

Two New Neotropical Genera of Drosophilidae (Diptera) Visiting Palm Flowers

DAVID GRIMALDI¹, FINN ERVIK², AND RODRIGO BERNAL³

ABSTRACT: Reports of Drosophilidae visiting palm and other spiked inflorescences are scattered in the literature, but this is the first systematic treatment of such flower visitors from the neotropics. Drosophilids in two new genera and four new species were found aggregating at inflorescences of palms in Ecuador and Colombia: *Palmophila ecuadoriensis* Grimaldi, n. gen., n. sp. on *Wettinia maynensis*; and *Palmomyia incerta* Grimaldi, n. gen., n. sp. on *Geonoma undata*, *Chamaedorea linearis*, and *Phytelephas seemanii*. *Palmophila rozeni* Grimaldi, n. sp., and *Palmophila dentata* Grimaldi, n. sp., were insecticide-fogged from the canopies of forests in eastern Ecuador. Both new genera are closely related to the IndoPacific genera *Baeodrosophila* and *Colocasiomyia*; species of the latter also visit columnar or spiked inflorescences, but mostly of aroids.

KEY WORDS: *Palmomyia* new genus, *Palmophila* new genus, pollination, palms, inflorescences

Terrestrial life is, without question, dependent upon plants. We define biomes from tropical forests to tundra on the basis of vegetation. Amongst all plants, the 250,000 species of angiosperms represent the most successful radiation in the nearly 450-million-year history of vascular plants. Most angiosperms, perhaps 85%, are pollinated by animals, and the preponderance of these are pollinated by insects (Faegri and van der Pijl, 1979; Proctor *et al.*, 1996). Indeed, insects and angiosperms engage in one of the most pervasive symbioses on earth, and it is likely that generalized insects already on stage 120–130 million years ago fueled the angiosperm radiations (Grimaldi, 1999). Bees, the Apoidea, receive most attention in pollination biology, as almost all of the approximately 20,000 species are obligate and efficient foragers of pollen and nectar, with which they provision their nests. But, numerous other insects visit flowers and transfer pollen, and pollinators of the great majority of angiosperms (especially tropical species) are unknown. Here, we contribute an original report on another interesting relationship between non-apoidean flower visitors and some tropical plants.

Biologists typically associate Drosophilidae only with decaying fruits, but the known life histories among the 3,200 described species are considerably more diverse. These include saprophages, larval predators and parasites, leaf miners, fungivores, and species that feed from and usually breed in flowers (Okada and Carson, 1982; Brncic, 1983). Anthophily is actually widespread throughout Drosophilidae, occurring in one species of *Cladochaeta* Coquillett, all species of *Colocasiomyia* de Meijere, many *Diathoneura* Duda and *Scaptodrosophila* Duda, some *Scaptomyza* Hardy and *Zygothrica* Wiedemann, all species in the related genera *Laccodrosophila* Duda and *Zapriothrica* Wheeler, and assorted *Drosophila* Meigen. Anthophilic *Drosophila* exist in the Neotropical subgenus *Phloridosa* Sturtevant (introduced to Hawaii); several species in the New World subgenus *Siphlodora* Sturtevant; several species in the *Drosophila* (*Sophophora*) *melanogaster* species group (i.e., the *elegans* subgroup); and many or all species (where known) in the *D.* (*Drosophila*) *floricola*, *onychophora*, and *tripunctata* species groups, among others.

In only a few cases have the behavior of the flies and pollination biology of the plants been studied, most of them dealing with aroids (e.g., Carson and Okada, 1980; Toda and

¹ Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024-5192, Email: grimaldi@amnh.org

² Universeum AB, Box 14365, 400, 20 Göteborg, Sweden.

³ Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia.

Table 1. Reports of Drosophilidae Visiting Palm Flowers in the Neotropics

Reference	Locality	Flies	Palm(s)
Bernal & Ervik, 1996	Colombia	"Drosophilidae"*	<i>Phytelephas seemanii</i> Borch-
senius, 1993	Ecuador	"4 spp. Drosophilidae"	3 spp. <i>Aiphanes</i>
Ervik, 1993	Ecuador	"Drosophilidae"	<i>Aphandra natalia</i>
Ervik & Bernal, 1996	Colombia	" <i>Drosophila</i> sp."	<i>Prestoea decurrens</i>
Ervik & Feil, 1997	Ecuador	"2 spp. <i>Drosophila</i> "	<i>Prestoea schultzeana</i>
Ervik & Feil, 1997	Ecuador	"Drosophilidae"	<i>Hyospathe elegans</i>
Ervik <i>et al.</i> , 1999	Ecuador	" <i>Drosophila</i> sp. 1, 2"	<i>Phytelephas seemanii</i>
Ervik <i>et al.</i> , 1999	Ecuador	" <i>Drosophila</i> sp."	<i>Phytelephas aequatorialis</i>
	Ecuador	" <i>Drosophila</i> sp."	<i>Phytelephas macrocarpa</i>
	Ecuador	" <i>Drosophila</i> sp."	<i>Aphandra natalia</i>
Henderson, 1986	Costa Rica	"Drosophilidae"	<i>Synechanthus warscewiczianus</i>
Henderson, 1986	Costa Rica	"Drosophilidae"	<i>Chamaedorea costaricana</i>
Henderson, 1986	Costa Rica	"Drosophilidae"	<i>Geonoma</i> sp.
Knudsen <i>et al.</i> , 1999	Ecuador	"Drosophilidae"	<i>Geonoma macrostachys</i>
Knudsen <i>et al.</i> , 2001	Ecuador	" <i>Drosophila</i> spp."	<i>Prestoea schultzeana</i>
Knudsen <i>et al.</i> , 2001	Ecuador	" <i>Drosophila</i> spp."	<i>Bactris gasipaes</i>
Knudsen <i>et al.</i> , 2001	Ecuador	" <i>Drosophila</i> spp."	<i>Chamaedorea linearis</i>
Knudsen <i>et al.</i> , 2001	Ecuador	" <i>Drosophila</i> spp."	<i>Geonoma macrostachys</i>
Listabarth, 1993	Peru	"Drosophilidae"	3 spp. <i>Geonoma</i>
Martín & Quesada, 2001	Costa Rica	"Drosophilidae"	<i>Geonoma epetiolata</i>
Olesen & Balslev, 1990	Ecuador	"2 spp. Drosophilidae"	<i>Geonoma macrostachys</i>
This report	Ecuador	<i>Palmophila ecuadoriensis</i>	<i>Wettinia maynensis</i>
This report	Ecuador	<i>Palmyia incerta</i>	<i>Geonoma undata</i> , <i>Chamaedorea linearis</i>

* Includes at least the species *Palmyia incerta*, described herein.

Okada, 1983). Where they have been studied, though, they appear to be significant pollinators, not merely visitors to flowers. Like most families of acalyptrate flies the species-level systematics of tropical faunas is seriously incomplete, and the description of two new genera and four new species herein is testament.

Twelve reports specifically mention drosophilids as visitors to inflorescences of New World palms (Table 1). At least this many more reports, though, simply cite "small Diptera" on palm flowers, which may also pertain to drosophilids (reviewed in Henderson, 1986). These twelve reports are only from four countries: Colombia, Costa Rica, Ecuador, and Peru. It is possible that palm-visiting drosophilids are restricted to northwestern South America and portions of southern Central America, but such confinement is highly unlikely when palm-visiting drosophilids are known even from the Old World tropics. For example, Essig (1973) reported numerous drosophilids on inflorescences of *Nypa fruticans* and *Hydriastele microspadix* (Arecaceae) in New Guinea, and Bøgh (1996) likewise reported abundant drosophilids visiting the rattan palm, *Calamus* (Arecaceae), in southern Thailand. Most likely, palm-visiting drosophilids are widespread throughout the neotropics and have simply been overlooked (e.g., Bullock, 1981).

Though most reports indicate that drosophilids are among the most abundant insects at some palm inflorescences, they are probably not as significant for pollination as are bees (especially meliponines, and some halictids), syrphids, and some beetles (especially nitidulids and curculionids). Indeed, several reports indicate that drosophilids had very small pollen loads, if any pollen at all. Almost certainly the drosophilids visiting palm flowers

are also breeding in them, and the mention of staminate flowers of *Geonoma* "infested" with the 4-filamented eggs of drosophilids supports this view (Olesen and Balslev, 1990).

Cladograms of palm relationships based on DNA sequences were recently reported (Assmussen *et al.*, 2000; Hahn, 2002), which help to interpret patterns of fly visitation. The palm genera that Neotropical drosophilids have been reported to visit are distantly related and belong to the arecoid, ceroxylid, and geonomoid lineages. This and subsequent reports will address whether flies are at all dedicated to particular palms, and if a phylogenetic pattern to visitation becomes apparent. Species of *Colocasiomyia*, for example, are typically monophagous to oligophagous on one or several species of aroids in Asia and the Indopacific (Carson and Okada, 1980; Okada and Carson, 1982), where they feed on flowers and breed in spadices. Neotropical palm-visiting species may have similar host fidelity, but determining this will depend on much more sampling. It may be very significant that four related genera of drosophilids are found on aroids and palms—plants whose inflorescences produce heat (thermogenesis) (Meeuse, 1975; Ervik and Barfod, 1999). Another report will treat the Neotropical *Drosophila dreyfusi* species group, various species of which have also been found to routinely visit palms based on field work by the junior authors.

It is a pleasure for the senior author to dedicate this paper to his colleague Dr. Jerome G. Rozen, Jr. ("Jerry"), for a Festschrift in honor of his 75th birthday anniversary. Zoology at the AMNH is narrowly restricted to phylogenetic analysis, so Jerry's interdisciplinary work on the systematics, pollination and nesting biology of bees has been refreshing, as has been his professionalism.

Methods and Materials

Flies were collected at several localities in Ecuador and Colombia. They were collected directly at inflorescences of various palms by Ervik and Bernal, or were fogged from the canopy of forests in eastern Ecuador by T. L. Erwin of the National Museum of Natural History, Smithsonian Institution. Protocols for canopy fogging are provided in Erwin (1983). Batches of insects (lots) collected by canopy-fogging, and preserved in ethanol, were sorted and the drosophilids removed. Lot numbers were kept associated with specimens, referred to in the specimen data below. Ethanol-preserved specimens were either critical point-dried or, for lots of only a few specimens, dehydrated using HMDS solvent (Hexamethyldisilazane, Polysciences Inc.), then point mounted. Morphological terminology follows Grimaldi (1990). Measurements were made with a digital stage micrometer (± 0.001 mm). Thorax length was used as a general measure of body size. Also measured were cheek depth (CD) and eye depth (ED), since comparisons of CD/ED showed significant variation.

Systematics

Palmophila Grimaldi, new genus

DIAGNOSIS: Face with very broad carina; arista pubescent, not plumose; eyes with short, dense pilosity; ov scape with numerous stiff, sharp setae (no pegs); male genitalia with surstylus lacking prensisetae pegs (having only fine setulae); paraphyses complex, sclerotized, flanking distiphallus but pivoting widely to the sides and outward.

TYPE SPECIES: *P. ecuadoriensis*, n. sp. By original designation.

ETYMOLOGY: "Palm lover," in reference to its habits; *-ophila* is a common suffix for drosophilid generic names.

RELATIONSHIPS: The new genus is unlike any other in the Western Hemisphere save for

the closely related new genus *Palmomyia*. Some Neotropical and southern Nearctic steganine drosophilids have a pubescent arista, and some species in the Neotropical drosophiline genus *Cladochaeta* have a bare arista (without even pubescence). This genus is clearly not related to either of those groups. It resembles most the IndoPacific genera *Baeodrosophila* Wheeler and Takada, and *Colocasiomyia*, known from the Caroline Islands and Micronesia, and from throughout southeast Asia, respectively. Indeed, the new genus appears closely related to these two genera, which were placed in a subtribe Colocasiomyina (Grimaldi, 1990). These genera were not discussed in a recent cladistic analysis of some drosophiline genera (Hu and Toda, 2001).

Most or all of the species in each of these two genera have a pubescent arista; a very broad, flat facial carina; and an oviscap with sparse or no marginal pegs. *Baeodrosophila*, however, has male genitalia quite different from those of the new genus and most similar to *Scaptodrosophila*, with jutting, setulose paraphyses or gonopods, and a pair of large apical setae on the hypandrium. *Baeodrosophila* also has the typical drosophiline surstylus bearing a row of marginal peg-like prensisetae; the new genus distinctively lacks these.

There are approximately 30 described species of *Colocasiomyia*, relationships of which have been most recently analyzed by Grimaldi (1992). *Colocasiomyia* has a basal clade (hereafter, "basal clade") of three species that plesiomorphically lacks distinctive teeth or pegs found in all other species of the genus (hereafter, "derived clade"). All species in the "derived clade" have lost marginal pegs on the oviscap, and most species have also lost prensisetae pegs on the surstylus. *Palmophila* n. gen. differs from the "basal clade" of *Colocasiomyia* by having no oviscap pegs, and two of the three species of *Palmophila* have well developed gonopods and lack surstylar teeth. It differs from the "derived clade" of *Colocasiomyia* by lacking foretarsal teeth; by having an oviscap that is not long and slender, nor with long, fine setae; and lacking the large, distinctive, keel-like aedeagal apodeme (cf. fig. 388 in Grimaldi, 1990).

Interestingly, at least *Colocasiomyia* has a habit similar to the new genus, of visiting columnar inflorescences (spadices) of aroids (reviewed in Grimaldi, 1992). *Baeodrosophila* has merely been reported as collected "on *Pandanus*" (Pandanaeae, "screw pines") (Wheeler and Takada, 1964). Palms, aroids, and *Pandanus* are all monocots, but rather distantly related (Bremer, 2000). Most significantly, one of the three species in the "basal clade" of *Colocasiomyia*, *C. arenga* (Okada), is reported visiting inflorescences of the palm *Arenga pinnata*, but not on aroids. This species is known only from Java. Thus, the compelling morphological evidence for a close relationship between the Neotropical genera and the two IndoPacific genera, *Baeodrosophila* and *Colocasiomyia*, is also reflected in their biology.

Palmophila ecuadoriensis Grimaldi, new species

Figs. 1, 2

DIAGNOSIS: Distinguished from the other species in the genus as given in the diagnosis for *P. rozeni*, below.

DESCRIPTION: Mean thorax length 0.92 mm (5 males), 0.94 (5 females). Color and vestiture: Body entirely light yellow, even on abdominal tergites. Most setae are sheared off specimens, but their positions discerned from sockets. Remaining setae all light yellow to golden, not black. HEAD: Frons and face broad. Eyes pink, not red; with short, dense interfacetal setulae. Each ocellus with dark brown rim. Anterior reclinate seta closer to ipsilateral proclinate than to posterior reclinate. Facial carina very broad, flat, with truncate (not rounded) ventral margin. Face with one pair of vibrissae. Cheek deep, CD/ED = 0.31.

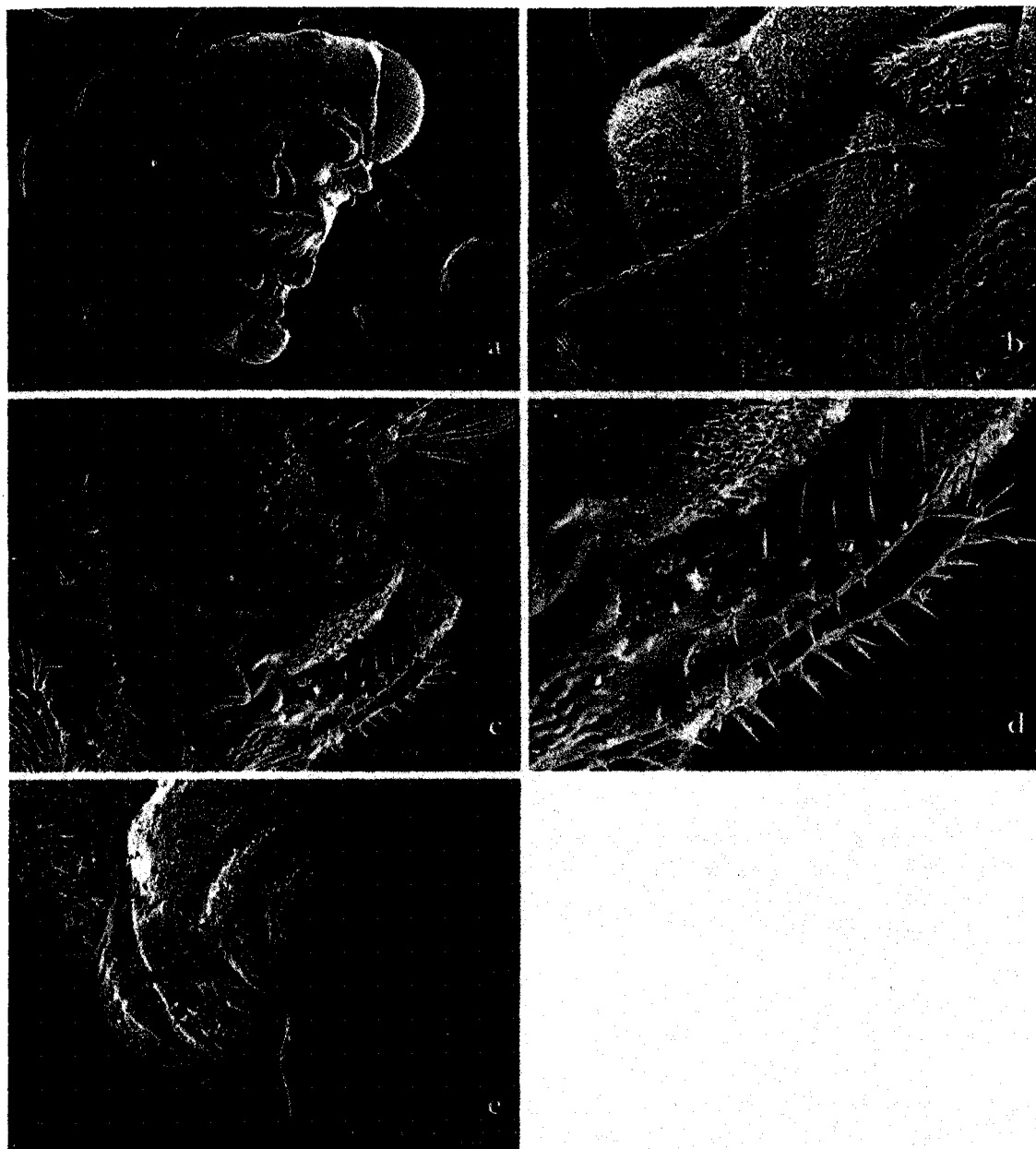


Fig. 1. Scanning electron micrographs of *Palmophila ecuadoriensis*, n. gen, n. sp.: a, Head; b, Detail of pubescent arista; c, Female terminalia; d, Detail of female oviscape; e, External male genitalia (terminal view), showing everted gonopods and aedeagus.

Antennae with bases well separated by distance equal at least to diameter of scape. Pedicel distinctively without large setae, only short, stout setulae. Arista with two segments, basal one small; apical arismere pubescent, not plumose. Clypeus fairly deep, palps broad. Labellar lobes each with 18 pseudotracheae. Floor of cibarium with following arrangement of sensilla (described for one side): pair of small sensilla trichodea at anterior end, then pair of campaniform sensilla, then row of 6 sensilla trichodea, a central sclerotized tube, and a central pair of campaniform sensilla at posterior end in line with central tube. A sclerotized, posterior bulb lacking on cibarium. THORAX: Acrostichal setulae in 6 rows; 2 pairs of dorsocentral setae, anterior pair 0.5× length of posterior dorsocentrals. One large katapisternal seta present. Legs without distinctive setae, combs, or spurs, though tarsi with dense microtrichia over most of surface. Wing hyaline, with no mark-

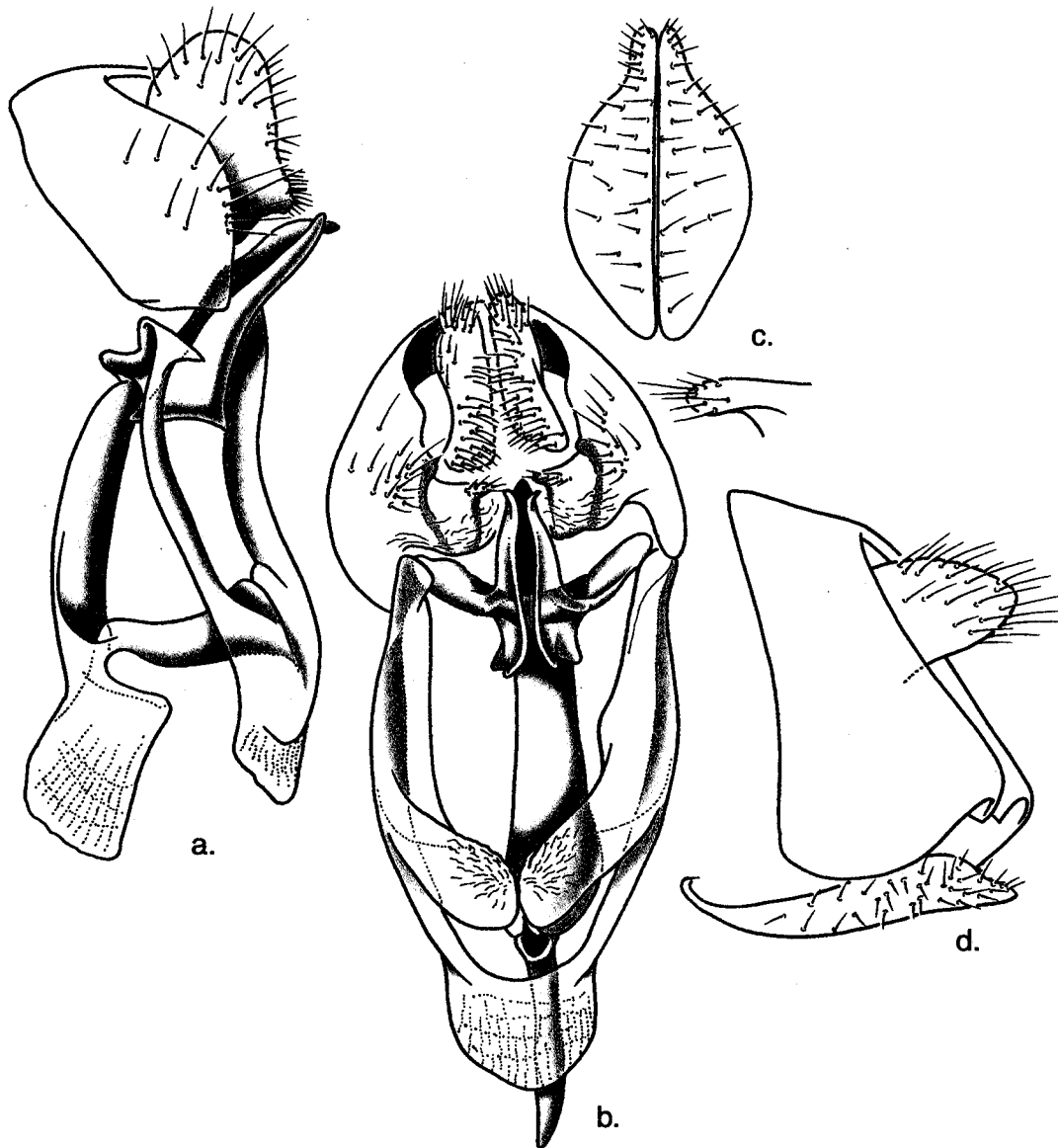


Fig. 2. Genitalia of *Palmophila ecuadoriensis*: a, b: Male genitalia, in lateral (a) and ventral (b) view, with detail of surstylus; c, d: Female. c, Oviscape, ventral view; d, Terminal tergite, cerci, and oviscape, lateral view.

ings; mean length = 1.87 mm (5 males), 1.92 (5 females). ABDOMEN: Without color patterns; having only short, sparse setae (setae on posterior margins of tergites barely longer than other setae). Male genitalia: Epandrium with sparse setae. Cerci narrow, long axis oriented dorsoventrally, with numerous fine setulae pointed medially. Surstyli very simple, the dorsomedial corner produced into a small lobe bearing fine setulae; no prenisetae pegs. Hypandrium small; aedeagal apodeme keel-like; paraphyses without large apical seta; gonopods well developed, with long, protruding arms that are folded close against distiphallus but pivot widely outward. Female genitalia: Oviscape acutely triangular, with narrow apex; having short, stiff setulae and three small marginal pegs preapically. Spermatheca not observed, so they are either extremely vestigial or absent.

HOLOTYPE MALE: **ECUADOR: Napo Province**, Napo River Basin, Jatun Sacha Biological Station (01°04'S, 77°36'W), among bracts and on inflorescences of the palm *Wettinia maynensis*. Holotype in AMNH.

PARATYPES: 57 males and 65 females, deposited in AMNH, Universidade Catolica (Quito), and NMNH.

ETYMOLOGY: from Ecuador, the only known locality.

Palmophila rozeni Grimaldi, new species

Fig. 3

DIAGNOSIS: Distinguished from *P. ecuadoriensis*, to which it is most similar, by the male and female genitalia. *P. rozeni* males have broader cerci; the terminal abdominal sternite sclerotized and folded between the penultimate sternite and the abdominal wall; surstyli more setulose; aedeagus shorter and broader in lateral view; hypandrium and posterolateral lobes thereof much broader; paraphyses (near center of hypandrium) more developed, with fine scales, and each with an elongate "window." Females of *P. rozeni* have oviscape valves less defined, and two pairs of membranous lobes covered in dense microtrichia.

DESCRIPTION: Mean thorax length 0.92 mm (5 males), 0.94 (5 females). Body entirely light yellow, no color patterns, even on abdominal tergites; all setae light yellowish to golden, relatively short. HEAD: Carina wide and flat, width equal to or slightly more than width of basal flagellomere. Eyes light pink, not red; with dense, very short pubescence. Ocelli light, with dark brown rim. Antennal pedicel with 2 very short, stout setae, plus numerous microtrichia. Arista 2-segmented; tiny basal segment yellow; apical segment long, pubescent, dark brown. Cheek of moderate depth (mean CD/ED = 0.31 [$N = 10$]); 1 pair of vibrissae present. Frons broad. Fronto-orbital setae short, very close together near mid-length of frons; anterior reclinate orbital seta minute, situated between ipsilateral orbitals. Postocellar setae small, 0.3× the length of ocellars. Vertical setae typical for drosophilids: inner verticals convergent, outer verticals divergent. Clypeus shallow, broad, yellow. Palps broad, yellow, with long apical seta. Labellum large, with 16 pseudotracheae per labellar lobe. THORAX: 2 pairs of dorsocentral setae, anterior pair short, length 0.5× that of posterior dorsocentrals. No prescutellar setae. Acrostichals thick, slightly flattened, in 6 rows. Scutellum with 2 pairs of setae, posterior pair longer. Pleural setae (per side): 2–3 postpronotal, 2 notopleural, 2 supraalar, 2 katepisternal. Anterior katepisternal seta 0.5× length of posterior one. Legs without long setae, spines, or spurs; tarsi with dense microtrichia. Wing hyaline (no patterns); mean lengths 1.87 mm (5 males), 1.92 (5 females); C extended to tip of M, with thick black spinules ending just before tip of R_{4+5} . Alula present; anal vein present but short. ABDOMEN: Entirely light yellow, with scattered short setae. Posterior margins of tergites without long setae, except last tergite before epandrium, with 3–4 setae per side laterally. Male with terminal sternite round, sclerotized, without setae; folded between penultimate sternite and body wall of abdomen. Male genitalia: Setae on epandrium restricted to posterolateral corners; no setae on dorsal arch. Cerci of standard drosophilid size, but ventrally with a brush of dense, short, stiff setulae. Surstyli small, lightly sclerotized, without peg-like prenisetae, having only about a dozen fine setulae. Surstyler lobes connected by extensive membranous area. Hypandrium, including posterolateral lobes, well developed. Paraphyses small, lightly sclerotized, covered with fine scales, each with an elongate "window" near center. Paraphysis without a large terminal seta. Aedeagus deep in lateral view, short, only slightly longer than aedeagal apodeme. Tip of phallus narrow, with two lateral valves. Gonopods sclerotized, with small ostiole in each, apices pointed; bases articulated to sides of distiphallus, pivoting outward but often folded and pointing posteriad. Female genitalia: Terminal tergite with sides wrapped ventrad, edges meeting beneath cerci. Oviscape with short, spicule-like setae, no pegs. Dor-

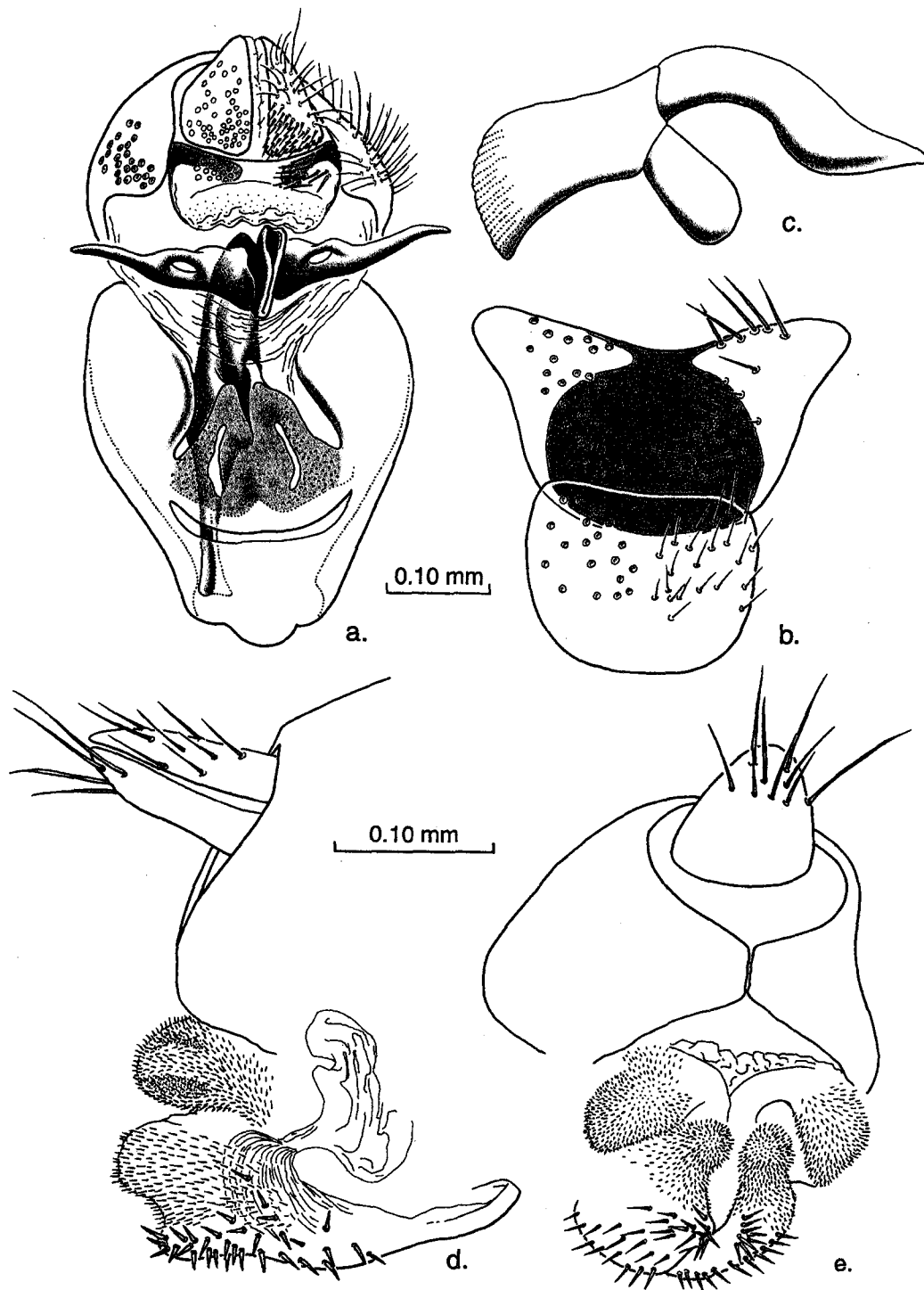


Fig. 3. Genitalia of *Palmophila rozeni*, n. sp.: a-c: Male. a, Ventral view; b, Terminal 3 sternites, showing sclerotized terminal sternite folded beneath penultimate one; c, Aedeagus and aedeagal apodeme, lateral view; d-e: Female. d, Lateral view of terminalia; e, Posterior view of terminalia.

sal edges of oviscape lobes not well differentiated from membranous dorsal lobes. Lobes covered with dense microtrichia. Oviprovector without scales, simply membranous. Spermathecal capsule either extremely minute and membranous, or completely absent.

HOLOTYPE MALE: **ECUADOR: Napo Province**, Orellana, Tiputini Biodiversity Area, near Yasuni National Park (00°37'55"S, 76°08'39"W), 220–250 m elevation, T.L. Erwin,

coll., canopy fogging, from Erwin fogging lot number 2072b1. Holotype in National Museum of Natural History.

PARATYPES: 15 males, 9 females from Erwin fogging lot numbers 2022 (1 specimen) and 2072b (10 specimens), both lots with same collecting information as holotype. Other paratypes: **ECUADOR: Orellana**, "Transect Ent 1 km Reserva Etnica W Onkone Gare 216 m", from lots 1113 (coll. 6 July 1995, 1 specimen), 1136 (coll. 9 July, 1995, 1 specimen), and 1137 (coll. 9 July 1995, 3 specimens). Paratypes in NMNH, AMNH and Universidade Catolica, Quito.

ETYMOLOGY: Patronym, for Jerome G. Rozen, Jr., senior curator in Entomology at the American Museum of Natural History.

Palmophila dentata Grimaldi, new species

Fig. 4

DIAGNOSIS: Distinguished externally from the other two species in the genus by the darker yellow color of the body, setae that are noticeably darker, and especially by the minute katapisternal setae. Distinguished on the basis of female genitalia by an oviscape having a very narrow apex; males with surstylar teeth, lack of gonopods, and a long, narrow aedeagus.

DESCRIPTION: Thorax lengths 0.92 mm (holotype male), 0.94 (paratype female). Body entirely dark yellow, without color patterns even on abdominal tergites; all setae dark copper-colored, not black nor golden. HEAD: Carina broad, flat, width equal to greatest width of basal flagellomere or slightly wider. Pedicel with two short, dark setae (plus numerous setulae). Arista with minute basal segment yellow; apical segment long, pubescent, blackish brown. Eyes light pink, not red; with dense but very short pubescence. Ocelli light, with dark brown rim. Face with 1 pair of vibrissae. Cheek relatively shallow (CD/ED = 0.22 [holotype], 0.20 [paratype]). Clypeus of moderate depth, broad. Palps yellow, broad, with an apical and subapical seta. Labellum with 16 pseudotracheae. Frons broad, with row of 6–7 minute setulae on fronto-orbital plate; 7–8 minute interfrontal setulae. Fronto-orbital setae situated near midlength of frons; anterior reclinate seta minute. Postocellar setae 0.65× length of ocellars. Inner vertical setae convergent, outer verticals divergent. Cibarial structure unknown (head not dissected). THORAX: Two pairs dorsocentrals, anterior ones 0.4× length of posteriors. Six rows short acrostichals. Scutellum with 2 pairs setae, posterior pair longer. Thoracic setae: 3 postpronotal, 2 notopleural, 2 supraalar, 2 minute katapisternals. Legs with few setae, save for apical bristle on apex of mid tibia. Tarsi with dense microtrichia. Wing: hyaline, slightly pointed; lengths 1.87 mm (holotype), 1.92 mm (paratype); C ending at apex of M; black spinules on C ending just before apex of R₄₊₅. Alula and anal vein well developed. ABDOMEN: Entirely yellow. Male genitalia: Epandrium dorsally bare, with group of approximately 20 short setae on ventral lobes. Cerci setose, but without brush of dense, stiff setulae ventrally. Surstyli well developed, with prensisetae pegs: mesal row of 9, laterally with 3, plus approximately 8 spicule-like, unsclerotized setae near apex. Hypandrium of moderate length, narrowest near middle; posterolateral lobes large. Paraphyses lobe-like, thicker apically, connected to hypandrium by very narrow strip. Aedeagus long and thin; distiphallus 1.5× width of shaft, with pair of ventral spines. Female: Oviscape without sclerotized pegs, bearing approximately 30 spicule-like setae scattered over each valve; plus approximately 15 thinner, spicule-like setae on lateral surface of apical tergite. Oviprovector without scales, entirely membranous. Spermathecal capsule either extremely minute and membranous, or completely lost.

HOLOTYPE MALE: **ECUADOR: "Orellana, Transect Ent 1 km Reserva Etnica W Onkone**

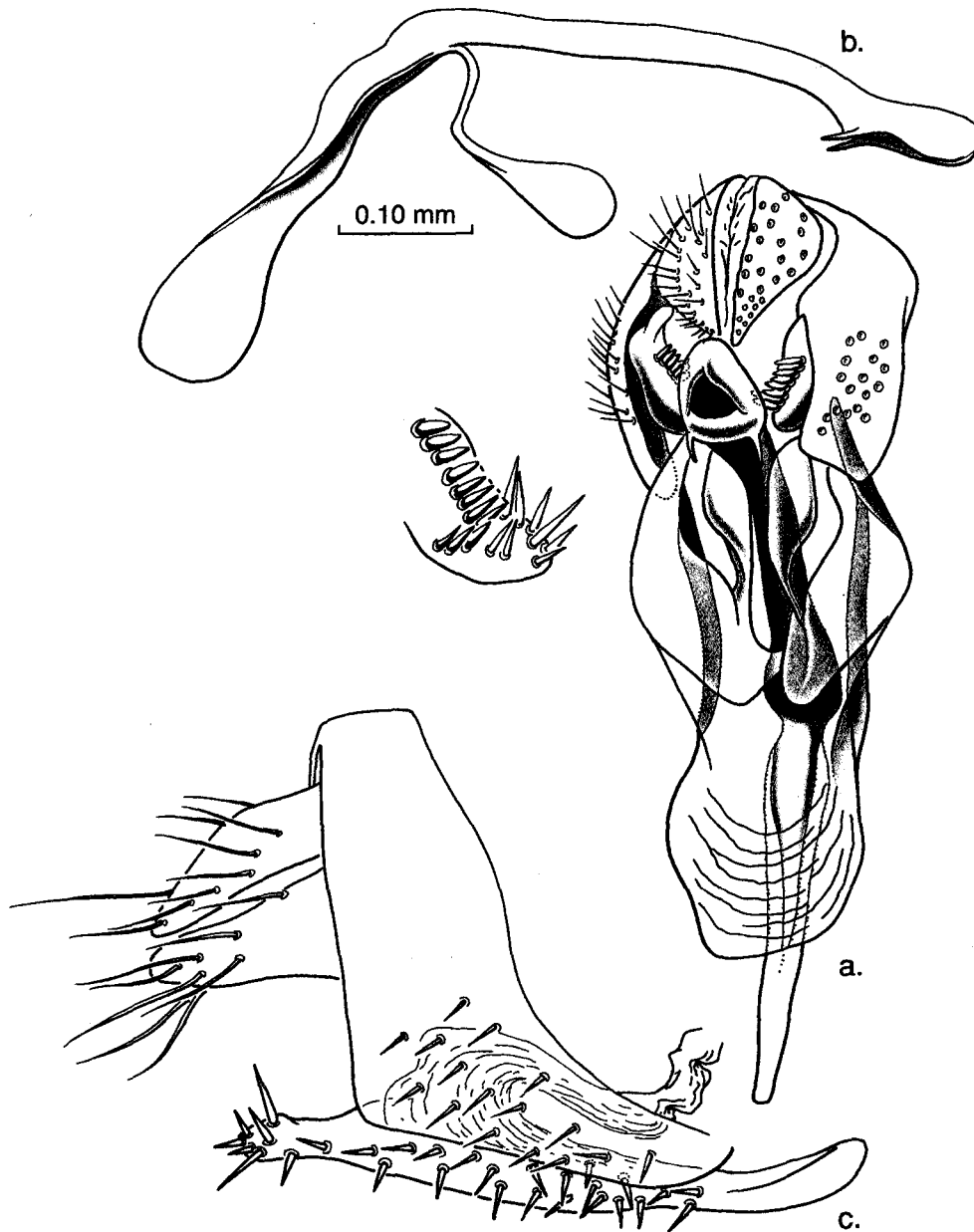


Fig. 4. Genitalia of *Palmophila dentata*, n. sp.: a-b: Male. a, Oblique ventral view; b, Aedeagus and aedeagal apodeme, lateral view, with detail of right surstylus; c, Female terminalia, lateral view.

Gare Can", 00°39'25.7"S, 76°27'10.8"W, 216 m, 6 July 1995, T.L. Erwin *et al.* (colls.). In National Museum of Natural History (NMNH). From Erwin fog sample lot number 1113.

PARATYPE: female, **ECUADOR**: from Erwin fog lot number 1086, same data as holotype except collected 2 July 1995, also in NMNH.

ETYMOLOGY: L., teeth, in reference to the prensisetae pegs on the male surstylus.

DISCUSSION: This species could arguably be included in a separate genus from the other two species of *Palmophila*, on the basis of lack of gonopods and the presence of pegs on the surstylus. On the other hand, definitive synapomorphies with the other two species include the broad carina; pubescent arista; distinctive, short body setae; a spiculate oviscape; and a spermatheca that is either extremely vestigial or absent. *Palmophila ecuadoriensis* and *rozeni* are clearly most closely related, so *P. dentata* would be a sister group to the other two.

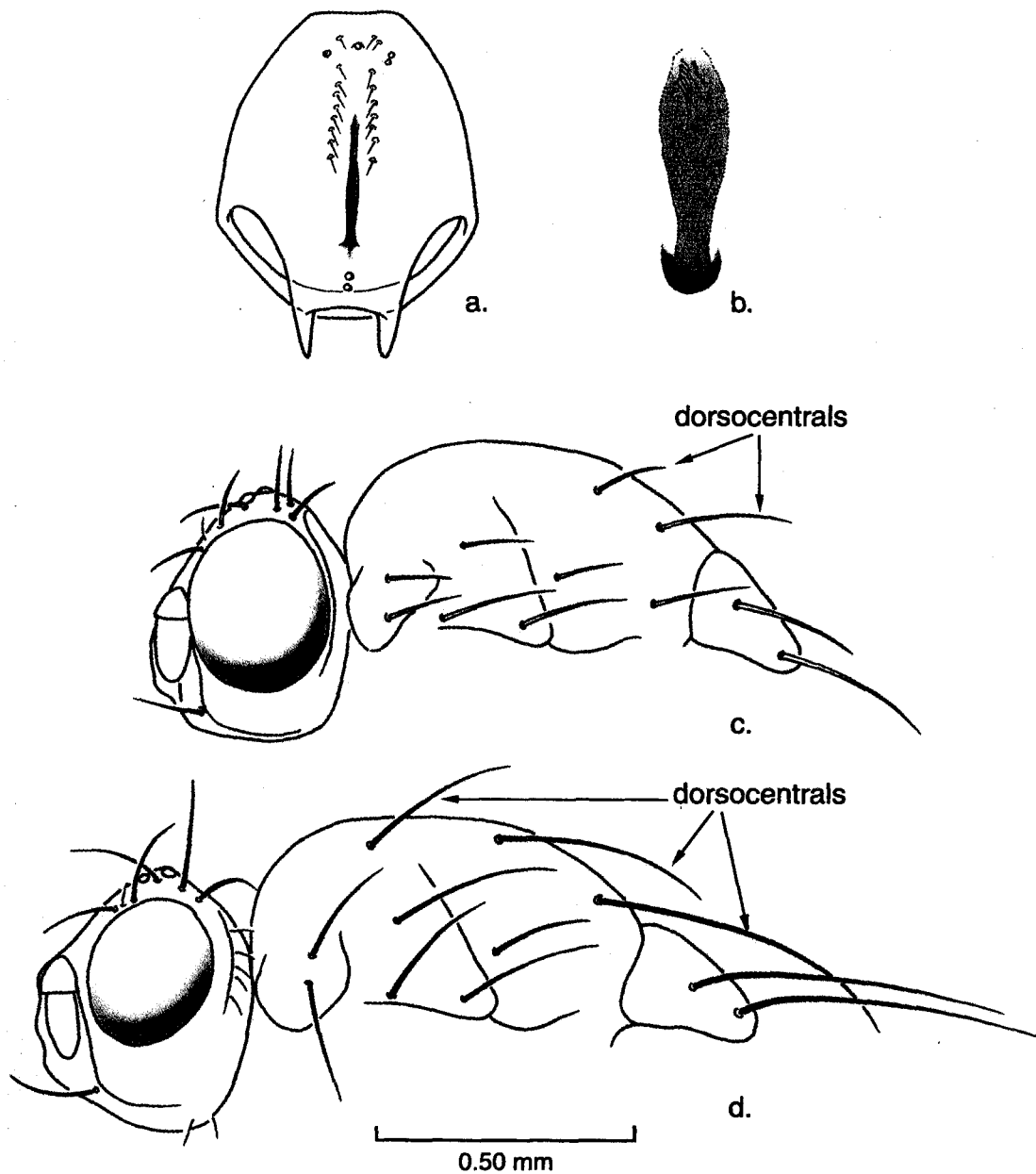


Fig. 5. Cibarial floor (a, b) and lateral view of head and thorax (c, d). a, *Palmomyia ecuadoriensis*; b, *Palmomyia incerta* (only middle part of cibarial floor shown); c, *Palmomyia rozeni*; d, *Palmomyia incerta*.

Palmomyia Grimaldi, new genus

DIAGNOSIS: Similar to *Palmophila* on the basis of a broad facial carina and an oviscape with spicule-like setae; differs from *Palmophila* by two plesiomorphic features: antenna plumose (not pubescent), and female with a pair of large, sclerotized spermathecal capsules. *Palmomyia* apomorphically differs from *Palmophila* by possessing 3 (vs. 2) pairs of dorsocentral setae, and male cerci with a large ventral lobe bearing sclerotized pegs; and all setae very long, instead of short.

TYPE SPECIES: *Palmomyia incerta*, new species. By original designation.

ETYMOLOGY: -myia (L., fly) is a standard suffix for fly names; the prefix referring to its habits.

RELATIONSHIPS: This new genus resembles basal species of *Colocasiomyia* as well as the

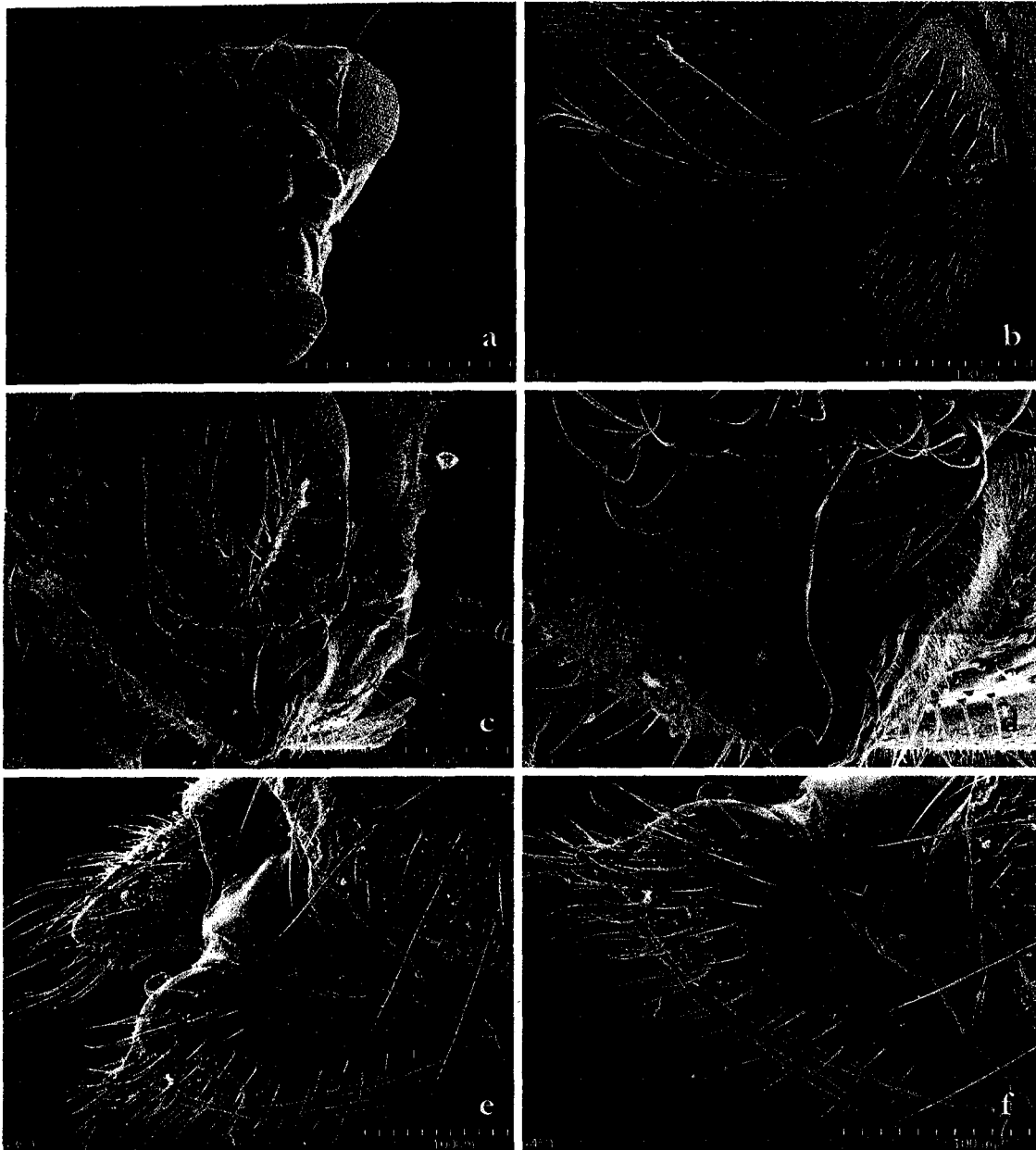


Fig. 6. Scanning electron micrographs of *Palmomyia incerta*, n. gen., n. sp.: a, Head; b, Detail of arista; c-d: Male terminalia. c, Posterior view; d, detail of ventral lobe of cercus and everted aedeagus; e-f: Female terminalia. e, Lateral view of terminalia; f, Oviscape in detail.

sympatric genus *Palmophila*, based on the broad carina and absence of oviscape pegs (only one basal species of *Colocasiomyia* possesses such pegs). Like basal species of *Colocasiomyia*, *Palmomyia* plesiomorphically retains a plumose arista, prensisetae on the surstylus, and no foretarsal teeth. Both *Palmomyia* and *Palmophila* lack the male epandrial hooks seen in basal species of *Colocasiomyia*. Lastly, *Palmomyia* is unique among the genera by the females possessing a pair of large, elongate, heavily sclerotized spermathecal capsules.

Palmomyia incerta Grimaldi, new species

Figs. 6, 7

DIAGNOSIS: As for genus.

DESCRIPTION: Mean thorax length = 1.04 mm (4 males); 1.03 mm (4 females). Coloration



Fig. 7. Genitalia of *Palmomyia incerta*: a-b: Male. a, Entire terminalia, posterior view; b, Entire terminalia, lateral view; c-e: Female. c, Tip of oviscape, lateral view; d, Entire oviscape, ventral view; e, Spermatheca (to same scale as c and d).

and vestiture: Body entirely light yellow, even on abdominal tergites. Setae long, slender, blackish, contrasting with light body color. HEAD: Frons of standard width among drosophilines; eyes pink (not red), with dense but very short interfacetal setulae. Ocellar triangle dark brown. Frontal-orbital setae in posterior half of frons; proclinate $0.7\times$ length

of posterior reclinate, close together; anterior reclinate minute, barely distinguishable from row of fronto-orbital setulae on fronto-orbital plate. Ocellar setae well developed, bases located within ocellar triangle. Inner vertical setae directed strongly inward, outer verticals strongly divergent. Facial carina well developed, flat, width approximately equal to width of basal flagellomere. Antennal pedicel with 2 longer setae typical of drosophilines; flagellomere 1 light brown (not yellow), unmodified; arista with 2 segments, basal one minute, apical one plumose with 3 dorsal branches and 1–2 ventral branches. One pair of vibrissae present. Cheeks deep, mean CD/ED = 0.50 (10 males + females). Each labellar lobe with 12 pseudotracheae. Floor of cibarium having following arrangement of sensilla (described for one side): anterior end with row of 6 moderately long sensilla trichodea, then pair of campaniform sensilla, then row of 4 sensilla trichodea, and finally a sclerotized, granulose bulb at posterior end. THORAX: Chaetotaxy distinctive, with 3 pairs (not 2) of dorsocentrals, anterior pair shortest, posterior pair longest. No prescutellar setae; 4 rows of acrostichal setulae, 2 postpronotal, 3 notopleural, 2 supra-alar setae, 1 long katapisternal. Legs: long, slender, entirely yellow. Foreleg with femur having two dorsal rows of setae, 1 row with short setae, other with setae twice the length of others, ventrally with two long setae (at base and apex). All tibiae and tarsi with dense microtrichia. Wing hyaline (no patterns), mean lengths 2.66 mm (3 males), 2.75 mm (3 females). Vein C ends at apex of M. ABDOMEN: Entirely yellow (no tergal patterns), setae on dorsal margins distinctively longer than others. Male genitalia (as based on illustrated specimens, males 13, 14): Epandrium narrow in posterior view, bare save for brush of 10 long setae at apex of pendulous ventral lobe. Cerci very highly modified: long and narrow, with pendulous ventral process that is flared at apex and bears row of 4–6 sclerotized pegs on margin. Surstylus with a long, narrow arm; apex flared; a row of 5–6 peg prenisetae on margin and row of 6 setae laterad. Sursyli virtually detached from epandrium. Hypandrium short, U-shaped, paraphysis with stout apical seta. Aedeagal apodeme keel-shaped, but short; aedeagus arched in lateral view, thick, with dorsoapical process and apicolateral flanges. Female genitalia: deep in lateral view, with abruptly narrowed tip bearing 4 sharp, stiff setae; no marginal pegs, but fine setae scattered over distal half of oviscape. Spermathecal capsule sclerotized, large and tubular, length approximately 0.5× that of oviscape, with very deep introvert.

HOLOTYPE MALE: **COLOMBIA: Chocó**, Sampichi, 4 April 1994, on female inflorescences of *Phytelephas seemanii*, in AMNH.

PARATYPES: **ECUADOR: Napo Province**, Baeza, 26 February, 1994, on male phase of *Geonoma undata* (1 male fly), male inflorescences of *Chamaedorea linearis* (9 males, 5 females), coll. F. Ervik; Jatun Sacha Biological Station, 27 February 1994, on male inflorescence of *C. linearis* (1 female fly), coll. F. Ervik. **COLOMBIA: Chocó**, Sampichi, 4 April 1994, on female inflorescences of *Phytelephas seemanii* (2 males, 4 females), coll. R. Bernal and F. Ervik. Paratypes in AMNH and Universidade Catolica (Quito).

ETYMOLOGY: in reference to its somewhat ambiguous phylogenetic position, a result of an unusual combination of features.

Acknowledgments

We are grateful to the following individuals for their assistance: Tam Nguyen (AMNH) for the scanning electron micrographs; Steve Thurston (AMNH) for rendering the inked drawings in Adobe PhotoShop; Craig Gibbs (AMNH) for assistance in preparation and sorting of canopy flies; Wayne Mathis and George Byers for reviewing the manuscript; and Molly Rightmyer, for offering the opportunity to contribute to this Festschrift.

Literature Cited

- Asmussen, C. B., W. J. Baker, and J. Dransfield. 2000. Phylogeny of the palm family (Arecaceae) based on rps16 intron and trnL-trnF plastid DNA sequences, pp. 525–536 *In* K. L. Wilson and D. A. Morrison (eds.), *Monocots: Systematics and Evolution*. CSIRO; Melbourne.
- Bernal, R., and F. Ervik. 1996. Floral biology and pollination of the dioecious palm *Phytelephas seemanii* in Colombia: an adaptation to staphylinid beetles. *Biotropica* 28:682–696.
- Bøgh, A. 1996. The reproductive phenology and pollination biology of four *Calamus* (Arecaceae) species in Thailand. *Principes* 40:5–15.
- Borchsenius, F. 1993. Flowering biology and insect visitation of three Ecuadorean *Aiphanes* species. *Principes* 37:139–150.
- Bremer, K. 2000. Early Cretaceous lineages of monocot flowering plants. *Proceedings of the National Academy of Sciences, USA* 97:4707–4711.
- Brcic, D. 1983. Ecology of flower-breeding *Drosophila*. *In* M. Ashburner, H. L. Carson, and J. N. Thompson (eds.), *The Genetics and Biology of Drosophila*, vol. 3d., pp. 333–382. Academic Press; New York/London.
- Bullock, S. H. 1981. Notes on the phenology of inflorescences and pollination of some rain forest palms in Costa Rica. *Principes* 25:101–105.
- Carson, H. L., and T. Okada. 1980. Drosophilidae associated with flowers in Papua New Guinea I. *Colocasia esculenta*. *Kontyû* 48:15–29.
- Ervik, F. 1993. Notes on the phenology and pollination of the dioecious palms *Mauritia flexuosa* (Calamoideae) and *Aphandra natalia* (Phytelephantoideae) in Ecuador, pp. 7–12 *In* W. Barthlott, C. M. Naumann, K. Schmidt-Loske, and K.-L. Schuchmann (eds.), *Animal-Plant Interactions in Tropical Environments*. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Ervik, F., and A. Barfod. 1999. Thermogenesis in palm inflorescences and its ecological significance. *Acta Botanica Venezuelana* 22:195–212.
- Ervik, F., and R. Bernal. 1996. Floral biology and insect visitation of the monoecious palm *Prestoea decurrens* on the Pacific coast of Colombia. *Principes* 40:86–92.
- Ervik, F., and J. P. Feil. 1997. Reproductive biology of the monoecious understory palm *Prestoea schultzeana* in Amazonian Ecuador. *Biotropica* 29:309–317.
- Ervik, F., L. Tollsten, and J. T. Knudsen. 1999. Floral scent chemistry and pollination ecology in phytelephantoid palms (Arecaceae). *Plant Systematics and Evolution* 217:279–297.
- Erwin, T. L. 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (eds.), *The Tropical Rain Forest: Ecology and Management*, pp. 59–75. Blackwell Scientific Publications; Oxford.
- Essig, F. B. 1973. Pollination in some New Guinea palms. *Principes* 17:75–83.
- Faegri, K., and L. van der Pijl. 1979. *The Principles of Pollination Ecology*, third edition. Pergamon Press; Oxford.
- Grimaldi, D. 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bulletin of the American Museum of Natural History* 197:139 pp.
- Grimaldi, D. 1992. Systematics of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae): cladistics, a new generic synonym, new records, and a new species from Nepal. *Entomologica scandinavica* 22:417–426.
- Grimaldi, D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* 86:373–406.
- Hahn, W. J. 2002. A molecular phylogenetic study of the Palmae (Arecaceae) based on atpB, rbcL, and 18S nrDNA sequences. *Systematic Biology* 51:92–112.
- Henderson, A. 1986. A review of pollination studies in the Palmae. *The Botanical Review* 52:221–259.
- Hu, Y.-G., and M. J. Toda. 2001. Polyphyly of *Lordiphosa* and its relationships in Drosophilinae (Diptera: Drosophilidae). *Systematic Entomology* 26:15–31.
- Knudsen, J. T., L. Tollsten, and F. Ervik. 2001. Flower scent and pollination in selected neotropical palms. *Plant Biology* 3:642–653.
- Listabarth, Ch. 1993. Pollination in *Geonoma macrostachys* and three congeners, *G. acaulis*, *G. gracilis*, and *G. interrupta*. *Botanica Acta* 106:496–506.
- Martén, S., and M. Quesada. 2001. Phenology, sexual expression, and reproductive success of the rare Neotropical palm, *Geonoma epetiolata*. *Biotropica* 33:596–605.
- Meeuse, B. J. D. 1975. Thermogenic respiration in aroids. *Annual Review of Plant Physiology* 26:117–126.
- Okada, T., and H. L. Carson. 1980. Drosophilidae associated with flowers in Papua New Guinea. II. *Alocasia* (Araceae). *Pacific Insects* 22:217–236.

- Olesen, J. M., and H. Balslev. 1990. Flower biology and pollinators of the Amazonian monoecious palm, *Geonoma macrostachys*: a case of Bakerian mimicry. *Principes* 34:181–190.
- Proctor, M., P. Yeo, and A. Lack. 1996. *The Natural History of Pollination*. Timber Press; Portland, Oregon; 479 pp.
- Toda, M. J., and T. Okada. 1983. Ecological studies of floricolous *Drosophilella* in Burma with descriptions of three new species from Burma and the Philippines (Diptera, Drosophilidae). *Kontyû* 51:169–184.
- Wheeler, M. R., and H. Takada. 1964. Diptera: Drosophilidae. Pp. 163–242 *In* *Insects of Micronesia*, vol. 14, number 6. Bernice Bishop Museum; Honolulu.