A new genus of Lygistorrhinidae from Vietnam (Diptera: Sciaroidea), and phylogenetic relationships in the family

[Eine neue Gattung der Lygistorrhinidae aus Vietnam (Diptera: Sciaroidea) nebst Aussagen zu den Verwandschaftsbeziehungen innerhalb der Familie]

by
David GRIMALDI and Vladimir BLAGODEROV

New York (U.S.A.)

Abstract The Lygistorrhinidae comprises a monophyletic, cosmopolitan family of 21 described species of fungus gnats occurring in tropical and warm temperate forests. A **new genus**, ***Loyugesa***, is described and illustrated, based on a new species from Vietnam, ***Loyugesa khuati* spec. nov.** A phylogenetic analysis of 33 morphological characters indicates that *Loyugesa* is an unambiguous sister group to the African genus *Seguyola* MATILE. The analysis also found that *Palaeognoriste* in Eocene Baltic amber is the sister group to all other (living) lygistorrhinids. Various features of *Palaeognoriste* are redescribed in detail. "*Lygistorrhina*" *asiatica* SENIOR-WHITE is the most primitive living species, and should be placed in its own genus pending possible discovery of apomorphic features. *Probolaeus* WILLISTON, classified by some as the New World sister genus to the Old World *Lygistorrhina*, is actually a clade within *Lygistorrhina* and is treated as a subgenus here and according to several prior taxonomic treatments. As such, *L.* (*P.*) *edwardsi* LANE, 1947 is a senior subjective homonym of *L. edwardsi* MATILE, 1990, and the latter is renamed as ***Lygistorrhina edwardsina* nom. nov.** An identification key to the genera is provided.

Key words *Loyugesa* gen. nov., Vietnam, Lygistorrhinidae, phylogeny, Baltic amber

Zusammenfassung Die Lygistorrhinidae sind eine monophyletische Familie mit kosmopolitischer Verbreitung. Insgesamt 21 Arten dieser Pilzmücken sind aus tropischen Wäldern und jenen der warm-temperierten Klimazone bekannt. Auf Basis der neuen Art ***Loyugesa khuati* spec. nov.** wird ***Loyugesa* gen. nov.** aus Vietnam beschrieben und abgebildet. Eine phylogenetische Analyse von 33 morphologischen Merkmalen erbringt den unzweifelhaften Nachweis, daß *Loyugesa* die Schwestergruppe der afrikanischen Gattung *Seguyola* MATILE ist. Ebenfalls wird nachgewiesen, daß *Palaeognoriste* aus dem eozänen Baltischen Bernstein die Schwestergruppe zu allen anderen (rezenten) Lygistorrhiniden bildet. Verschiedene Eigentümlichkeiten von *Palaeognoriste* werden detailliert beschrieben. „*Lygistorrhina*" *asiatica* SENIOR-WHITE ist die ursprünglichste der rezenten Arten und sollte möglicherweise nach dem Auffinden apomorpher Merkmale in ein eigenes Genus gestellt werden. Die auf die Neue Welt beschränkte Gattung *Probolaeus* WILLISTON wird von einigen Autoren als Schwestergruppe der in der Alten Welt verbreiteten Gattung *Lygistorrhina* angesehen. Erstgenanntes Taxon ist ein Verwandschaftszweig innerhalb von *Lygistorrhina* und wird hier im Einklang mit früheren taxonomischen Auffassungen als Subgenus angesehen. Daraus folgt, daß *L.* (*P.*) *edwardsi* LANE, 1947 ein älteres subjektives Homonym von *L. edwardsi* MATILE, 1990 ist und letztere Art wird deshalb als ***Lygistorrhina edwardsina* nom. nov.** benannt. Ein Bestimmungsschlüssel der Gattungen der Lygistorrhinidae wird gegeben.

Stichwörter *Loyugesa* gen. nov., Vietnam, Lygistorrhinidae, Phylogeny, Baltischer Bernstein

Introduction

The Lygistorrhinidae are one of the most morphologically distinctive and unquestionably monophyletic groups in the Sciaroidea, also referred to as the subfamily Lygistorrhininae of the family Mycetophilidae *sensu lato*. Wing venation is unique, by lack of the stem of the medial vein and even the base of the fork of M_1–M_2, as well as the base of vein CuA_1. At a

quick glance, then, the wing of lygistorrhinids has 3 incomplete, stemless longitudinal veins. With exception of one genus (*Seguyola*), they possess a fine, elongate proboscis, also unusual among the Sciaroidea but found in *Aphrastomyia*, *Gnoriste*, *Rhynchoheterotricha* (Mycetophilidae), several keroplatid genera, and *Eugnoriste* (Sciaridae). Mouthpart elements of these genera, however, are differentially modified, reflecting convergence. There are other synapomorphies of the lygistorrhinids, given below. Great modification of the wing venation, proboscis, and simplified genitalic morphology, has obscured relationships of the Lygistorrhinidae among the mycetophiloids. Indeed, controversy over the position of the family is still largely unsettled (TUOMIKOSKI 1966, THOMPSON 1975, MATILE 1990).

The Lygistorrhinidae is a cosmopolitan group, but represented in museum collections by relatively few specimens. Indeed, our collecting in Neotropical forests has revealed that species of *Probolaeus* are only occasionally found, but when present they are sometimes found in considerable series. Sampling for the midges is quite inconsistent, probably because the adult habits are largely unknown and the larval life history completely unknown. The function of the elongate proboscis, for example, is presumably for feeding from flowers, and for which anecdotal evidence exists. HENNIG (1966) originally considered the distribution of the Lygistorrhinidae and discussed that the distribution is either highly disjunct and relict, or the distribution is largely unknown. Based on material we have been studying and that is presented here, it is clearly the latter.

The family presently consists of four recognized genera and 20 living species, from tropical, subtropical and warm temperate regions of Africa, Asia, North America, and Central and South America (including the Caribbean) (EDWARDS 1912, 1932; ENDERLEIN 1910, LANE 1947, 1958; MATILE 1979, 1990a; OKADA 1937, SKUSE 1990, SENIOR-WHITE 1922, THOMPSON 1975, WILLISTON 1896). Two species are described from Eocene Baltic amber, in the genus *Paleognoriste* (MEUNIER 1904, 1912). It has been intimated (e. g., TUOMIKOSKI 1966) that the Sri Lankan species *Lygistorrhina asiatica* is actually a *Palaeognoriste*, which we have addressed below.

In 1998 one of us collected in Vietnam a series of interesting specimens representing a new species and genus of lygistorrhinid. In an attempt to understand the relationships of this new species, it was necessary to assess the monophyly of the genera of Lygistorrhinidae and examine their relationships. We have not included in the phylogenetic study a new genus (with 2 species) of primitive lygistorrhinids in Cretaceous amber from Canada and Siberia, since these are being treated in a larger work on fossil Sciaroidea (BLAGODEROV & GRIMALDI, in prep.). Suffice it to say, though, that the Cretaceous genus is plesiomorphic to the extant genera, and the extant genera represent a monophyletic group. We are also aware of numerous undescribed species of *Probolaeus* from the neotropics, and work on them is in progress. The purpose of this paper is simply to assess genera and their relationships. We take this opportunity to also briefly diagnose each genus and provide a key to genera and a catalogue of all described species.

Methods, materials

Specimens were borrowed or used from:

AMNH - American Museum of Natural History, New York (Division of Invertebrates)
CNC - Canadian National Collection of Insects, Ottawa (Agriculture Canada), loaned by Dr Richard VOCKEROTH
MNHP - Muséé national d'histoire Naturelle, Paris, loaned courtesy of Prof Loïc MATILE (†)
NHM - Natural History Museum, London (Entomology and Palaeontology), loans by Mr. John CHAINEY (Entomology) and Dr Andrew ROSS (Palaeontology)

NMNH - U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C., loaned by Dr Wayne MATHIS and Ms. Holly WILLIAMS

Specimens of the new genus were collected in a Malaise trap and by sweeping understory vegetation in slightly disturbed tropical forest near the village of Huong Son (Ha Tinh province, Truong Son mountain range), close to the Rao (River) An, at an altitude of approximately 350 m. The forest was primarily a tropical moist evergreen forest, with an ecotone of understory and emergent *Arenga* and *Liristona* (Palmae), *Cycas chevalieri* (Cycadaceae), Melostomaceae and some *Lithocarpus* (Fagaceae). The Malaise trap that captured most specimens was suspended about 5 meters above the ground on the narrow saddle of a ridge that faced northwest. Specimens were preserved in 70 % ethanol in the trap heads, and subsequently in vials, then critical point dried in New York.

Structures were surveyed by examining original specimens, including types and specimens authoritatively identified to species. 19 species were surveyed, including an undescribed species of *Probolaeus* from Costa Rica, which appears fairly typical of a complex of new species in this genus from the neotropics. Coding of *Paleognoriste* spec. – an extinct taxon in Eocene Baltic amber – was based on original observations of a pair of specimens in copula in the NHM collections (In. Paleo. 17705, identified as *P. sciariforme*, but see notes under that genus, below) and a newly discovered male specimen (AMNH B-JH8) (Fig. 2). Only two described species of the family were not studied here, which were *Lygistorrhina cincitcornis* EDWARDS and *L. cerqueirai* LANE.

Observations and drawings were generally done with a Leitz Wetzlar stereomicroscope (up to 144×) and a Zeiss compound microscope (up to 400×), each with camera lucidas. The weakly sclerotized frons and face of lygistorrhinids necessitates extremely careful observations of the head (e.g., presence of median ocellus, holoptic eyes, etc.), so dissections of specimens for which series exist allowed definitive observation of obscure structures. Specimens that were preserved in ethanol (50-80 %), then critical-point dried, were far superior for study than ones that were simply air dried. Critical-point drying keeps these fragile insects distended. To properly study the minute veins at the base of the wing necessitates slide mounting. Phylogenetic analysis used the program Winnona (GOLOBOFF 1999). Winclada (NIXON 2000) was used to edit and submit the matrix for analysis, analyze character distributions and visualize and print trees. Character states were polarized by outgroup comparison to ground plans of the Ditomyiidae, Keroplatidae, Manotidae, and Mycetophilidae.

Phylogenetic relationships

The apomorphic condition is listed first, the plesiomorphic condition second (in parentheses).

1. Proboscis long, ≥ 4× head height/length (vs. 2.5× or less) (Fig. 3).
2. Proboscis vestigial (vs. well developed, protrudent). Autapomorphic to *Seguyola*.
3. Palps nearly equal to length of labella (vs. 0.6× or less labella length) (Fig. 3).
4. Male eyes holoptic (vs. dichoptic, with frons never more narrow than width of outer margins of antennal bases) (Fig. 3). The membranous frons can obscure this character, since collapse of the head in this area draws the inner margins of the eyes together making them appear to be holoptic. Best seen in fresh or alcohol-preserved specimens. It is unknown if this is a sexually dimorphic character for *Loyugesa*, since only males are known.
5. Male eyes with dorso-ventral differentiation of facets, dorsal facets approximately 2× diameter of ventral ones (vs. no differentiation). Autapomorphic to *Seguyola*.
6. Antenna with 12 flagellomeres (vs. 14).

7. Antenna short, length less than height of head (vs. ≥ 1.2 × head height) (Fig. 3).
8. Flagellomeres moniliform (vs. rectangular shape in lateral view, with length greater than width) (Fig. 3).
9. Median ocellus lost (vs. present, albeit sometimes very small and obscured because this area is sunken) (Fig. 3).
10. Antenna with several middle and apical flagellomeres cream-colored, the remaining ones dark (vs. all flagellomeres dark, although *P. brasiliensis* has a yellowish base of the flagellum).
11. Vein Sc incomplete (vs. complete) (Fig. 6). A complete Sc is clearly plesiomorphic in *Paleognoriste*, but has apparently re-appeared in *Probolaeus barettoi*, *P. edwardsi*, and *Lygistorrhina carayoni*.
12. Basal fork of M_1 – M_2 completely lost (vs. present, albeit faint and diffuse) (Fig. 5).
13. CuA_1 and CuA_2 not connected in a distal fork (vs. connected/sessile) (cf. Figs 1, 5). While polarity of this character was based on widespread presence in the Mycetophiloidea of a CuA_1-CuA_2 fork, as well as presence in a very primitive genus of Cretaceous lygistorrhinid, it is most parsimoniously interpreted as a reversal (apomorphic fork).
14. Vein Rs highly reduced to lost, with no small br cell (vs. Rs present as a definite vein) (Fig. 6).
15. Great reduction/loss of anal cell (vs. present, although small) (Fig. 6).
16. Wing maculation: apical ¼ of wing dark (vs. completely hyaline).
17. Wing maculation: dark area/band over bases of M_1 and M_2 (vs. hyaline in this area).
18. Wing maculation: dark area over apex of CuA_2 (vs. hyaline in this area).
19. Costal swelling at apex of R_1 (vs. no swelling).
20. Costal edge darkly infuscate, with 2 clear "windows" in this area (vs. without such infuscation or windows).
21. Tip of wing broadly rounded (vs. apex more acute) (Fig. 1).
22. Mid tibia with 1 apical spur (vs. 2).
23. Apical half of hind tibia and entire hind basitarsus inflated (vs. slightly and gradually expanded distad, but not dramatically so) (Fig. 1).
24. Scutum dome-shaped (vs. flatter dorsally) (Figs 1, 4).
25. Laterotergite expanded outward, pendulous, almost flap-like, with a fringe of long setae on lateral edge (vs. laterotergite swollen, but not protruding, with at best several scattered setae) (Fig. 4).
26. Anterior edge of notum, including anteprontum, well anterior to fore coxa in lateral view (vs. just above fore coxa, or barely anteriad) (Fig. 4).
27. Concavity on proximal half of lateral surface of hind coxa (vs. smooth on this surface, not concave) (Fig. 4).
28. Metanepisternum extended dorsally beyond ventral margin of laterotergite (vs. not reaching ventral margin of laterotergite) (Fig. 4).
29. Tergite IX (G) without [loss] of dense tuft of short, stiff, spicule-like setulae on apex (vs. only fine, scattered setulae in this area) (Fig. 7).
30. Tergite IX (G) without anterior ramus/apodeme (vs. with). This structure could not be surveyed for *Paleognoriste* because of inadequate material (EE or fossils) (Fig. 7).
31. Gonostyli stout, W:L ratio = 2.2-2.4 (vs. 3.5-5.0) (Fig. 7).
32. Fore tibia without an apical spur (vs. 1 spur present). Autapomorphic to new genus (Fig. 1).
33. Laterotergite bare (vs. with scattered setae or a row of them on edge). Autapomorphic to new genus (Fig. 4).
34. Scutum with 3 rows of setulae: an incomplete median row, and 2 virtually complete paramedian rows (vs. scattered setulae). Autapomorphic to new genus.

Results of phylogenetic analysis

Analysis of 34 morphological characters of the adult using NONA used a search involving 100 replications of the bisection-reconnection method of branch swapping. This resulted in 13 trees with length 38 steps, CI=86, and RI=90. A consensus tree (Fig. 8) collapses 4

Table 1: Matrix of synapomorphies for Lygistorrhinidae

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Lygistorrhina carayoni	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. hamoni	1	0	1	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. insignis	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. legrandi	1	0	1	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. magna	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. nasreddinei	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. pictipennis	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
L. (Probolaeus) barettoi	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
L. (P.) brasiliensis	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
L. (P.) coxata	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
L. (P.) edwardsi	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
L. (P.) st-catherinae	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
L. (P.) urieki	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
L. (P.) spec. (Costa Rica)	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
Seguyola variegata	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0
S. vicina	0	1	0	?	?	?	?	?	?	0	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0
Loyugesa khuati	0	0	0	1	0	1	1	1	1	0	1	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	1	1
Paleognoriste spec.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
"Lygistorrhina" asiatica	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0

nodes, the result being a slightly longer tree with slightly less character consistency (L=40, CI=82, RI=87). The homoplasious characters were 15 (appearing twice within *Lygistorrhina*), 22 (appearing three times: once in *Seguyola* + gen. nov., and twice in *Lygistorrhina*), and 26 (appearing twice, in basal node of *Lygistorrhina* and of *Seguyola*). Monophyly of *Seguyola* and the new genus is unambiguous, as is monophyly of *Lygistorrhina* sensu lato. While *Probolaeus* is a monophyletic clade restricted to the western hemisphere, it is clearly embedded within *Lygistorrhina*. Imposing a sister-group relationship to *Lygistorrhina* and *Probolaeus* would require an additional 6 steps (15 % of the total length) – a highly unparsimonious hypothesis. Relationships among species of *Lygistorrhina* s.l. were largely unresolved, although the present study did not focus on a search for characters to resolve relationships in this genus. This should ideally be done in a revision of the genus, presently underway. *Lygistorrhina asiatica* is the most primitive living species, unfortunately not distinguished by any autapomorphies, although this could be due to inadequate study of the one available female specimen. It clearly does not belong in *Lygistorrhina* which is why we do not include it under taxonomy section. *Palaeognoriste* is unambiguously the sister group to all living lygistorrhinids, but no characters likewise were found that define its monophyly.

Taxonomy and classification

Family LYGISTORRHINIDAE

Type genus: *Lygistorrhina* SKUSE, 1890: 598. Type Species: *L. insignis* SKUSE, by monotypy.

Diagnosis: Apomorphic characters of the family include the following: Proboscis long, ≥1.5 × head height, up to 5 × head height/length (highly reduced in *Seguyola*); the 5 elongate mouthpart elements of the proboscis are the labella, palps, and hypopharynx. Eyes large, occupying nearly entire head in lateral view. Median ocellus small, ≤0.5 × diameter of

lateral ones, or lost. Frons generally weak to completely membranous, always sunken in air-dried specimens; face largely membranous. Wing with base of vein M lost; veins R_3 and R_4 lost; base of R_{4+5} weak to barely present; anal veins vestigial. Apical portion of hind tibia, and basitarsomeres, slightly to distinctively swollen. Male genitalia simple, gonostylus with apical tooth or pair of teeth (these lost in *Loyugesa* gen. nov.).

Genus *Lygistorrhina* SKUSE

Lygistorrhina SKUSE, 1890: 598. Type species: *L. insignis* SKUSE, 1890: 600)
Probolaeus WILLISTON, 1896: 261. Type species: *P. singularis* WILLISTON, 1896: 261 (by monotypy).
Aphanizophleps ENDERLEIN, 1910: 203. Type species: *A. coxatus* ENDERLEIN, 1911: 203 (by monotypy).

Diagnosis: Proboscis ≥4× length of head, including palps; vein Sc incomplete (except in *L. magna,* and an undescribed species from Costa Rica); basal portion of fork of M_1–M_2 lost; CuA_1 and CuA_2 not connected in distal fork; laterotergite expanded outward, flap-like, with fringe of long setae on edge; and several features of male genitalia (see phylogeny, above). Subgenus *Probolaeus* is defined by the presence of only one apical spur on the mid tibia (vs. two).

Species

***Lygistorrhina* s. str.:** *L. insignis* SKUSE, 1890 (Australia); *L. cincticornis* EDWARDS, 1926 (Borneo); *L. pictipennis* OKADA, 1937 (Japan); *L. nassreddinei* MATILE, 1979 (Grand Comore); *L. carayoni* MATILE, 1986 (New Caledonia); *L. edwardsina* **nom. nov.** for *edwardsi* MATILE, 1990b: 366 (Africa [eastern]); *L. legrandi* MATILE, 1990b (Africa [Gabon, Congo]); *L. magna* MATILE, 1990 (Africa [Congo]); *L. hamoni* MATILE, 1996 (Africa [Ivory Coast]).
Subgenus *Probolaeus* (all New World): *L. singularis* (WILLISTON, 1896)(St. Vincent, BWI); *L. coxatus* (ENDERLEIN, 1910) (Brazil); *L. urichi* EDWARDS, 1912 (Trinidad, Brazil); *L. brasiliensis* EDWARDS, 1932 (Brazil); *L. barretoi* LANE, 1947 (Brazil), *L. edwardsi* LANE, 1947 (Brazil); *L. cerqueirai* LANE, 1958 (Brazil), *L. sanctaecatherinae* THOMPSON, 1975 (south-eastern U.S.).

Comments: Recognition of *Probolaeus* as a genus separate from *Lygistorrhina* (e.g., Papavero, 1977; Matile, 1990a,b) would render the latter paraphyletic. The only feature distinguishing *Lygistorrhina* is a pair of spurs on the apex of the mid tibia, which is plesiomorphic. Thus, *Probolaeus* – which appears to be monophyletic on the basis of a single pair of mid tibial spurs – should be referred to at best as a subgenus of *Lygistorrhina*, as previously indicated (EDWARDS 1912, THOMPSON 1975).

Genus *Loyugesa* gen. nov.

Diagnosis: Very closely related to *Seguyola* by the holoptic eyes in males; flagellomeres reduced from 14 to 12, moniliform; median ocellus lost; broadly rounded wing tip; mid tibia with only I apical spur; scutum dome-shaped; apical half of hind tibia and entire hind basitarsus inflated; G tIX without a tuft of spicule-like setae at apex (spicules are sparse); gonostyli stout (W:L = 2.2-2.4). Plesiomorphic with respect to *Seguyola* by having all eye facets equal in size; the wings without maculation; possession of a proboscis (albeit small, only slightly longer than length of head), and several other features. Autapomorphically uniform greyish-brown over entire body, without banding patterns on legs or tergites; scutum with setulae in 3 rows, not scattered; fore tibia without an apical spur; and laterotergite bare.

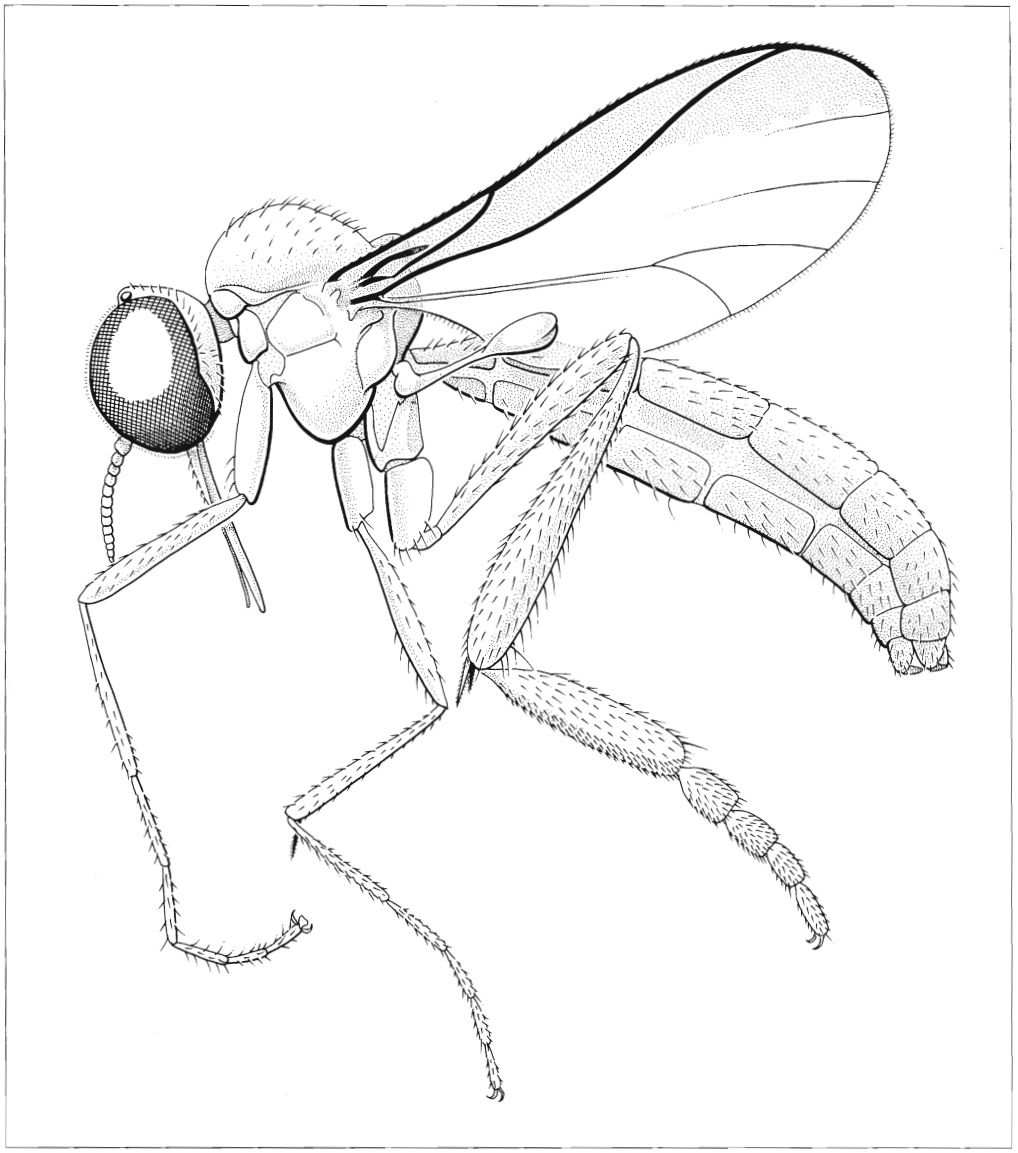


Fig. 1: Habitus of *Loyugesa khuati* gen. nov, spec. nov. Approximate length of fly is 2.2 mm.

Type Species: *L. khuati* spec. nov. Known only from central Vietnam.

Etymology: Anagram of *Seguyola*, sister group to the new genus, to be treated in gender as female.

Comments: Although there are several apomorphies of *Loyugesa* with respect to *Seguyola*, the latter genus is phenetically/autapomorphically more modified. Their close relationship and disjunct distribution in central Africa and southeast Asia indicates that additional species within this group should be expected in intervening areas, such as India and Madagascar.

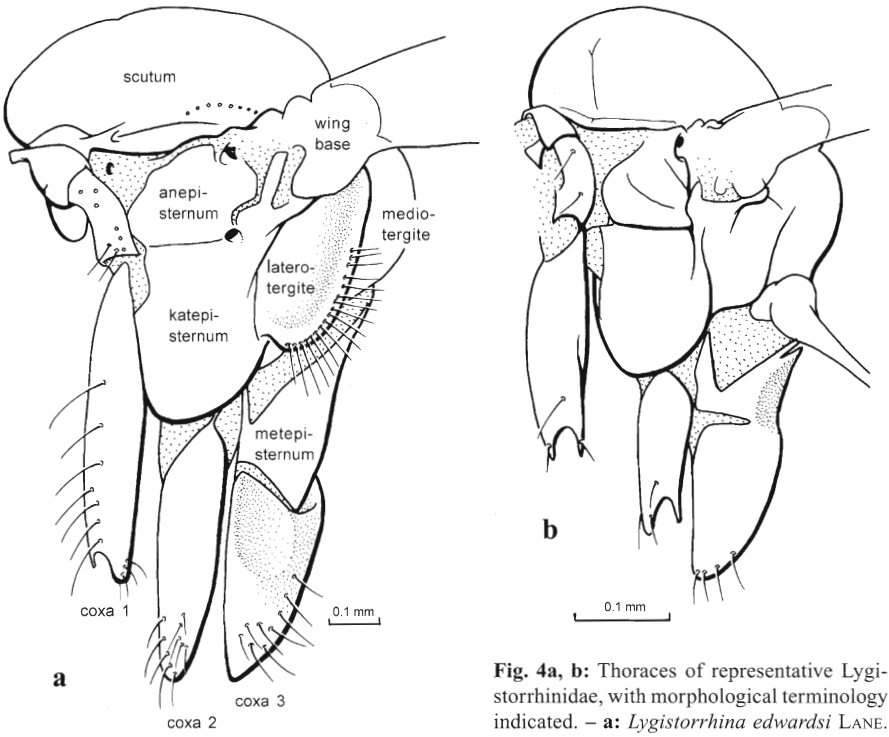


Fig. 4a, b: Thoraces of representative Lygistorrhinidae, with morphological terminology indicated. – **a:** *Lygistorrhina edwardsi* LANE. – **b:** *Loyugesa khuati* gen. nov, spec. nov.

flagellomeres present, flagellomeres moniliform, decreasing slightly in width apicad; length of flagellum slightly less than depth of head. Clypeus a small setose mound on face; face largely membranous, narrow, bounded laterally by margins of eyes. Labrum small, narrow, triangular (length approximately 2 × the width), apically pointed and length 0.3 × that of palps. Length of proboscis approximately equal to depth of head, longest portion is pair of labella; median hypopharynx slightly shorter, with serrate tip. Hypopharynx diaphanous, delicate. Palps relatively short, c. 0.4 × length of labella, with row of lateral setae along most of its length. Postgena membranous.

Thorax: Scutum dome-shaped, with median row of acrostichal setae extended from anterior margin to half the length of scutum; 2 paramedian rows of dorsocentrals extending nearly the length of scutum, dorsocentrals same size as acrostichals. Scutellum short, with marginal setae; median ones longest, lateral ones shortest. 7-8 notopleural and supra-alar setae. Pleura in lateral view as figured (fig. 4). Ventral margin of katepisternum rounded. Anterior margin of thorax slightly anterior to or at same level as fore coxa. Episternite with only 2 setae. Pleura bare, including laterotergite. Laterotergite not flat nor distended from pleural wall. Metanepisternum cleft, posterior lobe not reaching to ventral margin of laterotergite.
Legs: Mid coxa short, apex not reaching to apical level of hind coxa; hind coxa without depression on anterior end. All coxae with sparse setae. Legs of moderate length. Tibial spurs 0-1-2. Base of hind femur whitish. Hind tibia clavate, apical width 3 × proximal width,

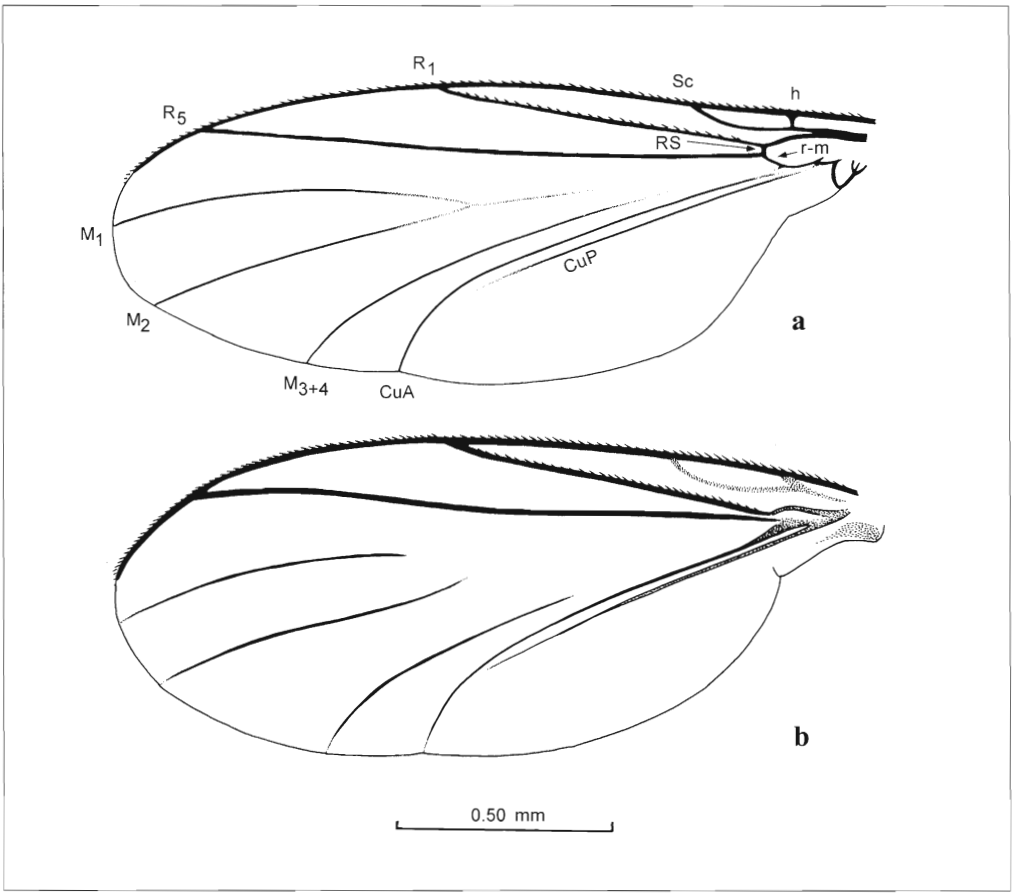


Fig. 5a, b: Wings of representative Lygistorrhinidae. – **a:** *Palaeognoriste* spec. (AMNH B-JH8) – **b:** "*Lygistorrhina*" *asiatica* SENIOR-WHITE, with venational terminology indicated.

apical third with longer, dense setae. Hind tibial spurs microtrichose, unequal in length; inner spur 2.5 × size of outer one. Hind basitarsomere large: width equal to apical width of tibia, length equals combined lengths of distal tarsomeres. Hind tarsomeres decreased in width apicad. **Wing:** Length approximately equal to length of abdomen; color fuscous, slightly darker apically. Apical margin very rounded. Sc incomplete; h not oblique; R_1 very short, length ca. 0.25x length of wing. R_{4+5} entirely bare. C ends midway between apices of R_{4+5} and M_1. Rs vestigial, incomplete. Base of R with acute angle and pinched; R_{4+5} with base incomplete, vein completely bare even at apex. Only apical third of veins M_1 and M_2 present (bases lost), length of M_2 is 1.3x length of M_1. CuA_1 and CuA_2 forked (sessile), with stem ca. 2.5x length of fork. CuP very close and parallel to stem of CuA. Very tiny cup and a cells at base of wing. No trace of vein A; anal lobe well developed. Halter white.

Abdomen: Tergites and sternites II-IV longest, decrease in length posteriad. Segment I small. Male genitalia with t IX relatively large, oval, with sparse apical spicules; gonocoxae stout; gonostyli very stout, length 2.3 × the width. Apex of gonostylus with dense spicules, apical tooth not observed.

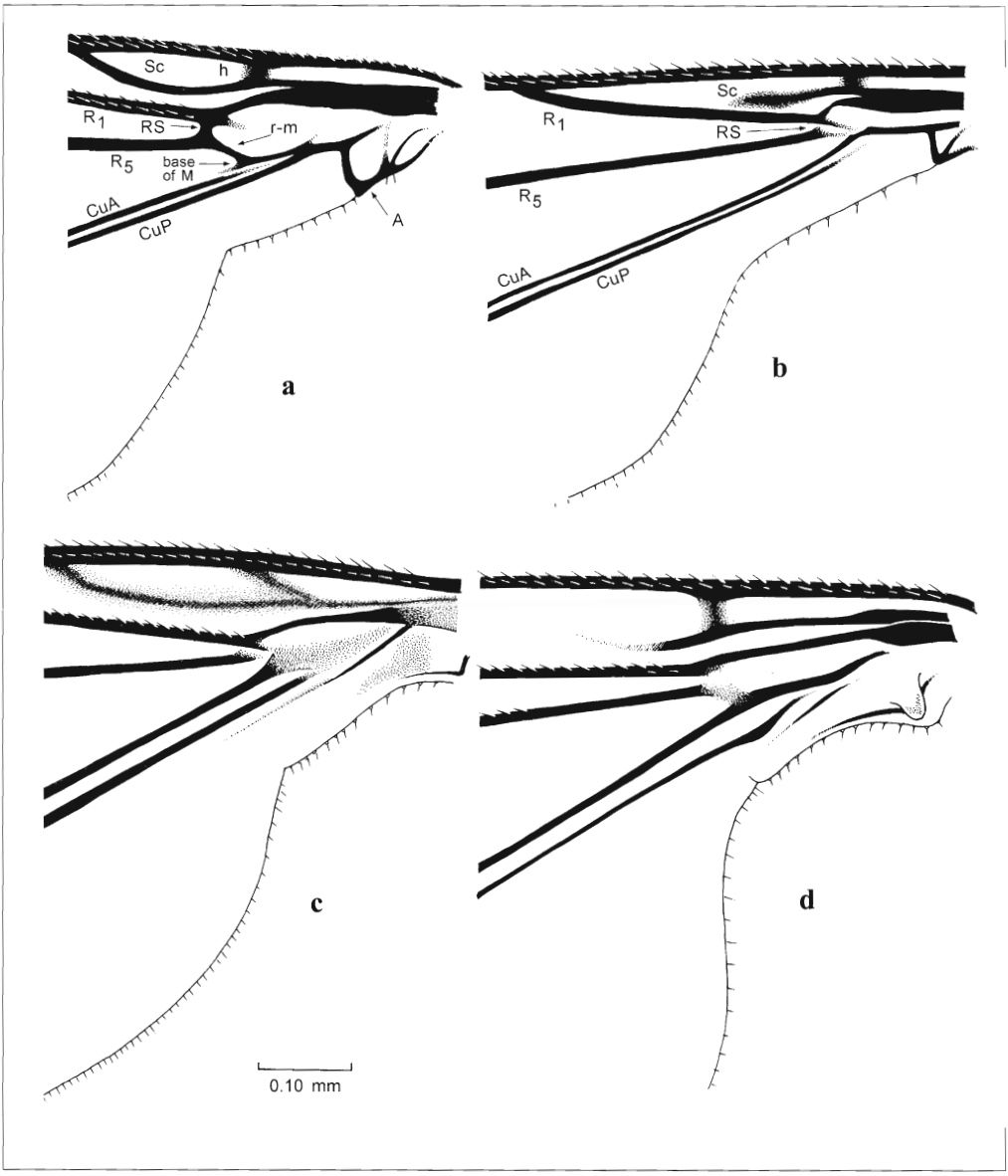
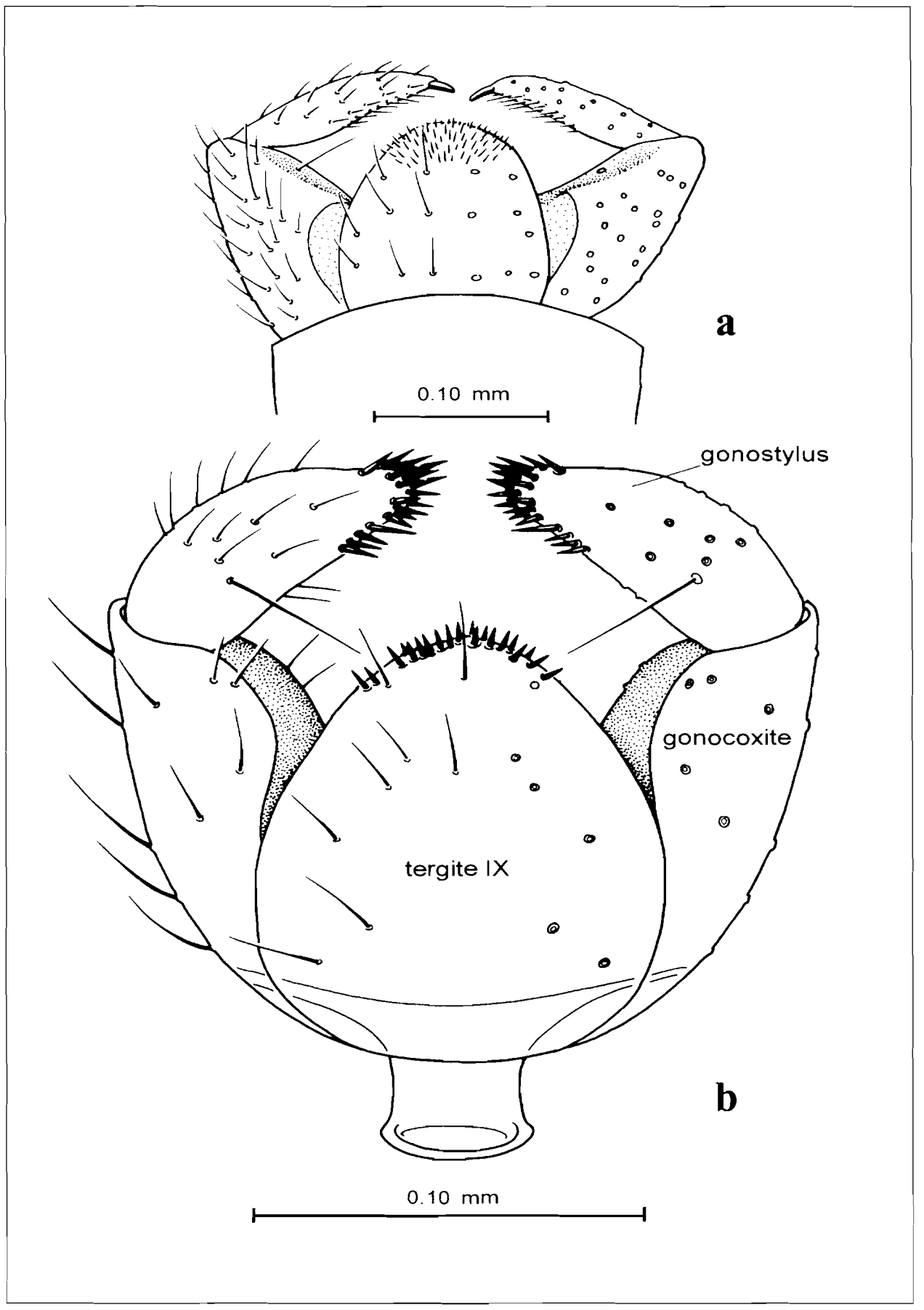


Fig. 6a-d: Bases of the wings of Lygistorrhinidae. – **a:** *Palaeognoriste* spec. (AMNH B-JH8). – **b:** *Loyugesa khuati* gen. nov, spec. nov. – **c:** "*Lygistorrhina*" *asiatica* SENIOR-WHITE. – **d:** *Lygistorrhina sanctaecatherinae* THOMPSON.

Type: Male, holotype: **Vietnam:** Ha Tinh, 13 km W Huong Son, 18°21'56"N, 105°13'18"E, near Rao An, 350 m., V/1998, collected by D. GRIMALDI (in AMNH). Series of 18 paratypes with same data (in IEBR, Hanoi; AMNH; MNHP).

Etymology: for Dr. KHUAT DANG LONG, entomologist at the Institute for Ecology and Biological Resources (IEBR), Hanoi, in recognition of his work and his collegiality in the AMNH-IEBR biotic surveys.



Genus *Seguyola* MATILE

Seguyola MATILE, 1990: 361. Type species: *S. variegata* MATILE, 1990.

Diagnosis: Closely related to *Loyugesa*, as given above, additionally distinguished by: virtually complete absence of proboscis; G eyes with dorsoventral differentiation of facets (dorsal ones larger); swelling of the costal margin at the apex of R_1; and infuscation on the costal margin, with 2 clear windows.

Species

S. variegata MATILE, 1990 (Africa [Cameroon]); *S. vicina* MATILE, 1990 (Africa [Cameroon]).

Fig. 7a, b: Male genitalia of Lygistorrhinidae. – **a:** *Palaeognoriste* spec. (AMNH B-JH8); – **b:** *Loyugesa khuati*, gen. nov, spec. nov.

Genus *Palaeognoriste* MEUNIER

(Figs 2a, b, 3c, 5a, 6a, 7a)

Palaeognoriste MEUNIER, 1904: 88. Type Species: *P. sciariforme* MEUNIER, 1904: 89.

Diagnosis: Monophyly highly questionable, defined entirely on the basis of plesiomorphic features: proboscis short, 1.7× head height; and complete Sc vein. Most distinctively, these are the only species of the family with a complete basal portion of fork of M_1–M_2; and vein Rs present, but small (e.g., dm cell present).

Species: *P. sciariforme* MEUNIER, 1904; *P. affinis* MEUNIER, 1912. Both are extinct species in Eocene Baltic amber.

Comments: Distinctions between the two species are subtle, especially given MEUNIER'S cursory descriptions and lack of mention of distinguishing features. Illustrations of the two species indicate that *affinis* has a definite stem to M_1–M_2; *sciariforme* does not, although the two veins meet or virtually so. MATILE (1990a) figured the venation of the holotype of *P. sciariforme*, which agrees very closely with the two specimens we have examined, except that we could not see a base of vein R bisecting cell dm, nor an anal vein that extends past the small anal lobe ("A1").

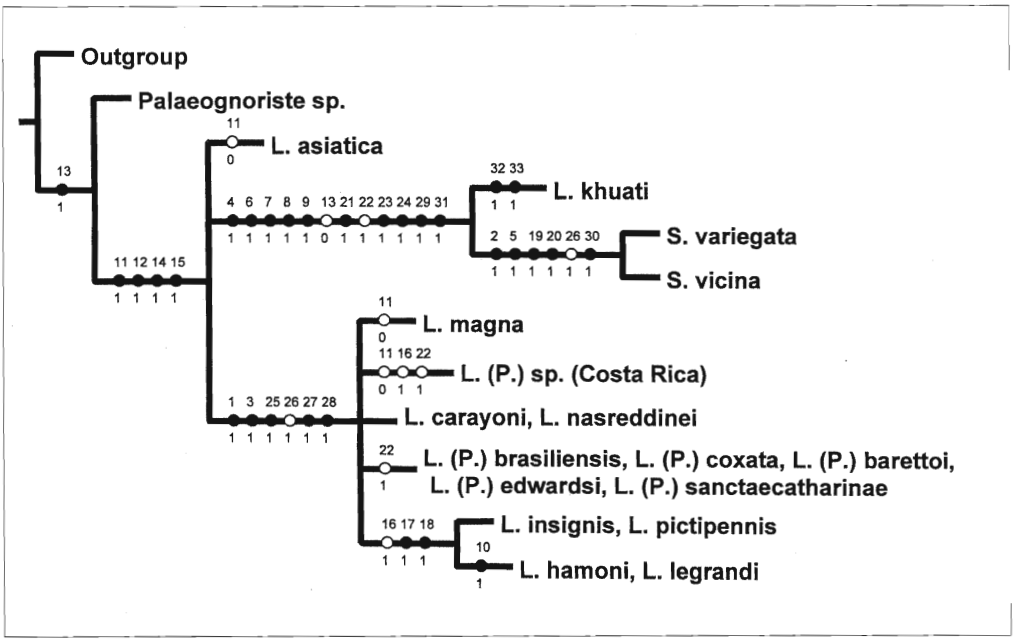


Fig. 8: Relationships of genera of Lygistorrhinidae, based on a consensus of 13 equally parsimonious trees. Length 40; CI 82; RI 87. Chararacters are numbered (above lines); all have a state of 1, except for those with polarity reversal (0)(below lines). Open circles are homoplasious characters.

Key to genera of Lygistorrhinidae

1. Proboscis very long, ≥4× height; abdomen generally longer than wings **2**
– Proboscis no longer than 2.5× head height; abdomen about as long as wings **3**
2. Mid tibia with 2 apical spurs; abdominal segments usually with basal light bands; Old World ..... Genus ***Lygistorrhina****
– Mid tibia with 1 apical spur; segments usually with apical light bands; New World ... . Subgenus ***Probolaeus***
3. 3 ocelli present; 14 flagellomeres; hind tibia and basal tarsomere not swollen .... Genus ***Palaeognoriste***
– 2 ocelli present; 12 flagellomeres; hind leg and basal tarsomere swollen **4**
4. Dorsal eye facets 2× size of ventral ones; mouthparts very small; costal margin of wing with swelling; laterotergite setose ..... Genus ***Seguyola***
– Dorsal and ventral eye facets equal in size; length of proboscis about thorax height; costal wing margin straight; laterotergite bare ..... Genus ***Loyugesa***

* includes "*Lygistorrhina*" *asiatica*, pending its classification in a separate genus (see above).

Acknowledgments

For the loan of crucial material we thank all those listed above; also, Jens VON HOLT provided a Baltic amber specimen to the AMNH. NSF grant BSR DEB 9870232 to the AMNH Center for Biodiversity and Conservation funded bioinventory work in Vietnam. Tam Nguyen, Senior Scientific Assistant at the AMNH, contributed to this and many other projects by the senior author. Lastly, the senior author is also grateful to Dr. KHUAT DANG LONG, for his patience and hard logistic work with the Vietnam surveys, and his friendship.

Literature

EDWARDS, F. W. (1912): XXI – *Lygistorhina urichi*, a new Mycetophilid from Trinidad. – The Annals and Magazine of Natural History. Ser. 8. **10**(56): 203-204; London.

EDWARDS, F. W. (1926): XIV. – Diptera Nematocera from the mountains of Borneo. – Sarawak Museum Journal **3**(10): 243-278 + 2 plates; Kuching.

EDWARDS, F. W. (1932): New Brazilian Mycetophilidae (Diptera). – Revista de Entomologia **2**(2): 138-149; São Paulo.

ENDERLEIN, G. (1911): Neue Gattungen und Arten außer-europäischer Fliegen. – Stettiner entomologische Zeitschrift **1911**: 135-209; Stettin.

GOLOBOFF, P. (1999): Winnona, ver. 2.0. Program and documentation. – Tucuman, Argentina.

HENNIG, W. (1966): The Diptera fauna of New Zealand as a problem in systematics and zoogeography [translation of the German original by P. WYGODZINSKY]. – Pacific Insect Monographs **9**: 1-81; Honolulu.

LANE, J. (1946). New Brazilian Mycetophilidae (Diptera, Nematocera). – Revista de Entomologia **17**(3): 339-360; São Paulo.

LANE, J. (1958): On Amazonian Mycetophilidae (Diptera, Nematocera). – Studia Entomologia **1**(1/2): 209-216; Rio de Janeiro.

LANE, J. (1960): Mycetophilidae from Trinidad, B. W. I. (Diptera, Nematocera). – Studia Entomologia **3**(1-4): 375-384; Rio de Janeiro.

MATILE, L. (1978): Diptères Mycetophilidae de l'archipel des Comores. – Mémoires Museum national d'histoire Naturelle A (Zoologie) **109**: 247-306; Paris.

MATILE, L. (1986): Diptères Mycetophiloidea de Nouvelle-Calédonie. I. Lygistorrhinidae. – Annales de la Societé entomologique de France **22**(2): 286-288; Paris.

MATILE, L. (1990a): Recherches sur la systématique et l'évolution des Keroplatidae (Diptera, Mycetophiloidea). – Mémoires Museum National Histoire Naturelle Paris (A) **148**: 682 pp; Paris.

MATILE, L. (1990b): Les Lygistorrhinidae de la région Afrotropicale (Diptera: Mycetophiloidea). – Annales de la Societé entomologique de France **26** (3): 359-370; Paris.

MATILE, L. (1996): Une nouvelle espèce afrotropicale du genre *Lygistorrhina* SKUSE (Diptera, Mycetophiloidea, Lygistorrhinidae). – Revue française Entomologique **18**(1): 30; Paris.

MEUNIER, F. (1904): Monographie des Cecidomyidae, des Sciaridae, des Mycetophilidae et des Chironomidae de l'ambre de la Baltique. – Annales de la Societé scientifique de Bruxelles **28**: 93-275; Brussels.

MEUNIER, F. (1912): Un nouveau Mycetophilidae de l'ambre de la Baltique (Dipt.). – Bulletin de la Societé entomologique de France **1912**: 88-90; Paris.

NIXON, K. (2000): Winclada, ver. 0.9.99.m24 beta. Program and documentation. – New York: Ithaca.

OKADA, I. (1937): Beitrag zur Kenntnis der Fungivoriden-fauna Japans V: Lygistorrhininae (Dipt.). – Insecta Matsumurana **12**: 45-48; Tokyo.

PAPAVERO, N. (1977): Family Lygistorrhinidae. – Pp. 1-2 in: PAPAVERO, N.: A Catalogue of the Diptera of the Americas South of the Unated States. **19D**, São Paulo.

SENIOR-WHITE, R. A. (1922): New Ceylon Diptera (Part II). – Spolia Zeylanica **12**: 195-206: Colombo.

SKUSE, F. A. A. (1890): Diptera of Australia. Nematocera, Supplement II. – Proceedings of the Linnaean Society of New South Wales **2**(5): 595-640 + 1 plate; Sydney.

THOMPSON, F. C. (1975): Notes on the genus *Lygistorrhina* SKUSE with the description of the first Nearctic species (Diptera: Mycetophiloidea). – Proceedings of the Entomological Society of Washington **77**(4): 434-445; Lawrence, Kansas.

TUOMIKOSKI, R. (1966): Systematic position of *Lygistorrhina* SKUSE (Diptera, Mycetophiloidea). – Annals Entomologica Fennica **32**(3): 254-260; Helsinksi.

WILLISTON, S. W. (1896): On the Diptera of St. Vincent (West Indies). – Transactions of the Entomological Society of London **1896** (3): 253-446; London.

Authors' address

David GRIMALDI and Vladimir BLAGODEROV
Division of Invertebrates
American Museum of Natural History
Central Park West at 79th St.
New York, New York 10024-5192, U.S.A.
E-mails: grimaldi@amnh.org
vblago@amnh.org.

The paper was accepted on 10 September 2000.
Editum: 15 August 2001.