

A NEW CLASSIFICATION OF *FICUS*

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ABSTRACT

The taxa of *Ficus* are classified on the basis of the specificity and morphology of their symbiotic wasps (Agaonidae), systems of pollination, and morphology and physiology of the figs. The new classification is a modification of Corner's system with the following changes. In subgenus *Ficus*, subsection *Eriosycea* is elevated to sectional rank. Series *Rivulares* and *Pseudopalmae* do not belong to the group of *Blastophaga*-pollinated figs and are transferred to the new *Ceratosolen*-pollinated complex of subgenus *Sycomorus*. Two subsections, *Scabrae* and *Varinga*, are recognized in section *Sycidium*, and series *Phaeopilosae* and subsection *Paleomorphe* are recognized as sections. The subgenus *Sycomorus* is much expanded to include eight sections: *Adenosperma*, *Neomorphe*, *Prostratae*, *Pungentes*, *Pseudopalmae*, *Rivulares*, *Sycocarpus*, and *Sycomorus*.

The object of this study is to group the taxa of *Ficus* into related groups considering the specificity and morphology of their symbiotic agaonids, the different systems of pollination, as well as the morphology and physiology of the figs.

The last systematic arrangement of *Ficus* was made by Corner (1965) and is summarized in Table 1. A parallel list of the pollinating agaonids (genera or subgenera reported up to now for each fig taxon) is also included. The list of agaonids was taken from Hill (1967) and modified by me. Parallel to the groups of wasps there are columns showing the absence or presence of corbiculae in the wasps (Ramírez, 1974).

THE NEW CLASSIFICATION OF *FICUS* AND ITS POLLINATORS

The proposed classification of *Ficus* is found in Table 3. Modifications are extended only to the level of series.

SUBGENUS *UROSTIGMA*

This group of figs remains as treated by Corner (1965) (Table 1).

Section Urostigma.—The figs are inhabited by *Blastophaga* (group E), which are characterized by the presence of coxal and sternal corbiculae (as in Figs. 3 and 4).

Section Leucogyne.—This section comprises two species. One of them (*F. tsiela*) is pollinated by *Maniella delhiensis*, with coxal and sternal corbiculae (as in Figs. 3 and 4).

Section Conosycea.—The species of this section are pollinated by several groups of wasps. The only *Blastophaga* (*B. arnottiana* and *B. errata*) known from this group of figs have sternal corbiculae and coxal combs. *Ceratosolen megarhopalus* (the *Megarhopalus* group) and the majority of *Waterstoniella* wasps are characterized by only very rudimentary sternal corbiculae (Figs. 5–6); some

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Waterstoniella (e.g., *W. sundaica* and *W. jacobsoni*) do not have corbiculae (Fig. 2). The other two groups of agaonids (*Eupristina* and *Parapristina*) found in section *Conosycea* have sternal and coxal corbiculae (as in Figs. 3 and 4).

Section Stilpnophyllum.—This section contains only *Ficus elastica* which is pollinated by *Blastophaga clavigera* (*Blastophaga* group B) a wasp with sternal and presumably coxal corbiculae (Wiebes, personal communication).

Section Malvanthera.—This group is unique in that its anthers have two pollen sacs which dehisce with one crescentic or equatorial slit. The section is pollinated by *Pleistodontes* wasps. However, there are apparently several *Pleistodontes* groups pollinating the different groups of *Malvanthera* figs (personal observation).

Pleistodontes imperialis is characterized by sternal and possibly coxal corbiculae while the other known *Pleistodontes* do not possess corbiculae at all. Series *Malvanthereae* is pollinated by wasps without corbiculae (*P. blandus*, *froggatti*, *rieki*, *plebejus*, and *regalis*). The only *Pleistodontes* (*P. inmaturus*) known from series *Cyclanthereae* apparently does not possess corbiculae. For more information on *Pleistodontes* wasps see Wiebes (1963b: 319, Table 1). It is probable that the group *Pleistodontes* as well as its *Ficus* hosts, will have to be reclassified when more is known of both groups.

Section Galoglychia.—This group of figs resembles the last section in the inflexed, not interlocking, apical and internal bracts of the ostium (Corner 1959: 376), but it has normal anthers with four pollen sacs. It is pollinated by two main groups of wasps: (a) those with only sternal corbiculae (*Agaon*, *Allotriozoon* and *Paragaon*) and (b) those with sternal and coxal corbiculae (*Alfonsiella* and *Elisabethiella*).

Section Americana.—According to Corner (1959: 376) this section is closely related to both sections *Urostigma* and *Conosycea*. It is pollinated by *Blastophaga* wasps of the subgenus *Pegoscapus* (Ramírez, 1970) with coxal and sternal corbiculae. However, *P. carlosi* and *P. mariae* (the pollinators of *F. tuerckheimii* in Costa Rica, Mexico and Panama) do not possess coxal corbiculae (Ramírez, 1970).

SUBGENUS *PHARMACOSYCEA*

Corner (1959: 407) considered that the Old World section *Oreosycea* has the same essential characters, and indeed, is with difficulty distinguished from New World *Pharmacosycea* species. However, in the descriptions of the two sections we find very important differences, some of which are pointed out in Table 2.

The Old World species have in the past been referred to the subgenus *Urostigma* where they are out of place, particularly in being independent trees and not banyans or stranglers. The species from New Caledonia have never been properly classified and they are the closest in several respects to the American species. Corner (1959: 407) stated that he divides the subgenus *Pharmacosycea* into two sections, maintaining the geographical distinction for convenience, but that redefinition will be necessary when the American species are better known.

TABLE 1. Recorded host specificity of Agaonidae (genera and subgenera) to different groups of *Ficus*. With particular reference to the presence or absence of coxal and sternal corbiculae among different groups of agaonids (modified from Hill, 1967). The systematic breakdown of *Ficus* is taken from Corner (1965).

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae		
						Absent	Sternal	Coxal
Urostigma	Urostigma		Religiosae		Blastophaga		+	+
			Superbae		Blastophaga		+	+
			Caulobotryae		Blastophaga		+	+
			Orthoneurae		Maniella		+	+
	Leucogyne Conosycea	Conosycea	Validae		Blastophaga		+	?
					Megarhopalus group		+	+
					Eupristina		+	+
					Eupristina		+	+
					Waterstoniella	+	+	+
					Eupristina		+	+
			Drupaceae Indicae Zygotrichaeae Crassirameae	Blastophaga		+	+	
				Waterstoniella	+	+	+	
				Waterstoniella				
		Dictyoneuron	Glaberrimae Dubiae Subvalidae Perforatae Benjamineae Callophyllaeae	Waterstoniella	+			
Stilpnophyllum Malvanthera		Benjamina	Malvanthereae	Eupristina		+	+	
				Parapristina		+	+	
				Blastophaga		+	?	
				Pleistodontes	+			
				Pleistodontes	+			
				Pleistodontes	+			
				Pleistodontes	+			
				Pleistodontes	+			
				Agaon		+	+	
				Paragaon		+	+	
Galoglychia			Cyclanthereae	Allotriozoon		+	+	
				Elisabethiella		+	+	
				Alfonsiella		+	+	
				Pegoscapus		+	+	
Americana								

TABLE I. (Continued)

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae		
						Absent	Sternal	Coxal
<i>Pharmacosycea</i>	<i>Oreosycea</i>		<i>Vasculosae</i>	<i>Albipilae</i>				
				<i>Vasculosae</i>	<i>Dolichorhis</i> <i>Blastophaga</i> <i>Blastophaga</i> <i>Blastophaga</i> <i>Tetrapus</i>		+	+
<i>Ficus</i>	<i>Pharmacosycea</i>	<i>Ficus</i>	<i>Nervosae</i>				+	+
			<i>Austrocaledoniceae</i>				+	+
			<i>Rivulares</i>				+	+
			<i>Pseudopalmeae</i>				+	+
			<i>Sinosyceae</i>				+	+
			<i>Cariceae</i>				+	+
			<i>Erythrogynaeae</i>				+	+
			<i>Podosyceae</i>				+	+
				<i>Podosyceae</i>	<i>Ceratosolen</i>		+	
					<i>Blastophaga</i> <i>Blastophaga</i> <i>Blastophaga</i>			
				<i>Basitepalae</i> <i>Eriosyceae</i> <i>Trichosyceae</i>	<i>Blastophaga</i>		+	
				<i>Deliscentes</i> <i>Cuneifoliae</i> <i>Auratae</i> <i>Monandreae</i>				
<i>Rhizocladus</i>			<i>Auratae</i>					
			<i>Plagiostigmaticae</i>					
			<i>Ramentaceae</i>					
				<i>Plagiostigmaticae</i> <i>Pogonotropheae</i> <i>Pantonianae</i> <i>Balanotae</i> <i>Irritantes</i> <i>Ramentaceae</i> <i>Excavatae</i> <i>Araneosae</i>	<i>Blastophaga</i>	+		
			<i>Distichoidaeae</i> <i>Distichae</i>					

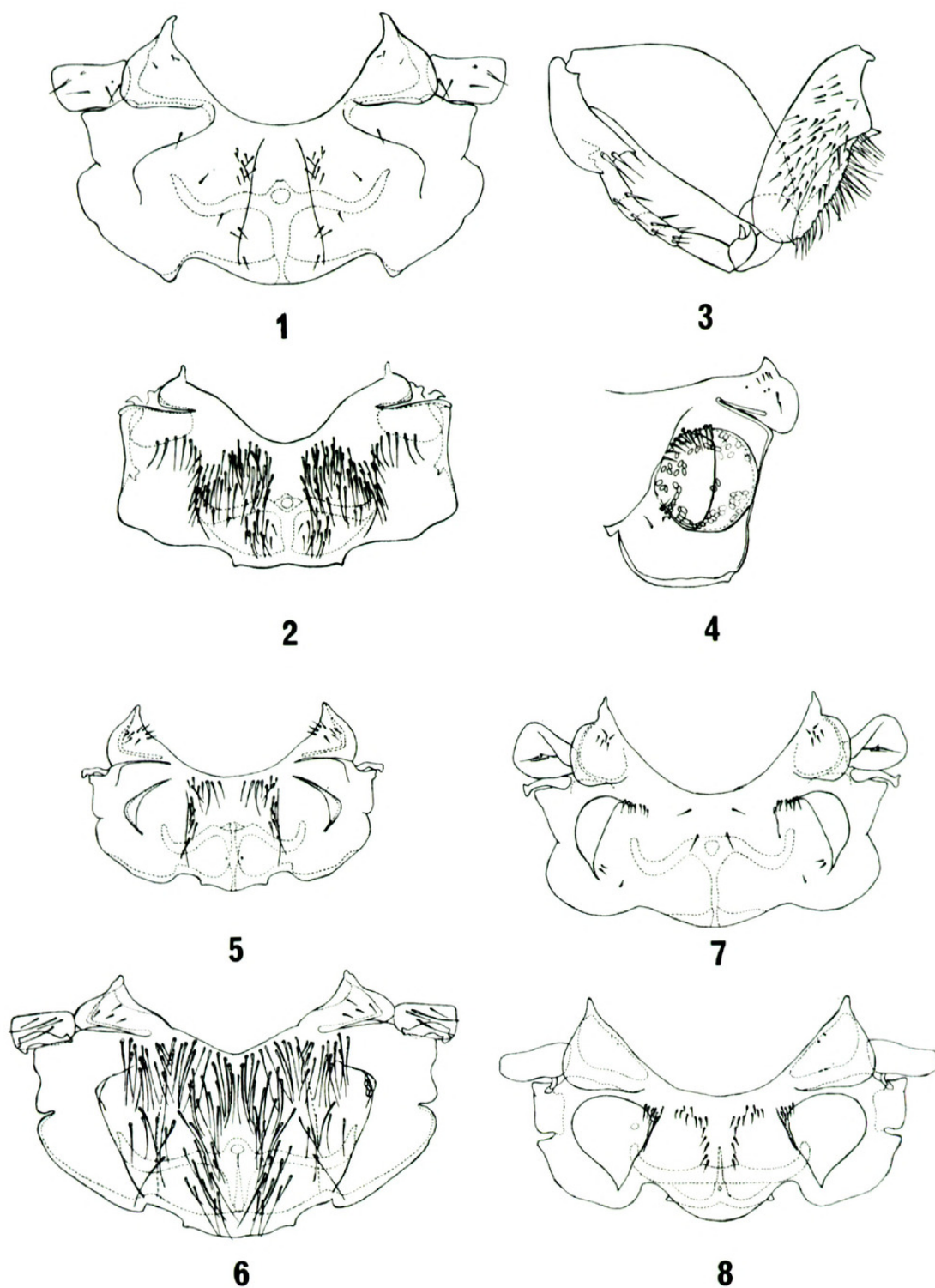
TABLE 1. (Continued)

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae		
						Absent	Sternal	Coxal
<i>Ficus</i>	<i>Kalosyce</i>		<i>Trichocarpeae</i>		<i>Blastophaga</i>	+		
			<i>Apiocarpeae</i>					
			<i>Punctatae</i>					
	<i>Sinosycidium</i> <i>Sycidium</i>	<i>Sycidium</i>	<i>Prostratae</i>	<i>Punctatae</i> <i>Ruginerviae</i>	<i>Ceratosolen</i>		+	
			<i>Pungentes</i>		<i>Ceratosolen</i>		+	
			<i>Phaeopilosae</i> ^a		<i>Blastophaga</i> ^a		+	
			<i>Copiosae</i>		<i>Blastophaga</i>		+	
		<i>Varinga</i>	<i>Scabrae</i>		<i>Blastophaga</i>		+	
	<i>Adenosperma</i> <i>Neomorphe</i>	<i>Paleomorphe</i>	<i>Heterophylleae</i>		<i>Blastophaga</i>		+	
			<i>Cyrtophylleae</i>		<i>Liporrhopalum</i>		+	
			<i>Exasperatae</i>		<i>Liporrhopalum</i>		+	
			<i>Pallidae</i>		<i>Liporrhopalum</i>		+	
			<i>Subulatae</i>					
			<i>Cuspidatae</i>		<i>Liporrhopalum</i>		+	
			<i>Minutiflorae</i>		<i>Liporrhopalum</i>		+	
			<i>Fibrosifoliae</i>		<i>Ceratosolen</i>		+	
			<i>Amphigenae</i>		<i>Ceratosolen</i>		+	
			<i>Hypogenae</i>		<i>Ceratosolen</i>		+	
<i>Sycocarpus</i>		<i>Auriculisperma</i>	<i>Auriculatae</i>	<i>Variegatae</i> <i>Laciniatae</i>	<i>Ceratosolen</i>		+	
			<i>Variegatae</i>					
			<i>Cynaroides</i>					
			<i>Theophrastoides</i>					
			<i>Vitienses</i>					
		<i>Danmaropsis</i> <i>Papuasyce</i>			<i>Ceratosolen</i>			+

TABLE 1. (Continued)

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae		
						Absent	Sternal	Coxal
<i>Sycomorus</i>		<i>Lepidotus</i> <i>Macrostylis</i> <i>Sycocarpus</i>	<i>Longetuberculatae</i> <i>Tuberculi-</i> <i>fasciculatae</i>	<i>Praestantes</i>				
				<i>Calopilinae</i>	<i>Ceratosolen</i>		+	
				<i>Congestae</i>	<i>Ceratosolen</i>		+	
				<i>Hispidae</i>	<i>Ceratosolen</i>		+	
				<i>Axillares</i>	<i>Ceratosolen</i>		+	
				<i>Fulcidulae</i>	<i>Ceratosolen</i>		+	
				<i>Geocarpicae</i>				
				<i>Tuberculi-</i> <i>fasciculatae</i>				
					<i>Ceratosolen</i>		+	

^a At present these species are placed in *Blastophaga*, but they show different degrees of intergrading with *Ceratosolen*, especially in the females (Hill, 1967).



FIGURES 1-8.—1. Mesosternum without corbiculae of *Blastophaga psenes*, the pollinator of the edible fig.—2. Mesosternum of *Blastophaga* (*Waterstoniella*) *sundaica*, a wasp without corbiculae but with abundant bristles which are probably used to carry pollen.—3. Front leg of *Maniella delhiensis* with coxal corbicula.—4. Right side of mesosternum of *Blastophaga* (*Pegoscopus*) *cumanensis* showing corbicula and some pollen in place.—5. Mesosternum of *Blastophaga* (*Waterstoniella*) *sundaica* with incipient corbiculae.—6. Mesosternum of *Ceratosolen megarhopalus* (the *Megarhopalus* group), right corbicula with some pollen.—7. Mesosternum of *Blastophaga javana* (*Blastophaga* group B) with developed open corbiculae.—8. Mesosternum of *Liporrhopalum mindanaensis* with closed corbiculae as in *Ceratosolen*.

TABLE 2. Presence or absence of some characters in the two sections of subgenus *Pharmacosycea*.

Section	Figs Single	Ostium Crateriform	Ovary with a Red Mark	Pachycaulous Trees	Anthers Numerous	Pollen Exposed at Male Phase
<i>Pharmacosycea</i>	+	+	+	-	+	+
<i>Oreosycea</i>	-	-	-	+	-	-

Corner (1967: 40) noted that the new look brought into the subgenus *Pharmacosycea* by the plants from New Caledonia is the brown hairiness, sometimes almost furriness, of twig, leaf, and fig, coupled with the rosettes of large leaves, the many-veined obovate lamina with cordate base and short petiole, and the large size of the fig. All of these characters are more or less primitive and pachycaul signs in *Ficus*. Section *Pharmacosycea* in the New World does not present all the pachycaulous characters mentioned by Corner (1967) for some Old World *Oreosycea*.

In order to explain the presence of pharmacosycean figs in both the Old and New World, Corner (1967: 41) postulated that there must have been a land connection with tropical Africa such as is suggested by the great extension of the 4,000 mile line to the west of Peru. In 1967 he further stated that this connection is demanded by other moraceous genera such as *Antiaris*, *Antiaropsis*, *Sparattosyce* and *Trophis*, as well as by the monocotyledons *Dianella*, *Heliconia* and *Spathiphyllum* in very diverse families.

Two hypotheses to explain the presence of *Pharmacosycea* in the Old and New Worlds are: (a) Sections *Pharmacosycea* and *Oreosycea* do not belong to the same subgeneric taxon and their species are more or less similar because of convergence. If this is true, each should be elevated to the subgeneric level, forming biological units separated geographically and by their respective pollinators, New World *Pharmacosycea* being the host of *Tetrapus* wasps (without corbiculae) and Old World *Oreosycea* of *Blastophaga* (*Blastophaga* group F) and of *Dolichoris vasculosae* (both with coxal and sternal corbiculae). (b) Sections *Pharmacosycea* and *Oreosycea* belong to the same subgeneric category, but section *Pharmacosycea* migrated to the New World before the agaonids evolved corbiculae. This line of thought would agree with the ideas of Corner (1967: 53), although not demonstrating the particular land connection that he postulated.

SUBGENUS *FICUS*

In the new classification the subsections *Ficus* and *Eriosycea* are elevated to sectional rank as suggested by Corner (1959: 417). The series *Rivulares* and *Pseudopalmeae* are not considered to belong to the group of *Blastophaga*-pollinated figs and are transferred to the new *Ceratosolen*-pollinated complex (the subgenus *Sycomorus*, Table 3). Corner (1969b: 326) stated that *F. pseudopalma* and *F. rivularis* (two Philippine species) differ from the rest of section *Ficus* and from each other markedly enough to require separate taxonomic series (Table

TABLE 3. Proposed classification of the genus *Ficus* considering the specificity and morphology of its symbiotic agaonids, the different systems of pollination, as well as the morphology and physiology of the figs; with a list of the agaonid pollinators (modified from Hill, 1967) of each group, and the presence or absence of corbiculae.

Subgenus	Section	Subsection	Agaonidae	Corbiculae		
				Absent	Sternal	Coxal
<i>Urostigma</i>	<i>Urostigma</i>		<i>Blastophaga</i> Group E		+	+
	<i>Leucogyne</i>		<i>Maniella</i>		+	+
	<i>Conosycea</i>	<i>Conosycea</i>	<i>Blastophaga</i>		+	+
			<i>Megarhopalus</i>		+	+
			Group			
			<i>Eupristina</i>		+	+
	<i>Stilpnophyllum</i>	<i>Dictyoneuron</i>	<i>Waterstoniella</i>	+		
			<i>Waterstoniella</i>		+	
			<i>Waterstoniella</i>	+		
			<i>Eupristina</i>		+	+
		<i>Benjamina</i>	<i>Parapristina</i>		+	+
			<i>Blastophaga</i>		+	+
			<i>clavigera</i> (= <i>Blastophaga</i> Group G)			+
	<i>Malvanthera</i>		<i>Pleistodontes</i>	+		
	<i>Galoclychia</i>		<i>Pleistodontes</i>		+	+
			<i>Agaon</i>		+	
			<i>Alfonsiella</i>		+	+
			<i>Allotriozoon</i>		+	
			<i>Elisabethiella</i>		+	+
			<i>Paragaon</i>		+	
	<i>Americana</i>		<i>Pegoscapus</i>		+	+
<i>Pharmacosycea</i>	<i>Oreosycea</i>		<i>Blastophaga</i> Group F		+	+
			<i>Dolichoris</i>		+	+
	<i>Pharmacosycea</i>		<i>Tetrapus</i>	+		
<i>Ficus</i>	<i>Ficus</i>		<i>Blastophaga</i> Group A	+		
	<i>Rhizocladus</i>		<i>Blastophaga</i> Group A	+		
	<i>Kalosyce</i>		<i>Blastophaga</i> Group A	+		
	<i>Sinosycidium</i> ^a					
	<i>Eriosycea</i>		<i>Blastophaga</i> Group B		+	
	<i>Sycidium</i>	<i>Scabrae</i>	<i>Blastophaga</i> Group B		+	
		<i>Varinga</i>	<i>Blastophaga</i> Group B		+	
	<i>Phaeopilosae</i>		<i>Blastophaga</i> Group C		+	
	<i>Paleomorphe</i>	<i>Paleomorphe</i>	<i>Liporrhopalum</i>		+	
		<i>Copiosae</i>	<i>Blastophaga</i> Group D		+	

TABLE 3. (Continued)

Subgenus	Section	Subsection	Agaonidae	Corbiculae		
				Absent	Sternal	Coxal
<i>Sycomorus</i>	<i>Adenosperma</i>		<i>Ceratosolen</i>		+	
	<i>Neomorphe</i>		<i>Ceratosolen</i>		+	
	<i>Prostratae</i>		<i>Ceratosolen</i>		+	
	<i>Pugentes</i>		<i>Ceratosolen</i>		+	
	<i>Pseudopalmeae</i>		<i>Ceratosolen</i>		+	
	<i>Rivulares</i> ^b				+	
	<i>Sycomorus</i>		<i>Ceratosolen</i>		+	
	<i>Sycocarpus</i>		<i>Ceratosolen</i>		+	

^a Probably pollinated by a wasp of *Blastophaga*, Group A.

^b Probably pollinated by a *Ceratosolen* wasp.

1). Wiebes (1963a: 101, 104) indicated that the pollinator of *F. pseudopalma* (*C. bakeri*) has aberrant characters for the genus *Ceratosolen*, but appears related to the *C. abnormis* and *C. armipes* groups (pollinators of figs of section *Sycocarpus*).

Sections Kalosyce and Rhizocladus.—These two sections are left in the taxonomic position given them by Corner (1965). They form two well-defined groups pollinated by *Blastophaga* (*Blastophaga* group A) wasps without corbiculae (Fig. 1). The pollinators of these two groups of figs are quite similar to the ones found with section *Ficus* (Table 3). These two sections are associated by their pollinators. Corner (1960: 3), however, suggested that sections *Kalosyce* and *Rhizocladus* might be considered to form a fifth subgenus.

Section Sinosycidium.—This section is left in the same taxonomic position given by Corner (1960: 24). It has a single species (*F. tsiangii*). Because of its dispersed diandrous flowers and the slightly bifid stigmata of the female flowers, I consider this section to be related to section *Ficus* (as in Table 3), although the ramiflorous bracteate receptacles are like those which occur in sections *Sycidium*, *Sycocarpus* and *Adenosperma* according to Corner (1960: 24–25). The pollinator of *F. tsiangii* is not known, but it could be a *Blastophaga* without corbiculae (as in Fig. 1) as those of *Blastophaga* group A.

Section Sycidium.—In the new classification this group has two subsections, *Scabrae* and *Varinga*. These groups are related by their pollinators of the *Blastophaga* group B, which are characterized by their open sternal corbiculae (Fig. 7).

Sections Phaeopilosae and Paleomorphe.—The series *Phaeopilosae* and subsection *Paleomorphe* (both sensu Corner, 1965) are elevated to sectional rank. *Phaeopilosae* is pollinated by *Blastophaga* group C with closed sternal corbiculae (Fig. 9). *Paleomorphe* has two subsections, *Paleomorphe* being pollinated by *Liporrhopalum* with closed sternal corbiculae (Fig. 8) and *Copiosae* (series *Copiosae*, sensu Corner, 1965) by *Blastophaga* group D having closed sternal corbiculae (as in Fig. 9).

SUBGENUS *SYCOMORUS*

In the new classification the subgenus *Sycomorus* is expanded and comprises eight sections: *Adenosperma*, *Neomorphe*, *Prostratae*, *Pungentes*, *Pseudopalmeae*, *Rivulares*, *Sycocarpus* and *Sycomorus* (Table 3). Of these sections, *Adenosperma*, *Neomorphe* and *Sycocarpus* were considered by Corner (1965) as sections of the subgenus *Ficus*; *Prostratae* and *Pungentes* as series of subsection *Sycidium*; *Pseudopalmeae* and *Rivulares* as series of subsection *Ficus*.

All the sections included here in *Sycomorus*, excepting *Rivulares*, are known to be pollinated by *Ceratosolen* wasps. The pollinator of *Ficus rivularis* (the only species of section *Rivulares*) is not known, but I suspect this species to be pollinated by a *Ceratosolen* with a short ovipositor and closed sternal corbiculae. All the dioecious sections (*Adenosperma*, *Neomorphe*, *Prostratae*, *Pungentes*, *Pseudopalmeae* and *Sycocarpus*) are inhabited by *Ceratosolen* wasps with short ovipositors. Nevertheless, Corner (1965: 85) included in section *Sycocarpus* (subsection *Papuasyce*) the species *F. microdictya* (of New Guinea) which has the perianth similar to that of *Sycocarpus*, but is monoecious like *Sycomorus*², which does not occur in New Guinea (Corner, 1958: 31, personal communication). Section *Sycomorus* is a monoecious group pollinated by *Ceratosolen* with long ovipositors.

RELATIONSHIPS AMONG GROUPS OF FIGS INCLUDED IN
SUBGENUS *SYCOMORUS*SECTION *ADENOSPERMA*

This section aligns with the unistaminate sections *Sycidium* and *Sycocarpus*, which differ in the form of the seed if not in that of the flower (Corner, 1969b: 320). The section is related to section *Sycocarpus*, subsection *Auriculisperma*, of the Solomon Islands, and connects with the origin of section *Ficus* through the Philippine species *F. pseudopalma* and *F. rivularis* (Corner, 1969b: 319).

SECTION *NEOMORPHE*

Corner (1967: 51) stated that this section has much in common with the subgenus *Sycomorus*. *Neomorphe* may have come from the stock of *Adenosperma* on the Melanesian Foreland, and this stock may have been connected with that of *Sycomorus*, so that *Neomorphe* is an eastern parallel of it (Corner, 1967: 51). *Neomorphe* must be divided into two series (Table 1), *Variegatae* and *Auriculatae*, which show alliance with the subgenus *Sycomorus* in the first case and section *Sycocarpus* in the second. Series *Variegatae* can be divided, likewise, into two subseries. The first Corner (1965: 32–33) called subseries *Laciniatae*. It has tepals characteristic of subgenus *Sycomorus*, but it is further removed geographically from the African subgenus *Sycomorus* (Corner, 1967). The second, subseries *Variegatae*, has only two species, *F. variegata* and *F. viridicarpa*. *Ceratosolen striatus* (= *C. appendiculatus*), an agaonid collected from *F. variegata* in Java, was illustrated by Grandi (1917:

² *Ficus pritchardii*, a monoecious fig, also belongs to *Sycocarpus* (Corner, 1970).

Fig. XII, 6) as a wasp with a long ovipositor like the wasps found in section *Sycomorus* (as in Table 3).

Neomorphe as well as subgenus *Sycomorus* of Corner (1965) are pollinated by *Ceratosolen* wasps which are apparently related. Wiebes (1963a: 104) reported that the species of the *Ceratosolen appendiculatus* group live in the receptacles of section *Neomorphe* and subgenus *Sycomorus* (sensu Corner, 1965), and one species is known from series *Prostratae*. The occurrence of a group of such closely related species of *Ceratosolen* in the figs of both dioecious *Neomorphe* and monoecious *Sycomorus* would suggest that the floral characters in which *Neomorphe* is close to *Sycomorus* are more important than the distribution of the flowers in the receptacles. A parallel is found in *F. microdictya*, which is a monoecious species in the dioecious *Sycocarpus*³ (Wiebes, 1963a: 104).

SECTIONS *PROSTRATAE* AND *PUNGENTES*

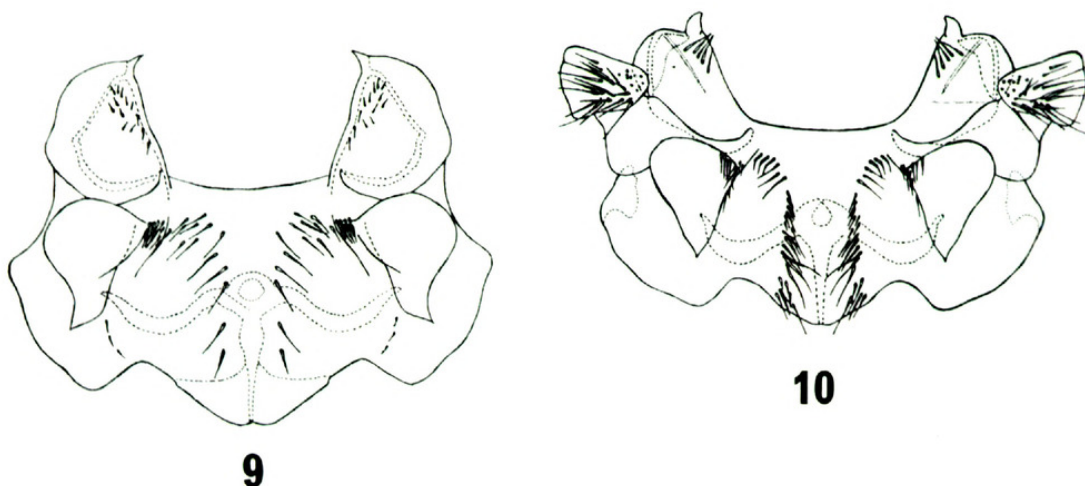
These sections are also pollinated by *Ceratosolen* wasps. Corner (1965) considers them to be two series of section *Sycidium*. According to Wiebes (1963a: 102), the greater part of the Indomalayan and Papuan species of *Ceratosolen* live in the sections *Neomorphe* and *Sycocarpus*, but some are known from *Prostratae* and *Pungentes*, two series of *Sycidium* (sensu Corner, 1965). These series have usually been placed in section *Sycocarpus* and only recently have been assigned to *Sycidium* (Wiebes, 1963a). Botanically these two series point to a common ancestor which would combine *Sycidium* with *Sycocarpus* and *Sycomorus*, including *Neomorphe* (Corner, 1958: 31). In the opinion of Wiebes (1963a: 102) the wasps from the series *Prostratae* connect those from the section *Neomorphe* with those of the subgenus *Sycomorus*, and the wasps from the series *Pungentes* appear to be related to the wasps from the section *Sycocarpus*. According to Corner (1959: 444), series *Prostratae* relates with section *Ficus* but habit and convenience place it in *Sycidium*.

SECTIONS *PSEUDOPALMEAE* AND *RIVULARES*

Each of these taxa has a single species. Corner (1965) included them as two series of the subgenus *Ficus*. Both species are found in the Philippines. *Ficus rivularis* is an advanced leptocaul shrub with lanceolate leaves, distinguished in section *Ficus* by the gamophyllous perianth with distinct tepal lobes, compressed auriculiform seed, and the more or less gynobasic style in the female flower. The perianth is intermediate between that of section *Ficus* and *Sycocarpus*. In perianth, style and seed, *F. rivularis* agrees with *Adenosperma*; it appears as a relic, fitting no section of the ancestral line of section *Ficus* from which those of *Auriculisperma* and *Adenosperma* diverged (Corner 1969b: 328).

Ficus pseudopalma connects as a pachycaul with *F. dammaropsis* (section *Sycocarpus*, subsection *Auriculisperma*) of New Guinea, and thus, with section *Adenosperma*. It connects also with the ancestry of the *F. deltoidea* complex (section *Ficus* series *Erythrogynae*) and has the three tepals of section *Ficus*

³ *Ficus pritchardii* (a monoecious fig) also belongs to *Sycocarpus*.



FIGURES 9-10.—9. Mesosternum of *Blastophaga jacobsi* (*Blastophaga* group C) with closed sternal corbiculae.—10. Mesosternum of *Ceratosolen pilipis* with closed corbiculae.

(Corner, 1969b: 326). *Ceratosolen bakeri* is the pollinator of *F. pseudopalma*. This wasp appears to be related to the *C. abnormis* and the *C. armipes* groups. *Ficus pseudopalma* was classified in section *Ficus* because of its bistaminate male flowers, but it does show some relationship with *F. dammaropsis* (section *Sycocarpus*), the host of *C. abnormis* (Wiebes, 1963a: 101).

SECTION SYCOCARPUS

This group of *Ficus* is mostly dioecious; however, *F. microdictya* and *F. pritchardii* are monoecious. It is pollinated by *Ceratosolen* wasps with short ovipositors, but the ovipositors of the pollinators of *F. microdictya* and *F. pritchardii* are probably much longer than the abdomens. The chief character of the section is the entirely gamophyllous perianth. In the male flower the perianth is saccate and covers one, or less often, two stamens (Corner 1960: 38). For the relationship of the pollinators of *Sycocarpus* with the pollinator of *F. pseudopalma* and those of section *Nemorphe*, see under sections *Pseudopalmeae* and *Neomorphe*. See also under section *Adenosperma*.

SECTION SYCOMORUS

In the new classification, this group contains all the monoecious figs included in the subgenus *Sycomorus* of Corner (1965). It is pollinated by *Ceratosolen* wasps with long ovipositors.

Galil (1973) noted that in spite of numerous structural differences between the syconia of the dioecious *F. fistulosa* (section *Sycocarpus*) and the monoecious *F. sycomorus* (section *Sycomorus* sensu Ramírez, 1974) which belong to different subgenera of *Ficus*, namely *Ficus* and *Sycomorus* (sensu Corner, 1965) respectively, the two have several biological features in common. In both, the pollinating wasps are species of *Ceratosolen* which behave very similarly in relation to the figs, and such likeness in behavior indicates that physiological conditions within the figs are probably also similar in both cases.

CHARACTERS OF THE SUBGENUS *SYCOMORUS*

Corner (1967: 51) stated that *Sycomorus*, *Sycocarpus*, *Adenosperma*, *Neomorphe*, and two series of *Sycidium* (*Prostratae* and *Pungentes*) are distinguished by having *Ceratosolen* as pollinating insects. Despite their differences, he suggests it may be necessary to combine them in the subgenus *Sycomorus* in contrast with the remainder of the subgenus *Ficus* pollinated by *Blastophaga*.

The newly defined subgenus *Sycomorus* is characterized by the following characters: *Male flowers*: (a) in 1 or 2 (in some cases 3) ostiolar rings; (b) few per fig; (c) usually without pistillode; (d) perianth with free petals, gamophyllous or utriculate; (e) mostly sessile; (f) usually with only one or two stamens (few species with three). *Anthers*: (a) enfolded by the perianth; (b) usually small; (c) pollen not exposed at male phase. *Female flowers*: (a) stigma simple; (b) styles usually short excepting those of section *Sycomorus* and of *F. microdictya* and *pritchardii*⁴. *Syconia*: (a) with internal bristles; (b) helicoidal ostiolar entrance with several (more than three) interleafing superficial bracts; (c) dioecious (excepting section *Sycomorus* and *F. microdictya* and *pritchardii*; (d) ostiolum usually does not open at male phase. *Leaf*: (a) stomata usually superficial; (b) leaf not coriaceous; (c) plicate in bud. *Trees*: independent, not epiphytic. *Pollinators*: *Ceratosolen* wasps which are characterized by closed sternal corbiculae (as in Fig. 10), and coxal combs, and which collect the pollen from detached anthers cut by the males (Galil, 1973); short ovipositors (except the *Ceratosolen* wasps of section *Sycomorus* and *F. microdictya* and *pritchardii*) and by the ability of the male to perforate the fig in order to gnaw an exit that allows the females to escape. The males in all species probably cut the stamens before the females emerge from the galls (Galil, 1973).

The figs of sections *Adenosperma*, *Sycocarpus*, and *Sycomorus* are parasitized by *Eukoebelea* wasps (tribe *Sycophagini*, Hill, 1967: 92), while the species of section *Sycomorus* are inhabited by *Sycophaga* wasps (tribe *Sycophagini*, Hill, 1967: 92).

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⁴ Corner (1970: 383) suggested that subsection *Papuasyce* (of section *Sycocarpus*), to which *F. itoana*, *microdictya* and *pritchardii* belong, should become a fifth subgenus as a monoecious group distinct from subgenus *Ficus* but with *F. itoana* as the dioecious product.

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