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POLLINATION IN THE NEW GUINEA ENDEMIC *ANTIAROPSIS DECIPIENS* (MORACEAE) IS MEDIATED BY A NEW SPECIES OF THRIPS, *THRIPS ANTIAROPSIDIS* SP. NOV. (THYSANOPTERA: THRIPIDAE)

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Fig pollination is a well-known example of obligate mutualism involving specialized fig wasps (Hymenoptera, Agaonidae) and *Ficus* (Moraceae). However, pollination is poorly understood in Castilleae, the recently identified sister group to *Ficus*. Here we report the first record of thrips pollination in a member of the paleotropical Castilleae. We used phenological measurements, insect trapping, and pollinator exclusion experiments to investigate the mode of pollination in *Antiaropsis decipiens*, a monotypic dioecious tree of lowland rainforests in New Guinea. We recorded a new species, described here as *Thrips antiaropsidis* (Thysanoptera, Thripidae), feeding on *Antiaropsis* pollen, breeding in the staminate inflorescences, and pollinating the carpellate inflorescences. It appears that thrips are lured from staminate to carpellate inflorescences by deceit. We combine these observations with evidence from the Neotropical Castilleae to suggest that thrips pollination may be common in the sister group to figs. We speculate that entomophily in the common ancestor of *Ficus* and Castilleae predated the origin of the fig pollination mutualism.

Keywords: Castilleae, Ficus, pollination by deceit, paleotropics, mutualism, reproductive ecology.

Introduction

Moraceae includes at least 1100 species, and more than two-thirds of these are figs (Rohwer 1993). The spectacular diversification of *Ficus* is often attributed to a coevolved, obligate mutualism between figs and pollinating fig wasps (Hymenoptera, Agaoninae) in which the plant relies on wasps for pollination and the wasps breed in figs (Janzen 1979; Weiblen 2002). The origin of this uniquely specialized pollination syndrome has remained a mystery, and remarkably little is known about pollination in the rest of the Moraceae (Berg 1990, 2001). The family comprises five tribes (fig. 1) that include monoecious, dioecious, androdioecious, and gynodioecious species with either unisexual or bisexual inflorescences (Datwyler and Weiblen 2004). Both wind and insect pollination syndromes are indicated by the diverse inflorescences of the family. In particular, members of the tribe Moreae usually have explosive pollen release and are presumed to be wind pollinated (Bawa et al. 1985; Rohwer 1993; Williams and Adam 1993; Kinjo et al. 1998; Berg 2001) while some Artocarpeae and Castilleae are believed to be insect pollinated and provide brood sites for insect larvae (Bawa et al. 1985; Sakai et al. 2000; Berg 2001). Some members of the Dorstenieae with condensed staminate inflorescences might also provide insect breeding sites (Berg 2001). Despite much speculation on pollination modes in the Moraceae, only a few empirical studies have been conducted. Sakai et al. (2000) demonstrated that pollination of *Artocarpus integer* (Thunb.) Merr. (Artocarpeae) is mediated by gall midges feeding on the mycelia of fungi that grow on staminate inflorescences. Momose et al. (1998*a*) concluded that diverse insects pollinate *A. integer* and *Artocarpus odoratissimus* Blanco, while *Artocarpus elasticus* Reinw. *ex* Blume appears to be wind pollinated (Momose et al. 1998*b*). Sakai (2001) demonstrated that a species of thrips (Thysanoptera, Thripidae) pollinates the Neotropical, androdioecious *Castilla elastica* Sessé (Castilleae) and breeds in the staminate inflorescences. Thrips have also been observed on three other genera of Neotropical Castilleae (Sakai 2001; Datwyler and Weiblen 2004).

Given the unique fig pollination syndrome and the great diversity of inflorescence forms in the Moraceae, elucidating pollination modes in close relatives of *Ficus* may provide insights on the ancestral condition of the fig and other correlates of pollinator specialization. Castilleae were recently identified as the sister group to *Ficus* (Datwyler and Weiblen 2004), and although the majority are Neotropical species, the earliest diverging lineages are paleotropical, including the monotypic New Guinea endemic *Antiaropsis decipiens* K. Schum. (figs. 1, 2).

Antiaropsis decipiens is a dioecious understory tree with staminate and pistillate inflorescences borne individually in the leaf axils of separate plants (fig. 2). Although some members of Castilleae are androdioecious (Sakai 2001), there is no evidence of this in *Antiaropsis*. The pistillate inflorescence is subglobose and comprises ca. 20 flowers, each containing a single ovule. Flowers are individually enclosed by bracts on

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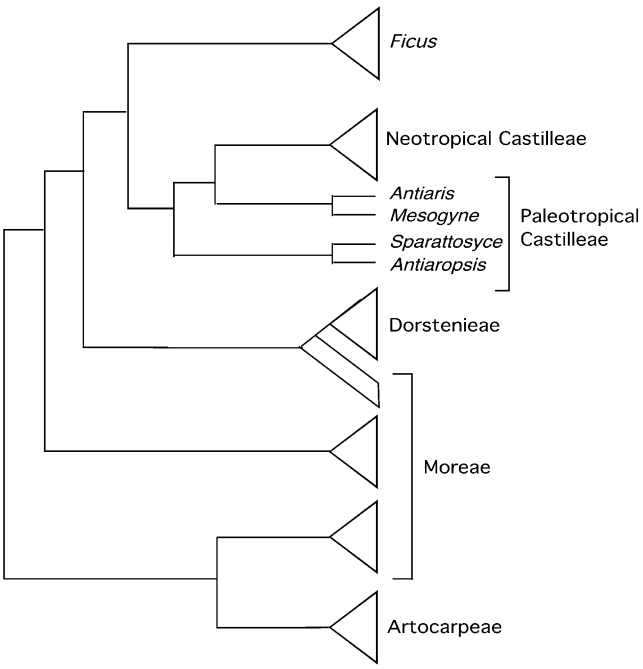

Fig. 1 Phylogeny of Moraceae tribes based on *ndhF* sequences (Datwyler and Weiblen 2004).

a discoid fleshy receptacle and collectively surrounded by an involucre of imbricate bracts (fig. 2*A*–2*F*). At receptivity (fig. 2*C*), bifid stigmas protrude from the protective involucre that persists and reddens after pollination (fig. 2*D*). The involucre reflexes as the receptacle expands in fruit to expose white, arillate seeds among the red bracts (fig. 2*E*, 2*F*). The staminate inflorescence is discoid and comprises dozens of tightly packed flowers, each with four stamens and four tepals (fig. 2*G*–2*K*). These are situated on a receptacle and surrounded by imbricate involucral bracts that expose the stamens before anthesis as the receptacle expands (fig. 2*I*, 2*K*). We investigated the pollination biology of *Antiaropsis* by monitoring its floral phenology, trapping flower visitors, and conducting pollinator exclusion experiments. This led to the discovery of a new species of thrips, described below, that appears to be involved in a pollination mutualism with *Antiaropsis* similar to that of the closely related Neotropical Castilleae (Sakai 2001).

Material and Methods

Study Site

This study was conducted in a primary rainforest remnant near the village of Baisarik, Madang Province, Papua New Guinea (5°16′0″S, 145°26′60″E, ca. 250 m above sea level) during November and December 2003. The climate in this region is perhumid with annual rainfall ca. 3500 mm and a moderate dry season between July and September. *Antiaropsis* is locally abundant on undisturbed hill slopes in this area. The study included 23 female trees, 19 male trees, and 12 trees of unknown sex that lacked inflorescences during the course of the study. Voucher specimens of *Antiaropsis decipiens* are deposited in the following herbaria: A, CANB, K, L, LAE, MIN, NY, and US.

Phenology

The timing of *Antiaropsis* flowering and fruiting was quantified by measurement of 72 carpellate and 80 staminate inflorescences over 37 d. On average, measurements were taken every third day during this period, and a reproductive category was assigned to each inflorescence. Staminate inflorescences were categorized as either (1) with involucral bracts enclosing the stamens (fig. 2*G*, 2*H*), (2) with stamens exposed before anthesis (fig. 2*I*, 2*J*), or (3) at anthesis (fig. 2*K*). Pistillate inflorescences were categorized as either (1) preflowering (fig. 2*B*), (2) flowering, with pink stigmas protruding from the involucre indicating receptivity (fig. 2*C*), (3) postflowering, with involucral bracts enclosing the carpels (fig. 2*D*, 2*E*), or (4) fruiting, with the involucre reflexed and arillate seeds exposed (fig. 2*F*). A timeline of phenology was extrapolated from these measurements because the study was of insufficient duration to follow pistillate inflorescences from inception to senescence. Extrapolation involved dividing inflorescences into size classes according to the date of first measurement, plotting diameter over time for each size class, and finding points of intersection between these curves.

Insect Trapping

Sticky traps were placed near inflorescences to collect insect visitors to *Antiaropsis* flowers at anthesis and at stigma receptivity. Traps were constructed by lining plastic petri dishes 5 cm in diameter with a thin layer of Tanglefoot Pest Barrier (Grand Rapids, Mich.). Traps were affixed to twigs with wire twists and oriented perpendicular to the inflorescence axis at a distance of ca. 2 cm from the flowers. The study included 18 carpellate and 29 staminate inflorescences and 12 control traps, the latter located on *Antiaropsis* trees bearing no inflorescences. Traps were removed either when the inflorescence dropped or after 20 d, whichever occurred first. Insects adhered to the traps were sorted to order and counted. Thrips, flies, and total arthropod abundance were compared among the three treatments with nonparametric Mann-Whitney tests because abundance was not normally distributed. Live insects collected from inflorescences were preserved in alcohol for taxonomic study.

Exclusion Experiments

Pollinator exclusion experiments were conducted to measure the impact of insect visitors on *Antiaropsis* fruit set. Preflowering pistillate inflorescences were divided into three treatments: (1) fine mesh bagging to exclude all insects but not pollen grains (ca. 12.5 μm in diameter), (2) coarse mesh with 1 mm^2 openings allowing the passage of small insects, and (3) open pollinated inflorescences as a control. Infructescences were harvested 37 d following treatment, and percent fruit set was calculated by dividing the number of developing fruits by the total number of flowers. Flowers and fruit set per inflorescence were compared among treatments with nonparametric Mann-Whitney tests.

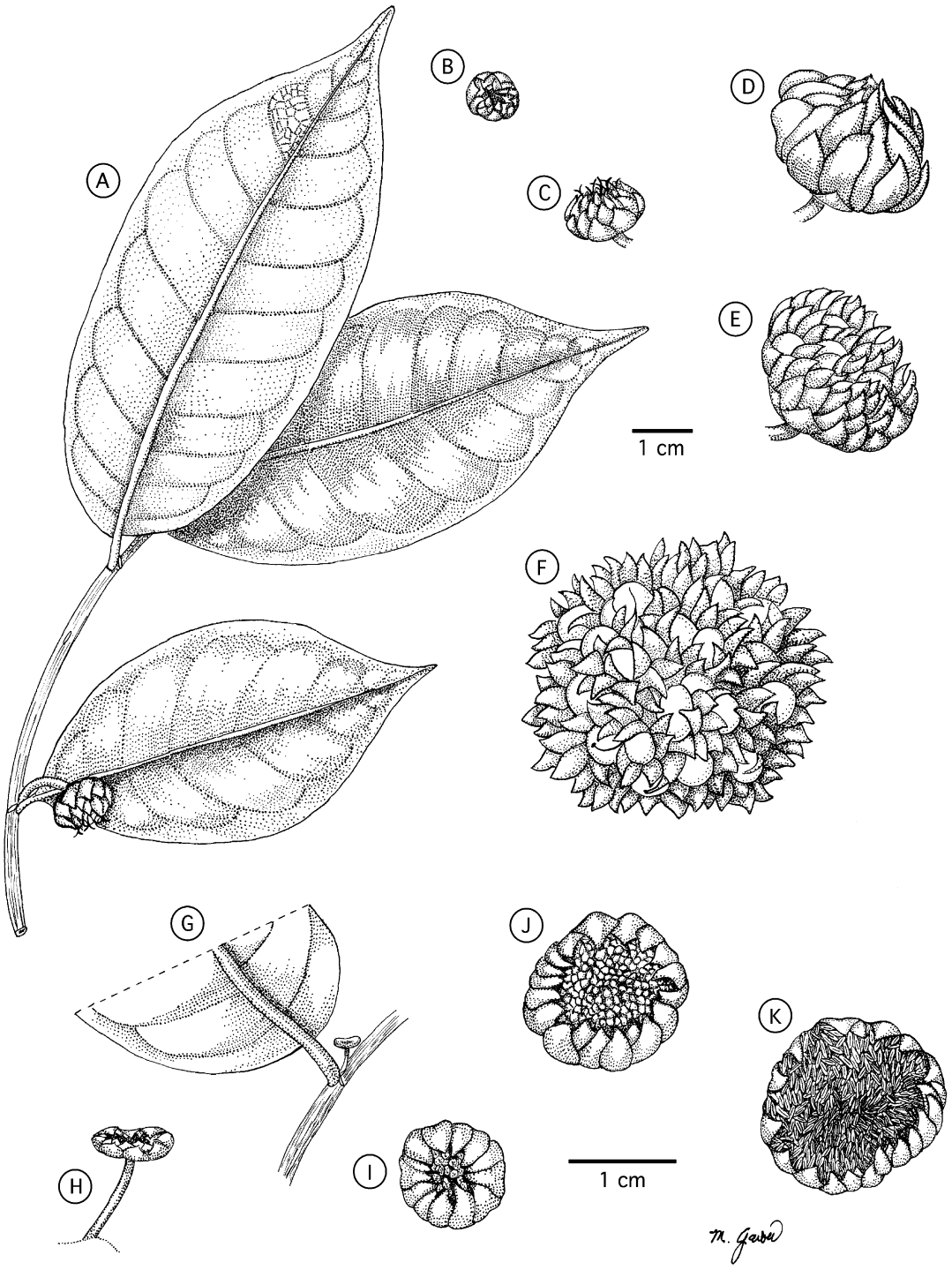

Fig. 2 *Antiaropsis decipiens* K. Schum. (Moraceae). Sequence of development for pistillate (*A–F*) and staminate (*G–K*) inflorescence. Upper scale bar refers to *A–F*. Lower scale bar refers to *G–K*.

Description of the Pollinator Thrips antiaropsidis *sp. nov. Female*

Color medium brown, tarsi yellow, distal half of tibiae variably yellow; antennae brown, segment III yellowish brown to yellow; forewing including clavus brown with small pale area between base of first and second veins. Antennae eight-segmented (fig. 2*H*), segments VII–VIII short with the suture between them sometimes incomplete; head with few lines of sculpture behind eyes, ocellar setae III small, arising usually just behind first ocellus within ocellar triangle (fig. 3*B*); postocular setae uniseriate. Pronotum with widely spaced transverse striae and few discal setae medially (fig. 3*C*); anterior

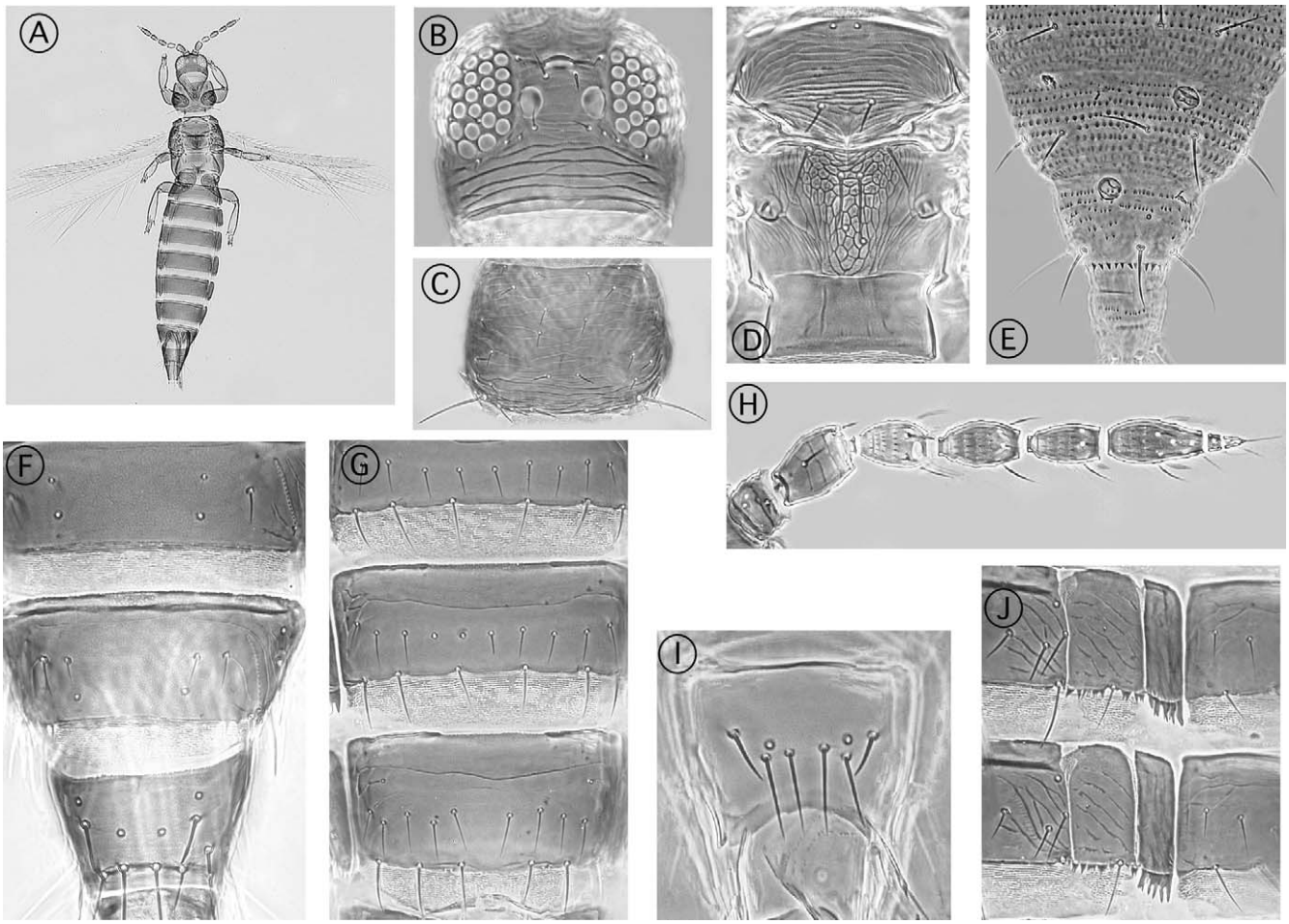

Fig. 3 *Thrips antiaropsidis*. *A*, Female. *B*, Head. *C*, Pronotum. *D*, Mesonotum and metanotum. *E*, Larva II tergites VII–X. *F*, Tergites VII–X. *G*, Sternites V–VII. *H*, Antenna. *I*, Male tergite IX. *J*, Pleurotergites.

angles with one or two pairs of prominent setae; posterior angles with only one pair of long setae, outer posteroangular setae shorter than each of the three pairs of posteromarginal setae. Prosternal basantra with stout microtrichia, ferna not divided medially. Mesonotum transversely striate without lines of sculpture close to the anterior pair of campaniform sensilla. Metanotum strongly reticulate (fig. 3*D*), median pair of setae not close to anterior margin, campaniform sensilla present. Forewing clavus with five marginal setae, terminal seta longest; first vein with about seven basal and three widely spaced distal setae, second vein with about 13 setae. Abdominal tergite II with three lateral marginal setae, a fourth seta present anterolaterally on pleurotergite; II–VII with paired median setae unusually small and fine, arising anterior to campaniform sensilla, no lines of sculpture present mesad of setae S2; tergite VIII posteromarginal comb represented laterally by few microtrichia but medially by weakly lobed craspedum (fig. 3*F*); tergite IX with two pairs of campaniform sensilla; tergite X with short longitudinal division. Ovipositor projecting beyond apex of abdomen. Pleurotergites with no discal setae (fig. 3*J*). Sternite II with two pairs of posteromarginal setae, III–VII with three pairs; sternite II with one or two discal setae, III–VII with eight to 12 discal setae (fig. 3*G*).

Holotype female in micrometers (smallest and largest paratypes in parentheses): body length 1050 (1000, 1200); head length 65; width across cheeks 105; ocellar setae III 10; pronotum length 95, width 135; outer pa setae 10; inner pa setae 48; posteromarginal median setae 20; forewing length 520; tergites VIII, IX, X median length 55, 48, 50; ovipositor length 200; antennal segments III–VIII length 30, 28, 28, 35, 5, 8.

Male

Color yellow, distal antennal segments light brown, forewings weakly shaded. Similar in structure to female but considerably smaller (body length 850 μm); tergite VIII with no trace of comb developed; tergite IX with two pairs of setae in transverse line posterior to campaniform sensilla, median pair slightly closer to lateral pair than to each other (fig. 3*I*); sternite II with one or two discal setae, III–VII with slender transverse glandular area and three to five discal setae.

Larva II

Body color yellow. Dorsal setae all finely acute; spiracles on abdominal segments II and VIII unusually small, scarcely wider than nearest setal base. Tergite IX with posteromarginal

fringe of small tubercles continuous dorsally and ventrally (fig. 3*E*); dorsal surface with many microtrichia, campaniform sensilla slightly further apart than median dorsal setae.

Insects Studied

Holotype female: Papua New Guinea, Madang Province, Baisarik (5°16′S, 143°26′E, altitude ca. 283 m), from *A. decipiens* staminate inflorescence, xi.2003 (Nyree Zerega), in the Natural History Museum, London. Paratypes: 16 females, three males taken with holotype; PNG, East Sepik Province, Wamangu, (3°47′S, 143°39′E, altitude ca. 230 m), 11 females, November 2002 (Barry Andreas). Paratypes are deposited in the following institutions: Australian National Insect Collection, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Natural History Museum, London, United Kingdom; and National Agricultural Research Institute, Port Moresby, Papua New Guinea.

Relationships

This new species has the typical character states of all members of the genus *Thrips*: ocellar setae pair I not developed, ctenidia present on tergites V–VIII, terminating laterally on VI–VII at tergal setae S3, but mesad of the spiracles on VIII (Mound 2002). However, within this genus the combination of character states displayed by this new species is unusual, and it cannot be placed within any of Palmer's (1992) five species groups in the genus *Thrips*. The metanotal sculpture is particularly similar to that of the southeast Asian species in Palmer's Group III, such as *Thrips orientalis* and *Thrips parvispinus*, but both of these lack discal setae on sternite VII and both of them have an almost complete row of setae on the first vein of the forewing. In the key to Oriental members of *Thrips* by Palmer, *T. antiaropsidis* will run to *Thrips unispinus*, a species that was described from three females and four males taken from an unknown plant at Koitaki, PNG. *Thrips unispinus* is a common polyphagous flower thrips around the northern coasts of Australia, and uniquely within this large genus, these two species share the character state of having only one pair of elongate pronotal posteroangular setae. However, *T. unispinus* is a small yellow species with the antennae 7 segmented, the metanotum with no markings within the sculptured reticles, the abdominal tergites with lines of sculpture present mesad of setae S2, and the pronotum and also the sternites with more numerous setae.

Results

Phenology

Starting from a diameter of 1 mm, staminate inflorescences of *Antiaropsis decipiens* took about 44 d to reach anthesis and senescence (fig. 4*A*). During this interval, three stages were discernable: (1) preanthesis with the involucre bracts enclosing the stamens for 16–25 d, (2) preanthesis with involucre bracts exposing the tightly packed stamens between 6 and 14 d, and (3) anthesis that lasted ca. 4 d until senescence. Female thrips bearing mature eggs were observed on preanthesis inflorescences while nymphs and adults of either sex, including females with immature eggs, were observed feeding on pollen of inflorescences at anthesis.

Starting from a diameter of 3 mm, the development of pistillate inflorescences took approximately three times as long as the staminate inflorescences, or ca. 120 d (fig. 4*B*). During this period, four stages were discernable: (1) a preflowering stage of at least 17–30 d, (2) a receptive, flowering stage of 3–30 d, depending on when and if pollination occurred, (3) postflowering of 36–50 d, when the involucre enclosing the carpels turned from green to pale pink, and (4) fruiting with red bracts reflexed and exposing white arillate seeds for up to 2 wk. Adult female thrips were observed on pistillate infloresences only during the receptive phase.

Insect Trapping

Thrips antiaropsidis was the single most abundant species trapped at *Antiaropsis* trees, but Diptera was the most abundant insect order (table 1). The mean abundance of Diptera per trap was not significantly greater for inflorescences than nonflowering trees, indicating that on average flies are not floral visitors specifically. Twenty-eight fly morphospecies were small enough to fit through our coarse mesh, but only three of these were trapped at both staminate and pistillate inflorescences more than once. The very high standard deviations of mean abundance per trap for these three species and the lack of significant differences between inflorescences and controls (table 1) indicated that even the most abundant flies were not consistently associated with *Antiaropsis* inflorescences.

Thrips antiaropsidis was by far the most abundant species on inflorescence traps, accounting for 31%, 23%, and 1.6% of all arthropods trapped at staminate inflorescences, pistillate inflorescences, and nonflowering trees, respectively. Mean numbers of *T. antiaropsidis* per trap at staminate and pistillate inflorescences were significantly different from controls but not from each other (table 1). *Thrips antiaropsidis* larvae and adults were observed feeding on pollen of staminate inflorescences, and female adults were observed on receptive pistillate inflorescences. Pollen was found on the bodies of adult females collected from staminate inflorescences and found next to thrips trapped at both types of inflorescences. Collecting by sticky traps and alcohol did not permit the determination of pollen load, and counts in the future should involve slide mounting in the field.

Exclusion Experiments

Inflorescence mortality was high in all three treatments. Fewer than half of the unbagged inflorescences, fine-mesh-bagged inflorescences, and coarse-mesh-bagged inflorescences were retained for the duration of the experiment. Among the survivors, the average percentage of fruit set per inflorescence varied from 0% for fine mesh to 30% for coarse mesh and 35% for the open-pollinated control (table 2). Fruit set did not differ significantly between the coarse mesh and control treatments (table 2). This indicates that a vector in the size class of *T. antiaropsidis*, smaller than 1.0 mm in diameter but larger than the diameter of the fine mesh, affected *Antiaropsis* pollination.

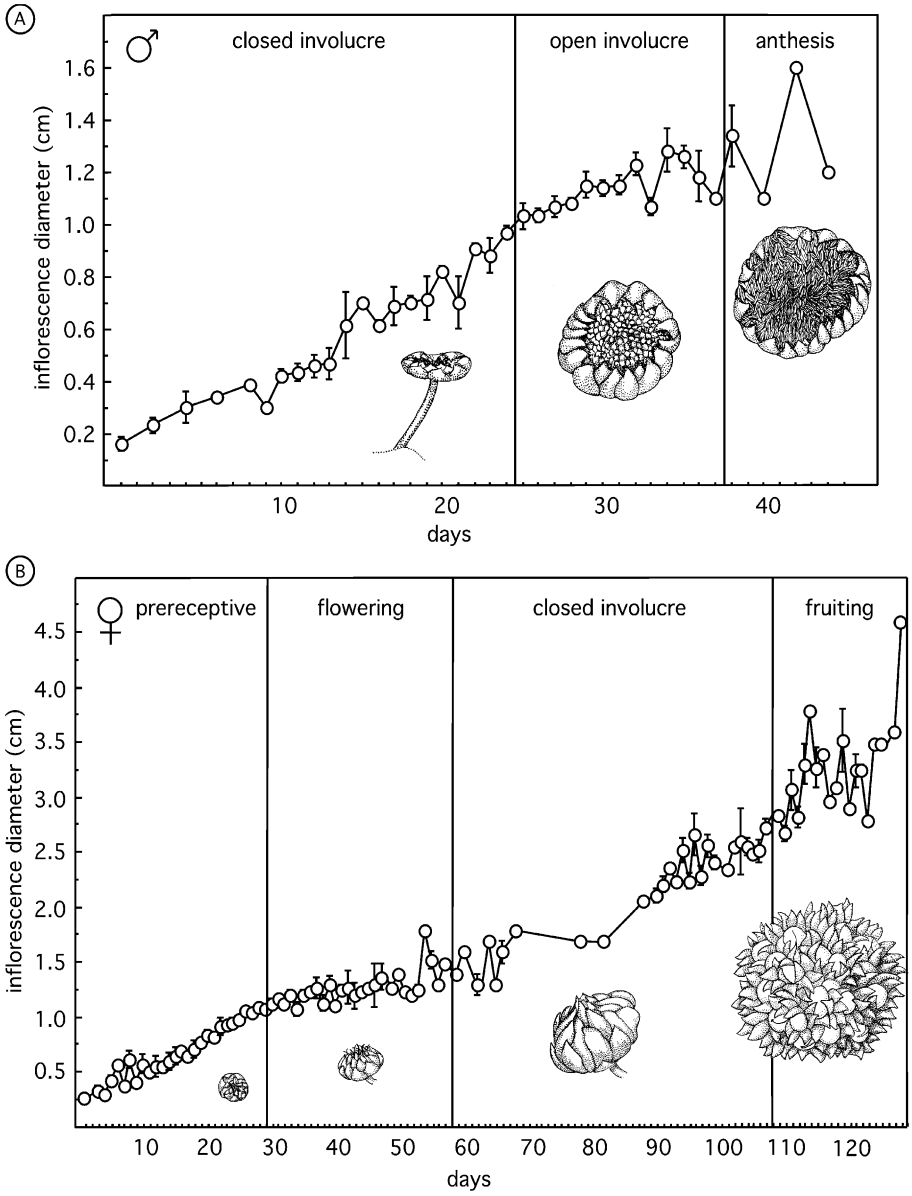

Fig. 4 Phenology of *Antiaropsis decipiens*. Staminate (*A*) and carpellate (*B*) phenology with developmental stages indicated. Times indicated for each stage are maximum times.

Discussion

Few pollination syndromes are understood in the Moraceae apart from the well-documented obligate mutualism between figs and fig wasps (Janzen 1979; Weiblen 2002). This study of *Antiaropsis decipiens* is the first report on the mode of pollination in a paleotropical member of the Castilleae, the sister group to the figs, and only the second study in the tribe (Sakai 2001). Diptera was the most abundant insect order trapped at *Antiaropsis* trees, but abundance at inflorescences was similar to that at nonflowering trees (table 1). That no particular fly species was consistently associated with inflorescences we interpret as evidence that Diptera are not specific pollinators of *Antiaropsis*.

Several lines of evidence indicate that thrips (Thysanoptera, Thripidae) are responsible for *Antiaropsis* pollination, as they are in *Castilla elastica* (Sakai 2001). *Thrips antiaropsidis* was the only species trapped at inflorescences in significantly greater abundance than at control traps (table 1). *Thrips antiaropsidis* nymphs and adults were also observed feeding on pollen in staminate inflorescences at anthesis, and adults were encountered on receptive pistillate inflorescences. *Antiaropsis* pollen was attached to *T. antiaropsidis* on sticky traps, and pollen smeared on traps near thrips may have dislodged from struggling insects. Fruit set in open pollinated inflorescences and coarse-mesh-bagged inflorescences was not significantly different, and there was no fruit set in the fine mesh treatment that excluded all floral visitors.

Table 1

Total Abundance of Arthropods on Sticky Traps Associated with Staminate and Carpellate Inflorescences and Nonflowering Branches of *Antiaropsis decipiens*

Order	M inflorescences ($N = 29$)	F inflorescences ($N = 18$)	Controls ($N = 12$)
Thysanoptera	92	74	2
Thrips antiaropsidis	91	73	2
M	28	33	0
F	63	40	2
Other Thysanoptera	1	1	0
Diptera	124	152	55
Hymenoptera	32	30	34
Coleoptera	12	18	7
Homoptera	5	11	12
Orthoptera	2	0	0
Lepidoptera	0	2	1
Collembola	0	1	0
Acarina	2	1	8
Araneida	5	0	0
Undetermined	15	33	9
Total abundance	289	322	128
Total arthropods per trap	10.0 (13.5)	17.9 (15.8)^{A}	10.37 (3.7)^{A}
Thrips antiaropsidis per trap	3.1 (5.0)^{A}	4.0 (6.5)^{A}	0.2 (0.4)
Diptera per trap	4.3 (11.3)^{B}	8.4 (14.1)^{A,B}	4.6 (2.5)^{A}
Species 1	1.9 (10.2)^{A}	3.7 (12.0)^{A}	0.42 (0.7)^{A}
Species 2	1.2 (1.9)^{A}	2.8 (8.2)^{A,B}	2.0 (1.4)^{B}
Species 3	0.4 (0.6)^{A}	0.2 (0.4)^{A}	0.1 (0.3)^{A}

Note. M = male, F = female. Abundance per trap of total arthropods, *Thrips antiaropsidis*, Diptera, and three frequently occurring Diptera species small enough to fit through the coarse mesh (X ± SD per trap) was compared between treatments with pairwise Mann-Whitney tests. Values with the same letter within columns not significantly different at $P = 0.05$.

This indicates that a small vector capable of passing through mesh 1.0 mm^2 in diameter, such as *T. antiaropsidis*, is responsible for pollination. Wind pollination appears extremely unlikely given that the pollen is sticky and the habitat is perhumid lowland forest. We have also observed *T. antiaropsidis* at inflorescences in two other localities: Wannang, Madang Province (5°13′S, 145°41′E, altitude 100 m) and Wamangu, East Sepik Province, Papua New Guinea (3°47′60″S, 143°39′0″E, altitude 239 m). The most distant of these sites is more than 160 km from Baisarik. We speculate that *Antiaropsis* pollination by thrips is ubiquitous, but continued study is necessary to establish the specificity of the association with *T. antiaropsidis*.

Apterous nymphs were observed only on staminate inflorescences, where they fed on pollen, but the abundance of adults trapped near pistillate and staminate inflorescences was not significantly different. Adults were observed more frequently and for longer periods on staminate inflorescences (N. Zerega, personal observation). In species with unisexual inflorescences where pollen is the only reward, pistillate flowers may deceive potential visitors by mimicking the attractive traits of conspecific staminate flowers.

Pollination by deceit has been demonstrated in *Begonia involucrata* Liebm. (Agren and Schemske 1991), while olfactory mimicry is important in *Myristica insipida* R. Br. (Armstrong and Irvine 1989) and *Macrozamia* cycads (Terry et al. 2004). Pollination by deceit has been suggested for three other Moraceae species with functionally unisexual inflorescences (Patel et al. 1995; Sakai et al. 2000; Sakai 2001; Weiblen et al. 2001). We propose that this is also the case in

Table 2

***Antiaropsis decipiens* Exclusion Experiments**

Treatment	Inflorescences		Flowers per inflorescence		Fruit set (%)
	Total	Retained	Total	Pollinated	
Control	18	8	12.2 (4.7)*	4.1 (2.2)*	35.0 (10.8)*
Fine	19	9	14.9 (2.8)*	0 (. . .)	0 (. . .)
Coarse	16	9	11.6 (3.8)*	3.1 (4.0)*	29.8 (34.6)*

Note. Total flowers per inflorescence (X ± SD), flowers pollinated per inflorescence (X ± SD), and percent fruit set per infructescence (X ± SD) were compared using pairwise Mann-Whitney tests.

* Not significantly different at $P = 0.05$.

Antiaropsis, where the pistillate inflorescence offers neither nutritional reward for adults nor brood sites. Galled ovules serve as the reward in fig pollination, but deceit pollination in *Antiaropsis* protects the ovules and offers inexpensive pollen as the reward instead. Berg (2001) suggested that this type of pollination coupled with insect breeding in staminate inflorescences could be quite common in Moraceae. What signals might be important in luring pollen feeders from staminate to carpellate inflorescences? Olfactory cues are thought to be important attractants for thrips (Kirk 1985), but *Antiaropsis* inflorescences have no obvious odor, and volatile profiles have yet to be investigated. Visual cues could be important, as the receptive carpellate inflorescence with pink stigmas protruding from a ring of yellowish bracts is of similar diameter and appearance to the preanthesis staminate inflorescence with pink stamens surrounded by a ring of yellowish bracts.

Thrips antiaropsidis *Life Cycle*

Staminate inflorescences of *Antiaropsis* appear to be brood sites for *T. antiaropsidis* based on the presence of pollen-feeding larvae. The exact timing of thrips development varies among species and depends on temperature and food quality. Tsai et al. (1995) demonstrated that at temperatures similar to those of our study site, the melon thrips, *Thrips palmi* Karny (Thysanoptera, Thripidae), needs ca. 4 d in the egg stage, 4 d for the two feeding larval instars, and 3 d for the two nonfeeding pupal instars. If eggs are laid in staminate inflorescences just a few days before anthesis, these times coincide well with the phenology of *Antiaropsis* staminate inflorescences (fig. 4*B*).

We have yet to observe pupae, but we postulate that *T. antiaropsidis* pupates in the litter because staminate inflorescences drop to the ground shortly after anthesis. As first and second instar larvae are abundant in the protected cavity formed by the receptacle, involucre bracts, and interwoven stamens, it is conceivable that last instar larvae ride the inflorescence to the ground as it senesces within a few days of anthesis (fig. 5).

Adult thrips probably copulate on the staminate inflorescence, as both sexes were observed there at anthesis. Two of four females from a single preanthesis inflorescence had preformed eggs, and a third female nearly so. At least three of seven females from an inflorescence at anthesis carried immature eggs. *Thrips antiaropsidis* females accommodate only one egg at a time, occupying about 70% of the abdominal volume. It is possible that eggs are formed after bouts of pollen feeding in a matter of hours. However, females must locate a preanthesis inflorescence in which to lay eggs, because egg development takes ca. 4 d, and anthesis only lasts as long. Anecdotal observations on population phenology suggest some degree of within-tree synchrony requiring with some probability that females locate a preanthesis inflorescence on another tree. This may indicate that adults seeking pollen and mating opportunity may find both at staminate inflorescences during anthesis, while pollen-bearing, gravid

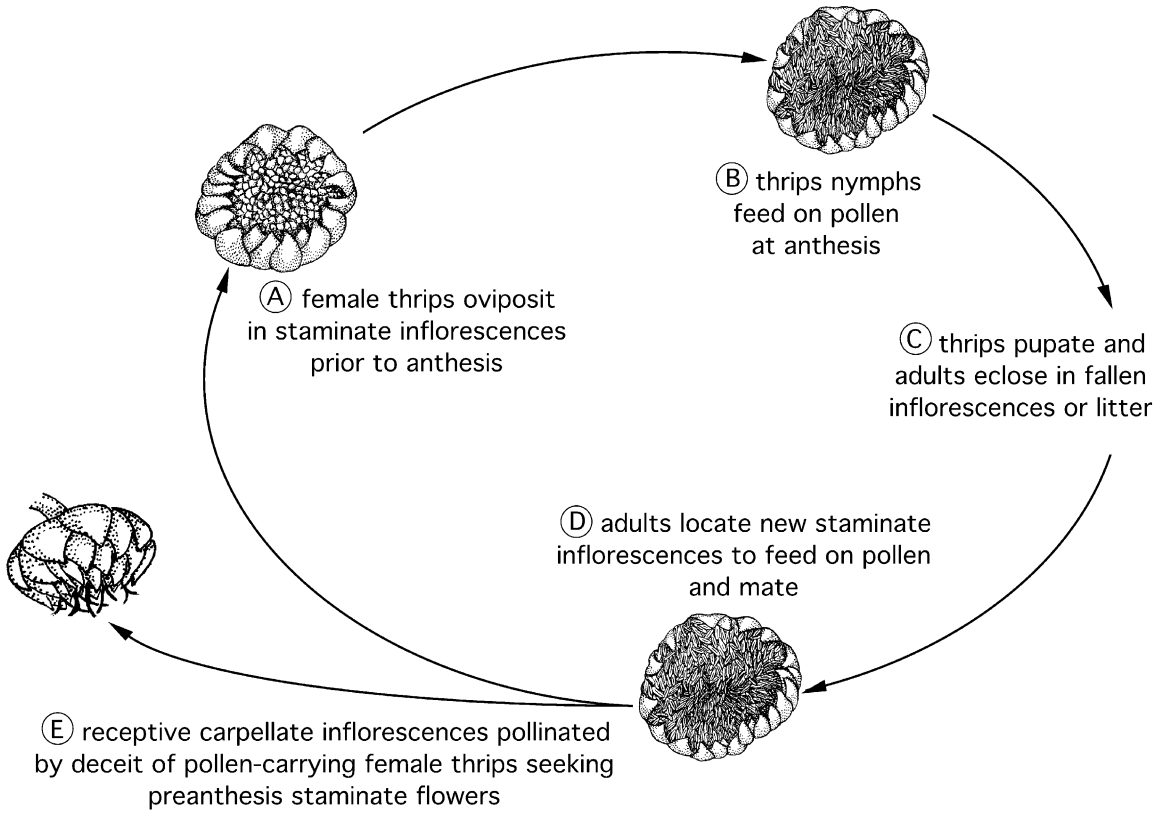

Fig. 5 Proposed life cycle of *Thrips antiaropsidis* in relation to *Antiaropsis decipiens* flowering phenology

females seeking oviposition sites in preanthesis inflorescences may be deceived into visiting pistillate inflorescences and thereby affect pollination (fig. 5).

Thrips *Pollination and Castilleae*

Thrips are well-known horticultural pests (Kevan and Baker 1983; Kirk 1984; Mound and Heming 1991), but they can also play an important role as pollinators. Thrips have been suggested as pollinators across a wide range of plant families, including Annonaceae (Webber and Gottsberger 1995; Momose et al. 1998*b*; Gottsberger 1999; Silberbauer-Gottsberger et al. 2003), Araceae (Rust 1980), Chloranthaceae (Luo and Li 1999), Dipterocarpaceae (Appanah and Chan 1981), Euphorbiaceae (Moog et al. 2002), Lauraceae (Norton 1984), Monimiaceae (Williams et al. 2001), Moraceae (Sakai 2001), Winteraceae (Thien 1980; Bernhardt and Thien 1987; Pellmyr et al. 1990), and Zamiaceae (Mound and Terry 2001). It is possible that thrips are overlooked as pollinators in many studies because the weave of cloth often used in pollinator exclusion experiments does not exclude thrips (Mound et al. 1998).

It appears that there is some level of *Anitaropsis* flowering year-round (G. Weiblen, personal observation), which could provide feeding and breeding sites for host-specific thrips. Host specificity among thrips is rare (Mound and Marullo 1996) but has been documented in the pollination of *Macrozamia* cycads (Terry et al. 2004). It is possible that *Antiaropsis* is a specific host, because *T. antiaropsidis* was found in *Antiaropsis* inflorescences over 160 km away from our study site, and this species is the dominant visitor to pistillate and staminate inflorescences in the size range indicated by pollinator exclusion experiments. These and previous observations implicate thrips in the pollination of the sister group to figs (Sakai 2001; Datwyler and Weiblen 2004). The pantropical occurrence of thrips pollination in Castillae (Sakai 2001) and the absence of any evidence to the contrary leads us to speculate that association between thrips and this plant lineage is ancient. *Thrips* may be attracted to Castilleae because of the tightly packed flowers and involucre bracts, which provide a protected brood site and satisfy a predilection for thigmotaxis, the habit of crawling into spaces such that maximal body surface area is in contact with the cavity. If thrips pollination proves to be ubiquitous in Castilleae, then entomophily coupled with mating on and breeding in the inflorescences may have preceded the origin of fig pollination. Like the figs, with their flowers enclosed inside an urn-shaped inflorescence that provides breeding sites for pollinators but excludes most other phytophagous insects, Castilleae protect their flowers from phytophagy in the enclosure formed by the receptacle and bracts while providing a breeding site for pollinators. The major difference between Castilleae and *Ficus* pollination then would appear to be the nature of the floral reward, pollen versus ovules.

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