

Moraceae diversity in a global perspective

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The Moraceae are tightly embedded in the Urticales, a clear-cut entity of the Angiospermae. It comprises c. 1050 species and 37 genera, many of which have 1 or 2 species, and a few are large: *Ficus* has nearly 750 spp., *Dorstenia* has c. 105 spp., and *Artocarpus* has c. 60 spp. The family is pantropical, with extensions to subtropical and warm-temperate regions. It is well-represented in all tropical phytogeographic regions, each with one or more primary and/or secondary centres of distribution. The family is very diverse in both woody and herbaceous life and growth forms, but even more so in reproductive structures, comprising by condensation and fusion complex inflorescences, of which some are pseudoflorous and others are pseudocarpous, such as those of *Ficus* in which stigmas and anthers are not exposed at anthesis. This is linked to an unique pollination system. For other Moraceae pollination is by wind and adapted to forest conditions, or they are pollinated by small beetles, flies, or thrips and based on breeding in staminate inflorescences, or the mode of pollination is unknown. Patterns of Moraceae diversification, its functional implications, patterns of distribution, and the distinctness of genera and tribes suggest that most of the differentiation of the family took place in a still coherent tropical continent. The distinctness of taxa is not reflected in cladograms based on molecular analyses; one may wonder why.

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Introduction

This paper summarizes various previously published aspects of the diversity and distribution of Moraceae (Berg 1977a, 1983, 1989, 1990, 1998, 2001) and discusses the overall taxonomic structure of the family and how they are linked to patterns of morphological and biological diversification and distribution. Finally, these morphological and biological aspects are compared with results of molecular analyses (Sytsma *et al.* 2002).

Urticales

Except for doubt about the position of some odd genera or families (*e.g.*, Barbeyaceae), the Urticales was soon recognized and generally accepted as a well-defined group in the process of defining “natural” entities, as by Bentham (1880), Baillon (1875), Eichler (1875), Engler (1889). The solidity of the order is in recent times confirmed, *e.g.*, by Baas *et al.* (2000) who considered the wood anatomy as well as by results of molecular analyses (Sytsma *et al.* 2002).

The position of the order within the angiosperms has been uncertain. Traditionally it is linked to the amentiferous families, grouped in the Hamamelidae (Cronquist 1981). A position near the Malvales (and Euphorbiaceae) has been advocated (Berg 1989). Molecular studies indicate a link to the Rosales (*e.g.*, Sytsma *et al.* 2002) and the order is then referred to as Urticalean rosids. Roses and nettles in the same taxonomic unit are, although they share the capacity to sting, difficult to accept for morphological reasons.

Moraceae

The Moraceae can be regarded as a “natural entity”, after exclusion of the genera in the subfamilies Conocephaloideae and the Cannaboideae in Engler’s classification, the former being included in the Cecropiaceae (Berg 1989) and the latter in the Cannabaceae (Cronquist 1981).

In its morphological differentiation, the family shows strong links to the other larger urticalean families currently recognized. These links are such that one could unite Moraceae, Cecropiaceae, and Urticaceae into a single family. If one is not too narrow-minded, even Ulmaceae (both Celtidoideae and Ulmoideae) can be included in this more broadly construed family Urticaceae, thus, largely coinciding with the order Urticales.

However, such a broadly construed family lacks the transparency one needs to analyse morphological differentiation and distribution patterns in relation to biological traits and evolutionary processes leading to its present taxonomic structure. In this respect, it is convenient to maintain a family Moraceae and its presumably natural subdivisions (Fig. 1).

Compared to many other tropical plant families, the Moraceae is with its 1050-1100 species small, but in many tropical lowlands it is ecologically and important in forest structure and sup-

ply of food to frugivorous animals (Balslev & Renner 1989; Gentry 1993; Berg 1998; Shananan *et al.* 2001).

Composition of the family

The genera are very unequal in species numbers; 13 genera have only one or two closely related species; 14 genera have three to 14 species; few have more, *Naucleopsis* and *Streblus* 20-25 species, *Artocarpus* c. 60 species, *Dorstenia* c. 105 species, and *Ficus* nearly 750 species and, therewith, one of the largest genera of woody flowering plants.

Habit

The family is predominantly woody. The two species of *Fatoua* are herbaceous. Eleven species of *Dorstenia* are woody, the others are herbaceous and represent a wide range of life and growth forms (Berg 1977a; Berg & Hijman 1999; Fig. 2).

The woody Moraceae vary from being small shrubs to tall trees with sympodial or monopodial growth. Few species are (sub)monocaul, *Dorstenia djettii* J. L. Guillaumet, *Naucleopsis stipularis* Ducke, and some *Ficus* species, *e.g.*, *F. pseudopalma* Blanco. Several *Ficus* species are rheophytic (van Steenis 1981).

The capacity of *Ficus* to produce aerial adventitious roots, contributes considerably to the diversity of the woody life and growth forms, as hemi-epiphytes, hemi-epiliths, and root-climbers.

The plants have a system of ducts extending from the stem to the leaves and containing milksap (not in *Fatoua*). Uncinate hairs occur in many genera, and pluricellular (“glandular”) trichomes in most (or all?) genera. Nearly all *Ficus* species have waxy glandular spots on the lamina, base of the petiole and/or nodes of leafy twigs.

The height of the plants varies from less than

Fig. 1. Distribution and subdivision of Moraceae. The survey gives the representation in the three main phyto-geographic regions and tribes with the numbers of species () per genus tribe, and region; in *Ficus* (Ficeae) per subgenus (for the entirely or mainly (gyno)dioecious subgenera (B) or for the (main) sections of the monoecious subgenera (A) *Ficus* = Ficeae), and the indigenous genera in []; * including a species in North America; □ all (gyno)dioecious. Africa includes Madagascar, adjacent Indian Ocean Islands, and the Arabian Peninsula with adjacent islands.

	America	Africa	Asia Australasia
Moreae (ca 70)	(11) <i>Maclura</i> (3*) <i>Morus</i> (3*) <i>Trophis</i> (5)	(12) <i>Maclura</i> (1) <i>Morus</i> (1) <i>Trophis</i> (2) <i>Bleekrodea</i> (1) <i>Broussonetia</i> (1) <i>Fatoua</i> (1) <i>Streblus</i> (3) <i>Milicia</i> (2)	(c 47) <i>Maclura</i> (7) <i>Morus</i> (c 8) <i>Trophis</i> (2) <i>Bleekrodea</i> (1) <i>Broussonetia</i> (7) <i>Fatoua</i> (1) <i>Streblus</i> (21)
Artocarpeae (c 70)		(3) <i>Treculia</i> (3)	(c 68) <i>Artocarpus</i> (c 60) <i>Hullettia</i> (2) <i>Parartocarpus</i> (2) <i>Prainea</i> (4)
Soroceae (23)	(23) <i>Bagassa</i> (1) <i>Batocarpus</i> (3) <i>Clarisia</i> (3) <i>Poulsenia</i> (2) <i>Sorocea</i> (14)		
"Antiaropsidae" (3)			(3) <i>Antiaropsis</i> (2) <i>Sparattosyce</i> (1)
Dorstenieae (128)	(64) <i>Dorstenia</i> (46) <i>Brosimum</i> (14) <i>Helianthostylis</i> (2) <i>Trymatococcus</i> (2)	(63) <i>Dorstenia</i> (58) <i>Bosqueiopsis</i> (1) <i>Scyphosyce</i> (2) <i>Trilepisium</i> (1) <i>Utsetela</i> (1)	(1) <i>Dorstenia</i> (1)
Castilleae (58)	(55) <i>Castilla</i> (3) <i>Helicostylis</i> (7) <i>Maquira</i> (4) <i>Naucleopsis</i> (22) <i>Perebea</i> (9) <i>Pseudolmedia</i> (10)	(2) <i>Antiaris</i> (1) <i>Mesogyne</i> (1)	(1) <i>Antiaris</i> (1)
Ficeae (c.735)	(c 120)	(105)	(c 510)
"A" (c 350)	(c 120) <i>Pharmacosyce</i> (c 20) <i>Americana</i> (c 100)	(83) <i>Oreosyce</i> (4) <i>Urostigma</i> (7) <i>Galoglychia</i> (72)	(c 150) <i>Oreosyce</i> (c 50) <i>Urostigma</i> (c 80) <i>Stilpnophyllum</i> (c 20)
"B" (c 360)		(22) <i>Ficus</i> (1) <i>Sycidium</i> (9) <i>Sycomorus</i> (12 [□])	(c 360) <i>Ficus</i> (c 60) <i>Synoecia</i> (c 80) <i>Sycidium</i> (c 100) <i>Sycomorus</i> (c 120)
	19[14] gen (c 270)	17[7] gen (185)	16[6] gen (c 610)

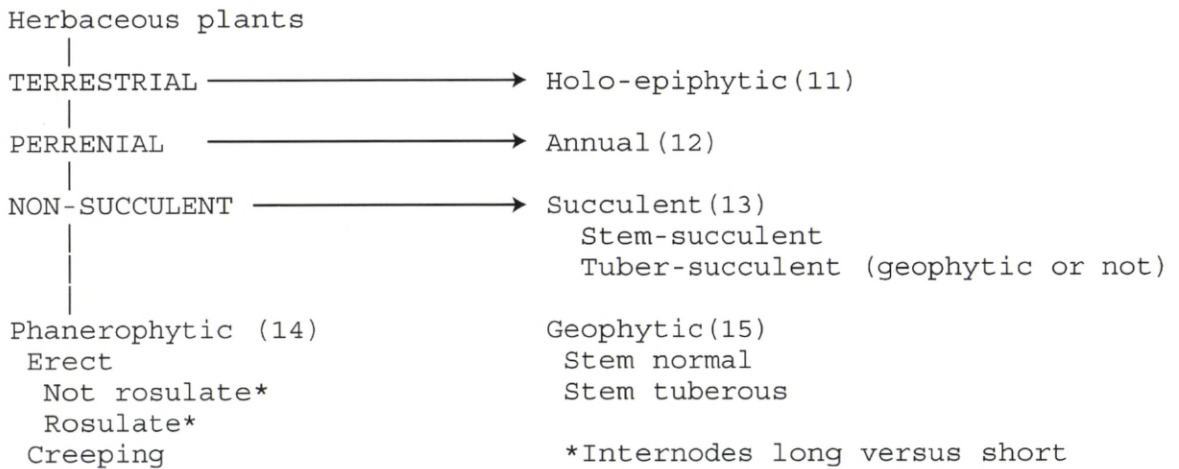
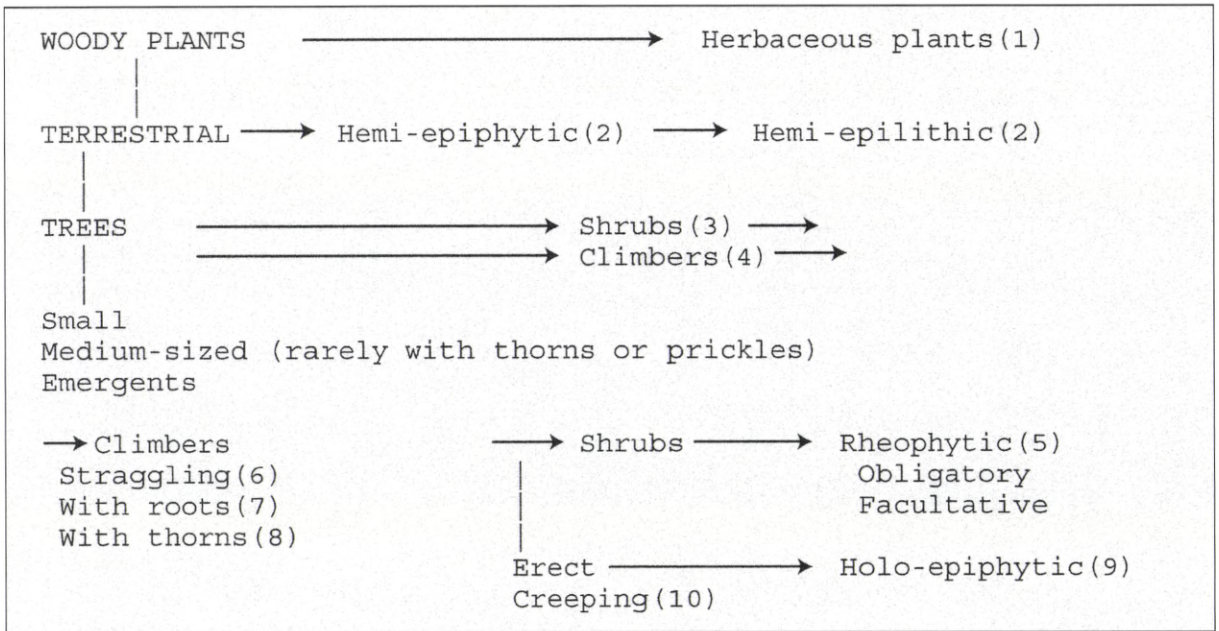


Fig. 2. Life and habit forms of Moraceae. The numbers indicate that the life and habit forms are represented in the following genera and species: (1) *Dorstenia* p.maj.p. (2) *Ficus* p.p. (3) *Bleekrodea*, *Brosimum* p.p., *Ficus* p.p., *Helianthostylis* p.p., *Perebea* p.p., *Scyphosyce*, *Sorocea* p.p., *Utsetlea*. (4) *Broussonetia kurzii*, *Ficus* p.p., *Maclura* p.maj.p., *Prairiea scandens*, *Trophis scandens*. (5) *Ficus* p.p. (6) *Broussonetia kurzii*, *Ficus* p.p., *Prairiea scandens*, *Trophis scandens*. (7) *Ficus* p.p. (8) *Maclura* p.p. (9) *Ficus deltoidea* (and *F. oleifolia*), facultatively. (10) *Ficus* p.p. (11) *Dorstenia astyanactis*. (12) *Dorstenia annua*. (13) *Dorstenia* p.p., *Fatoua*. (14) *Dorstenia* p.p.

5 cm as in some creeping *Dorstenia* species (Berg 2001) to 50 m tall, as in *Brosimum utile* (Kunth) Pittier and *Maquira coriacea* (Karst.)

C.C. Berg (Berg 1972), or possibly even taller in some *Ficus* species.

Leaves

The basic type of leaf has a short petiole and a basally attached, coriaceous, elliptic lamina with entire margin, pinnate to subtriplinerved brochidodromous venation with scalariform tertiary venation; the stipules are often fully amplexicaul, leaving the characteristic annular scars. Most of the variation in these features can be linked to life form or habitat.

Sexuality

Like in other Urticales families (with the notable exception of Cecropiaceae), monoecy (with either bisexual inflorescences or unisexual inflorescences) and dioecy are about equally represented. Bisexual inflorescences are mainly found in groups with cymose inflorescences and unisexual ones in racemous ones. Androdioecy is rare, it is found in *Castilla elastica* (Sakai 2001) and *Helianthostylis sprucei* (Berg 1972). Gynodioecy is found in *Ficus*, in which in c. 50% of the species the plants bear inflorescences with only long-styled pistillate flowers or with staminate flowers and short-styled pistillate ones, which, however, normally do not produce seeds. Gynodioecy or androdioecy may also occur in some (other) species of Castilleae in which pistillate and staminate inflorescences occur on the same tree, whereas others only bear pistillate or staminate ones; it is not clear whether differences in distribution of sexes in this tribe is related to age. For some species switch of sexuality is known: *Dorstenia cayapya* Vell. produces first staminate, later pistillate inflorescences, and *Brosimum alicastrum* Sw. first produces predominantly pistillate inflorescences then predominantly staminate ones (see Berg 2001). Changes in sexuality may also occur in Castilleae species of which some of the trees bear both staminate and pistillate inflorescences.

Inflorescences

The inflorescences are mostly condensed (unbranched) with similar parts (flowers) and dissimilar parts (flowers, bracts, and/or receptacles) often fused, resulting in structures which function as units of pollination, resembling either flowers, thus pseudoflorous, or fruits, thus pseudocarpous (Berg 1977a, 1989). Much of the differentiation of the inflorescences (and flowers) can be related to protection of developing stamens, pistils and fruits, which is essential for pollination based on breeding in staminate inflorescences (Berg 1990).

Most of the least condensed inflorescences (as racemes and cymes) are found in anemophilous taxa in which the staminate flowers need space for ballistic pollen release; the pistillate inflorescences of these taxa are often more condensed, but the flowers usually remain free.

The abaxial sterile strip commonly found in elongate inflorescences is caused by the basically adaxial orientation of the flowers.

The most complex and intricate inflorescence of the Moraceae (and angiosperms?) is that of *Trilepisium* (Berg 1977b: 298, t. 6 and 7).

The inflorescences occur basically in pairs in the leaf axils. In some groups, e.g., in Castilleae and in *Ficus* (e.g., in subg. *Urostigma*), inflorescences develop on axillary spurs (which may continue to elongate on the older wood) that often bear more than two inflorescences simultaneously, in some Castilleae even several staminate inflorescences and a single pistillate one. Cauliflory is found in *Artocarpus*, *Clarisia*, *Treculia* and in some subdivisions of *Ficus*: subg. *Urostigma* (sect. *Galoglychia*), subg. *Sycidium*, subg. *Sycomorus*, and subg. *Synoecia*; in subg. *Sycomorus*, many species are or can be flagelliflorous (or geocarpic).

Flowers

The flowers are small. Through reduction in size and numbers and through fusion of similar or dissimilar parts a wide range of flower types have developed from the basically (3-)4(-5)-merous, monochlamydous, unisexual flower, the pistillate one with a single (sub)apical ovule and two stigmas (Berg 1977a, 1989) and the staminate one with antitepalous stamens and often without pistillode. The perianth may become rudimentary or absent, and the number of stamens reduced to one. A single stigma is quite common. Pistillodes are present in all species with ballistic pollen release, as they seem to play a role in keeping the inflexed anthers under tension and in the correct position. Pistillodes are characteristic for *Ficus* subg. *Sycidium*, where they are in some species so large that they can function as breeding sites for fig wasps. Pistillodes with very long stigmas occur in *Helianthostylis sprucei* Baill. (Berg 1972).

In the species of the Moreae, with the exception of some Asian *Maclura* species, the stamens are like those of the Urticaceae, releasing the pollen suddenly. They differ from inflexed stamens of other Urticales in showing transverse (tension) lines on straightened filaments.

The differentiation of the flowers is tightly linked to the (degree of) complexity of the inflorescence and to protection of young flowers and developing fruits (Berg 1990).

Fruits and "fruits"

In addition to the "true" fruits (developed from a single ovary and being achenes or drupes (indehiscent or dehiscent!)), there is a wide range of "functional fruits", containing one or more seeds, and also consisting of perianths, bracts and/or receptacle, that usually function as units of dispersal. The most simple ones ("pseudodrupes") consist of a fruit (often with

a hard endocarp) enclosed by the fleshy fruiting perianth. Pseudodrupes may occur free or fused in (syncarpous) aggregates. The more complex fruit-containing structures show similarities to the "infructescence" of the pineapple.

Dehiscent drupes, or indehiscent ones with features clearly derived from the dehiscent ones are found throughout the family (Berg 1977a), even in *Ficus* (Berg & Wiebes 1992). The endocarp body is squeezed out of the fruit in macrospermous species, but it is ejected in microspermous ones (*Dorstenia* p.p. and *Fatoua*).

In many-seeded infructescences of *Dorstenia*, each single fruit (dehiscent drupe!) remains the unit of dispersal. This may also be the case in *Ficus*, depending on the "disperser" (a "seed-eater" rather than a "fruit-eater").

The units of dispersal vary from fruits or pyrenes of c. 2 mm length to syncarpous infructescences up to 100 x 50 cm in *Artocarpus heterophyllus* Lam. (Jarrett 1959-1960).

The fleshy fruits, pseudodrupes or infructescences vary in colour from green to yellow, orange, brown, red, purple or black (or white).

Seeds

The seeds are very variable in the size, the presence of endosperm, the texture of testa, the position/orientation of the seed in the fruit, the thickness, folding, and size (differences) of the cotyledons, and the length and position of the radicle (Corner 1962).

The majority of the genera are macrospermous; the seed lack (ample) endosperm and the cotyledons are thick, often folded, and/or unequal in size, conspicuously so in *Sorocea*, which is submonocotyledonous. Microspermous seeds are found in *Ficus*, the c. 95 herbaceous species *Dorstenia*, and several genera of the Moreae; the seed contains endosperm and the equal cotyledons are thin. Macrospermy is

linked to the rain forest habitat; microspermy is related to the herbaceous habit, hemiepiphytism, and occurrence of secondary growth. The protective function of the testa is transferred to the woody to leathery endocarp/pericarp; the testa is usually distinctly vascularized.

Pollination

The following modes of pollination are found.

Anemophily: (1) with sudden ballistic pollen release (in most Moreae) or (2) with \pm gradual pollen release, *e.g.*, from long pendulous staminate "catkins" (possibly in *Bagassa*, *Batocarpus*, *Clarisia* p.p., and reported for some species of *Artocarpus* without elongate staminate inflorescences). The first type, characteristic for Urticaceae, can be regarded as an adaptation to the rain forest understorey, in particular along small streams, where streaming water may cause (weak) air current by which pollen is carried.

Zoophily: (1) based on breeding in developing fruits by the small *Agaoninae* wasps (*Ficus*) or (2) based on breeding in staminate inflorescences by small beetles and flies. The latter mode is reported for some *Artocarpus* species, but probably widespread, to be found in genera with condensed staminate inflorescences (as those of Castilleae and Artocarpeae); insect larvae are nearly always present in these inflorescences.

Moreover, Sakai *et al.* (2000) described pollination in *Artocarpus integer* (Thunb.) Merr., carried out by gall midges, of which larvae feed on mycelium growing on staminate inflorescences; it is not clear whether the situation described is a local or a general phenomenon. Pollination by thrips is found in *Castilla elastica* Sessé (Sakai 2001). The racemose or spicate inflorescences of *Sorocea* resemble those of genera with ballistic pollen release (Moreae), but the stamens are short. As the perianths of pistillate flowers bear glandular trichomes which

are nutritious (providing a substrate for fungi) pollination may be carried out by collecting the trichomes (Berg 1990, 2001).

In several genera, in particular those with bisexual inflorescences of the Dorstenieae nothing is known about pollination and features of flowers and inflorescences do not point to possible modes of pollination other than (geitonogamous) autogamy. Agamospermy may play a role in reproduction of *Dorstenia* (Berg & Hijman 1999).

Dispersal

The following modes of dispersal are known.

Endozoochory in taxa with fleshy (true or functional) fruits: (1) by arboreal animals (majority), (2) by terrestrial animals (*Artocarpus*, *Ficus*, and *Treculia* with cauliflory or flagelliflory), or (3) by aquatic animals (*e.g.*, *Ficus* in riverine habitats).

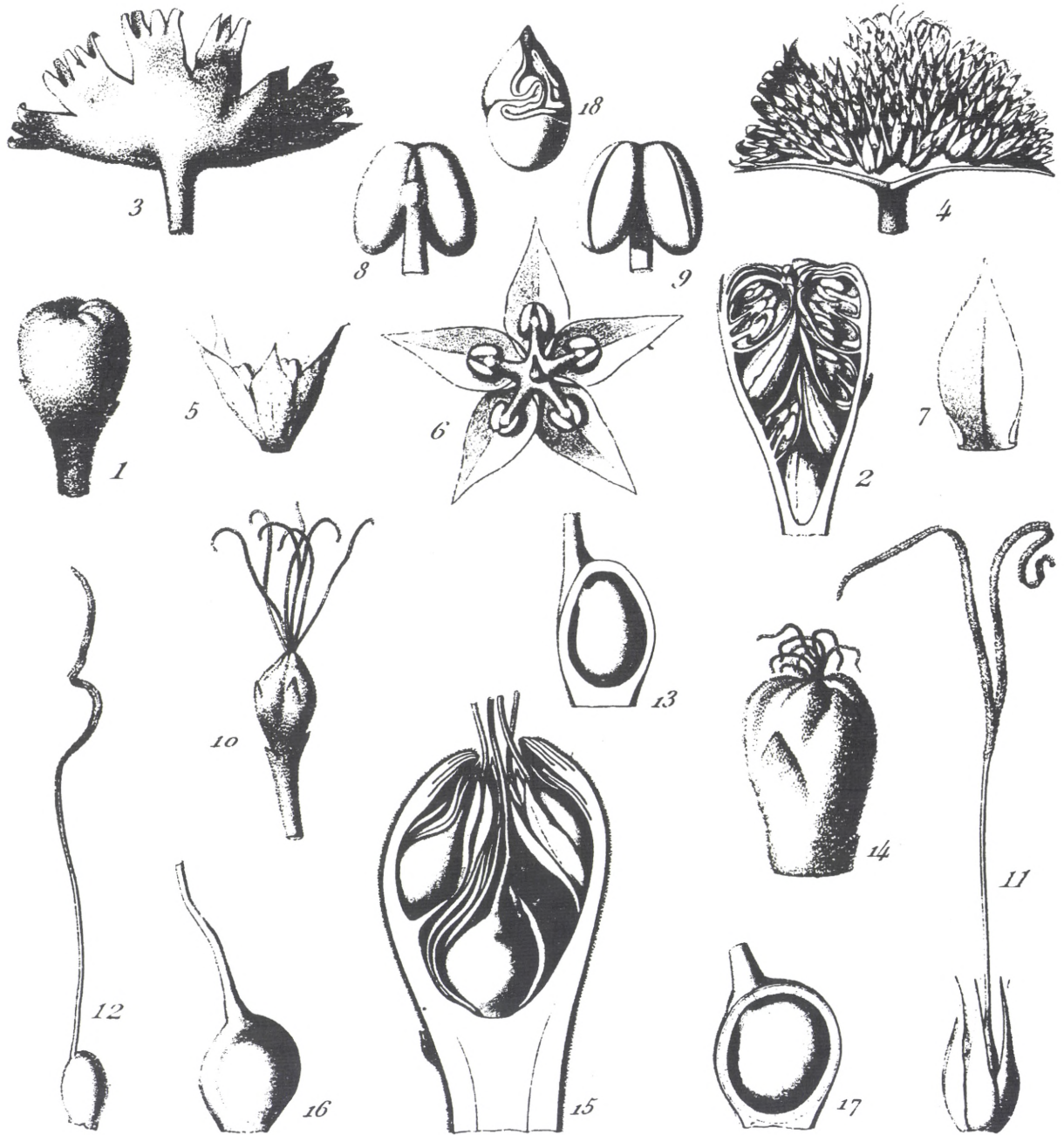
Exozoochory: (1) in taxa with fruits with a sticky outer layer (*Ficus*) or (2) in *Trymatococcus* of which the infructescences are covered with hooked hairs.

Fruits of *Ficus* deposited (by endo- or exochorous transport) on tree branches, may be carried on by ants (to more suitable germination sites).

Autochory in most taxa with dehiscent drupes, the endocarps of small ones are ejected, those of large ones dropped, and both transported further by water.

Hydrochorous in some *Ficus* species of which the syconia can float, either by air inside the infructescence or by a spongy wall of the inflorescence. The rheophytic species of *Ficus* (subg. *Sycomorus* subsect. *Macrostyla*) have retrorse hairs on the (very) long persistent style and on the fruit, apparently an adaptation to attach the fruits to the substrate.

The in general species-specific relations with pollinators limit the possibilities of long-distance establishment of populations.



Grabowski del.

Sparattosyce dioica. Bur.

Picart sc.

Imp. A. Salmon, r. Vieille-Estrapade, 15, Paris.

Tribal Taxonomy

The family comprises 1050-1100 species, accommodated in 37 genera, which as currently defined (see Fig. 1) can be regarded as natural (or monophyletic) entities.

Until recently (Berg 2001) five tribes were recognized:

Artocarpeae with 12 genera and 90-95 species, Castilleae with eight genera and c. 60 species, Dorstenieae with eight genera and c. 130 species, Ficeae with one genus and c. 720 species, and Moreae with eight genera and c. 70 species. All, except for the Artocarpeae are well-defined and can be regarded as natural entities. The Artocarpeae comprise the genera that could not be satisfactorily included in one of the other tribes. They comprise a group of five neotropical genera (with 23 species), a group of four Asian genera (*Artocarpus* and three allied Asian genera) and the African *Treculia* (in total with c. 65-70 species), and a group comprising two genera: *Antiaropsis* with two species from New Guinea, and the monotypic *Sparattosyce* from New Caledonia (Fig. 3). The neotropical group of genera resembles the Moreae in shape and structure of the inflorescences, but is clearly different in the structure of the staminate flowers. The small group formed by *Antiaropsis* and *Sparattosyce* resembles the Castilleae in the shape and structure of the inflorescences, but differs clearly in the presence of dehiscent drupes and scarious tepals of the pistillate flowers. The morphological links between these three groups are as weak as between the “natural tribes” and can, therefore, be regarded as tribes equivalent to the other four tribes and to be named Soro-

ceae, Artocarpeae, and “Antiaropsidae” (*ined.*), respectively. There might be a phylogenetic link between the “Antiaropsidae” and Ficeae.

The distribution patterns and the lack of clear affinities between the tribes suggest that the family was established and the genera to a largely shaped before the break-up of Gondawana, an opinion (Berg 1998) which is confirmed by research on *Ficus* (Molbo *et al.* 2003; Weiblen 2002).

The distinctness of the tribes is not only defined by their morphological make-up, but also by biological traits as expressed in the mode of pollination and habitat occupation.

Taxonomy of *Ficus*

Ficus is not only far more numerous than the other genera, but is also morphologically distinct in characters not found in other Moraceae, many of them related to the unique pollination system. Moreover, the systematic make-up tells the genus apart.

The unique pollination system is based on breeding in ovaries by Agaoninae (c 20 genera, numerous species, roughly as many as the number of *Ficus* species) of which the winged females transport pollen, penetrate the closed inflorescence, lay eggs in the ovules, and deposit pollen. The pollination system is in its basic traits uniform, but in details highly varied due to the pollinator groups involved and the variation of characters of flowers and inflorescence.

Characters that distinguish *Ficus* from other Moraceae are:

- (1). The flowers remain entirely enclosed in

← Fig. 3. *Sparattosyce dioica*, from *Ann. Sci. Nat. Bot., Sér. 5, 11*: t. 6 (1869): 1 and 2. Staminate inflorescences, closed; 3 and 4. staminate inflorescences, open; 5 and 6. staminate flowers; 7 tepal of staminate flower; 8 and 9. stamens; 10, 14, and 15. pistillate inflorescence, closed; 11. pistillate flower; 12. pistil; 13 and 16. ovary; 17. fruit; 18. embryo. The pistillate inflorescence opens like the staminate one to expose the ripe fruits and to release the endocarp bodies of the dehiscent drupes.

an urceolate receptacle (syconium) also during anthesis.

(2). Heterostyly (imperfect or perfect); the stigmas lined up (in monoecious taxa due to differences in the length of the pedicel (or also the shape of the ovary)).

(3). Pedicels of pistillate flowers distinctly different in length in the same inflorescence.

(4). The number of staminate flowers (per inflorescence or per plant) is mostly (very) small in relation to the number of pistillate flowers.

(5). Scarious tepals of the pistillate flowers.

(6). Formation of a coherent layer of stigmata (synstigma) in spite of style lengths in the same syconium.

(7). Waxy glandular spots on the lamina beneath and/or the nodes of leafy twigs in nearly all species.

Other differentiating characters:

(8). Pronounced protogyny: the staminate flowers are at anthesis when in the same inflorescence the seeds are (nearly) ripe.

(9). The perianth (and interfloral bracts and/or internal hairs) remained intact in spite of loss of the(ir) protective function.

In addition to these largely floral characters, *Ficus* differs from the rest of the Moraceae by the numerous species (c 390) that produce aerial roots, and for most of them (c 290) allowing them to be hemi-epiphytes and others to be root-climbers (c 70). Moreover, in (the monoecious subgenera) *Ficus*, the tertiary venation of the lamina can be parallel to the lateral veins.

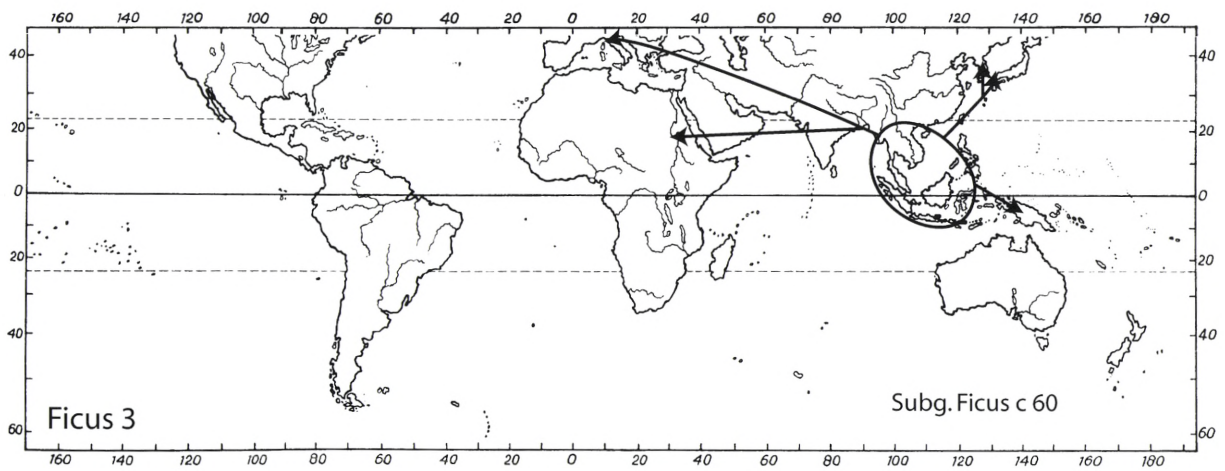
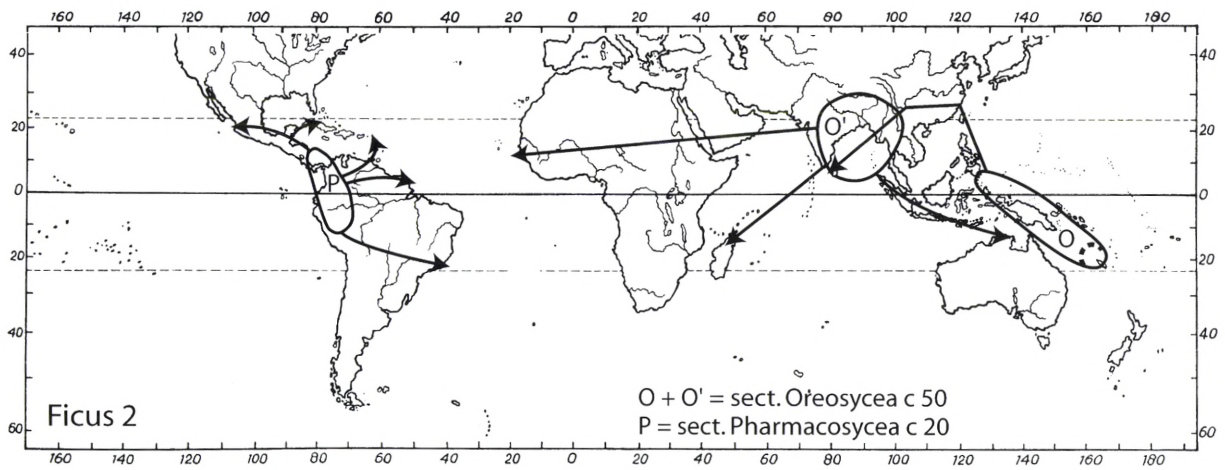
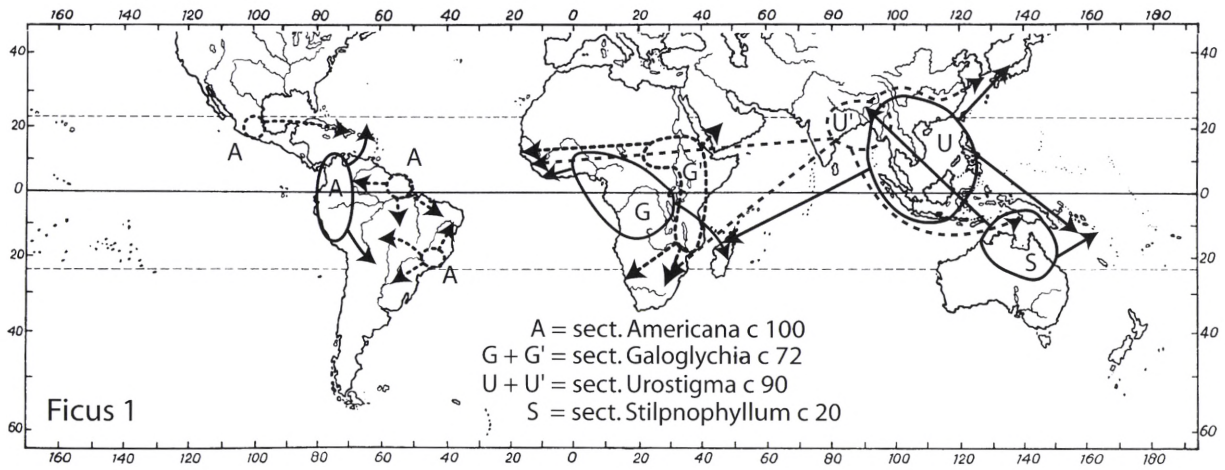
The only moraceous genus with inflorescences resembling of *Ficus* is *Sparattosyce* (Fig. 3), but the inflorescences are unisexual, the pistillate ones exposing the stigmas through

the apical opening and the receptacle splits to expose the dehiscent drupes; the staminate ones opens in the same way to expose the stamens at anthesis.

The subgenera of *Ficus* are in their numbers of species similar to several moraceous tribes. These numbers and the diversification within the genus makes it appear the genus is like “a family within a family” (Corner 1958), with a diversity that equals that of many large angiosperm families; subsections and sections currently recognised are more or less clearly equivalent to genera and subgenera to tribes. Far ahead of modern developments the Italian botanist Gasparrini (1844, 1845) started to split *Ficus* into new genera largely based on floral characters. This concept was adopted by the great Dutch “ficologist” Miquel (1847-1848), who expanded the number of genera, but finally he met the limits of the possibilities for systematization and had to include all those about 20 genera in *Ficus* (Miquel 1867). Many of those genera became subdivisions of the genus. The more recent and elaborate classification of the genus by Corner (1960, 1965) includes c. 125 entities: subgenera, sections, subsections, series, and subseries – too many trees to see the forest. A more concise classification is proposed (Berg 2003) of which outlines are presented in Fig. 1.

The morphological and ecological differentiation within the genus, the distribution patterns (Fig. 4, 5 & 8), the biological distinctness, the diversification in the pollination system as reflected in the number of genera of pollinating wasps and other groups of insects exploiting the system, and the differences with the “other” Moraceae suggest that *Ficus* established

Fig. 4. Distribution of three subgenera and sections of *Ficus* with the numbers of species for each. Continuous lines for the primary centres, broken lines for secondary ones; lines and arrows for main distribution tracks; G for groups of species associated with humid conditions, G' for groups of species associated with drier conditions; U for subject. *Conosycea*, associated with humid conditions, U' for subject. *Urostigma*, associated with drier regions. →



itself as distinct group early in the history of the Urticales (Molbo *et al.* 2003; Weiblen 2002). Also wood-anatomical features support the fairly isolated position of the genus (Koek-Noorman *et al.* 1984).

Molecular phylogeny of *Ficus* and Moreae

It is surprising that molecular data as presented by Sysma *et al.* (2002) do not support the profound distinctness of *Ficus* (Ficeae). It ends up in a cluster together with the tribe Castilleae, one would never consider to be related because of fundamental differences in the structure and function of the inflorescence. However, the Castilleae and *Ficus* share the absence of some characters, such as the absence of peltate bracts and, if one ignores the presence in three unrelated species of *Ficus* (*F. asperiuscula* Kunth & C.D. Bouché of subg. *Sycidium*, *F. recurva* Blume of subg. *Synoecia*, and *F. theophrastoides* Seem. of subg. *Sycomorus*) also the absence of uncinata hairs. If these characters express affinities, then one could predict that also *Antiaropsis* and *Sparattosyce* ("Antiaropsidae") will end up in the same cluster.

The indumentum character do not appear biologically important, and is in that respect, similar to macro- and micromorphological characters which are mostly used in the cited paper presenting the results of molecular analyses to explain clustering of taxa. The bracts character, may have more than subordinate, although somewhat ambiguous biological importance, if one assumes that basal attachment of bracts is a prerequisite for the establishment of rows of imbricate bracts with may close off access to the flowers, in *Ficus* perma-

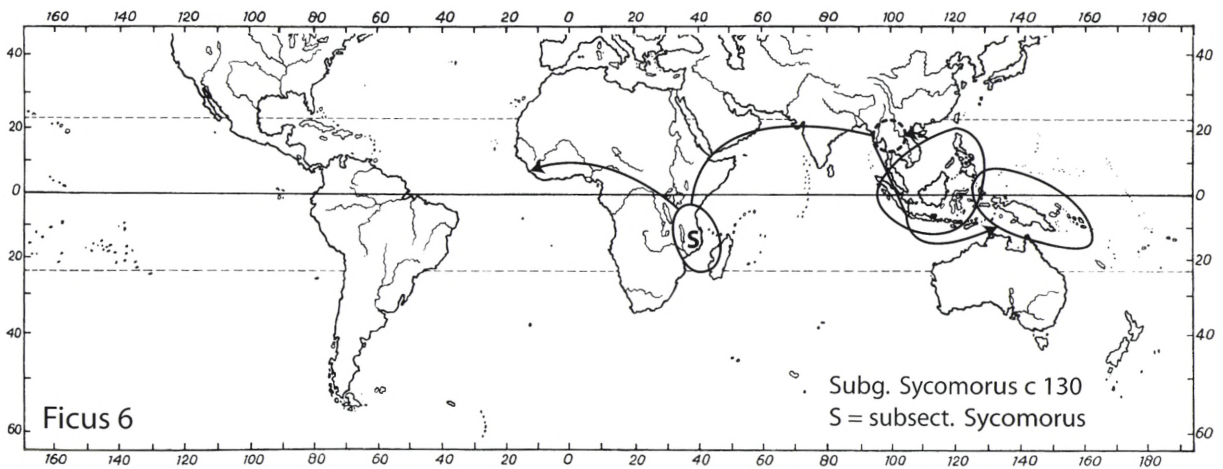
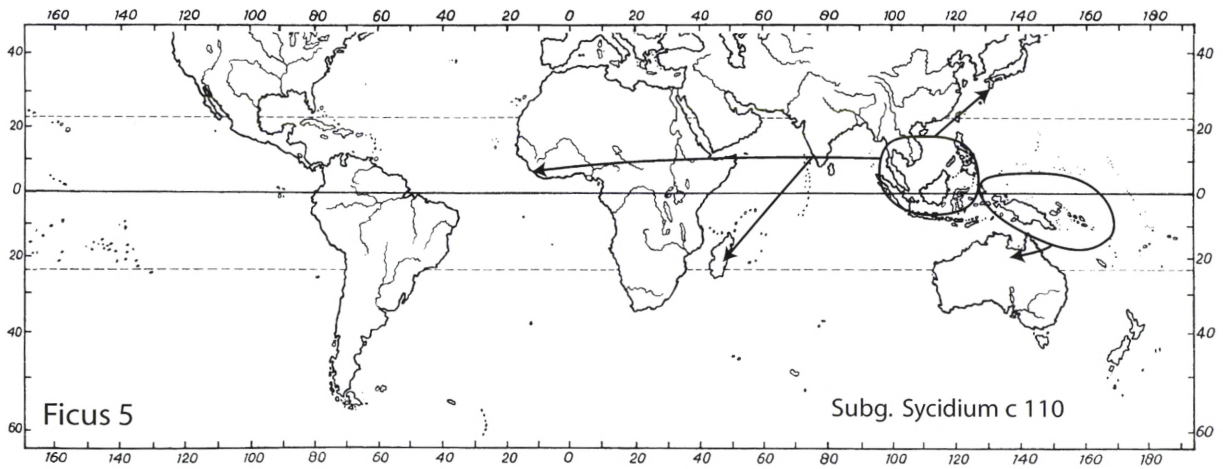
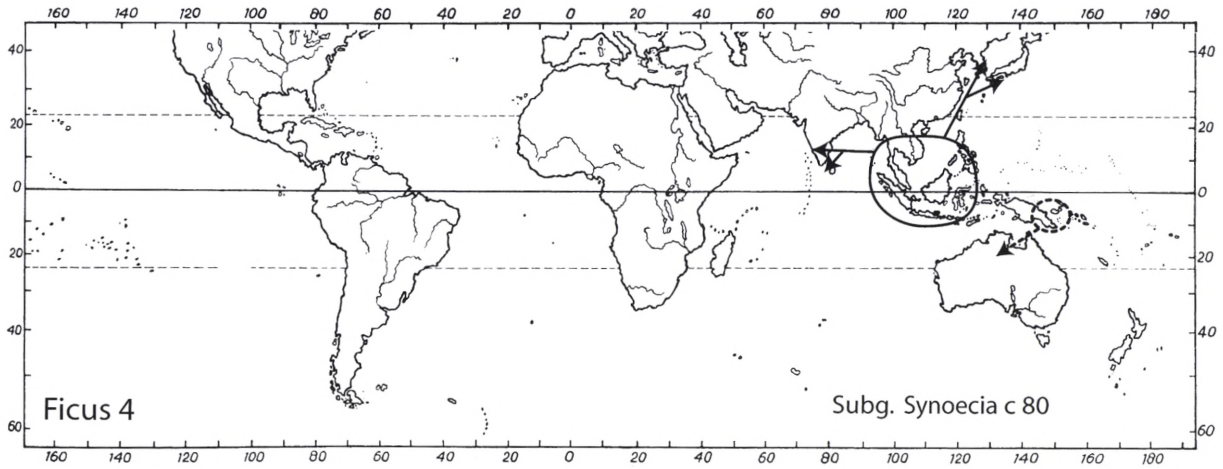
nently by ostiolar bracts, in Castilleae and "Antiaropsidae" temporarily by the upper involucre bracts, in the former tribe to staminate flowers and pistillate flowers in unisexual inflorescences, in the latter also pistillate ones with more than one pistillate flower. However, *Trophis caucana* (Pittier) C.C. Berg, which belongs to the tribe Moreae, also has involucres of imbricate bracts; in the genus the bracts are basally attached and also uncinata hairs absent.

Another result of the same molecular analyses (Sysma *et al.* 2002) that is clearly in conflict with a traditional concept, is the scattered occurrence of members of the Moreae which appears on the basis of morphological coherence and distribution to be such a nice natural group. It also raises the question how often the urticaceous type of androecium (staminate flower) can evolve or disappear without leaving any trace of an ancestral trait.

Molecular phylogeny of Urticales

Another case in this publication that does not reflect distinctness and presumably different evolutionary pathways is the presence of the neotropical lowland genus *Ampelocera*, that one could indicate as the most tropical of the Ulmaceae, in a cluster of genera which share abscission of the terminal meristems, a feature also found in the moraceous genera *Broussonetia* and *Morus*, and in *Tilia* (Tiliaceae). This feature links these genera (of which representatives may secondarily occur in the lowland tropics) to development under northern temperate conditions. The presence of a tiny hypanthium, although it is the most rosaceous character in the Urticales, but probably with lit-

Fig. 5. Distribution of three subgenera of *Ficus* with the numbers of species for each. Continuous lines for the primary centres, broken lines for secondary ones; lines and arrows for main distribution tracks; S for sect. *Sycomorus* subsect. *Sycomorus* with only monoecious species. →



the biological significance, is indicated as one of the unifying morphological characters. The other character, bisexuality of the flowers, is not consistent and also found in other Ulmaceae.

A similar case is the position of the five clearly related (West-Gondwanan) genera of the Cecropiaceae. They differ from Urticaceae in a good number of macromorphological, chemical and microscopic characters. More

important is that the group is biologically so different in the absence (loss?) of urticaceous stamens and it is, therewith, not anemophilous. Characters such as condensed inflorescences, fleshy staminate perianths, large protective stipules (and spathes) can be linked to disconnection from anemophily (if that would have been an ancestral trait at all). Adaptations to (secondary?) anemophily as in *Cecropia* are highly peculiar and diverse. Do the

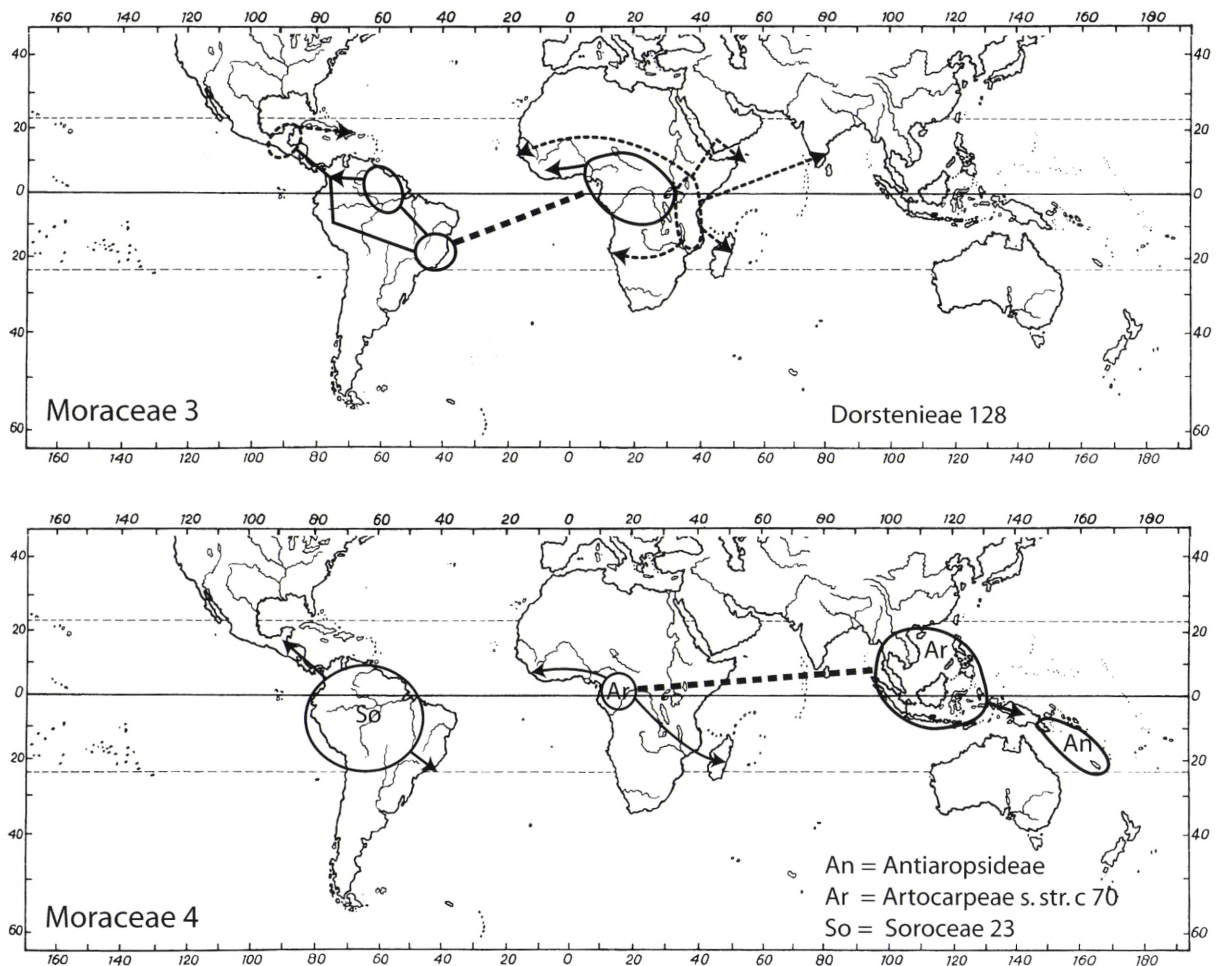


Fig. 6. Distribution of four tribes of Moraceae, with the numbers of species for each. Continuous lines for primary centres, broken lines for secondary ones. Thick broken lines for strong links between partial areas. Continuous and broken lines and arrows for main distribution tracks. Small circle for Artocarpeae in Africa for *Treculia*.

molecular bases of to characters like presence of arachnoid indumentum and pearl glands make that the bulk of the Cecropiaceae to cluster with the Boehmerieae?

Distribution

The family is pantropical (Fig. 1, 4, 5, 6, 7 & 8). The majority of the genera are truly tropical, but *Ficus* extends with some species to the sub-

tropical or even warm-temperate zones (Fig. 8). *Broussonetia* and *Morus* are clearly associated with the northern warm-temperate zone. They are morphologically adapted to nontropical climates through the abscission of the terminal meristem at the end of the growth season, so that elongation of branches happens through the meristem of the upper lateral bud. The buds are scaled. Even truly tropical lowland species of these genera, *Broussonetia greveana*

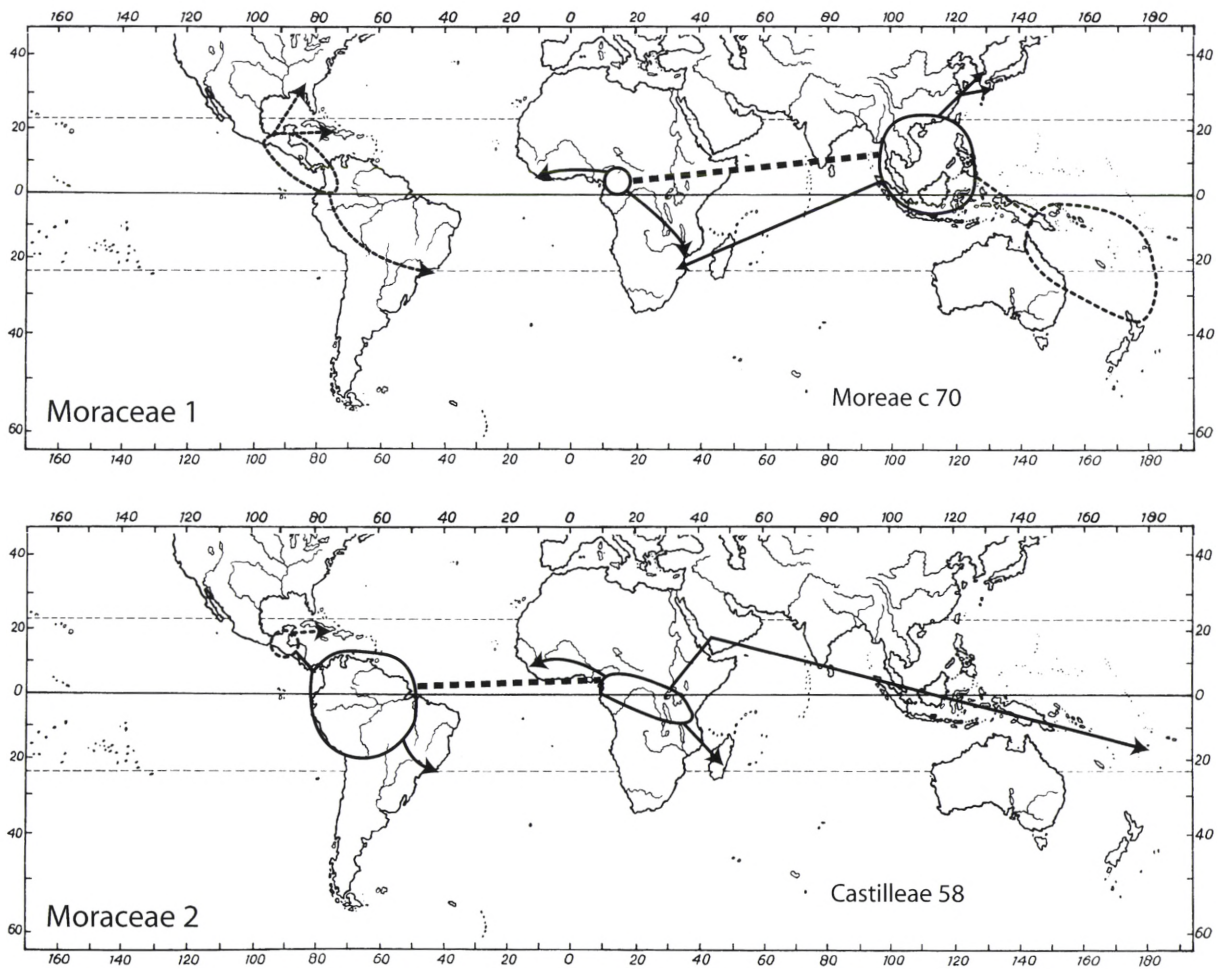


Fig. 7. Distribution of two tribes of Moraceae [Moreae and Castilleae] with the numbers of species for each. Continuous lines for primary centres, broken lines for secondary ones. Thick broken lines for strong links between partial areas. Continuous and broken lines and arrows for main distribution tracks. Small circle for Moreae in Africa for *Milicia*.

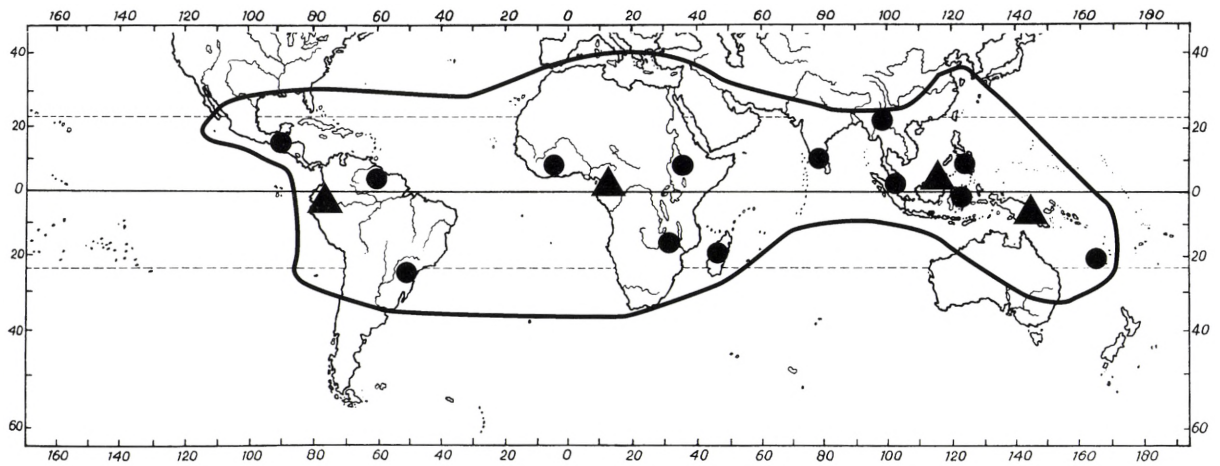


Fig. 8. Outline of the distribution of the Ficeae. Major concentrations on species indicated by triangles, lesser concentrations by circles.

(Baill.) C.C. Berg (Madagascar) and *Morus mesozygia* A. Chev. (Africa), show these features (Berg 1977b).

Most tropical Moraceae grow in humid lowland forest, relatively few are montane or submontane species or are found in drier conditions such as seasonal forests, or even in semi-deserts.

The tribes Castilleae (Fig. 7) and Dorsteneae (Fig. 6) show a clear trans-Atlantic (West-Gondwanan) connection. The other tribes do not. The Soroceae is the only tribe confined to the Neotropics, and the tribe "Antiaropsidae" (ined.) is confined to New Caledonia and New Guinea. The Artocarpeae and Moreae are centred in Malesia and the Sino-Himalayan region respectively; both are represented by a single genus in Africa. The Ficeae are centred in southeast Asia (Fig. 4, 5 & 8); some subgenera have (secondary?) centres in the Neotropics, Africa, and/or Australia. It is not possible to indicate a hypothetic centre of origin for the whole family. The richness of species in SE Asia is largely caused by "explosive" speciation in (gyno)dioecious segment of the genus *Ficus*; disregarding this fact, the representation of the

family in the main phytogeographic becomes more balanced, with regard to the numbers of both species and genera.

Based on distribution patterns of tribes and of sections or subsections of *Ficus*, primary and secondary centres can be recognized.

In the Neotropics, the northern Andes region and the adjacent part of Central American and the (upper) Amazon basin are primary centres and the Guianas, eastern Brazil, and southern Mexico and the adjacent part of Central America (with an extension to Greater Antilles) are secondary centres.

The primary centres in Africa are (humid western) Central Africa and (\pm dry) eastern and northern Africa (with an extension to Arabia); secondary centres are (humid) western Africa, (\pm humid) eastern Africa, and Madagascar.

Three main centres can be recognized in Asia: the Sino-Himalayan region, western Malesia (with northern Borneo as a hotspot), and eastern Malesia (with eastern New Guinea as a hotspot). The only rather clear secondary centre is Peninsular India (and Sri Lanka).

Other centres are northern Australia for

Ficus subsect. *Malvanthera* (of sect. *Stilpnophyllum*) the Pacific (with New Caledonia as hotspot) for *Ficus* sect. *Oreosycea* subsect. *Glandulosae* (*F. austrocaledonica*-group), see Fig. 4 and 8.

The number of genera represented in the main phytogeographical regions is rather similar, but the number of endemic genera differs clearly, and so does the number of species (Fig. 1). The high number of species in the Asian-Australasian region is caused by explosive radiation of the the (gyno)dioecious groups of *Ficus*.

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