Endemism in groups of Ethiopian geophytes ("Liliiflorae")

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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".

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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.

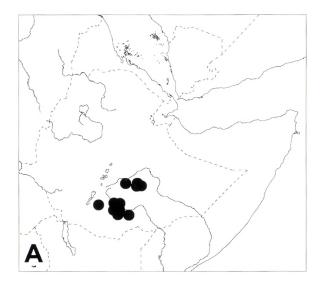
In Ethiopia and Eritrea the genus Anthericum is characterised by short rhizomes and +/-thick roots. The species belong to seasonally waterlogged areas. One species is near-endemic, i.e. A. jamesii Baker (Fig. 1C), occurring in the Harerge region, West Somalia, and North Kenya, very close to the Ethiopian 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%.

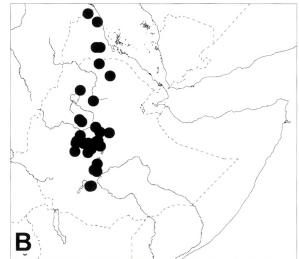
The genus *Chlorophytum* was revised for the Horn of Africa by Nordal & Thulin (1993). They revealed that this region represents an important area of diversity and described 9 new species that were endemic or nearendemic to the Horn of Africa. The species show a great diversity in subterranean storage 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 nearendemic 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.





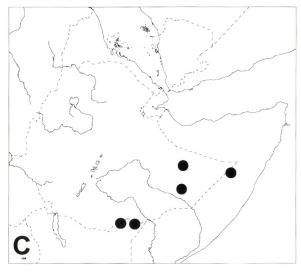


Fig. 1. Distribution patterns of endemic and near-endemic species in Anthericaceae: **A.** *Chlorophytum neghellense.* **B.** *Chlorophytum tetraphyllum*, the geographically unprecise type locality from SW Yemen is not indicated. **C.** *Anthericum jamesii.*

- 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-

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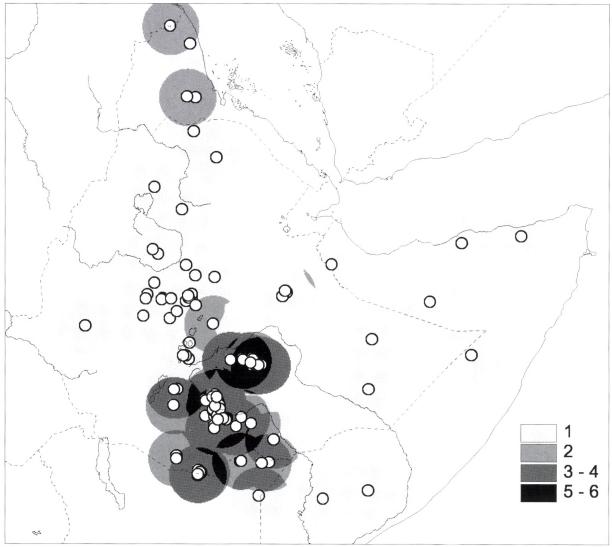


Fig. 2. The distribution of (near-)endemic taxa of Anthericaceae in Ethiopia. The shaded areas represent zones of overlapping species (see text).

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-

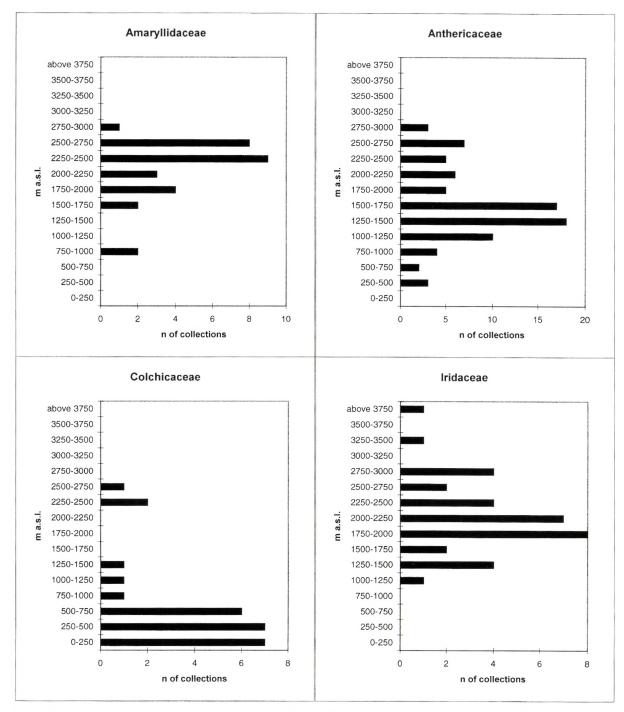


Fig. 3. The altitudinal ranges of endemic species within the families exhibiting a considerable degree of endemicity.

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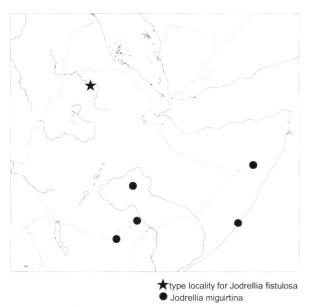


Fig. 4. The distribution of the genus *Jodrellia* on the Horn of Africa.

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.

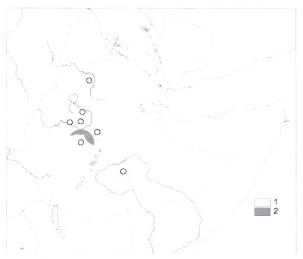


Fig. 5. The distribution of endemic taxa of Hyacinthaceae in Ethiopia. The shaded areas represent zones of overlapping species (see text).

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 Fritrea.

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

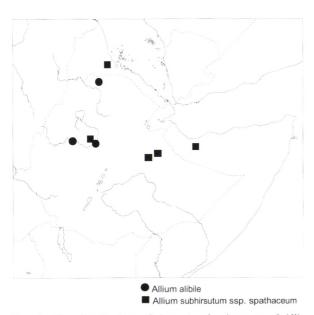


Fig. 6. The distribution of (near-)endemic taxa of Alliaceae.

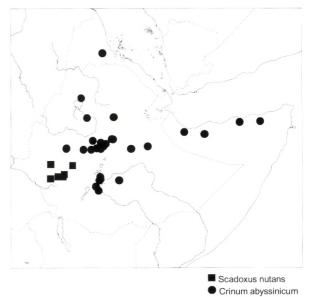


Fig. 7. The distribution of (near-)endemic taxa of Amaryllidaceae.

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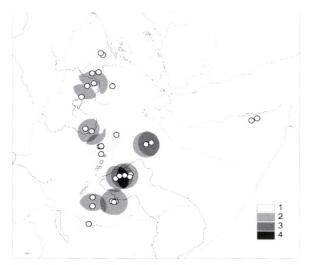


Fig. 8. The distribution of endemic taxa of Iridaceae in Ethiopia. The shaded areas represent zones of overlapping species (see text).

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

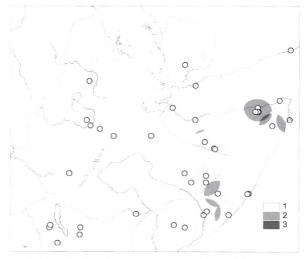


Fig. 9. The distribution of endemic taxa of Colchicaceae in Ethiopia. The shaded areas represent zones of overlopping species (see text).

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 nearendemics, 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 Hochst., is widespread schimperiana 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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