Classification and distribution of *Ficus*

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Summary. The classification of the genus *Ficus* has changed considerably in the course of time and is still the subject of further research and discussion. The main subdivisions in the most recent classification by Corner[12] are presented together with the genera of pollinating fig wasps (Agaonidae) associated with them. These subdivisions are discussed and grouped according to morphological and functional traits, in particular in connection with the unique pollination system. Two main groups are recognized: one with only monoecious species and the other with predominantly (gyno)dioecious species. The former comprises two subgroups (*Pharmacosycea* and *Urostigma*) and the latter three, more profoundly different subgroups (*Ficus, Sycidium,* and *Sycomorus*). The neotropical representatives of the genus are discussed in somewhat more detail. In addition, the distribution of the genus is summarized for the three main regions of distribution; Africa, America, and Asia-Australasia. Finally the concordance between subdivisions of *Ficus* and those of the Agaonidae is briefly discussed.
Key words. Ficus; subdivisions; distribution.

Introduction

In 1844–1845 Gasparrini[22,23] subdivided the genus *Ficus* into several genera. This concept was initially adopted by Miquel who studied the genus *Ficus* worldwide. He increased the number of genera and published many new species. Later on Miquel[25,26] decided to unite the genera previously distinguished into a single genus again, in which the former genera became elements of the primary subdivision of the genus. He gave a survey of the approximately 550 species recognized at that time. Since then, many students have contributed to the taxonomy of the genus and the number of species described has increased considerably. About 30 years ago Corner[11] started to publish revisional studies on the Asian and Australasian members of the genus. This work resulted in many publications, among which is the unpublished treatment for the Flora Malesiana. In 1965 he gave a revised classification of the genus and presented a check-list of the Asian-Australasian taxa he recognized at that time[12]. Several new species were added up to 1970[14]. In 1977 Berg started to work on the taxonomy of *Ficus* in the African flora region, which resulted in several regional revision[1,6–8] and a check-list for this region[4]. DeWolf[17,18] started revisional work on the neotropical *Ficus* flora; he has had to give up the work and it has been gradually taken over by Vázquez Avila[33] and Berg[3], both[9,34] at present mainly working on regional revisions.

Nowadays, systematic work on *Ficus* can be carried out within an increasingly better framework of knowledge about its reproductive biology. When Corner started his work, that knowledge was still largely based on observations on *F. carica,* and rather fragmentary taxonomic knowledge of the pollinators (Agaonidae). Many students have contributed to the increased knowledge, and only some major contributions will be referred to here: the work on pollen transport by and behaviour of the pollinators and the pollination system by Galil and coworkers[19–21], Ramirez[27–29] and Michaloud et al.[24], taxonomy of the pollinators by Ramirez[29] and Wiebes[38,39], improvement of the knowledge of pollination and reproduction by Valdeyron et al.[32], and recent studies on the anatomy of the syconium and flowers by Verkerke[35–37].

The present study is an attempt to re-group the main subdivisions (subgenera and sections) of Corner's classification[12], not only on the basis of morphological features, but also on the basis of traits related to reproduction and pollination systems. This may help in the understanding of evolutionary pathways in the differentiation of *Ficus* and its pollination. A brief survey of the distribution of *Ficus* may also contribute to that understanding.

Classification

The following subdivision of *Ficus* was proposed by Corner[12]. The survey includes (approximate) number of species, distribution of the entities and genera/entities of the Agaonidae.

Ficus	ca 750 spp.	worldwide	Agaonidae
subg. *Urostigma*	ca 280 spp.	worldwide	
sect. *Urostigma*	ca 20 spp.	Africa, Asia, Australasia	*Platyscapa*
sect. *Leucogyne*	2 spp.	Asia	*Maniella*
sect. *Conosycea*	ca 65 spp.	Asia, Australasia, Madagascar	5 genera; see below
sect. *Stilpnophyllum*	1 sp.	Asia	'Blastophaga G'
sect. *Americana*	ca 120 spp.	America	*Pegoscapus*
sect. *Galoglychia*	ca 75 spp.	Africa	7 genera; see below
sect. *Malvanthera*	ca 20 ssp.	Australasia, E. Malaysia	*Pleistodontes*

subg. *Pharmacosycea*	ca 75 ssp.	worldwide	
sect. *Pharmacosycea*	ca 20 spp.	America	*Tetrapus*
sect. *Oreosycea*	ca 50 spp.	Africa, Asia, Australasia	*Dolichoris*
subg. *Sycomorus*	13 spp.	Africa, Asia	*Ceratosolen*
subg. *Ficus*	ca 350 spp.	Africa, Asia, Australasia, Mediterranean	
sect. *Ficus*	ca 60 spp.	idem	*Blastophaga*
sect. *Rhizocladus*	ca 55 spp.	Asia, Australasia	*Blastophaga*
sect. *Kalosyce*	ca 20 spp.	idem	*Blastophaga*
sect. *Sinosycidium*	1 sp.	China	unknown
sect. *Sycidium*	ca 105 ssp.	Africa, Asia, Australasia	6 genera; see below
sect. *Adenosperma*	23 ssp.	Australasia, E. Malaysia	*Ceratosolen*
sect. *Neomorphe*	6 ssp.	Asia, Australasia	*Ceratosolen*
sect. *Sycocarpus*	ca 80 ssp.	Asia, Australasia	*Ceratosolen*

Further subdivisions of the sections as far as they are associated with more than one genus of the Agaonidae:

Subdivision of sect. *Conosycea* according to Corner[12]:

subsect. *Conosycea*	ca 30 ssp.	*Deilagaon, Eupristina, Platyscapa, Waterstoniella*
subsect. *Dictyoneuron*	ca 20 ssp.	*Waterstoniella*
subsect. *Benjamina*	ca 15 ssp.	*Eupristina, Parapristina*

Subdivision of *Galoglychia* according to Berg[2]:

subsect. *Galoglychia*	3 spp.	*Allotriozoon*
subsect. *Platyphyllae*	18 spp.	*Alfonsiella, Elisabethiella, Nigeriella*
subsect. *Chlamydodorae*	13 spp.	*Alfonsiella, Elisabethiella*
subsect. *Crassicostae*	8 spp.	*Elisabethiella, Nigeriella, Paragaon*
subsect. *Cyathistipulae*	19 spp.	*Agaon*
subsect. *Caulocarpae*	11 spp.	*Courtella*

Subdivision of sect. *Sycidium* according to Corner[12]:

subsect. *Sycidium*	ca 70 ssp.	*Ceratosolen, Kradibia*
subsect. *Varinga*	ca 15 ssp.	*Ceratosolen, Kradibia*
subsect. *Palaemorphe*	ca 20 ssp.	*Liporrhopalum*

The genera of Agaonidae involved in the pollination of *Galoglychia, Malvanthera* and *Pharmacosycea* belong to the subfamily Agaoninae and the other genera to the subfamily Blastophaginae[39].

Comments on the classification

There is great diversity in both vegetative and reproductive structures in the genus *Ficus*; this diversity would allow the distinguishing of several genera. The entities are held together by a number of features: the urceolate receptacle with a narrow entrance (ostiole), which is closed in one way or another by bracts, heterostyly, extended secondary protogyny (separation of receptiveness of the stigmata and the release of pollen by a considerable lapse of time). These features are connected with the unique pollination system found in the genus. Another feature, which may also be connected with the pollination system, is the common occurrence of waxy glandular spots on the leaves or twigs. A problem with the recognition of a single genus is the interpretation of traits of the genus based on findings in one or a limited number of species. Again and again, differences in many details become apparent. Therefore the generalizations in the discussion of morphological and functional groups that can be recognized in *Ficus* are provisional because of the lack of sufficient data.

Two main groups can be recognized in the genus: the first one (A) comprising the subgenera *Pharmacosycea* and *Urostigma*, and the other (B) comprising the subgenera *Ficus* and *Sycomorus* (sensu Corner).

Pharmacosycea–Urostigma group

This group comprises about 350 species and is represented both in the Old and in the New World. All members of this group are monoecious and the pistillate flowers show imperfect heterostyly (see Verkerke, this review). The stigmata are more or less filiform and cohere to form a more or less cobwebby synstigmatic layer. The flowers are densely packed, usually among interfloral bracts. The proportion of staminate flowers is relatively low (about 10%). These flowers are mostly dispersed among the pistillate flowers, less commonly concentrated near the ostiole; they have mostly one, but in subgenus *Pharmacosycea* they may have two (or three) stamens. The inflorescences are 'tomb blossoms' (from which the pollinators cannot egress except through tunnels made by male Agaonidae). Three types of arrangement of the ostiolar bracts occur (see Verkerke, this review).

The syconia vary from a few mm to about 10 cm in diameter, but are mostly between about 1 and 2.5–3 cm in diameter. They are mostly borne in the leaf axils, less

commonly on the previous season's growth or on older wood down to the trunk, and then usually on spur-like branchlets. Lateral bracts are rare (occurring in some species of the subgenus *Pharmacosycea*) and the basal bracts (three or two) are arranged in a whorl.

The flowering (and fruiting) is usually individually synchronous and intermittent, but in the population asynchronous and continuous. This implies that the pollinators have to fly from one tree to another to occupy new breeding sites. Pollination is, at least in *Urostigma* species, ethodynamic[19], involving active loading (and release) of pollen by the pollinator. This may also be the case in members of section *Oreosycea*, but in section *Pharmacosycea* the mode of pollination is probably topocentric[19], which implies (largely) passive loading (and release) of pollen by the pollinator. However, Ramirez[27] reported wasps eating pollen and regurgitating it when they have entered a syconium, which is possibly a primitive type of ethodynamic pollination. In contrast to the situation in other groups of monoecious species, the pollinators arrive undamaged in the fig cavity of the species of section *Pharmacosycea*.

The leaves are mostly coriaceous with an entire margin. In some species of *Oreosycea* the leaves can be lobate in juvenile forms; weakly lobate leaves can be found in juvenile forms of some species of the section *Pharmacosycea*. Tertiary venation parallel to the secondary veins can be found in most sections of the group. The leaf surface is mostly smooth. The waxy glandular spots occur on the lower leaf surface at the base of the midrib in one median spot or two lateral spots (in some of the *Pharmacosycea* species).

The two subgenera, *Pharmacosycea* and *Urostigma*, can be rather easily told apart and are probably natural entities.

1. Subgenus *Pharmacosycea*. The species of *Pharmacosycea* are usually terrestrial/free-standing trees (in *F. crassiuscula* sometimes hemi-epiphytic; Ramirez, pers. comm.). The style has normally two stigmatic branches. The two sections recognized by Corner are probably natural entities.

Section *Pharmacosycea* is probably the most primitive one of the subgenus (and also of the whole *Pharmacosycea–Urostigma* group) judging, for example, by the constant occurrence of two stamens in the staminate flower. The section is confined to the New World and (not very distinctly) concentrated in the Andean region and Central America. It is quite distinct in the pollination system, the type of ostiole, and traits of the pollinators.

The section *Oreosycea* is rather diverse, with some species reminiscent in many features of those in several subdivisions of the subgenus *Urostigma*, and with other species reminiscent of members of section *Pharmacosycea*. It is centred in Asia-Australasia with a few species extending to Madagascar and continental Africa.

2. Subgenus *Urostigma*. This subgenus is much more diverse than the former one and is characterized by the ability to form extensive systems of aerial roots, which allow the hemi-epiphytic life form to be adopted by many representatives of the subgenus. This may result in the spectacular habit of the 'strangler fig'.

The seedlings of hemi-epiphytes become established at a suitable place on the trunk or a branch of some tree, and send (in contrast to true epiphytes or holo-epiphytes) roots (often only one) down to the soil. When the soil is reached and ample nutrients become available, the plant starts to grow faster and will sooner or later start reproduction. In several *Ficus* species the supraterraneous root system can expand considerably and form a basket of anastomosed roots around the trunk of the host tree, which may contribute to the killing (strangling) of the host tree. Some (hemi-epilithic) species start their life on rock surfaces; some of them can be 'rock-splitters'.

The staminate flowers of the subgenus *Urostigma* have only one stamen. The styles mostly have a single stigmatic branch. Lateral bracts on the fig wall are absent.

In section *Malvanthera*, several derived characters can be found: anthers with a single theca, ovaries sunk into the receptacle, and all ostiolar bracts descending, resulting in a slit-shaped passage to the fig cavity and a slit-shaped bilabiate or triradiate entrance. Moreover, the tertiary leaf venation is predominently parallel to the secondary veins, the (two or three) basal bracts are often long and have a hooded apex, and the stipules are often relatively long. The section is centred in northern Australia and extends to New Guinea, the Solomon Islands and Celebes.

The members of section *Galoglychia* match those of section *Malvanthera* in having a slit-shaped passage to the cavity of the fig, but the entrance is (nearly) always a bilabiate slit. There are (nearly) always two basal bracts. This section is the most differentiated one among the sections of *Urostigma*, and this is reflected in the number of Agaonid genera involved in pollination. It is confined to the African flora region (incl. Madagascar and the Mascarene Islands and extending to the southern part of the Arabian Peninsula).

Section *Stilpnophyllum* comprises only one species: the Asiatic *F. elastica*. This species is very similar to several of the representatives of section *Malvanthera* in the leaf venation, the long stipules, and the long basal bracts with a hooded apex, but it clearly differs in the ostiole which is constructed as in the following sections.

The other sections of subgenus *Urostigma* are relatively less distinct. Distinction is largely based on differences in colours of the ovaries and the number of basal bracts.

Section *Urostigma* comprises a group of species with ovaries which are red-brown, entirely or in the upper part. Staminate flowers are often arranged near the ostiole. Interfloral bracts may be lacking or be replaced by bristles. The leaves often have relatively long petioles. The members of this section occur in Asia, Australasia and Africa; the section appears to be centred in the Asian mainland and shows distinct connections with the

African flora region, where the section is represented by five species. The section appears to be associated with relatively dry (and/or distinctly seasonal) climatic conditions.

Section *Leucogyne* comprises only two Asian species, both with entirely whitish ovaries. In other features these species match those of members of section *Urostigma*, and one could wonder whether separation of the two groups at the section level is justified. However, pollination is carried out by different genera of fig wasp.

The following sections are in many respects similar. The main morphological character used to distinguish the two sections is the number of bracts. The staminate flowers are always dispersed and interfloral bracts are always present. The ovaries often have a reddish spot.

The syconia of the species of the Old World section *Conosycea* normally have three basal bracts. Some of the species of this section (e.g. *F. benghalensis*) have the 'banyan' habit. The section is widespread in Asia and Australasia and extends with two species to Madagascar.

The syconia of the species of the New World section *Americana* have normally two basal bracts.

Ficus–Sycidium–Sycomorus group

The second main group comprises the subgenera *Ficus* and *Sycomorus* (sensu Corner). This group is confined to the Old World and is less uniform than the first group (A). About fifteen species are monoecious and have imperfect heterostyly; both types of pistillate flowers can form seeds. The majority of the species of this main group are (gyno)dioecious, heterostyly is perfect, and seeds are only formed in ovaries of the long-styled flowers (see Verkerke, this review).

The members of this main group are similar in that interfloral bracts are absent; these are often replaced by bristles among the flowers. Tepals and styles often bear hairs. The stigma is often clavate and funnel-shaped. The staminate flowers are usually arranged near the ostiole. The ostiole is often wide with several to many ostiolar bracts visible. Lateral bracts are common. The inflorescences are either 'tomb blossoms' or 'trap blossoms' (from which pollinators or their offspring can escape without needing tunnels made by male agaonids). Phenology is more diverse than in the former main group. Production of syconia can be basically continuous, may occur in overlapping crops, or can be intermittent. The phenology of plants with seed figs and those with gall figs is or can be different. Most species are terrestrial from the beginning and only a few are hemi-epiphytic or (facultatively) holo-epiphytic. The leaves often have more or less mesomorphic features (chartaceous texture, lobate to dentate to crenate margin, etc.). Cauliflory is quite common and in several groups, in particular section *Sycocarpus*, the geocarpic habit is found, with stolon-like branchlets arising from the base of the trunk, bearing figs at the soil surface or in the litter.

The subdivisions of the second main group are not yet established. One of the problems is the subgenus *Sycomorus*, which Corner[12] recognized only because of the occurrence of monoecy, in spite of striking similarities with members of section *Neomorphe* (one of the sections of subgenus *Ficus*), which consists of only (gyno)dioecious species. On the other hand, Corner accepted the presence of two monoecious species in *Sycocarpus*, another section of subgenous *Ficus*. The sharing of one genus of agaonids (*Ceratosolen*) as pollinators[29,39] and the occurrence of *Apocrypta*, a genus of parasitic wasps, only on species of *Sycomorus*, *Neomorphe*, and *Sycocarpus*[31], also suggest close relationships between these three entities. Uniting these three entitites into a single entity of higher rank can be justified on the basis of morphological characters. One of them is the presence of staminate flowers, which occur in a limited number (often 2–3% of the total number of flowers) near the ostiole. The perianth is tubular and the perianth lobes are hooded and overlapping, thus entirely enclosing the stamens. At anthesis the filaments stretch and tear the perianth. Moreover, the staminate flowers are enveloped by two large bracteoles. This type of staminate flower does not occur in any other group of *Ficus*.

Sycomorus and *Neomorphe* can be united in a rank equivalent to one for *Sycocarpus*, the former with about 2/3 of the species monoecious, the latter with only two monoecious species out of about 80 species. The two entities can be distinguished by differences in the perianth and the occurrence of hairs on the style in *Sycocarpus*.

A second, distinct, exclusively (gyno)dioecious subgroup comprises the species of section *Sycidium*. This subgroup is distinguished from the former and from the following one by the absence of neuter flowers (as substitutes for staminate flowers) in the 'gall figs'. The staminate flowers have well-developed pistillodes; in several species the 'staminate' flowers even have pistils similar to those of the short-styled pistillate flowers and can be regarded as (morphologically) bisexual. These two features suggest that (gyno)dioecy in section *Sycidium* may have developed differently from (gyno)dioecy in the former and in the third subgroup. In contrast to other groups of *Ficus*, a distinct whorl of basal bracts is lacking, but the bracts are usually borne on the peduncle. The staminate flowers are arranged near the ostiole. The pedicels, tepals, and styles are usually more or less hairy. The stigma is clavate and funnel-shaped. Lateral bracts are often present. The figs are often borne on the older wood. The inflorescences are of the 'trap blossom' type, that release the next generation of pollinators by a loosening of the ostiolar bracts[36]. Pollination is (always?) topocentric.

The leaves are often scabrous and unequal-sided. Just as in *Sycocarpus*, the waxy glandular spots can be nodal. Most of the members of this group are trees or shrubs. Some of them form aerial roots and can be (hemi-?)epiphytic; others are climbers.

The *Sycidium* group is centred in Asia and Australasia; it extends to Madagascar and the Mascarene Islands with five species, and with four species to continental Africa. The third, also exclusively (gyno)dioecious subgroup comprises the rest of the species of subgenus *Ficus* sensu Corner. The subgroup is more heterogeneous than the other two with regard to characteristics of the vegetative structures, the syconium, and flowers, and may be not a natural one. A distinct entity within this group is formed by a group of species that are root-climbers with more or less conspicuous differences in the size, shape and texture of the leaves of the sterile rooted/climbing branches and the fertile branches. This group comprises the more or less distinct sections *Kalosyce* and *Rhizocladus* sensu Corner, distinguishable for example by the number of stamens (usually one or two (or three), respectively). A remarkable trait shared with other members of *Ficus* sensu Corner is that the staminate flowers may occur dispersed (among the gall flowers) or near the ostiole.
The other members of this third main group are trees or shrubs (or creepers).
Section *Adenosperma* is a rather distinct group of trees or shrubs with a characteristic growth form (with the same type of branching as the genus *Terminalia* of the Combretaceae). The staminate flowers are ostiolar and the style is more or less distinctly lateral to gynobasic. Lateral bracts often occur. According to Corner[13] this group might be related to section *Sycocarpus*.
Section *Ficus* is quite diverse with regard to growth habits, life forms, leaves, position of staminate flowers, attachment of the style, hairiness of tepals, etc. It is apparently less homogeneous than the other sections and comprises several small subdivisions with one or a few species (like those with *F. carica, F. deltoidea,* and *F. pseudopalma*) that can be easily told apart, and some larger groups.

Neotropical taxa of Ficus

The taxa of *Ficus* of the Asian-Australasian and African regions have been revised in such a way that check-lists and treatments for floras could be prepared with consistent naming and acceptable delimitations of the taxa. The situation for the neotropics is different. Taxonomic studies were undertaken and several treatments for regional floras have been published[3,5,9,10,17,18,33] but the identity of the taxa involved is still problematical. The problems in subgenus *Pharmacosycea* are largely due to strong similarities between species; these problems can be solved by thorough revisional work. Some of the problems in subgenus *Urostigma* are quite different. Many species can be readily recognized, but in addition a number of complex entities occur, which were, in general, treated by DeWolf[17,18] as single species. Burger[10] did not accept this broad concept; correctly so. But for regional treatments it is easier to treat morphologically more or less distinct forms in such complexes as distinct species, in contrast to when one is dealing with such 'forms' throughout the usually wide ranges of distribution of these complexes.
The species complexes in *Urostigma* section *Americana* comprise a number of partly allopatric entities ('forms') that are morphologically so close that recognition is often very difficult or sometimes even impossible. Moreover, the pollinators of entities within the complexes can be different, possibly implying genetic isolation.

Main species complexes in Urostigma section Americana

F. citrifolia complex

This complex comprises several entities ('forms'). The typical 'form' occurs in the Greater and Lesser Antilles and extends to southern Florida. It is, however, replaced by a somewhat different 'form' in Jamaica; this (unnamed?) 'form' extends to Central America. In South America the complex is represented by *F. amazonica* (Lower Amazon Basin, Guianas, extending to Trinidad and Venezuela), *F. brittonii* (in dry regions in NW. Venezuela, NE. Colombia and Curaçao), and *F. eximia*. The latter ranges from E. Brazil to northwestern South America, where two other 'forms' also occur: *F. dugandii* (extending to Central America) and *F. subandina* (montane). *F. castellviana* may belong to this complex.

F. aurea complex

The typical 'form' occurs in the Greater Antilles and extends to southern Florida, Mexico and northern Central America, where a number of other 'forms' also occur, e.g., *F. isophlebia, F. jimenezii,* and *F. tuerckheimii*.

F. trigonata complex

This species complex extends from the Greater Antilles and Mexico to southern Brazil. It probably comprises three 'forms' in the Greater Antilles (*F. trigonata* s. str., and two entities with uncertain names). In Central America and Mexico the complex is represented by at least three 'forms': *F. goldmanii, F. morazaniana,* and *F. trigonata* s. str. (vel aff.), and in South America by at least two 'forms': one of them resembling *F. trigonata* s. str. and the other known as *F. gomelleira*.

F. pertusa complex

This complex of taxa extends from Jamaica and southern Mexico to southern Brazil and comprises several 'forms' known as *F. pertusa* (with relatively small figs), *F. padifolia* (with relatively large figs), *F. trachelosyce* (with a protruding apex of the receptacle), and probably also comprises *F. pallida* (with small figs in which the ostiole is hardly sunken) and *F. schumacheri* (rather similar to the former but with narrow leaves).

F. americana complex

This species complex extends from the West Indies to eastern Brazil. The 'typical' form, *F. americana* (known as *F. jacquinifolia* or *F. perforata*), occurs on most of the West Indian Islands, but in the southern Lesser Antilles

is replaced by one of the South American forms (*F. guianensis*) and in Jamaica by a form (*F. oerstediana*) also occurring in Central America and gradually passing into forms in the lowlands of the Andean region. The situation in South America is quite complex. The 'typical' form is known from a few localities in the mountains of Eastern Venezuela. In the lowlands of South America several forms (*F. guianensis, F. clusiifolia, F. mathewsii*) in which the figs are also borne below the leaves occur, as well as a form (*F. greiffiana*) with figs confined to the leaf axils. In the mountains in the Andean region and the Coastal mountains in Venezuela, several closely related forms (e.g., *F. maitin*) occur.

Distribution of the main subdivisions of Ficus

In the New World, *Ficus* is only represented by two, both relatively uniform sections; *Pharmacosycea* and *Urostigma* with ca 20–25 and ca 100 species, respectively. The closest relatives of both sections seem to be centred in the Asian-Australasian region and both sections are relatively well represented in the northwestern part of the Neotropics: Central America and the northern Andean region. The majority of the neotropical *Ficus* species are associated with more or less humid tropical lowland vegetation. About 10–15 species can be regarded as montane, and a few species are associated with more or less dry habitats.

The *Ficus* flora of Africa (including Madagascar and adjacent groups of islands), with a total of 105 species, is more diverse than the neotropical one. The largest group is section *Galoglychia* with 72 species and is the only one confined to the African flora region. This section is the most diverse one among the sections of subgenus *Urostigma*. The second largest group consists of 12 monoecious species of the *Sycomorus* (incl. *Neomorphe*) group which has the only other monoecious species (*F. racemosa*) in Asia. The fact that 7 of the 12 species are endemic to the Madagascar subregion, a greater number than in continental Africa, appears to indicate a close connection to the Asian-Australasian region. This pattern matches that found for the other sections of *Ficus* occurring in Africa; they all have their centres of distribution in the Asian-Australasian region and extend to the African region, being relatively well represented in the Madagascan subregion: section *Conosycea* with two species only in the Madagascan subregion, section *Urostigma* with two species in the Madagascan subregion and three species in continental Africa, the *Sycidium* group, with five species in the Madagascan subregion and four species in continental Africa, and section *Oreosycea* with two species in the Madagascan subregion and two species in continental Africa. Section *Ficus* is represented by only one species, *F. palmata,* extending from Nepal to northeastern Africa. The number of (gyno)dioecious species in the African flora region is confined to ten.

About 2/3 of the African species are more or less distinctly associated with humid tropical lowland forest or peripheral and transitional forest, most of these belong to section *Galoglychia*. A few taxa are associated with montane habitats, and the others are associated with drier habitats, mostly wooded grassland or habitats transitional to humid vegetation.

The Asian-Australasian region has taxonomically and morphologically the richest (more than 500 species) and most diverse *Ficus* flora with a dominance of (gyno)dioecious species. A survey of its distribution cannot be readily presented, and will, therefore, only be summarized briefly. The sections *Adenosperma* and *Malvanthera* are distinctly centred in the eastern (Melanesian-Australian) part of the region; the sections *Kalosyce* and *Rhizocladus,* as well as *Neomorphe* and *Sycocarpus,* are centred in Malesia; section *Sycidium* as a whole is centred in the central to eastern part of the region; section *Ficus* is in the eastern part of the Asian mainland and western Malesia, while *Pharmacosycea* and *Urostigma* occur widely through the region [13]. Data about ecological aspects of the distribution are scattered in the literature and are often incomplete, and therefore not easy to summarize. Approximate proportions of Asian-Australasian *Ficus* associated with lowland, montane, relatively dry habitats or temperate regions cannot yet be indicated. Unlike those in other regions some species are rheophytic, that is, adapted to live in (rapidly) flowing water [30].

Relations between genera of Agaonidae and subdivisions of Ficus

It is clear that neither the taxonomy and classification of *Ficus* nor those of the Agaonidae are fully sorted out [16, 40]. Wiebes [40] stated that the relation between a *Ficus* species and its pollinating wasp is as a rule species-specific; that only for about 200 *Ficus* species (about one-quarter of the total number of species) is the pollinating wasp known, and that related species of *Ficus* have related species of pollinating wasps.

From the survey given above it is clear that some genera of Agaonidae are confined to taxonomic entities (as presently recognized) at the level of section or subsection, both varying in the number of species they comprise. In other cases genera of Agaonidae (as presently recognized) occur in more than one section or subsection in *Ficus*. One may expect that part of the discrepancy between the classifications of the two groups of organisms will disappear in the course of time through further taxonomic studies and re-evaluation of characters, eventually leading to redefinition of the taxonomic entities.

There is one striking discrepancy between the classification of *Ficus* and that of the Agaonidae, namely the main subdivision of the latter. According to Wiebes [39], the genera acting as pollinators in the sections *Galoglychia, Malvanthera,* and *Pharmacosycea* belong to the Agaoninae (and the other genera to the Blastophaginae). The

sections *Galoglychia* and *Malvanthera* may be closely related, but section *Pharmacosycea* is (as far as we can see it now) certainly not closely related to the two *Urostigma* sections, but rather to section *Oreosycea*. One may wonder whether the subdivision of the Agaonidae should be related to the type of ostiole, which show similarities in the three sections. It may be worthwhile to try to trace patterns in the functional significance of features of the syconium, flowers, fruits, and (in the future) attractants for the pollinators in relation to both morphological and behavioural features of the pollinators.

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