Wight. & Arn.	Mimosaceae	MIP		•			
Dioscorea praehensilis Benth.	Dioscoreaceae	GEP(L)	•	•			
Diospyros mespiliformis Hochst. ex A. DC.	Ebenaceae	MEP	•				
Echinops longifolius A. Rich.	Compositae	HEC					•
Entada africana Guill. & Perr.	Mimosaceae	MIP			•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
Erythrococca cfr. abyssinica Pax	Euphorbiaceae	MIP	•				
Erythroxylum fischeri Engl.	Erythroxylaceae	MIP	•				
Ficus sycomorus L.	Moraceae	MEP				•	•
Flueggea virosa (Willd.) Voigt	Euphorbiaceae	MIP	•	•	•		
Gardenia ternifolia Schum. & Thonn.	Rubiaceae	MIP		•			
Grewia mollis Juss.	Tiliaceae	MIP		•	•	•	•
Grewia tenax Aschers. & Schweinf. ex E. Christ.	Tiliaceae	MIP	•				
Grewia cfr. velutina (Forssk.) Vahl	Tiliaceae	MIP				•	
Grewia sp.	Tiliaceae	MIP					•
Harrisonia abyssinica Oliver	Simaroubaceae	MIP	•	•	•	•	•
Hibiscus calyphyllus Cav.	Malvaceae	NAP	•				
Hibiscus cannabinus Linn.	Malvaceae	THP		•			
Hibiscus sp.	Malvaceae	?		•			
Hoslundia opposita Vahl	Labiateae	NAP		•		•	
Hyparrhenia confinis (A. Rich.) Stapf var. *nudiglumis* (Hackl.) W.D. Clayton	Gramineae	THP		•	•	•	
Hyparrhenia filipendula Stapf.	Gramineae	HEC(G)					•
Hyparrhenia sp	Gramineae	HEC(G)		•	•	•	•
Hyperthelia dissoluta (Nees ex Steud.) W.D. Clayton	Gramineae	HEC(G)				•	
Hypoestes forskaolii (Vahl) R. Br.	Acanthaceae	HEC	•	•			
Indigofera garckenana Vatke	Fabaceae	NAP		•		•	
Indigofera sp. aff. I. spicata Forsk.	Fabaceae	HEC		•			•
Indigofera trita L.f. var. *scabra* (Roth) Ali	Fabaceae	NAP		•			
Ipomoea blepharophylla Hallier f. ex Engl.	Convolvulaceae	GEP(L)				•	
Ipomoea eriocarpa R.Br.	Convolvulaceae	THP		•			
Ipomoea heterotricha F. Didr.	Convolvulaceae	THP				•	
Ipomoea sp.	Convolvulaceae	?				•	
Jasminum streptopus E. Mey. ex DC.	Oleaceae	NAP(L)		•		•	
Justicia ladanoides Lam.	Acanthaceae	HEC		•			
Justicia diclipteroides Lindau	Acanthaceae	HEC	•				
Lannea barteri Engl.	Anacardiaceae	MEP			•	•	
Lannea fruticosa Engl.	Anacardiaceae	MIP			•		•
Ledebouria revoluta (L.f.) J.P. Jessop	Hyacinthaceae	GEP			•		
Ledebouria sp.	Hyacinthaceae	GEP			•		

Species	Family	Life form	Site X	Site B	Site A	Site C	Site D
Lippia sp.	Verbenaceae	NAP					•
Lonchocarpus laxiflorus Guill. & Perr.	Fabaceae	MEP		•		•	•
Loudetia arundinaceae Hochst. ex Steud.	Gramineae	HEC(G)				•	
Loudetia sp	Gramineae	HEC(G)	•	•	•	•	•
Loudetia simplex (Nees) C. E. Hubbard	Gramineae	HEC(G)					•
Maytenus senegalensis (Lam.) Exell	Celastraceae	MIP		•		•	•
Maerua oblongifolia A. Rich.	Capparaceae	NAP/ (MIP)		•			
Maerua triphylla A. Rich.	Capparaceae	MIP	•				
Meyna tetraphylla Robyns	Rubiaceae	MIP	•				
Neorautanenia mitis (A. Rich.) Verdc.	Fabaceae	GEP(L)		•		•	
Ochna leucophloeos A. Rich.	Ochnaceae	MIP				•	
Opilia amentacea Roxb.	Opiliaceae	MIP(L)	•				
Panicum comorense Mez	Gramineae	THP	•				
Pennisetum polystachion Schult.	Gramineae	THP		•			
Periploca linearifolia A. Rich.	Asclepiadaceae	HEC(L)	•				
Plumbago zeylanica Linn.	Plumbaginaceae	HEC(L)	•				
Psilotrichum sp. cfr. P. elliotii Bak.	Amaranthaceae	CHP	•				
Pterocarpus lucens Lepr. ex Guill. & Perr.	Fabaceae	MEP	•	•			
Pyrenacantha kaurabassana Baill.	Icacinaceae	GEP(L)	•	•	•		
Sansevieria sp.	Agavaceae	SUC	•				
Siphonochilus aethiopicus (Schweinf.) B.L. Burtt	Zingiberaceae	GEP	•				
Solanum incanum Linn.	Solanaceae	NAP			•		
Spermacoce sphaerostigma Oliver	Rubiaceae	THP		•		•	
Sporobolus festivus A. Rich.	Gramineae	GEP(G)			•		
Sporobolus pyramidalis Beauv.	Gramineae	GEP(G)		•			
Sterculia africana (Lour.) Fiori	Sterculiaceae	MEP			•		
Stereospermum kunthianum Cham.	Bignoniaceae	MIP			•		•
Strychnos innocua Delile	Loganiaceae	MIP	•	•		•	
Tacca leontopetalodes Kuntze	Taccaceae	GEP	•	•			
Tamarindus indica Linn.	Leguminosae	MEP	•	•			
Terminalia laxiflora Engl.	Combretaceae	MEP		•		•	
Teramnus labialis Spreng.	Fabaceae	GEP					•
Tylosema fassoglensis (Schweinf.) Torre & Hillc.	Caesalpiniaceae	GEP(L)		•	•		

Species	**Family**	**Life form**	**Site X**	**Site B**	**Site A**	**Site C**	**Site D**
Triumfetta pentandra A. Rich.	Tiliaceae	THP		•			
Vangueria madagascariensis J. F. Gmel	Rubiaceae	MIP	•				
Vernonia turbinata Oliver	Compositae	GEP					•
Vigna ambacensis Welw. ex Bak.	Fabaceae	GEP(L)/ THP(L)		•			
Vigna unguiculata Savi	Fabaceae	GEP(L)/ THP(L)		•			
Zizyphus abyssinica Hochst. ex A. Rich.	Rhamnaceae	MIP		•	•		
Zizyphus mauritiana Lam.	Rhamnaceae	MEP			•		
Zizyphus pubescens Oliver	Rhamnaceae	MEP	•				
Ximenia americana Linn.	Olacaceae	MIP			•		

Soil seed bank dynamics and above-ground cover of a dominant grass, Hyparrhenia confinis, in regularly burned savanna types in Gambella, western Ethiopia

MENASSIE GASHAW & ANDERS MICHELSEN

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The spatial and temporal distribution of the soil seed bank of a dominant grass species, *Hyparrhenia confinis* (Hochst. ex A. Rich.) Stapf, was studied in regularly burned savanna in Gambella, western Ethiopia. The seedling emergence technique was employed to determine the density of the soil seed bank of six sites with different fire severity. The soil seed bank was largely dominated by graminoids as almost 90 % of the soil seed bank consisted of seeds of *Hyparrhenia confinis*. The seed density of *Hyparrhenia confinis* in the soil varied strongly between seasons, sites and depths and was not always closely correlated with the above-ground cover of *Hyparrhenia confinis*. This was high in the wooded grasslands and intermediate in the woodland, whereas the species, and other grasses, were absent from the more densely forested sites. The majority of the seeds were found in the uppermost 0.5 cm of the soil. Seed density was highest in the dry season and declined strongly in the beginning of the rainy season due to germination when conditions were favourable for plant growth. However, observations from the field suggest that sprouting from the base also may contribute to regeneration of the grass cover after the dry season. Our results show that the current fire regime of these savanna woodlands appears to maintain the dominance of *Hyparrhenia confinis* both as seeds in the soil and in the herbaceous stratum of the standing vegetation.

Menassie Gashaw, c/o Biology Dept., Addis Ababa University, P. O. Box 3434, Addis Ababa, Ethiopia. E-mail: nat.heb@telecom.net.et

Anders Michelsen, Botanical Institute, University of Copenhagen, Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark. E-mail: andersm@bot.ku.dk

Introduction

Vast areas of rangeland vegetation in many parts of the world are regularly cleared by natural and man-made fires, of which the latter play an increasing importance (Lock 1998). Fires are widespread in many African savanna woodland types and may result in open areas that may suppress the seed germination of some plant species, and stimulate that of other species. This is known to be an important phenomenon in forests (Swaine & Whitmore 1988), and probably also plays a role in wood-

lands. Thus, light-demanding species such as savanna grasses may benefit from burning. The gaps formed by slashing of vegetation or burning may quickly be colonized by plants recruited from the soil seed bank, from seed rain originating from the surrounding vegetation, as well as from pre-existing seedlings and sprouting shoots which may have escaped the disturbance (Demel Teketay 1997). Therefore soil seed banks are important as means of plant establishment after disturbance (Odgers 1996; Metcalfe & Turner 1998).

Soil seed banks enable plants to survive fire. Seeds buried in the soil are well protected from the direct effect of fire as the soil provides insulation from high surface temperatures during the course of fire (Whelan 1995). The mortality of seeds following burning depends on the intensity of fire and the depth of seed burial in the soil. According to Whelan (1995) seeds close to the soil surface could be killed by intense fire, whereas seeds in deeper soil layers may remain dormant. Water percolates into the soil and animal vectors such as small arthropods, *e.g.* insects, and other soil macroorganisms play major roles in the vertical and horizontal movement of seeds in the soil, facilitating the storage of seeds at deeper soil layers, and hence their survival in fires (Baskin & Baskin 1998).

The composition of a soil seed bank and its contribution to the restoration of a cleared or burned area depends on two important reproductive traits of the plants: (1) the capacity for seed dormancy, *i.e.* whether the species has persistent or short-lived seeds in the soil and (2) the potential for widespread seed dispersal (Dalling *et al.* 1997). The vegetation, particularly on disturbed sites, is often dominated by species that are abundantly represented in the site's seed bank (Uhl *et al.* 1981). Therefore, knowledge of the soil seed bank composition and dynamics in regularly burned sites may be used to predict the species composition of post-fire regeneration (Valbuena & Trabaud 1995). Species with large numbers of propagules already present in the soil seed bank, or dispersed to the site shortly or immediately after the fire disturbance have a great advantage over species arriving later, and over species with a small seed bank, or none at all (Swaine & Hall 1983). However, it has been questioned whether numerical dominance in the seed rain or seed bank puts the species at an advantage over others with few or no seeds in the soil seed bank (Swaine & Hall 1983; Uhl *et al.* 1981). This is because plants differ in their competitive ability, and competition for various resources among species also varies according to the timing of burning and the nature of the post-fire environment (Drake 1998).

Although grasses provide the major part of the primary production in savannas little is known about the regeneration strategies of some of the dominant species. This applies in particular to the importance of the soil seed bank for vegetation recovery after fire. The aim of this study was to reveal the spatial and temporal dynamics of the soil seed bank of *Hyparrhenia confinis*, and to compare the seed bank and above-ground cover of this species in vegetation types exposed to varying degrees of fire events. *Hyparrhenia confinis* is the dominant grass species in regularly burned savanna woodlands and grasslands in Gambella in western Ethiopia and is restricted to the border region between Ethiopia and Sudan from the Gamble region to Tigray (Phillips 1995).

Methodology

Study area

The study area is situated at about 500 m altitude on flat plains to undulating rocky areas with various types of savanna woodland in Gambella, western Ethiopia. The rainfall pattern in Gambella region is bimodal with a dry

season from October to March, little rain in the months of April and May, and a main rainy season between July and late September, with a peak of rainfall in July. Annual rainfall recorded in 1991, 1992 and 1993 ranged from 700 to 1000 mm in the drier part of the area (at sites B, C and D, see below) and from 1000 to 1900 mm in the wetter part (at site A). The climate is hot tropical with mean monthly minimum and maximum temperatures of 18°C and 40°C respectively.

Four regularly burned sites (A, B, C, and D) representing different vegetation types and fire severity were selected in the Gambella region. At each site three replicate plots with the size of 20 meters by 50 meters maximally 2 km apart were selected for the study. Sites were selected on the basis of differences in their vegetation types and biomass compositions and hence, difference in burning intensities (see Jensen & Friis 2001). The wooded grassland sites C and D burn relatively intensively, the woodland-wooded grassland intermediate site A burns moderately, whereas the woodland (B) site burns infrequently or less intensively. Fire intensity was roughly estimated from the amount of grass biomass measured in each respective site, following the method used in DeBano *et al.* (1998). Finding a control site (*i.e.* a site which was unburned or burned less frequently) proved difficult as almost the whole region burns every year. However, two plots with dry forest within the local airport area (X1 and X2) and one forested site called Gog (G site) could serve as controls or unburned plots, with the same plot sizes as the burned plots.

Above-ground cover estimation of Hyparrhenia confinis

In order to estimate the above-ground cover of *Hyparrhenia confinis*, 20 quadrates each with an area of 1 m^2 were positioned within each plot at 5 meters intervals along a 100 m transect line. The presence of *Hyparrhenia confinis* rooted within each of the 20 quadrates per plot were recorded both in February and in June 1998 as the percentage cover of stems and leaves in each quadrate, estimated by visual inspection.

Soil collection and treatment

Soil samples for seed bank studies were collected from each of the 3 plots at sites A, B, C, D, X and G. Six replicate spots for soil collection were randomly selected within each plot. Soil samples were taken from 0-0.5 cm, 2.5-3 cm, 5.5-6 cm, and 8.5-9 cm. Each subsample covered a depth of 0.5 cm. Soils between successive subsamples were discarded to minimize the risk of soil mix or contamination. Samples were taken with a knife and a spoon within a wooden frame measuring 15 by 15 cm. Samples were collected three times in a year. The first soil sampling was in February 1997, which was in the hot and dry period, the second one was in June 1997, *i.e.* the beginning of the wet season and the last set was taken during November 1997, at the end of the rainy season. At each occasion a total of 342 soil samples (comprising 90 soil columns normally with sampling at 4 depths, from 15 plots at the 6 sites) were collected. Each sample was kept separate, air dried and then passed through a 4 mm sieve to remove vegetative plant fragments. Seeds larger than 4 mm would be removed by this treatment, but few seeds of this size class were observed, and those found were added to the soil sample.

After sieving the soil was spread out in a 10 mm thick layer over washed and sterilized river sand in circular plastic pots with a diameter of 12 cm and depth of 6 cm. Pots were incubated in a glasshouse and watered as required. Air temperature in the glasshouse during the study period ranged from 20 to 43°C, which is a typical temperature range between day and night and the hottest and coldest months of the study site in Gambella. The major part of the

germination took place within a month and a half, but pots were kept for 3 to 6 months in the glasshouse to monitor later emergence of seedlings. Then all emerged seedlings were removed and the pots were stirred, watered and left for a further one month to stimulate germination of any remaining seeds in the soil. Emerging seedlings were identified, recorded and removed, or replanted for later identification. Identification was verified at the Royal Botanic Gardens, Kew.

Statistical analysis

Data were analyzed using analysis of variance (ANOVA) following the SAS General Linear Models procedure (Statistical Analysis Systems Institute 1997). The model used was a two way ANOVA with site and season (dates) as main factors.

Results

Seed bank sizes of Hyparrhenia confinis: effects of site and season

More than 90% of the soil seed bank in the burned sites was from a single graminoid species, *Hyparrhenia confinis*, whereas the remaining 19 taxa accounted for less than 10 % of the seed pool. The mean soil seed bank density of *Hyparrhenia confinis* as a function of site, depth and season is shown in Figure 1. Generally the number of seeds of this species varied greatly between sites, seasons and depths, whereas within sites the plots (which were at most 2 km apart and with similar vegetation) showed very similar patterns (Fig. 1). The two way ANOVA on effects of sites and seasons indicated that there was significant difference in the total soil seed densities of *Hyparrhenia confinis* between sites (Fig. 1, df.=3, F=13.40, P<0.01) and between seasons (Fig. 1, df.=2, F=41.49, P<0.01). No seeds of *Hyparrhenia confinis* were detected from the densely forested control plot (G) or from the dry forest control plots (X1 and X2). In contrast, seeds of *Hyparrhenia confinis* were abundant in the sites that burn more or less frequently (Fig. 1). At the beginning of the wet season (June) the soil seed pool of *Hyparrhenia confinis* was at a minimum in all burned sites. Thus, the soil seed banks were depleted during the wet season as a result of germination but were replenished in November and peaked in February, most markedly so in site A and site D. In November seeds of *Hyparrhenia confinis* were most abundant in site A followed by site B, C, D and X (in the order of decreasing seed abundance). However, in the dry period (February) the seed bank in site D was replenished too, resulting in relatively high seed numbers both in the woodland-wooded grassland intermediate (site A) and in one of the wooded grasslands (site D).

Vertical distribution of Hyparrhenia confinis seeds in the soil

Major changes in seed density of *Hyparrhenia confinis* with depth were observed. Most of the *Hyparrhenia confinis* seeds in the seed bank were found in the surface soil layer, *i.e.* between 0 and 0.5 cm depth (Fig. 1). The number of seeds at 2.5-3.0 cm depths was at most 20 % of that of the surface layer, with fewer seeds at even greater depth. A few viable seeds were found down to 9 cm depth in all burned sites.

Vegetation cover of Hyparrhenia confinis: changes with sites and season

Hyparrhenia confinis was absent from the densely forested and the dry forest sites. In the burned sites the cover of *Hyparrhenia confinis* was relatively higher in the wooded grassland sites A, C and D than in the woodland (site B) (Fig. 2). There were also significant differences in the cover of *Hyparrhenia confinis* between seasons (Fig. 2). In the plots of the wooded grassland sites C and D the cover of *Hyparrhenia confinis* was higher at the beginning of the

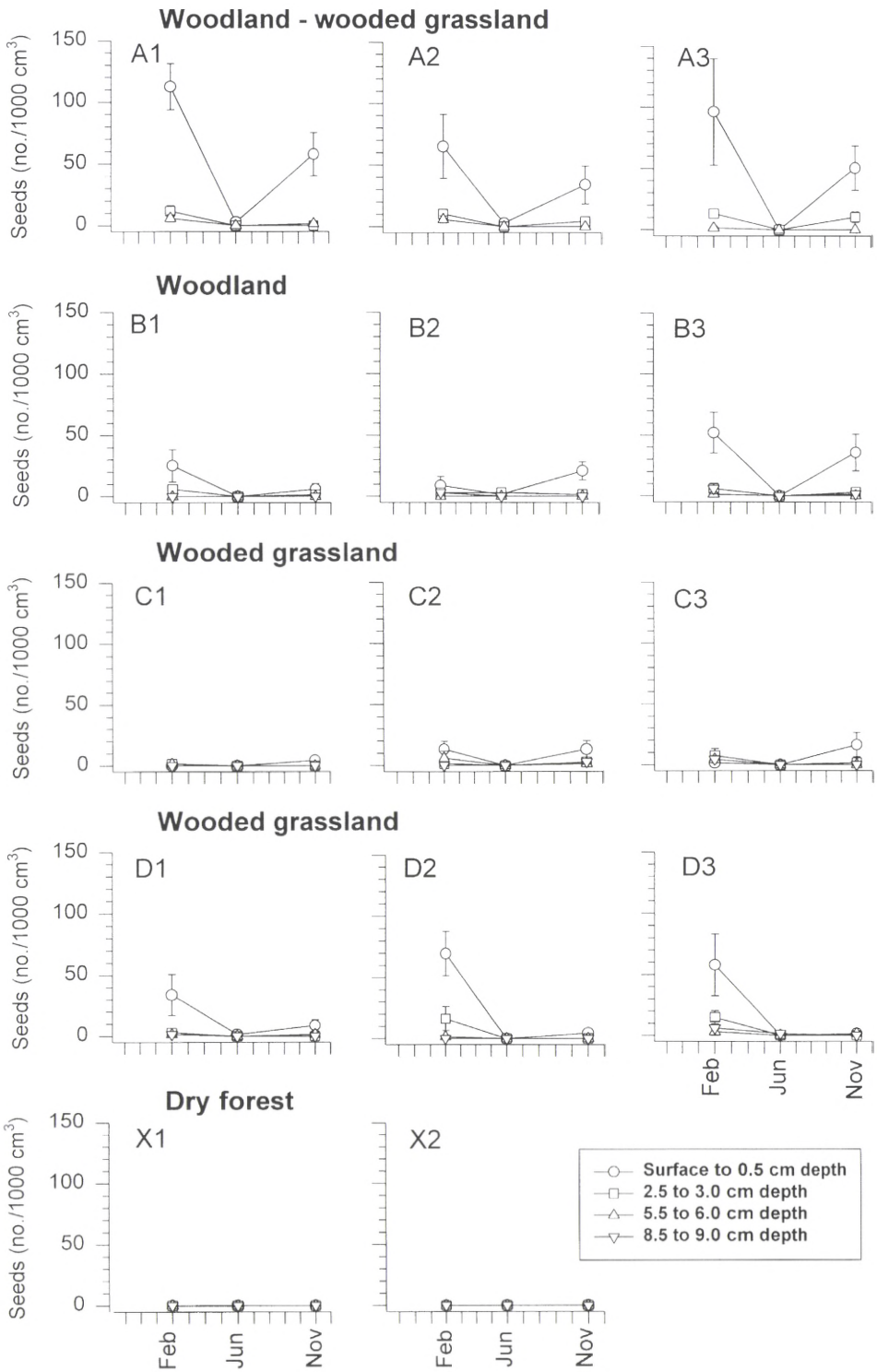

Fig. 1. Number of *Hyparrhenia confinis* seeds in February, June and November 1997 at four depths in soil profiles from three replicate plots of a woodland – wooded grassland intermediate site (A), a woodland site (B), two wooded grassland sites (C and D) and a dry forest site (X). Seeds of the grass were absent from the dry forest and densely forested sites (X and G). Each data point represents the mean of 6 replicate samples ±1 standard error.

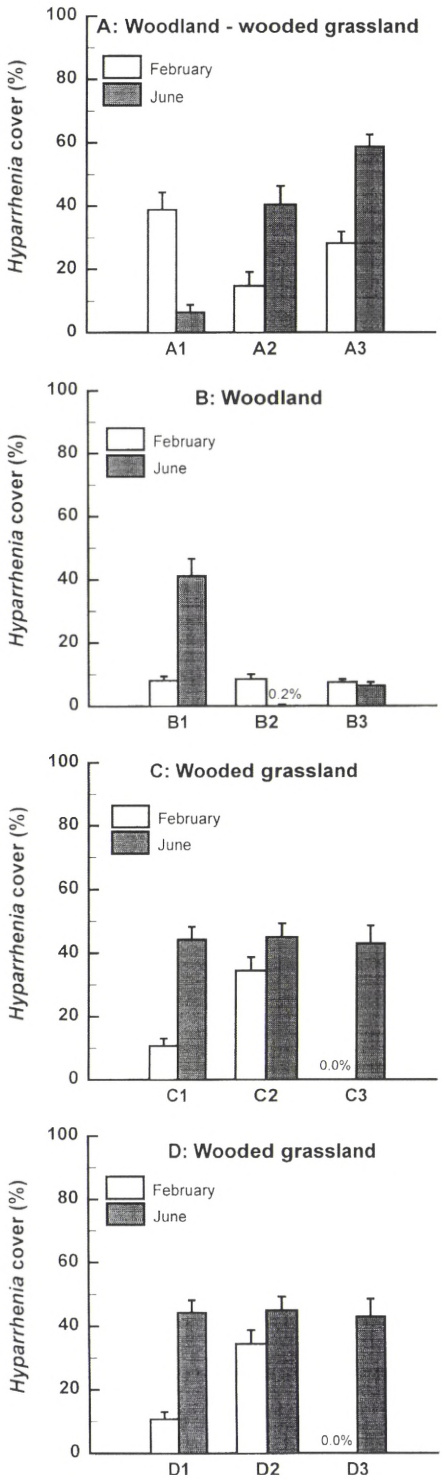

Fig. 2. Above-ground cover of *Hyparrhenia confinis* in February and June 1998 in a woodland – wooded grassland intermediate site (A), a woodland site (B), and two wooded grassland sites (C and D). The grass was absent from the dry forest and densely forested sites (X and G). Each bar represents the mean cover of *Hyparrhenia confinis* in 3 replicate plots per site, with 20 quadrats examined per plot, ±1 standard error.

rainy season (June) than in the dry season (February), at which time fire had removed the above-ground parts of *Hyparrhenia confinis* completely. In the woodland – wooded grassland intermediate (site A) and the woodland (site B) the variable grass cover in June between plots within sites was probably due to spatial differences in rainfall pattern right in the beginning of the rainy season.

Discussion

The soil seed banks of the regularly burned savanna woodland sites of the study area were almost entirely dominated by one grass species, *Hyparrhenia confinis*. According to Phillips (1995: 348) this species is an annual, and the high number of seeds recorded in the soil in the frequently burned sites in this study seems to support this notion. The herbarium specimens investigated for the Flora of Ethiopia pointed towards annual growth habit, although the material was scant when the account for the Flora was written (Sylvia Phillips, pers. com., 1999). However, our field observations of sprouting from stem bases in this species suggests that a large proportion of the individual grass shoots observed in the rainy season may actually come from perennial bases of individuals surviving light fires. These shoots were attached to the old stem bases and did not emerge from germinating seeds. Hence, the success of this species in the frequently burned savannas of the Gambella region could be ascribed to its dual modes of recovery after fires: by sprouts from the base and by germination from the large seed bank in the soil. More work is needed to elucidate the relative importance of the two means of regeneration of the *Hyparrhenia confinis* savanna after the dry season.

The major input to soil seed bank of *Hyparrhenia confinis* was largely in the beginning of the dry season, *i.e.* between November to January, similar to the seed dispersal of many other plants in the study area (pers. obs.). Consequently, *Hyparrhenia confinis* had the highest density of seeds in the soil in the dry season (February). Fire has usually taken place by this time (Jensen & Friis 2001), but there is still a high soil seed bank of this species to initiate growth after the fire when the rainy season begins and soil nutrient availability is increasing (*Jensen* et al. 2001). In addition, *Hyparrhenia* seeds from the study area tolerate temperatures up to 90°C for 1 and 5 minutes and 120°C for 1 minute (Menassie & Michelsen 2001). Seeds in the soil benefit from the scattered "small rains" in April and May, and by the end of June most of the *Hyparrhenia confinis* seeds have germinated and the seed bank is therefore exhausted. In the beginning of the dry season following the growing season, the grass dries up and disperses the seeds, leading to the restoration of the *Hyparrhenia confinis* seed pool in the soil between November and February. It follows that a late fire at the end of the dry season or beginning of the wet season (*i.e.* between May and June) which occurs with low frequency in the region (Jensen & Friis 2001) could be detrimental to this species as most seeds germinate during the "small rain" and the soil seed pool is very low in June.

The high cover of *Hyparrhenia confinis* in the wooded grasslands, the intermediate cover in the woodland and the absence of this and other grass species such as *Andropogon schimperianus*, *Hyparrhenia filipendula*, *Hyparrhenia rufa*, *Loudetia arundinacea* and *Penisetum polystachion* from the more densely forested control plots corresponds to the general pattern of grass cover in savannas across Africa (Menaut *et al.* 1995). The seed abundance in the soil partly reflects this pattern, with absence of *Hyparrhenia confinis* seeds in the densely forested control plots, relatively low seed density in the woodland, and high seed density in one of the grasslands and in the woodland-

grassland intermediate. However, the seed density of *Hyparrhenia confinis* was very low in the one of the grasslands (site C), possibly because of absence of fire the previous year causing a relatively high fire intensity the next year due to high fuel load (which might have led to the observed wood fires and fire damage to trees in this particular site, and to high mortality of seeds in surface soil).

Seasonal changes in the size of the seed pool were large but easily explained. The high above-ground cover of *Hyparrhenia confinis* recorded in the rainy season (June) corresponds to the low seed density at the same time, at which most of the seeds stored in the soil have germinated and contributed to the high cover of the species. In contrast, in the dry season (February) the grass cover is low and the species survives, at least partly, as seed propagules in the soil, which are high in number at that time. The seasonal fluctuations in grass cover observed in these Ethiopian savanna types differ from the lack of seasonal changes in the amount of grass biomass in higher altitude forests of Ethiopia (Michelsen *et al.* 1993) which experience less changes in climate through the year and in which fires are rare or absent.

The input of seeds, their capacity for dormancy and the loss from the seed pool determines the density of seeds and the seasonal changes in the abundance of viable seeds in the soil (Enright 1985; Demel Teketay & Granström 1995; Dalling *et al.* 1997). The almost complete lack of germinating seeds in June suggests that the vast majority of the seeds has either germinated, or does not survive more than half a year of burial. However, seeds deep in the soil may be important for regeneration after late, strong fires that could be detrimental to the survival of individuals of *Hyparrhenia confinis*. The current fire regime of the study sites, high frequency and relatively low intensity, seems to maintain the dominance of *Hyparrhenia confinis* both as seeds in the soil and in herbaceous stratum of the vegetation as a whole.

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Vegetation maps of Ethiopia and Eritrea. A review of existing maps and the need for a new map for the Flora of Ethiopia and Eritrea

Ib Friis & Sebsebe Demissew

Friis, I. & Sebsebe Demissew. 2001. Vegetation maps of Ethiopia and Eritrea. A review of existing maps and the need for a new map for the Flora of Ethiopia and Eritrea. *Biol. Skr.* **54**: 399-439. ISSN 0366-3612. ISBN 87-7876-246-4.

The main features of the existing vegetation maps of Ethiopia and Eritrea, especially those of R.E.G. Pichi-Sermolli from 1957, F. von Breitenbach from 1963 and F. White from 1983, are reviewed. The mapping units on these maps are compared in the light of modern classification of the characteristic species. Later modifications, especially those of I. Friis from 1992 and those of Sebesebe Demissew and others from 1996, are also reviewed. The majority of the long-known vegetation types in the central part of the region have been described, classified and interpreted rather differently by the different authors, and the maps they have produced are therefore at some points notably different. Human activity, especially agriculture for hundreds or thousands of years has had a major impact on the natural vegetation, especially in the highlands, and different authors interpret these secondary vegetation types differently. This is probably one of the main reason for the discrepancies between the maps. Another reason is that a number of characteristic vegetation types in remote areas, for example the vegetation of the Bale Mountains and various forests in the southwestern part of Ethiopia, have been explored and described in the international literature after printing of the maps of Pichi-Sermolli and Breitenbach. Something was known about these vegetation types while White produced his map, but our knowledge has been completed since. A debate at the 3rd International Symposium on the Flora of Ethiopia and Eritrea demonstrated the difficulties with the production of a new, informative vegetation map of Ethiopia and Eritrea at a reasonable scale. Such a map has been planned to accompany the general volume of the Flora of Ethiopia and Eritrea. Suitable criteria for mapping units and additional research that might lead to a satisfactory solution were suggested at the symposium and are discussed further here.

Ib Friis, Botanical Museum and Library, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark. E-mail: ibf@bot.ku.dk

Sebsebe Demissew, National Herbarium of Ethiopia, Addis Ababa University, P.O. Box 3434, Addis Ababa, Ethiopia. E-mail: nat.heb@telecom.net.et

Introduction

This is a review paper of the representation of the vegetation of Ethiopia and Eritrea on a map in one sheet covering the two countries. Such a representation will normally require a base map of a scale between *c.*1:2,000,000 and *c.*1:8,000,000, where the mapping of individual patches of forests, swamps, thickets, *etc.* is not

Rodolfo E. G. Pichi-Sermolli del.
Webbia, vol. XIII, 1957
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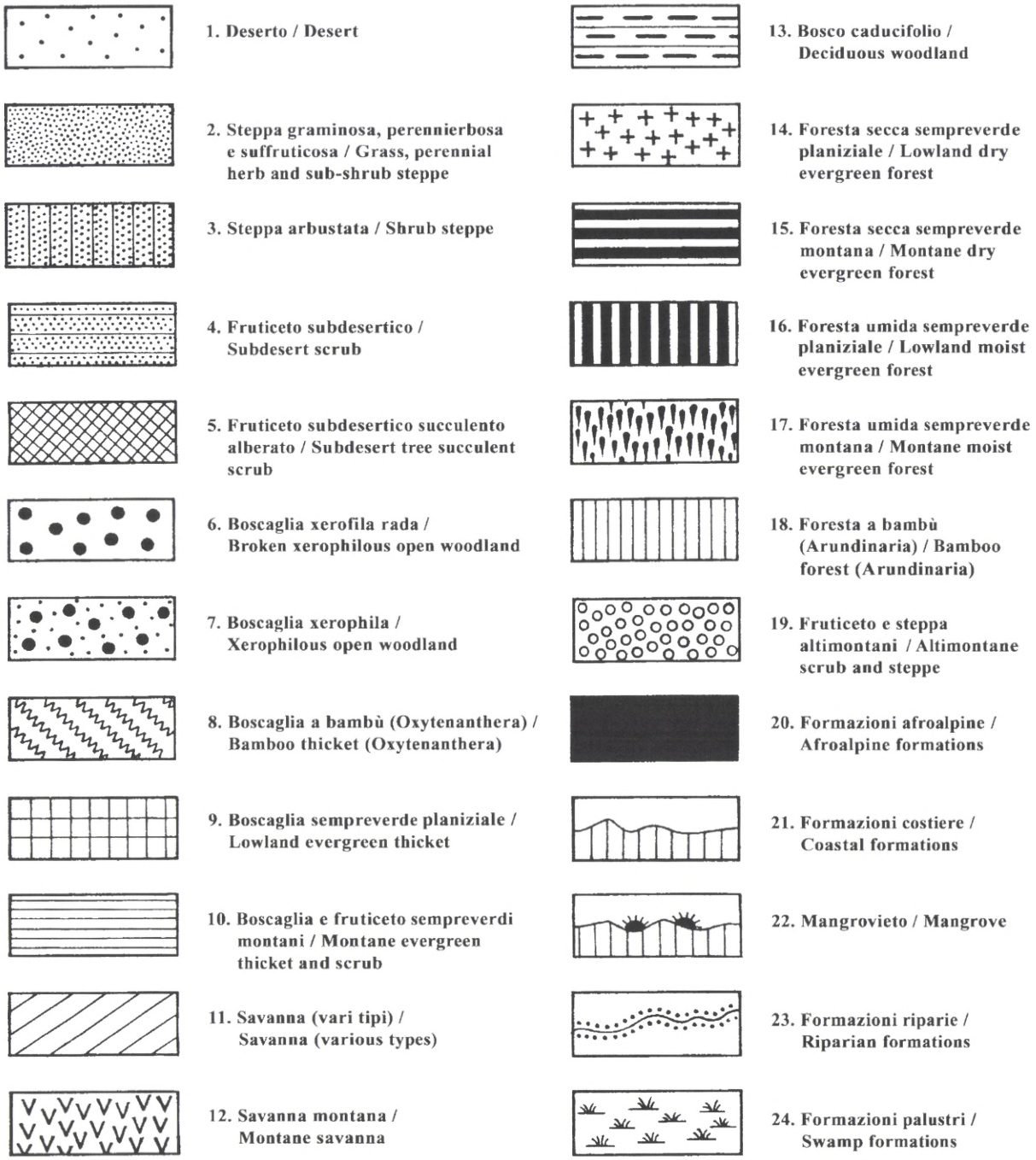


← **Fig. 1**. R.E.G. Pichi-Sermolli's vegetation map of Eritrea, Ethiopia and Somalia (Pichi-Sermolli). For detailed legend, see text. Published as appendix to *Webbia* 13 (1957). Reproduced with permission from Webbia and R.E.G. Pichi-Sermolli.

possible, but has to be replaced by mapping the predominant vegetation. This involves an element of generalisation of the directly observed vegetation types, and the concepts behind this generalisation become important. For this reason, the present paper will review the mapping units of the existing vegetation maps of that range of scales in detail. Several of the publications, where the descriptions of the mapping units and the maps themselves are printed, are not readily available, and some of the botanical nomenclature used in the description of the mapping units is now outdated. It has therefore been considered useful to provide a fairly detailed summary of the previously used mapping units, and to present a modernised nomenclature for the plant species mentioned. The review is also intended to bring together comments and opinions on vegetation mapping of Ethiopia and Eritrea of the botanists at the Symposium who had knowledge of the vegetation and flora of Ethiopia and Eritrea, and it is attempted to draw some conclusions.

In the paper, the total area of the two countries is referred to as the *Flora of Ethiopia and Eritrea* area, abbreviated the FEE area. We have tried to standardise and modernise the geographical terms. However, we have consistently used the names of old administrative regions (Shewa, Kefa, Bale, *etc.*) as these units are used for floristic entities in the *Flora of Ethiopia and Eritrea*. For the later representations of the vegetation in the western lowlands, some of the new administrative regions (Benshangul-Gumuz, Gambella) have been used, as they agree better with the areas with lowland vegetation than the traditional administrative units. The entire highland area is referred to as the Ethiopian Highlands. The plateau west of the Rift Valley is referred to as the Western Plateau, and the one east of the Rift as the Eastern Plateau. We have usually only presented our condensed version of the descriptions of the vegetation units as they were described by the original authors, but in a few cases we have added some comments of our own in sharp brackets.

The history of early vegetation mapping of Eritrea and Ethiopia has been outlined by Pichi-Sermolli (1957: 21-23). The earliest vegetation map of the study area was that of Schweinfurth (1868) in 1:10,000,000. However, this map is mainly of interest for Eritrea and the Sudan border-region, where Schweinfurth had travelled. The rest of the map is not based on original observation. Dove (1890) was the first to emphasise the altitudinal zonation of the Ethiopian vegetation, based on the classical Ethiopian distinction between the agro-ecological zones, in Dove's work referred to as "Quolla," "Woina-Dega" and "Dega." The maps from *c.*1890 to *c.*1945 that cover Ethiopia and Eritrea were basically on too small a scale to be of interest in our work. However, Logan (1946) published a detailed map of the forests of Ethiopia, which was based on rather limited ground survey, in *c.*1:5,000,000. The development that is of interest to us in the context of this paper begins with the map published by Pichi-Sermolli in 1957.

Pichi-Sermolli's physiognomic and floristic classification and vegetation map (1957)

Pichi-Sermolli made his first approach to a vegetation map of Ethiopia and Eritrea when he contributed an account and a map of the arid regions of Tropical East Africa, including our area. This descriptive text and the map only cover woodlands and more arid areas, and the map is on a very small scale, appearing as part of a review of arid regions around the world (Pichi-Sermolli 1955). Shortly after, he published a descriptive memoir and a map of all the vegetation types in the entire region and accompanied it with a detailed descriptive memoir. The map, which has a scale of

1:5,000,000, maps a total of 24 different vegetation types. A reproduction of the map and an enlarged legend are shown in Fig. 1. Of the 24 mapping units used by Pichi-Sermolli, only 21 vegetation types occur within the borders of Ethiopia and Eritrea (the types numbered 9, 14 and 16 only occur in Southern Somalia):

(1) Deserto / Desert
According to Pichi-Sermolli, there is no area absolutely devoid of vegetation in Ethiopia and Eritrea, but there are large areas where the plant cover is so scarce and degraded that it could be referred to as desert. The plant cover, which occurs in these sites, was not well studied before 1957, but Pichi-Sermolli assumed it to show great floristic similarity with that of the various kinds of steppe. On Pichi-Sermolli's map desert is indicated in the central and southern part of the Afar Depression.

(2) Steppa graminosa, perennierbosa e suffruticosa / Grass, perennial herb and sub-shrub steppe
According to Pichi-Sermolli, the steppe is not a homogenous vegetation type throughout the area it occupies in Ethiopia and Eritrea, neither physiognomically nor floristically. It ranges from almost vegetationless types, which can be referred to as subdesert steppe, to types with dense vegetation cover of sub-shrubs. There is no sharp floristic distinction between these two extremes, and they also grade into each other physiognomically. No attempt has been made to map these subtypes. On Pichi-Sermolli's map the vegetation type is indicated in the southern part of the Afar Depression, behind the coastal zone in Eritrea, and in a few places in eastern Ogaden.

(3) Steppa arbustata / Shrub steppe
According to Pichi-Sermolli, this is a vegetation that resembles the grass and perennial herb and sub-shrub steppe, but in the shrub stratum there are shrubs up to 4 m high, which are profusely branched from the base and either globular or obconical. These shrubs may be single or grouped in clusters of 2-4. The dominant shrubs are species of *Acacia*. On Pichi-Sermolli's map this vegetation is indicated in the Eritrean lowland below the subdesert scrub and extending into the Afar Depression to the south, and into Sudan to the north, and in a zone north of the northern escarpment of the Eastern Plateau in Harerge. Another area with this vegetation type extends from Somalia into the Ogaden.

(4) Fruticeto subdesertico / Subdesert scrub
According to Pichi-Sermolli, this vegetation consists of dwarf trees less than *c.*3 m high, shrubs, subshrubs and succulent herbs, all spaced out so that one can pass between them fairly easily. Between the woody plants there are tuberous or bulbous herbs and numerous annuals during the rains. Perennial grasses are absent. The shrubs are species of *Acacia*, *Commiphora, Jatropha,* Capparaceae, *etc.* On Pichi-Sermolli's map this vegetation type occurs in the Afar Depression in areas surrounding the desert vegetation, and it continues northwards in the lowlands, around the areas of higher ground to Western Eritrea and into the Sudan. In the south, this vegetation is indicated near the southern border of Ethiopia to the east of Dolo-Odo and east of Lake Turkana.

(5) Fruticeto subdesertico succulento alberato / Subdesert tree succulent scrub
According to Pichi-Sermolli, this is a scrub of rather scattered shrubs and subshrubs with a sparse upper layer of trees. The shrubs are 1-2 m high, and both the shrubs and subshrubs are usually solitary or in small groups. Many species of both shrubs and subshrubs have succulent features. The trees are up to 6 or 7 m high and usually deciduous, with leaves clustered at the end of the branches or with succu-

lent leaves scattered along the stems, or are cactiform or with dilated trunks. The vegetation incompletely covers the soil, and it mainly occurs on rocky ground and on slopes. Succulent species of the genus *Euphorbia* are well represented. Pichi-Sermolli's map indicates that this vegetation type occurs mostly at the base of the eastern escarpment of the Western Plateau and the northern escarpment of the Eastern Plateau in Harerge. It is also indicated to occur on the mountains in the Afar Depression near the border with Eritrea.

(6) Boscaglia xerofila rada / Broken xerophilous open woodland

According to Pichi-Sermolli, the Broken xerophilous open woodland (6) and the Xerophilous open woodland (7) are very closely associated vegetation types. The differences are in the density of the canopy and in the floristic composition, rather than in the general physiognomy. Pichi-Sermolli defines xerophilous open woodland as an open vegetation with woody plants and hemicryptophytes, in which the large shrubs and the perennial grasses are dominant, and in which there are scattered trees of the taxonomic groups which are characteristic of this vegetation type. The large shrubs are 3-5 m high and branched from the base, and they are so widely spaced that it is usually possible to pass between them. The herbaceous stratum is discontinuous, leaving some of the soil bare to be covered by annuals during the rains. The tree stratum is open. The density of the shrub layer is very dependent on the grazing pressure from the herds of the nomadic people in the areas where this vegetation occurs. Among the trees and shrubs, species of *Acacia*, *Commiphora* and Capparaceae dominate. On Pichi-Sermolli's map this vegetation type is very widespread in the Ogaden and in less arid parts of the Afar Depression.

(7) Boscaglia xerophila / Xerophilous open woodland

According to Pichi-Sermolli, this vegetation type differs from the previous one by the higher density in the tree stratum and in the floristic composition. On Pichi-Sermolli's map this vegetation type occurs on the western slopes of the Eritrean highlands, in the southern part of the Afar Depression and in a zone round the highlands of Harerge and Bale south to Dolo-Odo and across to the northern tip of Lake Turkana. [It seems from this that there are also floristic differences within this vegetation type, as the Sahel vegetation in western Eritrea is somewhat different from the zone round the highlands of Harerge and Bale south to Dolo-Odo and across to the northern tip of Lake Turkana.]

(8) Boscaglia a bambù (Oxytenanthera) / Bamboo thicket (Oxytenanthera)

According to Pichi-Sermolli, this vegetation type consists predominantly of the lowland bamboo *Oxytenanthera abyssinica*, the culms of which reaches a height of 10-12 m. It forms almost pure stands with rather few other species as infrequent components. On Pichi-Sermolli's map it forms extensive stands in mosaic with the deciduous woodland. This mosaic forms a zone along the western escarpment of the western highlands from Eritrea to Kefa.

(9) Boscaglia sempreverde planiziale

This vegetation type occurs only in Somalia.

(10) Boscaglia e fruticeto sempreverdi montani / Montane evergreen thicket and scrub

According to Pichi-Sermolli, there are two vegetation types here, distinguished on physiognomy: scrub and thicket. The evergreen scrub consists of evergreen shrubs, small trees or lianas, but with only few taller trees. Tall, candelabra-shapes species of *Euphorbia* may occur.

The shrub stratum is 2-3 m high and consists of sclerophyllous plants or plants with green, leafless and more or less succulent stems, mixed with some deciduous species. Lianas, often with succulent features, are very common. This vegetation type is characteristic of slopes. The evergreen thicket is dominated by 3-5 m high shrubs, from which numerous trees emerge. The trees do not form a continuous canopy above the shrubs. Perennial herbs and grasses are not dominant except in open spaces. Generally, the scrub develops at lower altitudes and in drier places than the thickets. Pichi-Sermolli cites as common species for example *Acokanthera schimperi*, *Carissa edulis*, species of *Euclea*, *Rhamnus*, *Rhus* and *Maytenus*, *etc.* He includes vegetation with *Juniperus procera*, shrubby *Olea europaea* subsp. *cuspidata* and *Barbeya oleoides* or *Buxus hildebrandtii* under this vegetation type, as well as the almost pure stands of candelabra-shaped species of *Euphorbia* on slopes and escarpments. On Pichi-Sermolli's map this vegetation has been indicated on large areas of the highlands below *c.*2000 m. Together, the general vegetation type, including both the scrub and the thicket, is indicated throughout the highlands from the northern part of Eritrea southwards to Sidamo and eastwards into Harerge at altitudes between 900 and 2400 m.

(11) Savanna (vari tipi) / Savanna (various types)

According to Pichi-Sermolli, savanna is a physiognomically defined vegetation type consisting of mainly xeromorphic herbaceous plants, among which grasses and species of Cyperaceae are the dominant. These plants form a continuous ground cover at least 80 cm high with scattered trees or shrubs, or with grouped trees and clumps of shrubs. African savanna is frequently subject to burning. Pichi-Sermolli has listed a range of rather different vegetation types, which fall within the limits of this physiognomic definition. From western Eritrea he describes a vegetation type with a grass stratum dominated by species of Andropogoneae, small shrubs and scattered trees of *Balanites aegyptiaca* and/or *Acacia seyal*; the type continues southwards in the western lowlands to the Blue Nile. From areas around Lake Tana he describes savanna dominated by *Acacia abyssinica*, *A. seyal* and *A. bavazzanoi* with a short grass stratum on alluvial soils, and a stratum up to 1.8 m on the hills. From the valleys of the Didessa and the Baro Rivers are recorded another savanna with *Acacia*, *Gardenia*, *Protea* and *Stereospermum*. In the Rift Valley between Shewa and Gamo-Gofa the dominant tree species are *Acacia albida*, *A. seyal*, *Balanites aegyptiaca*, and various grasses, of which only some are of the tribe Andropogoneae. On Pichi-Sermolli's map it is also indicated that this vegetation type occurs in the southern lowlands from west of the Omo River to near Dolo Odo, but very little evidence for this is quoted.

(12) Savanna montana / Montane savanna

According to Pichi-Sermolli, this vegetation type can be neatly distinguished from all other types of savanna on its physiognomy, ecology and its floristic composition. It consists of a herbaceous stratum usually not higher than 30-80 cm, very rich in perennial grasses and species of Cyperaceae, but also with sub-shrubs and perennial herbs, among which bulbous and rhizomatous plants occur. The monotony of this grassy sward is broken by scattered shrubs or trees, usually rather small. Sometimes the shrubs form clusters or thickets, in the shelter of which larger herbs may occur. This vegetation covers the extensive gently undulating areas of the highlands. In places where the flat ground meets a steep slope, the change to montane evergreen thicket and scrub is abrupt. It is found at altitudes between 1800 and 3000 m. The vegetation occurs in the areas where human activity has been longest

and most intense, and the vegetation is probably in most places derived from forest and other woody vegetation types. This is indicated by the fact that the essential woody species in this vegetation type are all the same that occur in various kinds of forest. It occurs from northern Eritrea to Gamo-Gofa, and from Arsi to Harerge. A small area at Mega is not marked on the map.

(13) Bosco caducifolio / Deciduous woodland
According to Pichi-Sermolli, this vegetation consists of deciduous trees, which are 5-12 m high and form a very open canopy, under which there is a heterogeneous ground cover with small trees, shrubs and perennial herbs and grasses. There is a marked seasonality of the flowering and litter-fall of these trees. This vegetation occurs on the western escarpment of the Western Plateau where it forms a zone from western Eritrea to northwestern Gamo-Gofa, interrupted by areas of Bamboo thicket (*Oxytenanthera*). It is found between *c.*700 and 1800 m, and it also penetrates into the highlands along the big rivers. Characteristically, the canopy contains species of *Boswellia, Anogeissus, Terminalia, Combretum, Lannea, Lonchocarpus, Stereospermum, Commiphora, Erythrina, Dalbergia, Gardenia, Dombeya, Balanites, Piliostigma, etc.*

(14) Foresta secca sempreverde planiziale
As defined by Pichi-Sermolli, this vegetation type occurs only in Somalia.

(15) Foresta secca sempreverde montana / Montane dry evergreen forest
According to Pichi-Sermolli, this vegetation has a canopy in several stories. The tallest storey is very open and irregular, below which there is a more closed stratum of trees and large shrubs, and on the forest floor a stratum of shrubs and herbs. Lianas and epiphytes are frequent. This vegetation type develops at rather high humidity, but the rainfall is less than that which supports the following type, and a clearly marked dry season exists. Coniferous species (*Juniperus procera* and *Podocarpus falcatus*) dominate most examples of this forest type. A type dominated by *Podocarpus* occurs on both the Western and the Eastern Plateau in association with broad-leaved species. *Juniperus procera*-dominated forest occurs in the driest places. Mixed *Juniperus-Podocarpus* forest is found in the central part of the highlands, particularly Shewa, Harerge and Sidamo. However, other forest types are included here. For example the *Mimusops kummel*-forest around and west of Lake Tana. Finally, Pichi-Sermolli includes here a type called *Acacia abyssinica*-forest, which is found from Lake Tana to Sidamo.

(16) Foresta umida sempreverde planiziale
As defined by Pichi-Sermolli, this vegetation type occurs only in Somalia.

(17) Foresta umida sempreverde montana / Montane moist evergreen forest
According to Pichi-Sermolli, this vegetation has a canopy in several stories, and consists typically of a fairly compact canopy stratum at 18-25 m, above which 30-50 m tall trees reach. Below there is a stratum of shrubs or small trees up to *c.*8 m high and a forest floor stratum of herbs or small shrubs. Epiphytes and lianas are common. The stratum of tall trees includes species of *Pouteria* (*Aningeria*), *Morus, Olea, Trilepisium* (*Bosqueia*), *etc.* Tree ferns (*Cyathea sp.*), *Ensete ventricosum*, species of *Dracaena* and large, candelabra-shaped species of *Euphorbia* occur in these forests. There are, according to Pichi-Sermolli, at least two or three different associations in this formation, but he felt unable to distinguish between them before further research had been carried out. According to Pichi-Sermolli these forests occur between 1300 and 2300 m in Welega, Ilubabor, Kefa and Sidamo. The extensive forests, the

Harenna Forest, on the southern slope of the Bale Mountains, were then completely unrecorded in the literature.

(18) Foresta a bambù (Arundinaria) / Bamboo forest (Arundinaria)
According to Pichi-Sermolli this is an almost pure vegetation type, dominated by dense stands of the mountain bamboo (*Arundinaria alpina*), associated with a limited number of trees, shrubs and herbs. Pichi-Sermolli has recorded this formation in the southwestern part of Ethiopia between 2300 and 3200 m in very humid areas of Welega, Ilubabor and Kefa.

(19) Fruticeto e steppa altimontani / Altimontane scrub and steppe
These formations are, according to Pichi-Sermolli the scrub and steppe vegetation of the highest part of the mountains. They are found at altitudes between 3000 and 3700 m in restricted areas below the Afroalpine formations described as the subsequent number. The formations can develop into two rather different types of vegetation, but many intermediate forms occur. One of the types is the high-mountain scrub, with patches of 3 to 6 m high thickets with *Erica arborea* as the dominant species. The *Erica* shrubs may be associated with *Hypericum*, *Rosa*, *Rapanea*, *Myrica*, *Myrsine*, *etc.* The other type is the high-mountain steppe, which is much less distributed than the previous type, and may according to Pichi-Sermolli represent degraded high-mountain scrub. Pichi-Sermolli records these formations from the Semien, a number of mountains east of Lake Tana, including Lasta (Mt. Abuna Yosef), the areas around Mt. Guna, etc, mountains in Gojam (Choké Mountains.), mountains west of Addis Ababa, the Chillalo and Galama Mountains in Arsi, the Amaro Mountains in Sidamo, and the Gughe Highlands in Gamo-Gofa. It should be noted that in Pichi-Sermolli's account there is no record of the extensive areas of this vegetation in Ethiopia found on the Bale Mountains. This extended area only became known in the international literature at a later point.

(20) Formazioni afroalpine / Afroalpine formations
Pichi-Sermolli has, because of the rather limited extent of the highest mountain peaks when shown on a map in 1:5,000,000, gathered a number of high altitude vegetation types under this heading, including at 4000-4350 m high-mountain steppe with *Lobelia rhynchopetalum*, dominated by grasses and low *Erica arborea* on rock-formations. At higher altitudes the steppe passes very gradually into various rocky communities with species of *Helichrysum*, grasses, *etc.*, and in damp places massive communities with species of *Carex*, chiefly *Carex monostachya*. According to Pichi-Sermolli, Afroalpine formations are found above approximately 4000 m. On his map, it is indicated the Semien Mountains, in various high mountain massifs east of Lake Tana (Lasta, Guna, *etc.*), in the Choké Mountains of Gojam, in a few, small mountain massifs west of Addis Ababa, in the Chillalo and Galamo Mountains in Arsi, and in the Gughe Highlands in Gamo-Gofa. However, Pichi-Sermolli points out that associations with characteristic Afroalpine plants can also be found at lower altitudes. It should be noted that in Pichi-Sermolli's account there is no record of the most extensive Afroalpine vegetation in Ethiopia, that on the Sannetti Plateau in the Bale Mountains. This extended area of Afroalpine vegetation only became known in the international literature at a later point.

(21) Formazioni costiere / Coastal formations
Pichi-Sermolli gives a detailed account of the coastal formations, but much of his description relates to areas in Djibouti and Somalia. Here, we will only deal with the formations inside the

FEE area. The rocks and the derived soil types at sea level are coralline in origin. The coast is rocky or sandy, often with low scrub rich in Capparaceae, Zygophyllaceae, Chenopodiaceae, Plumbaginaceae, Salvadoraceae, *etc.*, and many grasses. In some places dwarf shrubs may form extensive areas. Salt pans have often specialised grasses. Mangrove vegetation is described separately below.

(22) Mangrovieto / Mangrove
Pichi-Sermolli has recorded this formation from a number of localities along the Red Sea coast of the FEE area, where it has the aspect of a daily partly submerged scrub or thicket up to *c.*6 m high. The dominant species woody species is *Avicennia marina*, in places supplemented with *Rhizophora mucronata*.

(23) Formazioni riparie / Riparian formations
Pichi-Sermolli has gathered under this heading a number of formations, which occur along temporary or permanent water courses, as well as on lake shores. Along temporary streams (wadis), there are usually riparian woodlands with species of *Acacia*, *Ficus*, *Hyphaene*, *etc.* Particularly *Hyphaene* is characteristic of lowland riparian vegetation both on the western and eastern side of the Ethiopian highlands. At more permanent streams species of *Tamarix, Tamarindus indica, Diospyros mespiliformis, Syzygium guineense* and a number of evergreen scrubs or climbers are common. In higher rainfall areas there may be more species trees in the riverine forest, for example *Mimusops kummel* and *Phoenix reclinata*. The examples of lake shore vegetation described by Pichi-Sermolli are very varied, they include riparian forests of, for example, *Aeschynomene elaphroxylon* or *Mimusops kummel*, riparian scrub of species of *Sesbania*, reed swamps with species of *Phragmites*, *Typha* and *Cyperus papyrus*, *etc.*

(24) Formazioni palustri / Swamp formations
Pichi-Sermolli pointed out that swamp forests hardly occur in the area he described and that there might be great floristic similarity between types of lake shore vegetation and swamp formations. Swamps dominated by grasses and species of Cyperaceae and *Typha* cover extensive areas. Halophile swamps have many species of Chenopodiaceae, especially *Salsola* and *Salicornia*.

Characteristic features of Pichi-Sermolli's map

The most notable feature of Pichi-Sermolli's classification is the classification of the open vegetation in the lowlands and the vegetation on the plateaux. Large areas of the lowlands surrounding the Ethiopian Highlands are classified as *(6) Broken xerophilous open woodland* and *(7) Xerophilous open woodland* (the *Lowland Steppes* of Breitenbach) or *(11) Savanna (various types)*. The Afar Depression and parts of the western lowlands of Eritrea are characterised by desert (1), various steppes (3-4) and deciduous scrub (4-5). According to Pichi-Sermolli the predominant vegetation types on both the Western and the Eastern Plateau are *(12) Montane savanna* at the higher altitudes (the *Mountain Savannahs* of Breitenbach) or *(10) Montane evergreen thicket and scrub* at the lower altitudes (the *Lowland woodland* of Breitenbach).

Pichi-Sermolli's map formed the basis of the representation of the vegetation of Eritrea, Ethiopia, Djibouti and Somalia on the AETFAT vegetation map of Africa in 1:10,000,000 (Keay 1959). The distribution and classification of the woodlands, wooded grasslands, savanna, bushland, semi-desert bushland, grassland and semi-desert grassland according to Pichi-Sermolli do not agree with modern views. This is particularly the case with his vegetation type no. 11, which is now split into a number of unrelated types of Sudanian woodland and

Somalia-Masai *Acacia-Commiphora* deciduous woodland, bushland or scrub. Specifically, it is our impression that it is incorrect to indicate *(7) Xerophilous open woodland* for the western lowlands of the Gambella and Benshangul-Gumuz Region.

In the highlands, it is an oversimplification to indicate that *(12) Montane savanna* is the dominant vegetation in the northern part of the Western Plateau and in the central part of the Eastern Plateau, and that *(10) Montane evergreen thicket and scrub* is dominant in the southern part of the Western Plateau and the peripheral parts of the Eastern Plateau. It is also an oversimplification to say that there is a sharp distinction between *(10) Montane evergreen thicket and scrub* and *(12) Montane savanna.* These two vegetation types have considerable overlap, and were merged for mapping purpose by White (1983). However, there is no doubt that the mapping of the plateau-vegetation is a very complicated problem even today.

Breitenbach's physiognomic and floristic classification and vegetation map (1963)

Breitenbach's classification of the vegetation types of Ethiopia (then including Eritrea) and vegetation map appeared in the introduction to his mimeographed book *The indigenous trees of Ethiopia* (Breitenbach 1963). The main difference to the classification used by Pichi-Sermolli is a much more detailed and rigid classification of the vegetation based on physiognomy and seen in relation to altitude, humidity and presumed stage in succession. A generalised diagram of altitude and humidity was included in order to position the vegetation types in relation to these factors. The diagram is reproduced here as Fig. 2. Breitenbach has described the problem of fitting the vegetation of a site into a large-scale classification as identifying its "vegetational character, *i.e.* the developmental or devastational stage as well as the successional trend ..." The philosophy behind the classification is described as follows (Breitenbach 1963: 16-17):

> "This vegetational character as expressed by a certain plant community, however, cannot be properly recognised by simple reference to the climax-scheme, for the theory that can be represented in such a simplified and static graph would necessarily become a fiction if applied to the dynamic system of succession.
>
> The true climatic climaxes are very rare, especially in arid and semi-arid zones where the moving forces of succession are weak and the final development-stage held back by degenerative forces, such as fires, grazing, or the various activities of man, so that plant communities of great permanence are perpetuated at subfinal levels, the so-called subclimaxes. In the regions of the nomads and on shifting-cultivation areas, as well as in forests subject to low-grade operations, succession is kept in pro- and retrogressive fluctuation. There are also completely undisturbed sites where the vegetation has not yet reached the climatic climax, due to the immaturity of the soil. On many extreme localities, where continued soil erosion, resistant rock, hyperalkality, high water-table, or other negative influences act as permanent natural barriers, succession stopped at an initial or intermediate stage, the so-called physiographic or edaphic climax. Over and above, the mountainous orography of the greater part of Ethiopia exercises additional modifying influences on the arrangement of the plant communities, that are most confusing in the zones of climatic inversion as found in draughty ravines and shady valleys, at exposed escarpments, and in humidity- and cold-depressions.
>
> It is impossible to set up a fully satisfying and reliable detail-scheme of all those mosaic-like intermingling – initial, intermediate, transitory and permanent – vegetation forms and types. The recognition of the vegetational character of a particular site requires a thorough analysis of its static and dynamic elements as indicated by the respective, individual plant community, provided that at least its dominant members and their ecological and sociological range are known.
>
> For the purpose of a general introduction, however, a more summarising method may be useful, as employed in the geobotanical map [discussed later] and surface-cover quotation ... [quoted later], as well as in the following description of the major plant communities of Ethiopia [described in detail later]."

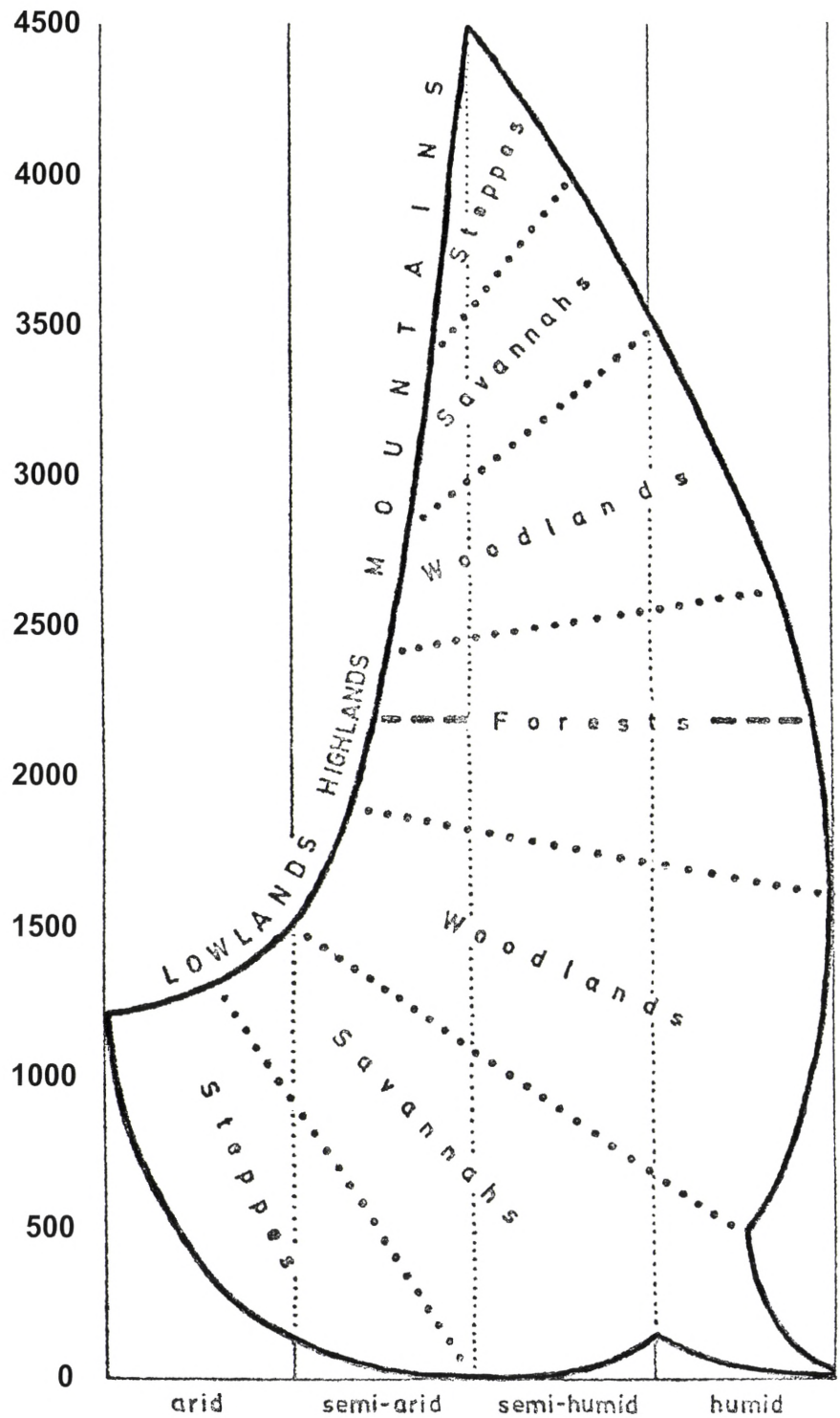


Fig. 2. Diagram of relation between altitude and humidity in the vegetation of Ethiopia and Eritrea, according to Breitenbach (1963). Reproduced with permission from J. von Breitenbach.

Breitenbach's book is now rather rare, and we have therefore decided to describe his highly complex and hierarchically arranged system of vegetation types in some detail in order to make it available for future discussion. We do not think that the strong emphasis on physiognomy and seral stages and climax vegetation in the classification are workable features in connection with vegetation mapping on the scale of 1:5,000,000 to 1:10,000,000, especially not where the topography is as complicated as is the case with Ethiopia and Eritrea. Yet, Breitenbach's classification reflects some very useful observations of characteristic features of Ethiopian and Eritrean vegetation, and it is well worth keeping in mind in the future.

Since many of the species mentioned in Breitenbach's text have now been re-identified, our description of the system will also to some extent be a modern interpretation of Breitenbach's work. Where unambiguous, we have simply replaced Breitenbach's plant names with the ones used in the *Flora of Ethiopia and Eritrea* or other modern sources. Two of his vegetation types have unfortunately names that are outdated for this reason, the *Faidherbia-Thicket* (1.334) because *Faidherbia albida* is now *Acacia albida*, and the *Aningeria-Forest* (2.233) because *Aningeria adolfi-friedericii* is now *Pouteria adolfi-friedericii*; in this account we have chosen not to change the names for these vegetation types.

The four levels in the hierarchy are outlined here in such a way that the typography and indentation indicates the hierarchy, and all generalised statements in the following review are, unless the contrary is clearly indicated, based on the chapter on vegetation in Breitenbach (1963). The lowermost level in the hierarchy is a classification based on altitude (lowlands, highlands, and mountains). The second level represents a sequence of presumed seral stages leading to a climax type (usually steppe, savannah, woodland, and forest). The third level indicates a moisture gradient (arid, semi-arid, semi-humid, and humid). The fourth level is related to the amount of woody species in the vegetation.

(1) LOWLANDS

According to Breitenbach, the lowland vegetation includes only steppes (including semi-desert), savannahs, scrub and woodlands.

(1.1) Lowland-Steppes.

According to Breitenbach, these have an irregular or broken ground cover and scattered shrubs or small trees.

(1.11) Arid Lowland-Steppe.

According to Breitenbach, this vegetation occurs up to 1300 m on a wide range of soil types, including very degraded skeletal soils; it has sometimes a mosaic of the various subtypes.

(1.111) Semidesert

According to Breitenbach, this is the most open type, often occurring on sandy soil; it is reported especially from the Danakil (Afar) Depression and the Ogaden. The usually low plants are very scattered.

(1.112) Grass-Steppe

According to Breitenbach, this vegetation type is reported from the Southern Danakil (Afar) Depression and eastern Eritrea; the vegetation is dominated mainly by annual grasses, *e.g. Aristida, Chrysopogon, Sporobolus, etc.*

(1.113) Shrub-Steppe

According to Breitenbach, this vegetation type is reported from the Eritrean lowlands and the western Danakil (Afar) Depression; it consists of scattered, mostly deciduous shrubs up to 3 m high, especially species of Capparaceae, *Acacia, Commiphora, Grewia, Euphorbia, etc.*, and many annual grasses.

(1.12) Semi-Arid Lowland-Steppe
According to Breitenbach, this vegetation is, in spite of its classification as steppe, composed of low, thicket-forming shrubs and scattered small trees.

(1.121) Subdesert-Scrub
According to Breitenbach, this is reported from the lower foothills of the eastern escarpment of the Western Plateau; physiognomy and floristic composition much like Shrub-Steppe, with a ground cover of annual or perennial grasses and small subshrubs.

(1.122) Succulent-Scrub
According to Breitenbach, this is reported from areas along the eastern escarpment of the Western Plateau and the Danakil Alps; it contains deciduous shrubs and trees, for example *Sterculia, Boswellia, Acacia, Lannea, etc.*, with an understorey of scattered shrubs and undershrubs and many succulents, for example species of *Euphorbia, Adenium, Sansevieria, Aloe, etc.*

(1.123) Scrub-Steppe
According to Breitenbach, this is recorded from the Eritrean lowlands, the Awash Basin, the eastern part of Harerge and the western lowland parts of Ilubabor and Welega; it contains a stratum of thicket-forming shrubs of for example *Acacia, Commiphora, Zizyphus, Capparis, Maerua, etc.*, and scattered 3-5 m tall trees, for example species of *Delonix, Acacia, Adansonia, Dobera, Lannea, etc.*

(1.2) Lowland-Savannahs
The lowland savannahs are, according to Breitenbach, reported to occur over vast areas in the Rift Valley, on the plains surrounding Lake Tana, in the western lowland plains towards the Sudan, on the lower escarpments of both the Western and the Eastern Plateau, and in the lowlands of southern Kefa, Gamo-Gofa, Borana and Welega.

(1.21) Arid Lowland-Savannahs
According to Breitenbach, these are floristically related to the Grass- and Shrub-Steppes and occur under very arid conditions at 800-1500 m.

(1.211) Grass-Savannah
According to Breitenbach, this is a fairly closed vegetation type with two layers of drought-adapted grasses, an upper with species of *Andropogon, Hyparrhenia, etc.*, and a lower one with species of *Pennisetum, Panicum, Eragrostis, etc.* Species of Cyperaceae may also be present.

(1.212) Shrub-Savannah
According to Breitenbach, this is a vegetation type with a stratum of scattered small trees, for example *Acacia* and *Ficus, etc.*, and shrubs, for example *Gardenia lutea*, over a grass stratum.

(1.22) Semi-arid Lowland-Savannah
According to Breitenbach, this group of vegetation types is characterised by larger and more prominent trees than in the previous group.

(1.221) Scrub-Savannah
According to Breitenbach, this type is floristically correlated with the Scrub-Steppe. The trees are for example species of *Delonix, Acacia, Ficus, Sterculia, Dobera, Combretum, Moringa, etc.* A shrub stratum may consist of species of *Maerua, Grewia, Zizyphus, Commiphora, etc.* There is no recording of a grass stratum; however, a grass stratum must be present in this vegetation type in order to qualify it as a type of savannah.

(1.222) Incense-Scrub
According to Breitenbach, this type is recorded as being common on the western escarpment of the Western Plateau and in the deep river valleys of the plateau at 500-1300 m. The dominant tree is *Boswellia papyrifera*. A stratum of shrubs or shrubby trees includes species of *Pte-*

rocarpus, Lonchocarpus, Anogeissus, Sterculia, Combretum, Commiphora, Pseudocedrela, Lannea, Sclerocaria, etc. We do not agree with this characterisation, which fits very large areas of the western escarpment, as many of the species here referred to as scrubs in fact usually reach tree height. Again, there is no recording of a grass stratum; however, a grass stratum must be present in this vegetation type in order to qualify it as a type of savannah.

(1.223) Tree-Savannah
According to Breitenbach, this type is recorded as being floristically related to *Acacia*-Thicket (1.311), and is best developed at 800-1500 m. It consists of trees and big shrubs, for example species of *Piliostigma, Cassia, Entada, Ficus, Sterculia, Terminalia, Combretum, Balanites, Stereospermum, etc.* Again, there is no recording of a grass stratum; however, a grass stratum must be present in this vegetation type in order to qualify it as a type of savannah.

(1.23) Semi-humid Lowland-Savannah
According to Breitenbach, this is a very heterogeneous assembly occurring under widely different ecological conditions.

(1.231) Coastal-Plain Thicket, Salt-Marsh Thicket
According to Breitenbach, the Coastal-Plain Thicket occurs along the coasts of Eritrea from sea level up to 700 m; it consists of rather few species, for example a species *Lycium*, with groups of the palm *Hyphaene thebaica.* Salt-Marsh Thicket also contains species of *Tamarix, Suaeda, etc.*

(1.232) Thicket-Savannah
According to Breitenbach, this is a vegetation type occurring from sea-level up to 800 m, with many species of shrubs and small trees, but Breitenbach does not state where it occurs. The woody stratum contains species of *Acacia, Dalbergia, Ficus, Euphorbia, Phyllanthus, Ximenia, Zizyphus, Balanites, Lannea, Strychnos, Gardenia, Steganotaenia, Cordia*, and the bamboo *Oxytenanthera.* The ground cover is a continuous grass and Cyperaceae stratum. It is said to be floristically related to Scrub-Savannah (1.221) and Lowland-Bamboo-Thicket (1.233). We think that from its floristic composition it is likely that this type represents a dense form of the vegetation types, which occur on the western escarpment of the Western Plateau.

(1.233) Lowland-Bamboo Thicket
This type occurs up to 1300 m on the western escarpment of the Western Plateau and in the deep river valleys of the plateaux. It is a tall thicket strongly dominated by the bamboo *Oxytenanthera abyssinica*, which in many places forms almost pure stands.

(1.24) Humid Lowland-Savannah
Under this heading is, according to Breitenbach, gathered a number of coastal and riparian scrub formations.

(1.241) Mangrove-Scrub
According to Breitenbach, this vegetation type is only found on the Red Sea coast of Eritrea; dominated by *Avicennia marina* and *Rhizophora mucronata.*

(1.242) Riparian Scrub
According to Breitenbach, this type is found along seasonal and permanent water courses below 700 m. Dominant trees and shrubs are *Acacia, Ficus, Tamarix, Zizyphus, Hyphaene, etc.*

(1.3) Lowland-Woodlands
According to Breitenbach, the woodlands have an upper storey up to 12 m high, which form a more or less closed canopy over a thicket of up to 3 m high shrubs. They occur on the more elevated plains and plateau-escarpments.

(1.31) Semi-arid Lowland-Woodland
According to Breitenbach, these types are common at lower altitudes of both the Western and the Eastern Plateau.

(1.311) Acacia-Thicket
According to Breitenbach, this type occurs at 1000-1800 m and is floristically related to the Tree-Savanna (1.223) and *Acacia*-Forest (2.111). Its tree stratum is dominated by species of *Cassia, Acacia, Entada, Ficus, etc.* A shrub stratum includes species of *Grewia, Euphorbia, Maytenus, Zizyphus, Rhus, etc.*

(1.312) Euphorbia-Thicket
According to Breitenbach, this type is found in drier habitats than the previous one and is characterised by the big, candelabra-shaped species of *Euphorbia* which form dense stands up to 12 m high. A number of trees and shrubs are associated, especially species of *Acacia, Cassia, Maytenus, Euclea, Rhus, Carissa, etc.* A number of climbers, for example *Pterolobium stellatum*, are characteristic.

(1.32) Semi-humid Lowland-Woodland
According to Breitenbach, these types occur at the same altitudes as the previous types, but at slightly higher rainfall, and the species are mainly composed of broad-leaved species.

(1.321) Combretum-Thicket
According to Breitenbach, this type is recorded at 700-1600 m and contains a number of deciduous trees over a mainly deciduous thicket. The tree stratum contains species of *Annona, Albizia, Cussonia, Entada, Combretum, Terminalia, Stereospermum, etc.* The lower strata contain species of *Grewia, Securidaca, Croton, Maytenus, Harrisonia, Gardenia, etc.*

(1.322) Croton-Thicket
According to Breitenbach, this type is recorded at 1200-1800 m and contains a number of deciduous trees over a mainly evergreen thicket. The tree-stratum contains species of *Acacia, Albizia, Ficus, Croton, Combretum, Terminalia, Olea, Ehretia, etc.* The lower strata contain species of *Gnidia, Croton, Catha, Carissa, Maytenus, Bersama, Ozoroa, Rhus, etc.*

(1.33) Humid Lowland-Woodland
According to Breitenbach, this is a heterogeneous assembly of vegetation types in higher rainfall areas, along streams and in places with high ground water table.

(1.331) Balanites-Thicket
According to Breitenbach, this is a vegetation type, which develops on flood plains where the water table is near the surface, and is found up to 1600 m. The tree stratum is dominated by *Balanites aegyptiaca.* Other important trees are species of *Acacia, Dichrostachys, Ficus, Tamarindus, Kigelia, Vitex, etc.*

(1.332) Albizia-Thicket
According to Breitenbach, this is a vegetation type found at 1200-1700 m in areas with fairly high precipitation. The dominant trees are species of *Albizia*; other trees in the canopy are species of *Millettia, Schefflera, Trema, Ficus, Ritchiea, Croton, Euphorbia, Maesa, Diospyros, etc.* Lower strata include species of *Bridelia, Bersama, Dodonaea, Pistacia, Carissa, Vernonia, etc.* Although not specifically mentioned by Breitenbach, there seems from his floristic enumeration to be considerable similarity between this vegetation type and some of his types of Semi-Humid Lower Highland-Forests (2.12).

(1.333) Tamarindus-Thicket
According to Breitenbach, this type occurs on river banks at 500-1200 m. The dominant canopy species is *Tamarindus indica*, together with species of *Acacia, Ficus, Salix, Tamarix, Zizyphus, etc.*

(1.334) Faidherbia-Thicket
According to Breitenbach, this type occurs on river-banks and lake-shores, and in humid valleys with high water table at 1000-1700 m. The dominant canopy species is *Acacia (Faidherbia) albida*. A wet stage in the development of this vegetation at river-lagoons and on lake shores is a thicket with the pioneer species *Aeschynomene elaphroxylon*.

(2) HIGHLANDS
According to Breitenbach, forests, ranging from the uppermost forms of the lowland vegetation to the mountain vegetation, at 1600-2600 m constitute the natural climax vegetation of the highlands.

(2.1) Lower Highland-Forests
According to Breitenbach, these forests are floristically related to the more closed types of Lowland-Woodlands.

(2.11) Semi-Arid Lower Highland-Forests
According to Breitenbach, this is only represented by one vegetation type, the *Acacia*-Forest.

(2.111) Acacia-Forest
According to Breitenbach, this type is characteristic of the dryer areas at 1800-2200 m, and is prevalent on south- or west-facing slopes. The vegetation has a canopy of the flat-crowned *Acacia abyssinica* under which there is a lower storey of big, mainly evergreen shrubs and smaller trees with species of *Carissa, Calpurnia, Celtis, Dombeya, Maytenus, Allophylus, Rhus, Olea, Vernonia, etc.* Trunks of the larger trees have epiphytes, and climbers may be prominent.

(2.12) Semi-humid Lower Highland-Forests
According to Breitenbach, these are prominent in semi-humid areas at 1700-2200 m.

(2.121) Celtis-Forest
According to Breitenbach, this type is found on north- and east-facing slopes or in cool depressions. The 25-35 m high, dominant canopy species is *Celtis africana*. Other trees in the upper part of the canopy are species of *Prunus, Croton, Syzygium, Apodytes, Ekebergia, Olea, etc.* In the lower part of the canopy are species of *Millettia, Schefflera, Trema, Pittosporum, Dombeya, Bersama, etc.*

(2.122) Polyscias-Forest
According to Breitenbach, this type is developed in warmer positions than the previous one. *Polyscias fulva, Prunus africanus*, species of *Albizia*, etc dominate the upper canopy. The lower strata have considerable floristic similarity with the previous type and the *Acacia* forest (2.111).

(2.123) Podocarpus-Forest
According to Breitenbach, this is be the climax of the two previous types, the *Celtis*-Forest (2.121) and the *Polyscias*-Forest (2.122). The dominant species in the 40-45 m high upper canopy is *Podocarpus falcatus*. The lower strata are less well developed, but may in open spaces contain trees, which also occur in the two previous types.

(2.13) Humid Lower Highland-Forests
According to Breitenbach, these forests include the broad-leaved rain forests of Ethiopia, as seen by Breitenbach. They occur at 1600-2200 m in the humid parts of Kefa and Ilubabor, but with isolated patches in Welega (Didessa Valley, Dembidollo), Southern Shewa (Gibat), and Sidamo (Jem-Jem). [As will be seen further on in this account, later authors have reported more sites].

(2.131) Syzygium-Forest
According to Breitenbach, this is a pioneering association in cool places. The canopy is dom-

inated by *Syzygium guineense* subsp. *afromontanum*. The lower strata are floristically rather similar to those of the *Celtis*-Forest (2.121) and the *Polyscias*-Forest (2.122).

(2.132) Cordia-Forest
According to Breitenbach, this is a pioneer type in warmer sites, especially on south- and west-facing slopes. *Cordia africana* and species of *Albizia* dominate the canopy. The lower strata are floristically rather similar to those of the *Celtis*-Forest (2.121) and the *Polyscias*-Forest (2.122), but the forest floor is richer in species, and there are many epiphytes and climbers.

(2.133) Olea-Forest
According to Breitenbach, this is the climax of the two previous types, the *Syzygium-Forest* (2.131) and the *Cordia-Forest* (2.132). It ascends in humid and warm sites into the Upper Highland-Forests. The upper canopy is 40-50 m high, the dominant species are *Olea welwitschii* (*Olea capensis* subsp. *welwitschii*), *Trilepisium madagascariensis* (*Bosqueia phoberos*), *Morus mesozygia*, *Pouteria (Aningeria) adolfi-friedericii*, *Pouteria (Aningeria) altissima*, *Manilkara butugi* and *Fagaropsis angolensis*. [However, this has been demonstrated to be incorrect. Apart from *Olea welwitschii*, all other enumerated species belong to a forest type, which descends the western escarpment, but was unknown to Breitenbach in 1963].

(2.134) Mimusops-Forest
According to Breitenbach, this is a type which is mainly confined to riverine and lake-shore forests at 1600-2000 m. The dominant canopy species is *Mimusops kummel*; many lower canopy species are common with the *Syzygium-Forest* (2.131) and the *Cordia-Forest* (2.132).

(2.135) Ficus-Forest
According to Breitenbach, this is also a riverine type said to be restricted to altitudes at 1800-2200 m. The dominant canopy species is *Ficus sur* (*F. mallotocarpa; F. riparia*).

(2.2) Upper Highland-Forests
According to Breitenbach, these forests have a close floristic relation to the Mountain-Woodlands.

(2.21) Semi-arid Upper Highland-Forests
According to Breitenbach, these forests occur in more arid areas at 2200-2500 m. They are floristically connected with the Semi-arid Lower Highland-Forests and likewise represented by only one type (*Acacia-Forest* (2.111)).

(2.211) Acacia-Forest
According to Breitenbach, these are very similar to the *Acacia-Forest* (2.111) of Semi-arid Lower Highland-Forests.

(2.22) Semi-humid Upper Highland-Forests
According to Breitenbach, these forests develop in semi-humid regions at 2200-2500 m and represent serial stages in the upper part of the coniferous forests.

(2.221) Sideroxylon-Forest
According to Breitenbach, this is one of the early stages (or stages in regrowth) of the forests on cold, north- and east-facing slopes. The 10-20 m high canopy is dominated by *Sideroxylon oxyacantha* (*Spiniluma oxyacantha*). Other trees in the canopy are species of *Olinia*, *Schefflera*, *Cussonia*, *Dombeya*, *Croton*, *Ekebergia*, and *Olea*.

(2.222) Galiniera-Forest
According to Breitenbach, this is an analogous forest type on warm, south- and west-facing slopes. A prominent member in the 10-15 m high canopy is *Galiniera saxifraga* (*Galiniera coffeoides*). Other trees in the canopy are species of *Prunus*, *Dombeya*, *Croton*, *Ilex*, *Apodytes* and *Olea*.

(2.223) Juniperus-Forest
According to Breitenbach, this is the climax of the two previous types, the *Sideroxylon-Forest* (2.221) and the *Galiniera-Forest* (2.222). The canopy is in some places at higher altitudes almost completely dominated by *Juniperus procera*. At lower and moister places this forest type overlaps and mingles with the *Podocarpus-Forest* (2.123). [*Juniperus procera* also occurs in a rather different association in dry parts of the Borana region and in other southern localities, where it represents an evergreen forest stage surrounded by deciduous scrub].

(2.23) Humid Upper Highland-Forests
According to Breitenbach, this is the highest altitude part of the broad-leaved forests.

(2.231) Ekebergia-Forest
According to Breitenbach, this is the forest type developed in more cold sites. The most prominent tree in the canopy is *Ekebergia capensis* (*Ekebergia rueppelliana*). Other canopy trees are species of *Ficus, Croton,* and *Syzygium.* Lower canopy trees are species of *Millettia, Olinia, Trema, Pittosporum,* and *Bersama.*

(2.232) Apodytes-Forest
According to Breitenbach, this is the type developed in warmer sites. The most prominent tree in the canopy is *Apodytes dimidiata.* Other canopy trees are species of *Prunus, Ficus, Croton, Trichilia, Allophylus,* and *Phoenix.* Lower trees are species of *Poslyscias, Schefflera, Dombeya, Maesa, Galiniera, etc.*

(2.233) Aningeria-Forest
According to Breitenbach, this is the climax of the two previous types, the *Ekebergia-Forest* (2.231) and the *Apodytes-Forest* (2.232). The upper part of the canopy is dominated by *Pouteria (Aningeria) adolfi-friederici.* According to Breitenbach, other trees in the canopy are *Pouteria (Aningeria) altissima, Morus mesozygia* and *Fagaropsis angolensis.* [These latter species are in fact characteristic at lower altitudes and at high rainfall].

(2.234) Schefflera-Forest
According to Breitenbach, this is the riverine and riparian forest type among the Humid Upper Highland-Forests. The most prominent member of the canopy is *Schefflera abyssinica.*

(3) MOUNTAINS
According to Breitenbach, the physiognomical types at mountainous altitudes are woodlands above the forests, and above savannahs and steppes.

(3.1) Mountain-Woodlands
According to Breitenbach, an open canopy of 5-12 m high trees above a scrub-stratum dominates the physiognomy of these vegetation types.

(3.11) Semi-arid Mountain-Woodlands
These can, according to Breitenbach, be found on dry, stony slopes at 2400-3000 m and is in Ethiopia and Eritrea only represented by one type.

(3.111) Protea-Thicket
According to Breitenbach, this type is associated with the *Acacia-Forest* (2.111 and 2.211) and the mountain savannah types *Grass-Savannah* (3.211) and *Scrub-Savannah* (3.212). The dominant woody species is *Protea gaguedi,* which is sometimes accompanied by a number of other woody plants, for example species of *Gnidia, Pittosporum, etc.* [Breitenbach does not mention the ground cover; in our experience these woody plants are almost always associated with a dense grass layer which frequently burns].

(3.12) Semi-humid Mountain-Woodlands
According to Breitenbach, these develop in more humid sites at 2400-3400 m.

(3.121) Juniperus-Thicket
According to Breitenbach, this vegetation type is mainly found in sites on warm, south- and west-facing slopes. It is open, and between the often poorly developed specimens of *Juniperus procera* there are species of *Cussonia, Gnidia, Dombeya, Croton, Maytenus, Rapanea, etc.* [We have been in doubt whether this could possibly be taken to represent the *Juniperus*-dominated vegetation of the Borana region, but are convinced that it must represent high-altitude *Juniperus*-dominated vegetation in the northern part of the Western Plateau, for example in Tigray].

(3.122) Hagenia-Thicket
According to Breitenbach, this vegetation type, mainly found in cooler sites on north- and east-facing slopes, has *Hagenia abyssinica* as its dominant species. The canopy also contains species of *Olinia, Schefflera, Dombeya, Ilex, Hypericum, Maytenus, Nuxia, Galiniera,* and patches of the montane bamboo, *Arundinaria alpina.* [There is no mentioning of a ground cover, but according to our experience, the woody species listed are usually associated with a fairly continuous grass and herb stratum].

(3.13) Humid Mountain-Woodlands
According to Breitenbach, these, only represented by one vegetation type, *Arundinaria-Thicket,* are only developed in areas of high humidity at 2500-3400 m.

(3.131) Arundinaria-Thicket
According to Breitenbach, this vegetation type is dominated by dense and almost monospecific stands of the montane bamboo, *Arundinaria alpina.* A few individuals of *Juniperus, Hagenia, Schefflera, Dombeya, Ilex, Hypericum, Galiniera, etc.* may also occur. [The ground cover is sparse and consist of herbs with turgid fleshy stems and low grasses].

(3.2) Mountain-Svannahs
According to Breitenbach, these occur mainly above the Mountain-Woodlands at altitudes up to 3500 m in dry regions and 4000 m in humid regions. The main physiognomic feature is a blanket of Poaceae and Cyperaceae dotted with spots of isolated or irregularly grouped shrubs or small trees. Breitenbach points out that although he thinks this vegetation naturally occurred at fairly high altitudes above the forests and the mountain woodlands they now also occur as secondary vegetation (seral stages) following clearing for cultivation or pastures at lower altitudes over large areas of both the Western and the Eastern Plateau.

(3.21) Semi-arid Mountain-Savannahs
According to Breitenbach, these are restricted to the fairly dry sites, which at this altitude are not very extensive.

(3.211) Grass-Savannah
According to Breitenbach, this vegetation type occurs on wind-exposed sites of the high mountain plateaux. It has virtually no shrubs or trees.

(3.212) Scrub-Savannah
According to Breitenbach, this vegetation type is very like the previous one, but has scattered groups or larger, but broken thickets of species of *Erica, Protea, Hypericum, Rhus, Rosa, etc.*

(3.22) Semi-humid Mountain-Savannahs
According to Breitenbach, these more humid types are floristically very variable.

(3.221) Shrub-Savannah
According to Breitenbach, this vegetation type has isolated or small groups of small trees or large shrubs, for example species of *Acacia, Erica, Hypericum,* and *Echinops.*

(3.222) Tree-Savannah
According to Breitenbach, this more humid type has scattered taller trees, for example species of *Acacia* and *Maytenus*, and groups of shrubs, for example species of *Olinia, Erica, Agauria, Buddleja, Brucea, etc.* At the highest altitudes, stands and scattered individuals of giant lobelia, *Lobelia rhynchopetalum*, may be common.

(3.3) Mountain-Steppes
According to Breitenbach, this is reported from the highest parts of the mountains at 3200-4500 m.

(3.31) Semi-arid Mountain-Steppe
According to Breitenbach, this is a mosaic of pioneer associations on rocky slopes at 3200-4500 m.

(3.311) Rupestrian Steppe
According to Breitenbach, this is a complex vegetation type with a thin blanket of grass and herbs between rocks, dominated by species of *Carduus, Urtica, Arabis, etc.*

(3.32) Semi-humid Mountain-Steppe
According to Breitenbach, these vegetation types are found under less extreme conditions at 3500-4500 m.

(3.321) Shrub-Steppe
According to Breitenbach, this vegetation type is found in more sheltered places and consisting of a mosaic of patches of *Erica arborea* scrub, sometimes with *Lobelia rhynchopetalum*, and a blanket dominated by grasses, especially species of *Poa, Festuca, Agrostis, etc.* [We are surprised that Breitenbach has nowhere in these high altitude vegetation types found reason to mention the extensive areas dominated by species of *Helichrysum*, for example *Helichrysum spinosum*].

(3.322) Grass-Steppe
According to Breitenbach, this is found in the highest, moist and most wind-swept peaks and consists of tufts *Carex monostachya, Deschampsia caespitosa, etc.*

Characteristic features of Breitenbach's map

The basic categories in this system are physiognomic. The subordinate categories are based on local rainfall aspects (in each basic category arranged in the sequence arid, semi-arid, semi-humid, and humid) and succession (in each subordinate category arranged in a sequence from pioneer types to climax types). Breitenbach has therefore decided to map only seven basic categories. These are *(1.1) Lowland-Steppes, (1.2) Lowland-Savannahs, (1.3) Lowland-Woodlands, (2.1 + 2.2) Highland-Forests, (3.1) Mountain-Woodlands, (3.2) Mountain-Savannahs* and *(3.3) Mountain-Steppes.*

Breitenbach's surface-cover quotations refer to these categories and are as shown in Table 1.

Table 1. The areas in sq.km. and the land areas in % of total area covered by Breitenbach's major vegetation types. Data from Breitenbach (1963: 19)

	Area (sq. km.)	%
Mountain-Steppes	10,000	1
Mountain-Savannahs	167,000	15
Mountain-Woodlands	8,000	1
Highland-Forests	42,000	4
Lowland-Woodlands	275,000	24
Lowland-Savannahs	147,000	13
Lowland-Steppes	485,000	42
Total land area	1,134,000	100
Rivers and lakes	10,000	
Total	1,144,000	

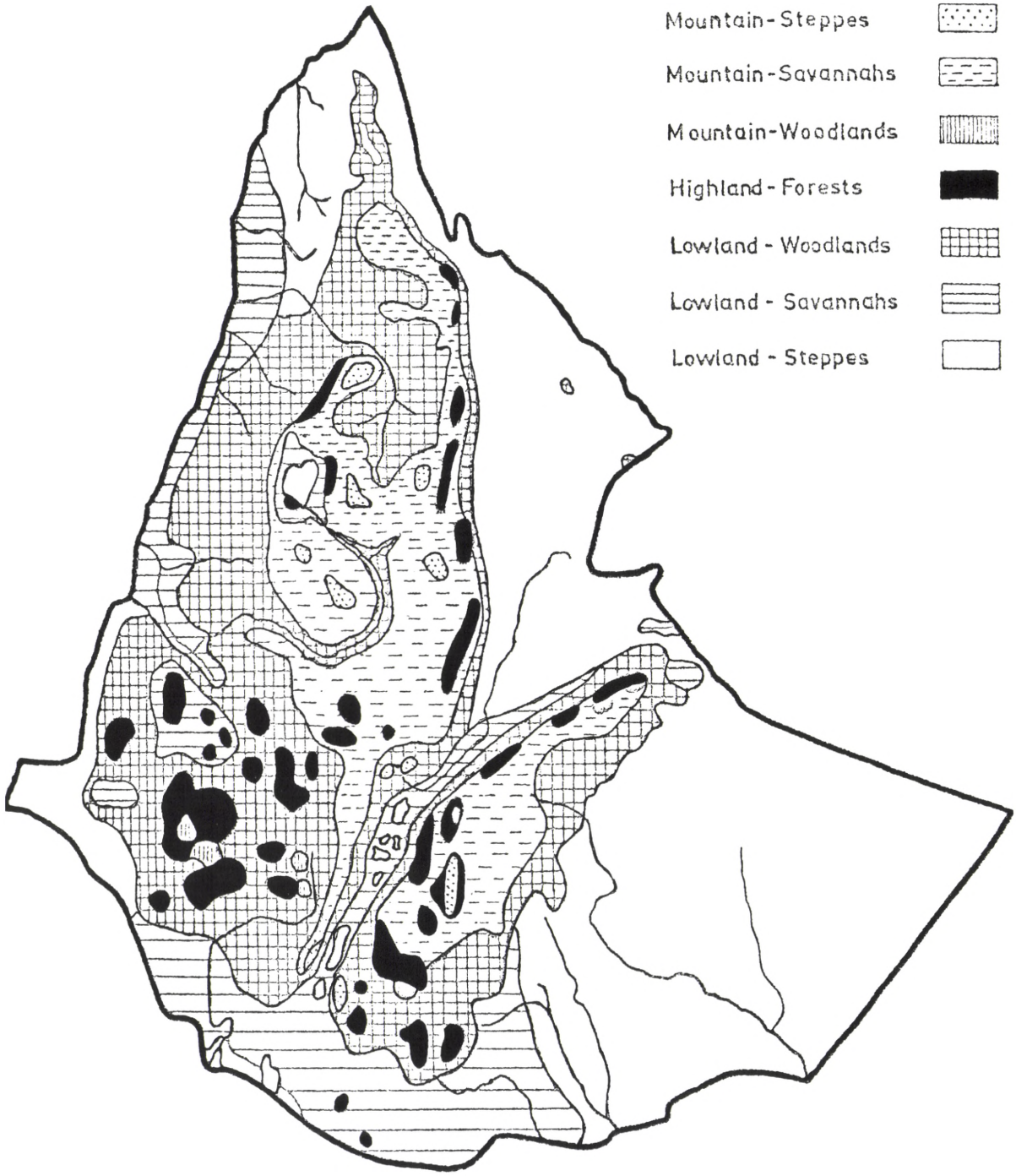


Fig. 3. Map of the vegetation of Ethiopia and Eritrea, according to Breitenbach (1963). Reproduced with permission from J. von Breitenbach.

The borders drawn on the vegetation maps of Pichi-Sermolli (1957) and that of Breitenbach (1963) are surprisingly similar, as can be seen from a reproduction of the map in Fig. 3. Hence the extent and delimitation of the mapping units are almost identical, but the descriptions and the terminology of the mapping units are conspicuously different. It can be seen from Breitenbach's map that he considers the major parts of lowlands to be covered by *(1.1) Lowland-Steppes* and *(1.2) Lowland-Savannahs*. The former is indicated in the places where Pichi-Sermolli has *(6) Broken xerophilous open woodland*, *(7) Xerophilous open woodland* and desert and various steppes. The latter is indicated in the places where Pichi-Sermolli had *(11) Savanna (various types)*. Both the higher, northern part of the Western Plateau and the central part of the Eastern Plateau are, according to Breitenbach, largely covered by *(3.2) Mountain-Savannahs*, while Pichi-Sermolli has indicated *(12) Montane Savanna* in exactly the same areas. The most striking difference between the maps of Breitenbach and that of Pichi-Sermolli relates to the western and southern parts of the Western Plateau (incl. most of Kefa, Ilubabor and Welega and the western parts of Gojam, Gonder and Tigray). In these areas Breitenbach has indicated the presence of *(1.3) Lowland-Woodlands* in the places where Pichi-Sermolli has two rather different vegetation types, *(10) Montane evergreen thicket and scrub* and *(13) Deciduous woodland*. On Breitenbach's map the conventional signs for Highland-Forests, representing both *(2.1) Lower Highland-Forests* and *(2.2) Upper Highland-Forests*, is indicated in the place of Pichi-Sermolli's *(15) Montane dry evergreen forest* and *(17) Montane moist evergreen forest*. Breitenbach has indicated very small areas with *(3.1) Mountain-Woodlands*, these areas agree almost exactly with Pichi-Sermolli's areas indicated for *(18) Bamboo thicket* (*Arundinaria*), while there is no indication of the geographical position of the other vegetation types which Breitenbach has placed under *(3.1) Mountain-Woodlands*. Finally, *(3.3) Mountain-Steppes* are indicated in the place of Pichi-Sermolli's *(19) Altimontane scrub and steppe* and *(20) Afroalpine formations*.

It is positive feature with Breitenbach's system that it makes it very clear that each major vegetational unit consists of a whole series of subunits that have some mutual relationship, often representing humid or drier aspects on adjacent mountain slopes, or seral stages of a succession. The drawbacks are that it often difficult to relate his very complex hierarchical system to what we actually see in the field, and that it will be impossible to map such a complicated set of units on a map at a scale of *c.*1:5,000,000.

F. White's chorologically based vegetation map (1983)

White's important map from 1983 covered the whole of Africa; 14 vegetation types and mosaics were recorded from Ethiopia and Eritrea. The part of the map which covers Ethiopia is reproduced in Fig. 4. Only seven of the 14 vegetation types recognised from the area by White are widespread, viz. *(19a) Undifferentiated montane vegetation (Afromontane)*, *(29b) Sudanian undifferentiated woodland (Ethiopian type)*, *(38) Evergreen and semi-evergreen bushland and thicket*, *(42) Somalia-Masai Acacia-Commiphora deciduous bushland and thicket*, *(43) Sahel Acacia wooded grassland and deciduous bushland*, *(54b) Semi-desert grassland and shrubland (Somalia-Masai type)*, and *(65) Altimontane vegetation in tropical Africa*. Two vegetation types, *(19a) Undifferentiated montane vegetation (Afromontane)*, including forests, and *(38) Evergreen and semi-evergreen bushland and thicket*, dominate both the Western and the Eastern Plateau according to White's classification, while the higher parts of the plateau are classified as *(65) Altimontane vegetation in tropical*

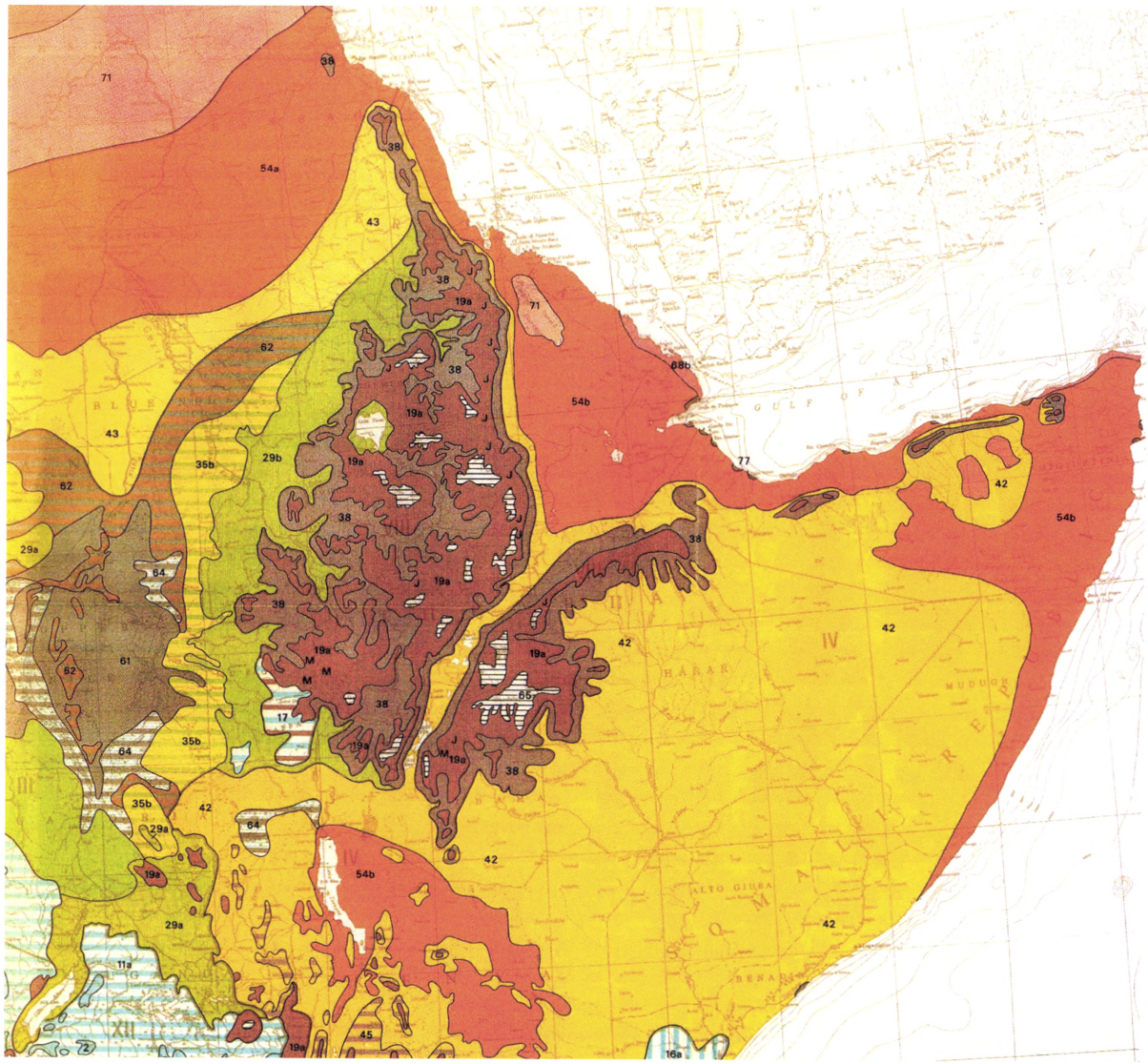


Fig. 4. Map showing the Ethiopian and Eritrean part of F. White's vegetation map of Africa (White 1983). For detailed legend, see text where the relevant numbers can be found. Reproduced with permission from UNESCO (UPO/D/A/2000-088 of 13 July 2000).

Africa. The lowlands are dominated by *(29b) Sudanian undifferentiated woodland (Ethiopian)* to the west, and *(42) Somalia-Masai Acacia-Commiphora deciduous bushland and thicket, (43) Sahel Acacia wooded grassland and deciduous bushland* and *(54a) Semi-desert grassland and shrubland (Somalia-Masai)* to the north, east and south. Below all fourteen types are enumerated.

FOREST TRANSITIONS AND MOSAICS

(17) Cultivation and secondary grassland replacing upland and montane forest (African)
This mapping unit represents areas where the original vegetation, now destroyed, probably originally contained a mixture of Afromontane and lowland species. Ib Friis recollects having informed Frank White at the time when the latter compiled the vegetation map about the mixed forests in Kefa and Ilubabor, and about how quickly these forests were disappearing. On White's vegetation map this vegetation is indicated for the southwestern part of Kefa.

(19a) Undifferentiated montane vegetation (Afromontane)
["J" indicates *Juniperus procera* forest; "M" indicates Mixed forest]. This mapping unit contains a number of vegetation types in White's phytochorion Afromontane archipelago-like regional centre of endemism. In White's descriptive memoir, he has subdivide this mapping unit into the following types, which are difficult to distinguish:

Afromontane rain forest, a multi-storeyed forest with *Pouteria (Aningeria) adolfi-friedericii* as a characteristic species in the highest stratum.

Undifferentiated Afromontane forest, usually shorter than the previous type, with for example *Apodytes dimidiata, Ilex mitis, Ocotea kenyensis, Podocarpus falcatus, Prunus africana, Juniperus procera, etc.*; most of the species in this type a very widespread.

Single-dominant Afromontane forest, including *Juniperus procera forest*, in dry areas, and *Hagenia abyssinica forest*, at the upper limit of the Afromontane forest, sometimes mixed with *Hypericum revolutum.*

Afromontane bamboo, dominated by *Arundinaria alpina*, and with few other tree and shrub species.

Afromontane evergreen bushland and thicket is according to White's concept almost synonymous with the *Ericaceous* belt of Hedberg (1951), but *Ericaceous bushland* occurs also at lower altitudes and on rocky outcrops, *etc.*

Afromontane and Afroalpine scrubland is according to White also dominated by Ericaceous species, but is shorter and have more forbs (especially geophytes), grasses and Cyperaceae. It seems to be defined as a high-altitude vegetation type.

Afromontane and Afroalpine grassland is according to White mostly a derived vegetation type, although small areas of grassland may have existed before the coming of man. Characteristically, many of the grass species in this vegetation belong to the Festuceae, Aveneae and Agrosteae, as opposed to the many Andropogoneae and Paniceae at lower altitudes. When not too heavily grazed or burnt, the vegetation is often invaded by forest-precursor shrubs, small trees and climbers that may form thickets.

On White's vegetation map this vegetation is indicated for the highlands throughout from northern Eritrea to Gamo-Gofa and to Harerge. It surrounds small islands of *(65) Altimontane vegetation in tropical Africa.*

WOODLAND

(29b) Sudanian undifferentiated woodland (Ethiopian type)
While most of the Sudanian woodland is characterised by many woody species of Leguminosae subfam. Caesalpinoideae, these species are rather infrequent in the eastern part, and one of the characteristic species, *Isoberlinia doka*, does not cross the Nile except for a short distance in Uganda. The Ethiopian type is dominated by widespread species, for example *Anogeissus leiocarpus, Balanites aegyptiaca, Boswellia papyrifera, Combretum collinium, Dalbergia melanoxylon, Erythrina abyssinica, Gardenia ternifolia, Lonchocarpus laxiflorus, Piliostigma thonningii, Sterculia setigera, Stereospermum kun-*

thianum and *Terminalia brownii*. A few tree species, for example *Combretum hartmannianum*, are endemic to the Sudanian woodlands east of the Nile. On White's vegetation map this vegetation type is indicated along the western escarpment of the Western Plateau from western Eritrea to Gamo-Gofa, descending to the Nile Valley and penetrating into the highland along the large river valleys. On White's vegetation map the area round Lake Tana has been marked with the conventional sign (colour) of the *(29b) Sudanian undifferentiated woodland (Ethiopian type)*, which must be based on a misunderstanding.

WOODLAND MOSAICS AND TRANSITIONS

(35b) Transition from undifferentiated woodland to Acacia deciduous bushland and wooded grassland (Ethiopian type).

According to White, this unit forms the transition from the edaphic grasslands of the Flood Region of the Nile [and its tributaries] to the *Anogeissus-Combretum hartmannianum* woodland flanking the Ethiopian highlands on their western side. *Acacia seyal* and *Balanites aegyptiaca* occur throughout, except for patches of thornless woodland dominated by *Combretum hartmannianum, Sterculia setigera, Stereospermum kunthianum* and *Adansonia digitata*. On White's vegetation map this vegetation type forms a zone on the western side of *(29b) Sudanian undifferentiated woodland (Ethiopian type)*.

BUSHLAND & THICKET

(38) Evergreen and semi-evergreen bushland and thicket.

According to White, this unit often forms transition between the Somalia-Masai and Afromontane Regions. For cartographic reasons it has on his vegetation map been places partly in the former and partly in the latter. White quoted Ib Friis as the authority for a note on evergreen bushland on the Ethiopian escarpment: the bushland was stated to be of several types. For the above-mentioned cartographic reasons, White included within the borders of Ethiopia and Eritrea most of the evergreen bushland and thicket within the boundary of the Afromontane region, although some might occur at low altitudes and be of different type. Some of the evergreen bushland with *Buxus, Barbeya* clearly belongs with the Somalia-Masai Region. On White's vegetation map this vegetation forms a zone around *(19a) Undifferentiated montane vegetation (Afromontane)* on both the Western and the Eastern Plateau. The largest areas of this vegetation are indicated in the deep river valleys of the western part of the Western plateau, but also elsewhere there are extensive areas indicated.

(42) Somalia-Masai Acacia-Commiphora deciduous bushland and thicket.

White includes under this unit the climax vegetation over the greater part of the Somalia-Masai Region. Characteristically, it is a dense bushland, 3-5 m tall with scattered emergent trees up to 9 m. Locally it is impenetrable and then forms thickets. The dominant species of *Acacia* and *Commiphora* are spiny shrubs that branch from near the base, and thus impede progress even in open types except along game or cattle tracks. Most species are deciduous. Only a few species have clearly developed trunks, especially *Acacia tortilis*, species of *Delonix* and *Terminalia, etc.* On White's vegetation map very large areas are indicated as covered by this vegetation type, from the lower Omo Valley and the southernmost part of Gamo-Gofa to the border with Somalia, in the Rift Valley, surrounding the Eastern Plateau, and forming a narrow band along the eastern escarpment of the Western Plateau.

(43) Sahel Acacia wooded grassland and deciduous bushland.
According to White, the Sahel wooded grassland is a widespread type in the southern higher rainfall areas of the Sahel, where annual rainfall is between 250 and 500 mm. It occurs on sandy soil, which is less common than the black, cracking clays in the Nile Valley. On White's vegetation map this vegetation type occurs in western Eritrea, where *Acacia senegal* dominates it.

SEMI-DESERT VEGETATION

(54a) Semi-desert grassland and shrubland (Northern Sahel type)
According to White, these grasslands and shrublands occur at annual rainfall lower than 250 mm, and predominantly on sandy soils. The dominant grasses are annual species. There is usually an admixture of bushes and small bushy trees, the density of which is partly determined by local conditions. The canopy covers less than 10%. The chief woody species are *Acacia tortilis*, *Balanites aegyptiaca*, and species of *Commiphora* and Capparaceae. On White's vegetation map this vegetation type occurs in the north-western Eritrea.

(54b) Semi-desert grassland and shrubland (Somalia-Masai type)
According to White, vegetation in the Somalia-Masai region at annual rainfall between 100 and 200 mm is often semi-desert grassland, which usually grows on deep sand, while shrubland occurs on stony soils. Gypseous soils support a considerable number of endemic succulents, especially species of *Euphorbia*. M.G. Gilbert is quoted for the information that Stapeliad succulents are usually found on limestone rather than gypsum. On White's vegetation map this vegetation type occurs extensively in the Afar Depression and along the coast along the Red Sea and the Gulf of Aden. There are also marked areas with this vegetation along the border between Ethiopia and Kenya from south of Mega to just west of Lake Turkana, but here the vegetation does not penetrate far into Ethiopia.

GRASSLAND

(61) Edaphic grassland in the Upper Nile basin.
According to White, the Upper Nile basin has extensive areas of dark, cracking Pleistocene clays. The grasses are as in mapping unit (62). On White's vegetation map this vegetation type is only indicated from the extreme western part of the Ilubabor lowlands (now Gambella Region), but it is very likely that other areas of pure grassland may occur in the seasonally flooded areas also closer to the western escarpment of Western Plateau.

EDAPHIC GRASSLAND MOSAICS

(62) Edaphic grassland mosaics with Acacia wooded grassland.
According to White, this vegetation is characterised by grass species of *Schoenfeldia*, *Cymbopogon*, *Sorghum*, *Hyparrhenia*, *Sehima*, *etc.* At rainfall above 570 mm *Acacia nilotica* and *A. seyal* is the dominant species, while *Acacia mellifera* dominates at lower rainfall. On White's vegetation map this vegetation occurs only in a small area around and south of Humera at the triple border between Sudan, Ethiopia and Eritrea and in a small area west of Jikau in western Ilubabor. Otherwise it forms a zone in the adjacent parts of Sudan outside *(35b) Transition from undifferentiated woodland to Acacia deciduous bushland and wooded grassland (Ethiopian type).*

(64) Edaphic grassland mosaics with semi-aquatic vegetation
According to White, this is a mosaic of various types of Sudanian wooded grassland, grassland

and swamp communities. By far the largest constituent is seasonally flooded grassland dominated by *Hyparrhenia rufa* and *Setaria incrassata*. On White's vegetation map there is indicated a patch of this vegetation west of the lower part of the Omo River and other areas in the lowlands near the border between Kefa and Sudan.

ALTIMONTANE VEGETATION

(65) Altimontane vegetation in tropical Africa
Under this mapping unit White has included a number of types that are cartographically difficult to separate.

Afromontane evergreen bushland and thicket, pro parte
As mentioned above, this is according to White's concept almost synonymous with the Ericaceous belt of Hedberg (1951). Here only the high altitude Ericaceous belt is included.

Afromontane scrubland, pro parte.
As mentioned above, this is according to White's concepts also dominated by Ericaceous species, but is shorter and have more forbs (especially geophytes), grasses and Cyperaceae.

Afromontane and Afroalpine grassland, pro parte
As mentioned above, most montane grassland is believed to be secondary, including some Afroalpine grassland types.

Mixed Afroalpine communities in tropical Africa
According to White, Afroalpine vegetation is physiognomically very mixed, being based on five distinctive Afroalpine life-forms, which do not fit the major physiognomic categories of areas at lower altitudes, but are closely paralleled in the paramo-vegetation in South America. There are also less specialised life forms in the Afroalpine communities.

On White's vegetation map the Altimontane vegetation is indicated in the Semien, in various massifs to the east of lake Tana, in the Choké Mountains of Gojam, in high mountains north-east and west of Addis Ababa, in the Guraghe Mountains in Shewa, in the mountains of Gamo-Gofa, Arsi, and Bale, and in the Amaro Mountains in Sidamo.

DESERT

(68b) Red Sea coastal desert.
According to White, the Red Sea coastal plain is 15-20 km wide and receives very little rainfall. There are halophytic communities and littoral salt marches on the coast itself, and no other vegetation except in the wadis. On White's vegetation map there is a belt of this vegetation marked along the Red Sea coast from the border with Djibouti.

(71) Regs, hamadas, wadis
On White's vegetation map the part of the Afar Depression which is largely below sea level is marked as mapping unit (71), and on a map of the Somalia-Masai Region in the descriptive memoir there is indication of *(71) "Stony desert"* in the "Danakil Depression," but we have not been able to find any references to this in the text of the descriptive memoir.

AZONAL VEGETATION

(77) Mangrove
According to White, the mangrove of Eritrea occurs on sandy mud over coral rock in shallow bays and is dominated by Avicennia marina. On White's vegetation map no areas along the Red Sea coast of Eritrea are indicated as mangrove.

White's classification of vegetation is primarily based on his phytochoria, which in our area involve *(1) the Sudanian regional centre of endemism,*

(2) the Afromontane archipelago-like centre of endemism, including *(3) the Afroalpine archipelago-like region of extreme floristic impoverishment*, *(4) the Somalia-Masai regional centre of endemism*, and *(5) the Sahel regional transition zone.*

The following is an indication of how the vegetation types are distributed like this on White's phytochoria.

Sudanian region
(29b) Sudanian undifferentiated woodland (Ethiopian type).

(35b) Transition from undifferentiated woodland to Acacia deciduous bushland and wooded grassland (Ethiopian type).

(61) Edaphic grassland in the Upper Nile basin.

(62) Edaphic grassland mosaics with Acacia wooded grassland.

(64) Edaphic grassland mosaics with semi-aquatic vegetation.

Afromontane archipelago-like centre:
(17) Cultivation and secondary grassland replacing upland and montane forest (African).

(19a) Undifferentiated montane vegetation (Afromontane). ["*J*" indicates *Juniperus procera* forest; "*M*" indicates Mixed forest].

(38) Evergreen and semi-evergreen bushland and thicket (partly).

Afroalpine archipelago-like region:
(65) Altimontane vegetation in tropical Africa (partly, also *(2) Afromontane archipelago-like centre*).

Somalia-Masai region:
(42) Somalia-Masai Acacia-Commiphora deciduous bushland and thicket.

(54b) Semi-desert grassland and shrubland (Somalia-Masai type).

(38) Evergreen and semi-evergreen bushland and thicket (partly, also *(2) Afromontane archipelago-like centre*).

(68b) Red Sea coastal desert.

(71) Regs, hamadas, wadis.

Sahel transition zone:
(43) Sahel Acacia wooded grassland and deciduous bushland.

(54a) Semi-desert grassland and shrubland (Northern Sahel type).

This classification is not quite detailed enough to fit the requirements for a vegetation map to accompany the *Flora of Ethiopia and Eritrea*, and areas particularly rich in species are not easily noticed as a separate vegetation type. It lacks some of the forest types, which have been discovered in southwestern Ethiopia after the publication of White's map in 1983.

Friis (1992)

Friis (1992) made an attempt to classify the forests on the Horn of Africa based on direct observations on collecting trips to hitherto less known forested areas, mainly in SW Ethiopia, and on the mapping of distributions of a considerable percentage of the distribution of the forest trees. This resulted in an improved understanding of the extent of the forests, their floristic composition and the relationship between the rainfall and the floristic composition in the forests on both the Western and the Eastern Plateau. The classification and terminology of the vegetation types largely followed that of White (1983), but some vegetation types not recognised from Ethiopia by White were nevertheless found to be present in previously less studied parts of the country. The detailed floristic work also rested on the intensive work of the Ethiopian Forest Inventory (Chaffey 1978a, 1978b, 1978c, 1979). The most important step was the recognition and floristic characterisation of the lowland semi-deciduous forest (*Dry peripheral semi-deciduous Guineo-Congolian forest*) and the altitudinally transitional forest (*Transitional rain forest*) not known from the region by White. These forests are described as no. (1) and (2) below. Friis (1992) did not produce a new vegetation map of the

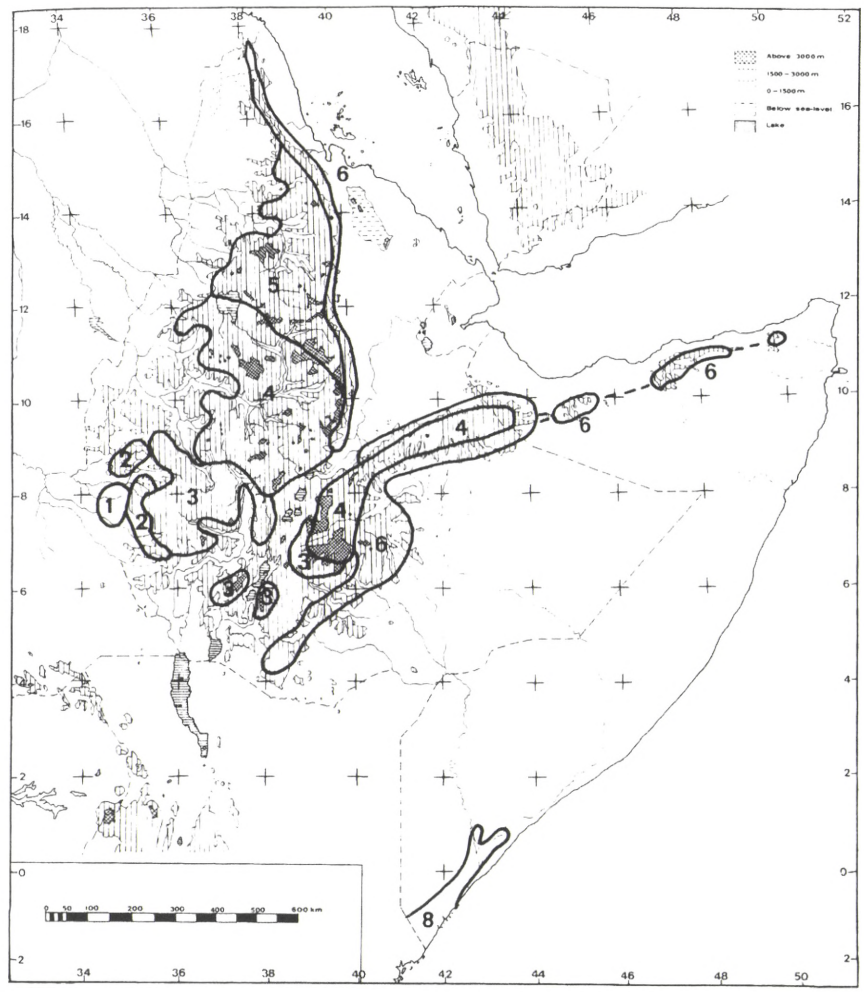


Fig. 5. Map showing the approximate outline of areas with the floristic forest types recognized by Friis (1992): (1) lowland dry peripheral semi-evergreen Guineo-Congolian type forest; (2) transitional rain forest; (3) broad-leaved Afromontane rain forest; (4) undifferentiated Afromontane forest, including various types of upland forest with *Podocarpus*; (5) dry single-dominant Afromontane forest, with *Juniperus procera* in the canopy and *Olea europaea* subsp. *cuspidata* in the understorey; (6) transition between dry single-dominant Afromontane forest and East African evergreen and semi-evergreen bushland and thicket; (8) transition between Zanzibar-Inhambane undifferentiated forest, the Zanzibar-Inhambane scrub forest and the Zanzibar-Inhambane evergreen and semi-evergreen bushland and thicket (southern Somalia). Riverine forest (7) and mangrove (9) are not shown. Reproduced with permission from author and publisher.

area, but he attempted to illustrate the general areas where his forest types could be found as enclaves in farmland, the map is reproduced here as Fig. 5.

(1) Dry peripheral semi-deciduous Guineo-Congolian forest

According to Friis, these forests are restricted to the Baro Lowlands of western Ilubabor, and have only become known in fairly recent years. Chaffey (1979) made the first inventory of a forest of this type. The name of this vegetation, adopted from White (1983), who used it for forest in the Sudanian Region, may sound almost nonsensical in an Ethiopian context, but comparison of the floristic composition of these Ethiopian forests with lowland forest types in the woodland regions of Ghana, as presented by Hall & Swaine (1981), shows that the Ethiopian forest would fall within the West African type referred to by Hall & Swaine as *Dry semi-deciduous forest*. These Ethiopian forests occur on sandy soils, and are semi-deciduous, with a 15-20 m tall, more or less continuous canopy of *Baphia abyssinica* (endemic to south western Ethiopia and adjacent areas of the Sudan), mixed with

less common species of *Celtis*, *Diospyros*, *Lecaniodiscus*, *Malacantha*, *Trichilia*, *Zanha*, and *Zanthoxylum*. Above the main canopy emerge species of *Alstonia*, *Antiaris*, *Celtis*, and *Milicia*). Below the closed canopy is a more or less continuous stratum of small trees and shrubs The ground is mostly covered by thick litter, and there are apparently very few species on the forest floor, for example the widespread forest grass *Streptogyna crinita*.

(2) Transitional rain forest

According to Friis, scattered examples of these forests are known from the western escarpment of the Ethiopian Highlands, in Welega, Ilubabor and Kefa. The forests occur between 500 and 1500 m. The rainfall is close to 2000 mm per year, with rain all year round. Chaffey (1979) provided some information, but most information is based on recent observations. The transitional rain forests are most similar in physiognomy and composition to the humid broad-leaved Afromontane rain forests of south western Ethiopia described below, with the addition of species from the lowland forest described above, and some species only known from humid forests of other countries, probably because the true lowland forests in Ethiopia are too dry for them. The canopy includes *Pouteria (Aningeria) altissima*, species of *Anthocleista*, *Campylospermum*, *Celtis*, *Elaeodendron*, *Ficus*, *Garcinia*, *Manilkara*, *Morus*, *Phoenix*, *Trichilia* and *Trilepisium*.

(3) Afromontane rain forest

According to Friis these forests occur in the south-western part of the Ethiopian Highlands at altitudes between 1500 and 2600 m, at annual rainfall between 700 and 1500 mm. The Harenna Forest on the southern slopes of the Bale Mountains is the easternmost example of these forests. The forests characteristically contain a mixture of *Podocarpus* and broad-leaved species in the canopy, but *Podocarpus* is never a single dominant and becomes gradually more infrequent towards the southwest in Kefa and Ilubabor as the rainfall increases, while *Pouteria (Aningeria) adolfi-friederici* becomes more prominent in the same direction. The drier parts of these forests are floristically very similar to those in the humid parts of the central highlands. The more or less continuous canopy consists of medium-sized trees, 10-30 m tall, including species of *Albizia*, *Ilex mitis*, *Prunus africana*, *Ocotea kenyensis*, *Polyscias fulva*, *Prunus africana*, *Sapium ellipticum*, *Syzygium guineense* subsp. *afromontanum* and *Olea capensis* subsp. *hochstetteri* or *O. welwitschii*. There are only one or two emergent species from the 20-30 m high canopy, *Pouteria (Aningeria) adolfi-friederici* or *Podocarpus falcatus*. The smaller trees and large shrubs form a discontinuous stratum. The most humid forests have dense stands of tree ferns (*Cyathea*) in the ravines. The epiphytes included ferns, orchids, and *Peperomia*. Lianas are present, and about 25 species have been recorded. The ground cover is comparatively lush, and rich in ferns, grasses, and herbaceous dicotyledons. *Arundinaria alpina* is not uncommon at higher altitudes in this area. A transition between *Acacia abyssinica* woodland and this type of forest exists and is described under the following type.

(4) Undifferentiated Afromontane forest

Friis sees the forests on both the Western and the Eastern Plateau as a gradient from wet to dry types, and generally the vegetation on the plateaux as a mosaic. The mosaic consists of humid sites, where areas of forest and evergreen (or semi-evergreen) bushland are now largely replaced by derived vegetation due to agriculture, and more well drained sites or sites in rain shadow, where the original vegetation had been wooded grassland, woodland or deciduous bushland. The undifferentiated Afromontane forests are either *Juniperus-Podocarpus* forests, or single dominant *Podocar-*

pus forests, both with an element of broad-leaved species. They occur especially on the plateaux of Shewa, Welo, Sidamo, Bale and Harerge at altitudes from 1500-2700 m, with annual rainfall between 700 and 1100 mm. Presently, the few larger patches still extant appear widely separated by areas of cultivation and wooded grassland. The canopy is usually dominated by *Podocarpus falcatus* with *Juniperus procera, Croton macrostachyus, Ficus spp., Olea europaea* subsp. *cuspidata, etc.* There is usually a rather well developed stratum of small to medium-sized trees. Scrambling species and true lianas are common. Epiphytes include species of *Peperomia,* ferns and orchids. The ground cover is rich in ferns, grasses, sedges, and small herbaceous dicotyledons. At the upper limit of this type of forest, between 3000-3400 m, there is often a more open type of woodland or evergreen bushland with *Erica arborea, Gnidia glauca, Hagenia abyssinica, Hypericum revolutum, Jasminum stans, Morella (Myrica) salicifolia, Myrsine africana, Myrsine (Rapanea) melanophlöeos, Rosa abyssinica,* and *Nuxia congesta.* Clumps of the mountain bamboo (*Arundinaria alpina*) may occur, but on the plateaux the species does not appear to form extensive stands such as are found in East Africa. *Acacia abyssinica* may form a very dense stand, a dense woodland or a forest, the canopy of which is mixed with broad-leaved species. Lianas and a ground cover of partly hygrophilous herbs may occur.

(5) Dry single-dominant Afromontane forest of the Ethiopian Highlands

According to Friis, this forest occurs especially on the Western and the Eastern Plateau in Tigray, Gonder, Welo and Harerge at altitudes from (1600-) 2200-3200 (-3300) m with an annual rainfall between 500 and 1500 mm. The typical dominant species in the upper storey of these forests is *Juniperus procera,* with *Olea europaea* subsp. *cuspidata* and a number of other species in the lower storeys.

(6) Dry single-dominant Afromontane forest of the escarpments and transition between single-dominant Afromontane forest and East African evergreen and semi-evergreen bushland

According to Friis, this category includes a range of physiognomic types, from typical forest to evergreen scrub with dispersed trees, but floristically the whole range is connected. The forest-like types exist in parts of Eritrea, on the eastern escarpment of the Ethiopian Highlands, and on the northern escarpment of the Somali Highlands; the bushland-like types with trees occur scattered in the previous areas, on the south eastern slope of the eastern Highlands. It extends along the mountain chain in northern Somalia. Throughout the range of the type it occurs on rocky ground with unimpeded drainage from an altitude of about 1500 m to about 2400 m at an annual rainfall of between 400 and 700 mm. The dry juniper forests of Sidamo occur at altitudes between 1500 and 2000 (-2200) m at an average rainfall of 400-700 mm. In an open stratum of smaller trees species of the following genera occur *Acokanthera, Apodytes, Barbeya, Berchemia, Brucea, Cadia, Halleria, Mimusops, Olea europaea* subsp. *cuspidata, Pistacia, Rhus, Schrebera, Sideroxylon* and *Tarchonanthus.* The dry juniper forests of Sidamo form the southern extension of this type. Other characteristic species include (in Bale and Harerge) *Dracaena ellenbeckiana, Buxus hildebrandtii* and *Barbeya oleoides.*

(7) Riverine forests

According to Friis, the riverine and riparian forest vegetation of the study area is very variable, and the floristic composition is dependent on altitude and geographical location. Only a brief summary can be given here. Common tree species in these forests are species of *Ficus, Lepisanthes senegalensis, Nuxia oppositifolia, Salix mucronata, Trichilia emetica, Diospyros mespiliformis, Mimusops kummel, Tamarindus indica, Acacia albida, Tamarix nilotica, Breonadia*

salicifolia, and *Phoenix reclinata*. There is often a shrub layer, and lianas and vascular epiphytes occur. The ground cover includes grasses, ferns, and a few herbaceous dicotyledons.

Riparian vegetation at larger lakes may include *Acacia albida*, species of *Ficus*, *Phoenix reclinata* and *Aeschynomene elaphroxylon*.

(8) Transition between Zanzibar-Inhambane undifferentiated forest, ZI scrub forest and ZI evergreen and semi-evergreen bushland and thicket

This woody vegetation from the coastal areas of southern Somalia is a forest type that does not occur in the FEE-area.

(9) Mangroves

Mangrove vegetation occurs along the Red Sea coast, where the major component is *Avicennia marina*, but in a few places *Rhizophora mucronata* is locally also important.

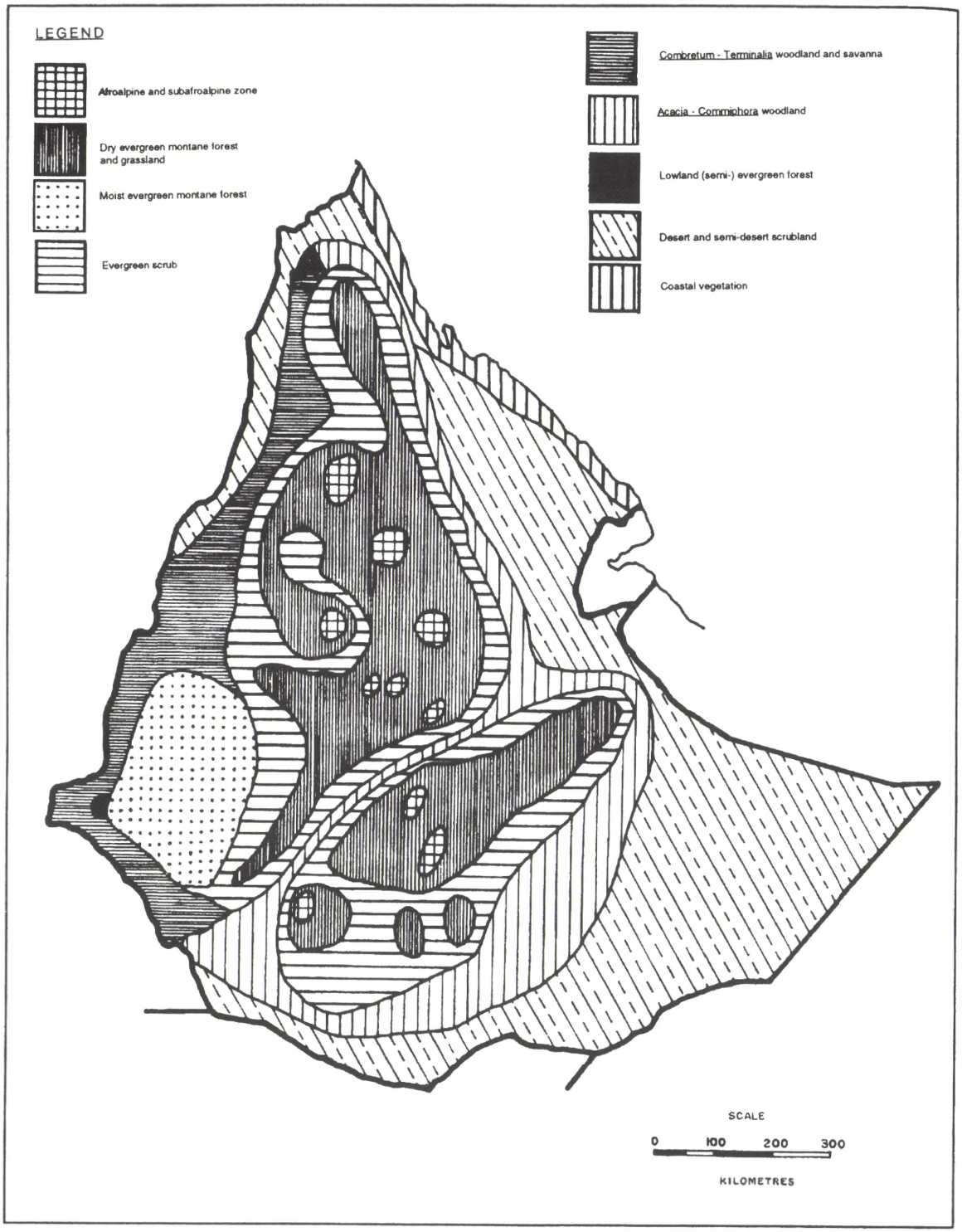
This attempt only deals with the forests. It assumes that the vegetation in the forest areas has been dominated by forests as described before human disturbance and farming changed the landscapes and attempts to map the extent of the forests by mapping characteristic species of forest trees also where they have been left outside the intact forests.

Sebsebe Demissew, Mengistu Wondafrash and Yilma Dellellegn (1996)

Sebsebe, Mengistu and Yilma (1996) published the descriptions of the mapping units and a vegetation map of Ethiopia. These vegetation types and the map reflects discussions going on among Ethiopian botanists and conservationists, and they are summarised in the Conservation Strategy of Ethiopia (CSE 1997). The importance of deforestation and the expanding man-made grasslands was stressed in a paper by Tewolde B.G. Egziabher (1988) which attempt to discuss the vegetation of the Afroalpine and Afromontane zones as a whole, based on the author's long experience from all parts of the highlands. The paper also makes a number other interesting observations, for example that the vegetation limits differ considerably between the different parts of the country, and that eastern facing escarpments are generally dryer than western facing ones. The *Juniperus procera* forest occurs only above 2200 m in the north, but down to 1500 m in the south. The upper limit of the montane *Acacia* wooded grassland [*'Acacia* woodlands' in the paper] is at 1900 m in the north, but at 900 m in the southwest. These differences are the effect of rainfall and moisture superimposed on the effect of the temperature decline with increasing altitude. But the clearly visible effects of these two factors are blurred by the long period of intense human interference almost everywhere in the Ethiopian highlands. In view of these complications, Sebsebe Demissew *et al.* (1996) decided to simplify the vegetation map as much as they thought possible and accepted only eight vegetation types for Ethiopia proper. The map is reproduced as Fig. 6. The mapping units are:

Desert and-semi desert scrubland

According to Sebsebe Demissew *et al.* this vegetation is highly drought tolerant, but due to external influence, for example around watering points, the land can locally be completely devoid of vegetation. The soils are alluvial. Small trees and shrubs occur, including species of *Acacia, Commiphora, Boscia, Cadaba, Maerua* and *Zizyphus*, as well as succulents, including species of *Euphorbia* and *Aloe*. The grass species are mainly annual, such as *Dactyloctenium aegyptium*, while another characteristic species, *Panicum turgidum*, is perennial. This vegetation type occurs in the Afar Depression, the Ogaden, around Lake Chew Bahir and the Omo delta.


LEGEND
Afroalpine and subafroalpine zone
Dry evergreen montane forest and grassland
Moist evergreen montane forest
Evergreen scrub
Combretum - Terminalia woodland and savanna
Acacia - Commiphora woodland
Lowland (semi-) evergreen forest
Desert and semi-desert scrubland
Coastal vegetation
SCALE
0 100 200 300
KILOMETRES

Acacia-Commiphora, small-leaved, deciduous woodland

According to Sebsebe Demissew *et al.* this vegetation is characterised by drought resistant trees and shrubs, either deciduous or with small, evergreen leaves. The trees and shrubs include species of *Acacia, Balanites, Commiphora, Capparis, Combretum,* and *Terminalia.* The ground cover is rich in subshrubs, including species of *Acalypha, Barleria,* and *Aerva.* This vegetation type occurs in the northern, eastern, central and southern part of the country at 900-1900 m.

Moist evergreen forest

According to Sebsebe Demissew *et al.* this vegetation type is characterised by one or more closed strata of evergreen trees. There are tall emergent trees, medium-sized trees that normally form a canopy, and understorey of shrubs. Characteristic emergent trees include *Pouteria (Aningeria) adolfi-friedericii, Albizia gummifera, A. grandibracteata, Macaranga capensis* and *Ocotea kenyensis.* None of the tall trees are endemic to Ethiopia. Typical understorey species include *Chionanthus mildbraedii* and *Psychotria orophila.* There are many epiphytes and lianas, some of which are endemic. The ground cover is not continuous, it includes a number endemic species. This vegetation type occurs in the western and south-western part of the country, in south Bale (including the important Harenna forest), north Borana, west Welega, Ilubabor and Kefa. It occurs in the western part of its range at altitudes at 1500-2400 m, with average annual temperature of 18-20° C, and annual rainfall of 1500-2400 mm. In the southern part of the range (Borana and Bale) it occurs up to 2800 m at annual rainfall around 1500 mm.

Lowland, semi-evergreen forest

According to Sebsebe Demissew *et al.* this vegetation type is characterised by one or more closed strata of trees, which may be deciduous or evergreen. There are tall emergent trees, including *Celtis toka, Diospyros abyssinica, Malacantha alnifolia,* and *Zanha golungensis,* medium sized trees which often form a closed canopy, and a low shrubby understorey with species like *Alchornea laxiflora, Oncoba spinosa* and *Whitfieldia elongata.* [In fact the "tall emergent species" mentioned by Sebsebe Demissew, Mengistu and Yilma are more frequently species of the upper, closed canopy. The truly emergent species are very large, individual trees that belong to the genera *Alstonia, Antiaris, Celtis* or *Melicia.* In places, the near-endemic *Baphia abyssinica* forms an almost monospecific canopy. Lianas may occur. The forest floor is often very dark and poor in species.] The forests categorised in this vegetation type occur in the Gambella region (previously the western lowland part of Ilubabor) at 450-650 m with average maximum temperatures of 35-38° C, mean annual temperatures of 18-20° C, and annual rainfall of 1300-1800 mm. The forests occur mainly on sandy soils, but usually with high ground water table.

The account by Sebsebe Demissew *et al.* lacks the altitudinal transitional forest described by Friis (1992). It is, as mentioned previously, known from altitudes around 1000 m in Kefa, at similar altitudes in Ilubabor north of Tepi, and is also represented in Welega at Dembidollo.

← **Fig. 6**. Map showing the vegetation types of Ethiopia and Eritrea according to Sebsebe Demissew *et al.* (1996). The legend includes the following vegetation types, which are further described in the text. (Left column, from top down): *Afroalpine and subalpine zone; Dry evergreen montane forest and grassland; Moist evergreen montane forest; Evergreen scrub.* (Right column, from top down): *Combretum-Terminalia woodland and savanna; Acacia-Commiphora woodland; Lowland (semi-) evergreen forest; Desert- and semi-desert scrubland; Coastal vegetation.* Reproduced with permission from author and publisher.

Combretum-Terminalia, broad-leaved, deciduous woodland and savanna
According to Sebsebe Demissew *et al.* this vegetation type is characterised by small to moderately sized trees with fairly large deciduous leaves. Species of *Terminalia, Combretum, Lannea, etc.* and *Boswellia papyrifera, Anogeissus leiocarpus* and *Stereospermum kunthianum* are common. The solid-stemmed lowland bamboo *Oxytenanthera abyssinica* is prominent in river valleys [and locally on the escarpment] of western Ethiopia. The ground cover is a tall stratum of perennial grasses, including species of *Cymbopogon, Hyparrhenia, Echinochloa, Sorghum* and *Pennisetum.* This vegetation type has been burning annually for such a long time that the plants show clear adaptation to fire, and it must be assumed not to be adversely affected by controlled annual fires. It occurs along the western escarpment of the Western Plateau, from the border region between Ethiopia and Eritrea to western Kefa and the Omo Zone; it is the dominant vegetation in what is now Benshangul-Gumuz and Gambella Regions, where it occurs at 500-1900 m. At the upper limit it frequently abuts on to Afromontane Moist Evergreen forest. It penetrates into the Western Plateau along the large river valleys.

Dry evergreen Montane Forest and Grassland Complex
According to Sebsebe Demissew *et al.* this vegetation type represents a complex system of successions involving extensive grasslands rich in legumes, shrubs and small to large-sized trees. The common tree species include *Juniperus procera, Olea eurpaea* subsp. *cuspidata, Celtis africana, Euphorbia ampliphylla, Mimusops kummel* and *Ekebergia capensis.* A number of shrubs are also characteristic. The grasses include genera from several tribes, and not only predominately temperate ones. The ecotone between forests and grassland is occupied by *Acacia* woodland with *Acacia abyssinica, A. negrii* and *A. pilispina.* This is a zone where sedentary, cereal-based agriculture has been going on for thousands of years. Very few areas have what can be described as natural vegetation. In many places the forests have been replaced by woodlands and grassland on the gentle slopes with deep soil, and by evergreen bushland on the steeper slopes with thin soil.

Afroalpine and sub-Afroalpine vegetation
According to Sebsebe Demissew *et al.* this vegetation type is characterised by small trees, shrubs and shrubby herbs at the lower altitudes and giant herbs, small herbs and grasses (the five distinctive Afroalpine life forms of Hedberg (1951) mentioned previously under White (1983)). The evergreen shrubs include *Erica arborea* and *Hypericum revolutum.* Typical shrubby-based herbs are a number of species of *Helichrysum. Lobelia rhynchopetalum* is alone among the giant rosette herbs with stems. The grasses mainly belong to tribes dominant in the temperate regions, and include species of *Festuca, Poa* and *Agrostis.*

Riparian and swamp vegetation
According to Sebsebe Demissew *et al.* this vegetation type consists of at least two physiognomically different types, riverine and riparian forest, and open, almost treeless swamp vegetation. Typical trees in riverine forest are *Celtis africana, Ficus sycomorus, Mimusops kummel, Tamarindus indica, Syzygium guineense, Kigelia aethiopum* and species of *Acacia.* The swamps are dominated by species of Cyperaceae, grasses and many herbs.

Coastal vegetation
Sebsebe Demissew *et al.* do not describe this, since their account only deals with Ethiopian vegetation.

On the map of Sebsebe Demissew *et al.* both the Western and the Eastern Plateau are dominated by *Dry evergreen montane forest and grass-*

land, surrounded at slightly lower altitudes by *Evergreen scrub*. Still lower on the western escarpment were extensive areas of *Combretum-Terminalia* woodland and savanna, and on the eastern escarpment equally extensive *Desert and semi-desert scrubland* which continued in the Sahel area in northwestern Eritrea.

There is some similarity with the map of Pichi-Sermolli in the distribution of the *Dry evergreen montane forest and grassland* at higher altitudes and in the northern parts of the Western Plateau and in the central part of the Eastern plateau. This is the distribution of Pichi-Sermolli's *(12) Montane savanna*. The distribution of the *Evergreen scrub* at lower altitudes and in large parts of the southern end of the Western Plateau is somewhat reminiscent of Pichi-Sermolli's (10) *Montane evergreen thicket and scrub*.

This is an simple representation, but some of the information in White's vegetation map on the lowland vegetation has been lost, and the problem of how to map and refer to the complex plateau vegetation is not yet completely solved.

In the Conservation Strategy of Ethiopia (1997) the following vegetation types are used as the basis for discussions and plans: *Desert and semi-Desert Scrubland*, *Acacia-Commiphora (Small Leaved Deciduous) woodland*, *Lowland Semi-Evergreen Forest*, *Combretum-Terminalia (Broad-Leaved Deciduous) Woodland*, *Moist Evergreen Forest*, *Evergreen Scrub*, *Dry Evergreen Montane Forest and Montane Grassland*, *Afro-alpine and Sub-afroalpine Vegetation*, and *Riparian and Swamp vegetation*.

Discussion

The above reviews of the classifications of the mapping units proposed by previous workers demonstrates that identical or at least closely analogous data sets on vegetation can be rather differently represented, resulting in considerable discrepancies between the maps. It is easy to see that the same physiognomically and floristically defined vegetation units are included in different complexes when viewed by different authors. However, the descriptions and the interpretations of the vegetation types do not agree, and it is therefore not possible simply to rearrange the mapping units of the existing classifications and maps. We have to discuss and find the best possible solutions on at least three outstanding questions.

1. The existing maps demonstrate the difficulties with the representation of complex vegetation mosaics and gradients, especially where the altitude changes drastically within a short distance. It is not realistic to have a map on a bigger scale than *c.* 1:5,000,000 for the *Flora of Ethiopia and Eritrea*. Should a new vegetation map in the *Flora of Ethiopia and Eritrea* be equivalent to, more detailed or more generalised than those previously published?
2. The representation of the lowland vegetation in the previous maps is rather different from map to map, but broadly speaking White's map has cleared up the difficulties, with the exception of the lowland forests in western Ethiopia added on the map by Friis. Is the lowland vegetation reasonably represented by a slight modification of White's ideas?
3. The plateau vegetation seems to represent the greatest unsolved difficulties. Is it possible to find a representative way to interpret this very complex system of grasslands, bushland, woodlands and forests in the highlands, taking into account the intensive farming that has been going on in these areas for hundreds or thousands of years? White (1983) has used a map unit (his no. 17, see Fig. 4) to indicate secondary vegetation following upland and montane forest in southwestern Kefa. Slightly illogically, he has not used a comparable map unit to indicate

the secondary vegetation of the plateaux. To what extent should a new vegetation map use map units for seconday vegetation types for the highlands?

With the printing of *c.* 50% of the *Flora of Ethiopia and Eritrea* completed and much more already at hand in manuscripts, it is appropriate and timely to being planning the vegetation map of Ethiopia and Eritrea, which would be part of the consolidated Volume, Vol. 8 of the Flora. The background for the need to have the vegetation map appears from the discussion above.

The characterisation of the lowland vegetation seem according to the authors rather satisfactory in White's vegetation map while the intermediate and the montane vegetation types are still incompletely characterised. The authors therefore suggested a simplification of White's vegetation map of the highlands by making them appear on the map as a mosaic of woodland (in rain shadow areas), forest (in areas receiving more rain), grassland and evergreen bushland and scrub (quite often degraded sites or areas of intensive farming for a long time).

Sebsebe Demissew, second author of this paper, indicated that the 1996 vegetation map (Sebsebe Demissew *et al.* 1996) was initiated as part of the report which aimed at presenting the natural resources of Ethiopia for the UN Conference held in Rio de Janeiro in Brazil in 1992 at the Secretariat office for the Conservation Strategy of Ethiopia under the Ministry of Planning. He also indicated that this vegetation map has been used since then for a number of scientific and practical purposes, but needed improvement and was hence presented here at the symposium for comments, suggestions, *etc.*

The following comments were forwarded:

Mike G. Gilbert (Natural History Museum, UK) suggested (1) to make use of the map in Science (1984/85) for the preparation of the vegetation map; the map in Science was the maps which Kåre Lye had used for his presentation during the symposium; (2) to use satellite imagery which is based on chlorophyll productivity and also takes care of the seasonality and provide information on the growing conditions.

Tewolde Berhan Gebre Egziabher (Environmental Protection Authority, Ethiopia) indicated that the use of the satellite imagery would not be realistic, as it is difficult to decide when to use it (either at the end or at the beginning of a wet season), and exactly where the satellite image would give reliable results. He suggested instead to include information in the preparation of the map (or in separate maps) on (1) the distribution of rainfall (unimodal and bimodal) from existing sources, and (2) the evapotranspiration to supplement the rainfall data on species distribution of certain key taxa (not only woody plants), and that these species should be mapped on the present agricultural system in order to incorporate these in the vegetation types.

Zerihun Woldu (Addis Ababa University, Ethiopia) informed about the presence of vegetation map tools which can integrate information on the various environmental factors such as rainfall, evapotranspiration, *etc.*, and which can show the average of 10 years climatic events for a given season.

Sue Edwards (Ethiopian Flora Project, Ethiopia) indicated that (1) the existing map puts more emphasis to woody plants than grasses and this should be adjusted in the future, (2) wetlands are not shown and should be included; (3) the number of species used to describe vegetation types should be limited to a reasonable size, and suggested (4) the present land-use map should be taken into consideration.

Roger Polhill (RBG, Kew, UK) suggested that there could be different kinds of vegeta-

tion maps, (1) a general map for students; (2) a detailed map for the flora which shows the mosaics, and refer to subsidiary vegetation maps with more detailed information. He warned against only adopting Friis' idea of a simplified vegetation map (a map where the highlands were only indicated as a mosaic of forest, woodland, grassland and evergreen bushland), as such a map might mislead people to think that the pattern was simple.

Ib Friis repeated as a general comment what had been said earlier during discussions that the indication of the lowland vegetation types was too simplified in the 1992 map, and as a reply to Dr Polhill that a better indication of some of the vegetation types in the highlands could be achieved if a method used for the Ethiopian highlands by White was elaborated: White has used various letters to indicate patches of special vegetation in the highlands. Examples of this are "J" for Juniperus-forest, "M" for evergreen montane forest, *etc.*

Kåre Lye (Norwegian Agricultural university, Ås, Norway) informed that the present vegetation map of Norway included 125 vegetation types, and that this was very useful for nature conservation, as it could indicate which vegetation types were rare and which were widespread in Norway. However, this requires a large scale map and detailed knowledge of the vegetation, including a system that can characterise secondary vegetation types.

Kaj Vollesen (RBG, Kew, UK) indicated the use of the production of several types of maps, depending on the intended use of the maps.

Robert B. Faden (Smithsonian Institution, USA) suggested: (1) to include as much detail as possible; (2) to have as many vegetation types as could possibly be recognised.

Ensermu Kelbessa (Addis Ababa University, Ethiopia) emphasised the existence of considerable variation in vegetation and species composition in even a small restricted area in many places, thus underlining the complications that Friis had pointed out. Ensermu cited the zonation of the vegetation around Lake Chamo in the Rift Valley as an example: Here the vegetation ranged from many types of shore vegetation surrounding the lake (for example swamps, reed swamps, swamp forest) to *Acacia* woodland close to the lake to deciduous thickets a few kms away from the lake. Dr. Ensermu also agreed with Prof. Friis in the view that the development of the scrub vegetation in the highlands is largely a result of human interference. He finally pointed out that these points need to be considered in order to come up with satisfactory vegetation types that could be mapped.

Mike G. Gilbert indicated the presence of mosaics such as the Somali-Masai region which are mainly based on geological factors and suggested the inclusion of geological information.

Tewolde Berhan Gebre Egziabher suggested that in order to improve the existing vegetation map: (1) a combination of species distribution, distribution of environmental factors and common sense needed to be used, (2) that as many sources as possible should be consulted, and (3) the work should start as soon as possible.

With the above comments, the session was concluded. At the end of the session it was understood that the suggestions presented will be looked into by the organisers of the session, Ib Friis and Sebsebe Demissew, and a report presented to the Editorial Board of the *Flora of Ethiopia and Eritrea.*

Conclusion

The authors of this paper both feel that a fairly simple map on the scale of 1:5,000,000 (or near) will be what is needed for reproduction with the last volume of *Flora of Ethiopia and Eritrea.* We think that it would be most feasible essentially to follow the advice of Dr Tewolde Berhan Gebre Egziabher and base the outlines

of this map on climatic and altitudinal data, supplemented with existing knowledge of vegetation and data on species distribution of certain key taxa. The vegetation types mapped will have to be fairly broadly defined, with approximately fifteen mapping units. The lowland vegetation will probably be reasonably well represented by this method, and we think that the results of the application of these methods will be fairly similar to that shown by White (1983), except where vegetation types were poorly known when he made his map. For areas with complex vegetation patterns, especially in the highlands where the vegetation is much influenced by agriculture, it will probably be feasible to use an elaboration of the non-hierarchical system of White (1983). According to this, letters or other specialised conventional signs are used to indicate the presence of special mapping units of very restricted range, such as small forest patches, swamps, outcrops of particular rocks, for example gypsum, with particularly species-rich, succulent flora, *etc.* It seems a practical idea on a map of the scale of *c.*1:5,000,000 to indicate vegetation types which represent seral stages in a fairly well defined succession under the same heading, as was done by Breitenbach, but simpler. In some cases it may be necessary to indicate with the same conventional signs (*i.e.* the same mapping unit) phytogeographically defined vegetation complexes of small extension, for example Afroalpine or montane vegetation types, coastal mosaics, *etc.* It will be possible, and indeed very desirable, as a parallel enterprise to start compiling data of use in the production of a map on a larger scale to be produced later, especially distribution maps of more key taxa. This is likely to compensate for some of the shortcomings of the more crude vegetation map in 1:5,000,000.

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