

The Phylogeny of the Lophopidae and the Impact of Sexual Selection and Coevolutionary Sexual Conflict

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A cladistic analysis of Lophopidae was performed, using 73 observed morphological characters and 41 taxa. This analysis involved 36 genera belonging to the Lophopidae family and 5 outgroups. For a better understanding of the selected characters some illustrations are provided. The most parsimonious cladograms obtained show that the Lophopidae cannot be considered as a monophyletic lineage unless two genera are withdrawn from this family: *Hesticus* Walker, 1862, and *Silvanana* Metcalf, 1947. The systematic position of these two genera remains uncertain. They cannot yet be included in another family of Fulgoromorpha. A cladistic analysis of each of the 19 remaining Fulgoromorphan families must be performed first. A new family could be created for these two genera, but not before we are sure that these two genera are in no way members of an existing family. The outgroup problem is discussed. The monophyletic lineage represented by the Lophopidae can be divided into four natural groups: Carriona⁺, Makota⁺, Sarebasa⁺, and Bisma⁺. When a cladistic analysis is completed using a data matrix without characters linked to females, the cladogram obtained presents a disrupted basal resolution. Female characters appear to bring a phylogenetic signal

important basally in the evolution of the Lophopidae but also apically, directly between the relationships of some genera. A similar analysis, using a matrix without characters linked to males, provides a phylogeny disrupted between the groups that form the Lophopidae and in the basal resolution in these groups. The respective impacts of the genitalic characters are discussed in relation to sexual selection conflict. © 2001 The Willi Hennig Society

INTRODUCTION

Different authors have worked on the classification of the Lophopidae, including Melichar (1915), Baker (1925), Muir (1930), and Metcalf (1955). Here we propose a morphology-based phylogeny according to a cladistic methodology. The Lophopidae are confined to the tropical regions. Only two genera are present on the African continent: *Lophops* and *Elasmoscelis*. In South America the genera *Hesticus*, *Silvanana*, and *Carriona* are the representatives of the family. Most of the genera are distributed from Southeast Asia throughout New Guinea to the Fiji Islands. Only little is known about their host plant and their ethology. The establishment of the phylogeny for this group is an opportunity

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to observe and study the different topologies for the cladograms obtained; this is directly linked to the order in which the taxa of the outgroup are entered in the matrix (Barriel and Tassy, 1998). A sexual conflict between males and females over the control of fertilization could be at the origin of morphological changes in the genitalia. "Each change in one sex that helps its members with the change secure their own interests to a greater degree is likely to be countered by changes in the other sex" (Alexander *et al.*, 1997). The changes in strategy in each sex could be observed in an alteration of the behavior but also in the morphology of the genitalia. Could we, on a phylogeny, observe and follow the successive modifications in the female and male characters, over time? Could a cladistic analysis underscore the type of sexual selection that has been dominant in the evolution of a monophyletic lineage?

MATERIALS AND METHODS

Morphological Phylogeny

The phylogeny presented here is based on 73 characters, 61 of which are informative. Five outgroups are used: two Eurybrachidae, *Loxocephala* sp. Schaum and *Aspidonitysp* sp. Lallemand; one Tettigometridae, *Tettigometra* sp. Latreille; and two Ricaniidae, *Ricania* sp. Germar and *Pochazia* sp. Amyot and Seville. The Eurybrachidae were chosen because they are considered to be the sister group of the Lophopidae (Emeljanov, 1990) and, like the Ricaniidae, they belong to a group of recent families (e.g., Issidae, Acanaloniidae, Nogodiniidae, Flatidae, Hypochthonellidae, Tropiduchidae, and Gengidae) within the Fulgoromorpha (Asche, 1988). Tettigometridae was chosen as a "curiosity"; the hypothesis of its place in the Fulgoromorpha families depends upon the authors. Emeljanov (1990) and Asche (1988) place the Tettigometridae at the most basal position within the Fulgoromorpha phylogeny, whereas Bourgoïn *et al.* (1997) present these families as being within the most recent. Thirty-three of the 37 lophopid genera known and a further three new taxa are included in the matrix (Soulier-Perkins, 1998). Four genera (*Ridesa* Schumacher, 1915; *Katoma* Baker, 1925; *Epiptyxis* Gerstaecker, 1895; and *Meloenopia* Metcalf, 1952) were not accessible for study. The analysis was

performed using the programs PAUP version 3.1.1. (Swofford, 1993) and MacClade version 3.07 (Maddison and Maddison, 1992). The characters used for this phylogeny were selected from the head capsule, legs, wing venation, dorsal part of the thorax, and female and male genitalia (see Bourgoïn, 1993, and Bourgoïn and Huang, 1990, for terminology).

Cladistic Methods

When a taxon presents different states for one character, this character for this taxon is considered as polymorphic. Among higher taxa, characters that were polymorphic in the constituent taxa were eliminated from phylogenetic analysis. Characters that are present in only one state for each of the constituents except for a single polymorphic taxon were retained in the analysis (characters 10, 35, and 40). In PAUP, polymorphism is chosen in the option "Multistate taxa." Rooting the cladogram is done by outgroup comparison with a basal polytomy. All the uninformative characters are ignored. All the characters have the same weight. "Nonsensical" characters are coded with a dash and the characters that have not been observed are coded by a question mark. PAUP treats them both as uncertain characters. The characters are not ordered or oriented. The three options of optimization available in PAUP have been used: Acctran (favors reversion), Deltran (favors convergence), and Minf (favors changes on the terminal taxa and at the base of the cladogram). These options present different possibilities of evolutionary history for some characters. We performed a heuristic search with TBR. The option "collapse zero-length branches" was deactivated. This option was then reactivated when we performed heuristic searches without female characters and again without the male characters. The order in which the outgroups are entered in the matrix is modified, in order to perform a cladistic analysis with each of the outgroups entered first in the matrix. If different cladograms are found, the suggested solution of Barriel and Tassy (1998) could be explored. The index of Bremer (1994) would then be performed for the resolved nodes of the retained cladogram. Clades will be referred to using the name of the first included taxon followed by the plus sign, as done by Amorim (1982).

CHARACTERS AND CHARACTER STATE DEFINITIONS

Legs

The fore femur can present a pattern with regular line of brown spots along its length. It is on the hind legs that most of the characters have been selected, especially on the tibia and on the first segment of the tarsus. On its external side, the hind tibia can bear some strong spines. Two to 3 spines are observable for the Lophopidae (Fig. 1), but this is not restricted to this family of Fulgoromorpha. Within the Eurybrachidae, 4 or more spines can be observed (Fig. 2), whereas for

the Tettigometridae these spines are absent (Fig. 3). The apical part of the hind tibia bears some spines as well. They can be quite strong but are never more than 12 in number (Fig. 4) or much smaller and generally very numerous (Fig. 5). Only the genus *Elasmoscelis* presented a pad of microsetae striated lengthwise, flanked by two groups of small spines (Fig. 6). The first segment of the hind tarsus is ornamented with spines for which the layout can be a line (Fig. 3) or a triangular surface (Fig. 4), or if this segment is partially covered with a pad of microsetae, the spines are organized in two lots (Fig. 5). *Elasmoscelis* is the only genus presenting a pad of microsetae striated lengthwise on the first segment of the hind tarsus. All the Lophopidae observed possess a hind tarsus with its second segment reduced to a lobe without any spines (Figs. 4–6), which is also the case for the Eurybrachidae and Ricaniidae. The Tettigometridae present 2 apical spines on the second segment of the hind tarsus (Fig. 3).

Head Capsule

The lateral ocelli are present in all the Lophopidae and in the outgroups except for the genera *Carriona* and *Buxtoniella*. Each lateral ocellus (o) is generally located below the compound eye (CE) and slightly anterior to it (see Fig. 7). The frons is usually longer than it is wide and bears some carinae. The median carina (McF) stretches longitudinally on the middle of the frons. On each side of this carina the sublateral carinae (SbcF) are observable and delimit an area: the frontal disc (Fd). The lateral margin of the frons (LmF) can be carinate and are named lateral carinae of the frons. The median carina can be absent as in *Pyrilla* (Fig. 8) and *Elasmoscelis* (Fig. 10). The frontal disc can be more or less flat, sometimes hollowed longitudinally and gutter shaped (Fig. 8). The sublateral carinae, reduced or not, are generally present and for the genus *Aluma* they are swollen (Fig. 9). The lateral carinae of the frons are often continuous from the frons–vertex suture to the frontoclypeal suture but they can also be incomplete (Fig. 10). The ornamentation of the frons is diverse, first with the colors and second with the presence of protuberances. *Asantorga* is the unique genus studied presenting these protuberances that cover the frons between the sublateral carinae and the lateral margins. In dorsal and lateral views, these protuberances cannot be ignored. On the clypeus three carinae

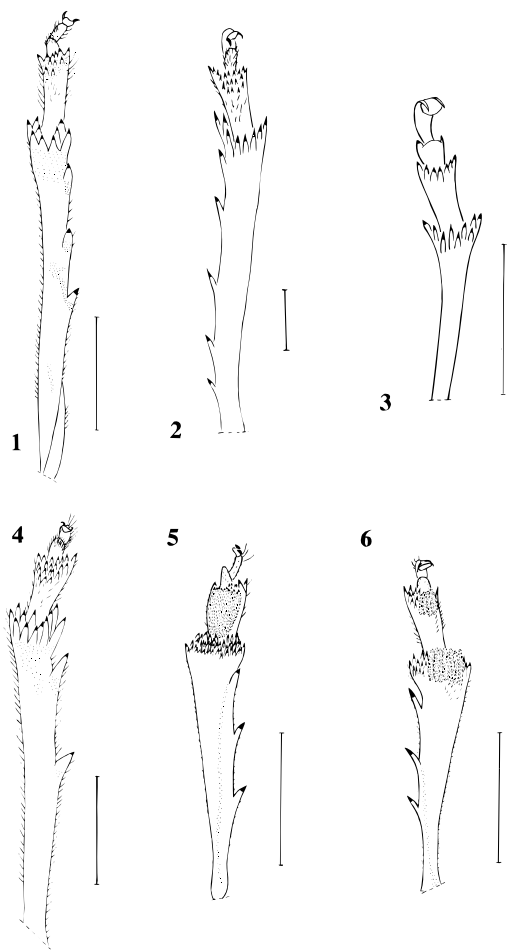


FIG. 1–6. Hind tibia and tarsus; (1) *Makota* sp. (Lophopidae); (2) *Loxocephala* sp. (Eurybrachidae); (3) *Tettigometra* sp. (Tettigometridae); (4) *Bisma* sp. (Lophopidae); (5) *Lacusa* sp. (Lophopidae); (6) *Elasmoscelis* sp. (Lophopidae).

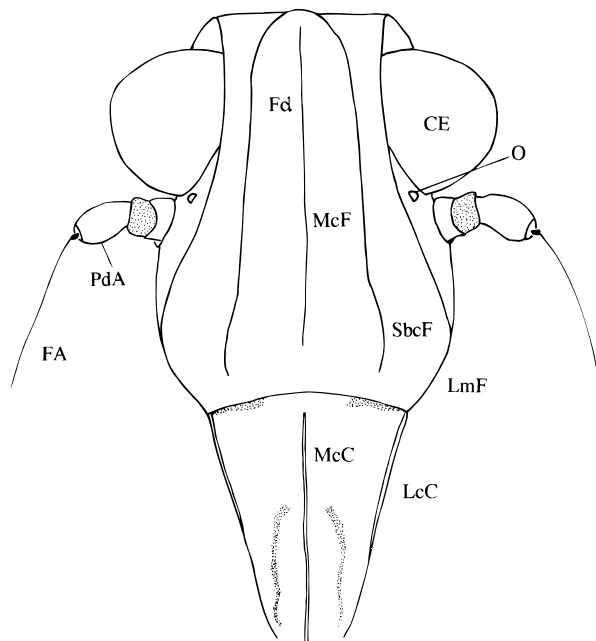


FIG. 7. Lophopid head capsule in frontal view; CE, compound eye; FA, flagella of the antenna; Fd, frontal disc; LcC, lateral carina of the clypeus; LmF, lateral margin of the frons; McC, median carina of the clypeus; McF, median carina of the frons; O, ocellus; PdA, pedicel of the antenna; SbcF, sublateral carina of the frons.

are observable (Fig. 7): the median carina (McC) and the lateral carinae (LcC). The presence or absence of lateral carinae is a character traditionally used to separate the Lophopidae from the Eurybrachidae. In effect some genera within the Lophopidae do not possess those carinae. In a lateral view of the cephalic capsule, two carinae can be observed. The ocellar carina links the ocellus to the lateral margin of the frons (Fig. 12) and the genal carina crosses the gena from the lateral margin of the frons to the posterior margin of the gena (Fig. 13). It is generally admitted that a vertex longer than it is wide is a character diagnostic to separate the Lophopidae from the Eurybrachidae. It is not verified here because some genera within the Lophopidae present a vertex wider than it is long. The Lophopidae present the classic antennae of the Fulgoromorpha. They are composed of a scape, a pedicel enlarged (PdA), frequently shaped as a bulb and bearing characteristic sensorial organs, and a flagella (FA) that is basally thicker and bears the "organe de Bourgoïn" (Cobben, 1988). For the genus *Hesticus*, the pedicel is three times longer than its diameter. The foramen of the

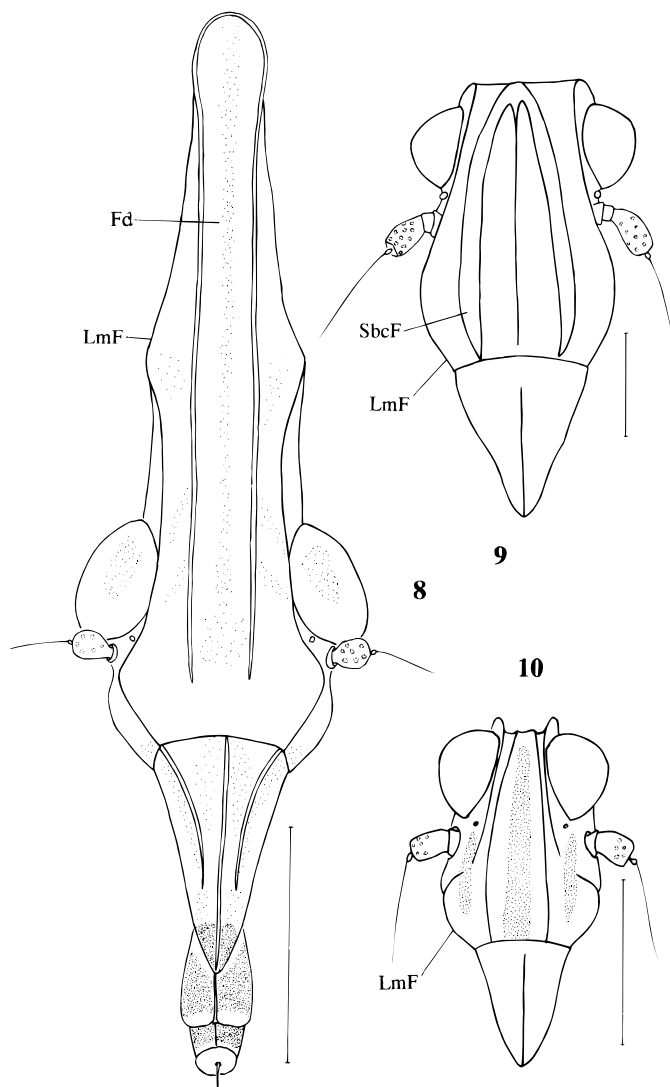


FIG. 8–10. Lophopid head capsule in frontal view: (8) *Pyrilla* sp.; Fd, frontal disc; LmF, lateral margin of the frons; (9) *Aluma* sp., LmF, lateral margin of the frons; SbcF, sublateral carina of the frons; (10) *Elasmoscelis* sp.; Lmf, lateral margin of the frons.

antennae is generally well separated from the compound eye base with the exception of the genera *Hesticus* and *Buxtoniella* in which the foramen of the antenna touches the compound eye base.

Wings

The fore wings or tegminae of all the genera studied, with the exception of *Buxtoniella*, present subcostal (Sc) + radial (R), median (M), costal (C), anal (A), cubital

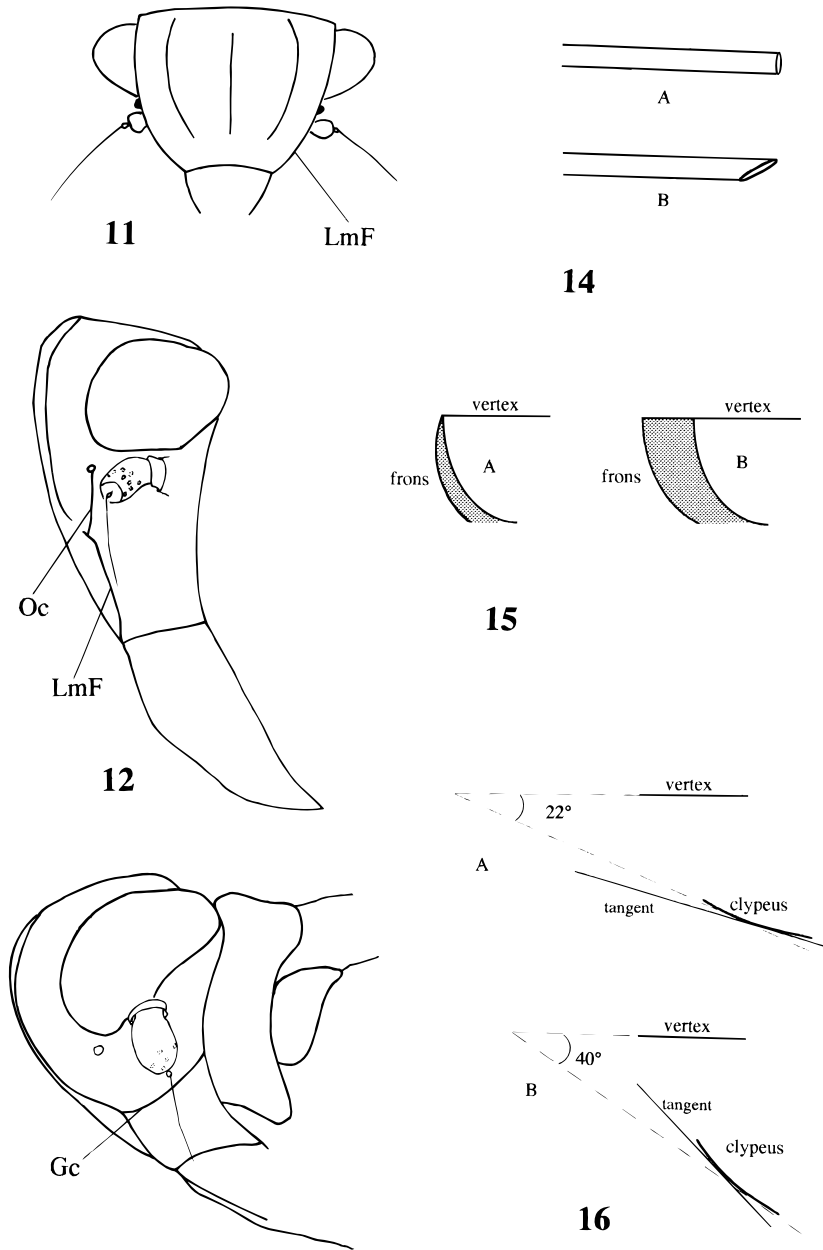


FIG. 11. Head capsule in frontal view of *Ricania* sp. (Ricaniidae); LmF, lateral margin of the frons.

FIG. 12. Head capsule in lateral view of *Zophiuma* sp. (Lophopidae); LmF, lateral margin of the frons; Oc, ocellar carina.

FIG. 13. Head capsule in lateral view of *Virgilia* sp. (Lophopidae); Gc, genal carina.

FIG. 14. Apex of the labium, schematic drawing; (A) cut perpendicular to its longitudinal axis; (B) bevelled edge.

FIG. 15. Schematic drawing for the relative position of the frons and the vertex in lateral view; (A) base of the frons does not continue the vertex; (B) base of the frons continue the vertex.

FIG. 16. Angle between the clypeal tangent and the vertex plan, schematic drawing; (A) less than 22° , (B) more than 40° .

(Cu), and postcubital (Pcu) veins that are clearly observable (Fig. 17). For many genera studied the costal vein is distinct from the costal margin (Cm) and delimits a costal area. This area can be more or less wide and crossed by some transverse veins. Dworakowska (1988) refers to this costal vein as being a composite vein: Pc + CP present in numerous Fulgoromorpha. Four genera studied here do not present a distinct costal vein: *Kasserota*, *Magia*, *Onycta*, and *Acarna*. The genus *Acarna* shows an autapomorphy on its tegmina with its cubital vein lying very close to the postcubital vein as noticed by Baker in 1925. With a median vein presenting a branch M2 strongly curved to the hind wing articulation, the Tettigometridae possess an autapomorphy recognized by Bourgoïn (1987) and Asche (1988). The venation was identifiable for each of the genera studied except for one: *Buxtoniella*. For this genus, the vein pattern was so intricate that only the postcubital vein was identified.

Thorax

On the mesothorax some carinae are observable and particularly the median carina, which can stretch from the anterior margin to the posterior apex. This carina is generally simple but it can be double, partially welded, or completely separated. On the central area of the prothorax, three carinae are observable. The median carina frequently joins the sublateral carinae anteriorly. The anterior margin, where these carinae meet, is generally rounded except for the genus *Pitambara*, which presents an anterior margin pointed toward the head.

Female Characters

Most of the Lophopidae anal tubes present an apex swollen in two lobes (Fig. 19). These lobes (LAn) can be of diverse shapes and sizes. All the outgroups and the genera *Hesticus* and *Silvanana* do not possess these lobes (Fig. 18). Even for the Eurybrachidae, which present an elongated anal tube, its apex is not even swollen but flattened laterally. For only two genera has a median extension (MeAn) located posteriorly and ventrally to the anal tube been observed (Fig. 20). The segmentary and appendicular structures present some characteristics (Fig. 21). The bilobate gonopods rest directly on the fulcrum with the gonocoxal base IX being absent for the Lophopidae except for *Hesticus* and *Silvanana*. (Fig. 22). The Eurybrachidae present a pair of bilobate gonopods maintained by a reduced gonocoxal base IX. *Hesticus* and *Silvanana* exhibit multilobate gonopods and the Ricaniidae bear monolobate gonopods ornamented by tooth-shaped spines. The Ricaniidae, *Silvanana* and *Hesticus*, present a gonocoxal base IX. Within the Lophopidae the upper gonopod lobe can be extremely reduced as for the taxa on *Elasmoscelis*. The gonapophysis IX or valve I (Snodgrass, 1933) is reduced and sometimes absent but quite developed for the genera *Loxocephala*, *Ricania*, *Pochazia*, *Hesticus*, and *Silvanana* and unique for *Aspidonitys* by their size, shape, and position (Fig. 22C). The tergites VIII are well sclerotized for the genera *Hesticus* and *Silvanana*. The gonocoxae VIII are observable within the taxa studied but can be more or less developed and may or may not bear a sacculiform structure. Ventrally a pair of endogonocoxal processes prolongs these

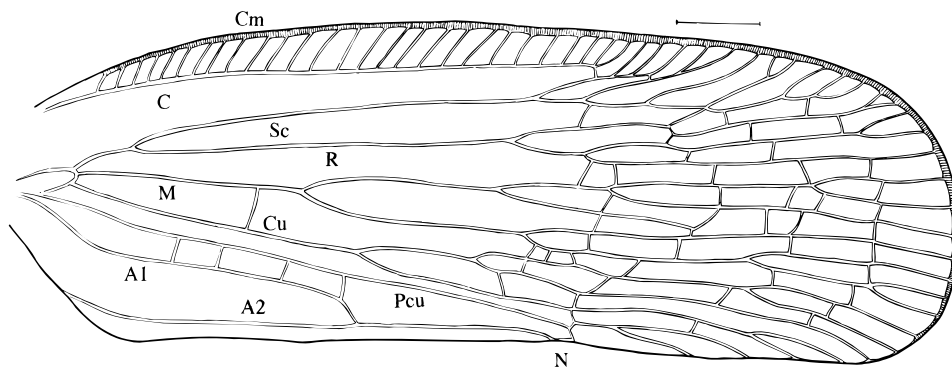
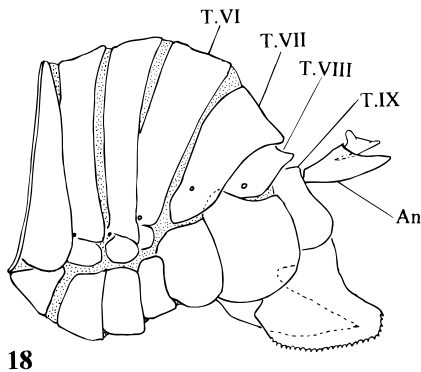
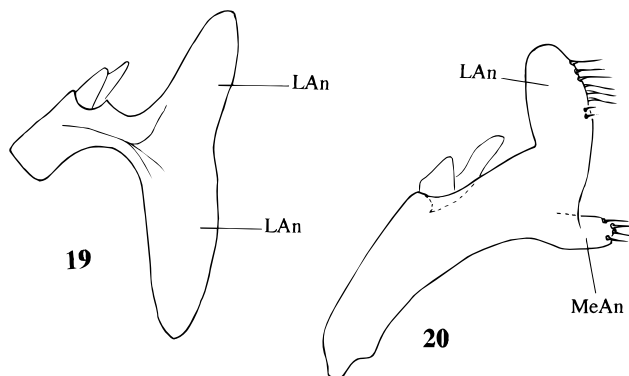


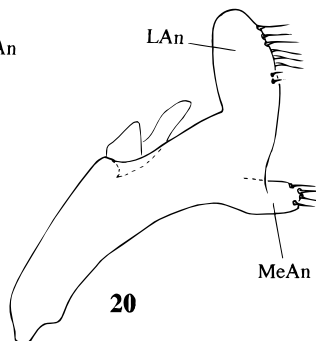
FIG. 17. Tegmina, *Pyrilla* sp. (Lophopidae); A1, anal vein 1; A2, anal vein 2; C, costal vein; Cm, costal margin; Cu, cubital vein; M, median vein; N, node; Pcu, postcubital vein; R, radial vein; and Sc, subcostal vein.



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FIG. 18. Abdomen in lateral view, *Ricania* sp. (Ricianiidae), An, anal tube; T.VI, tergite VI; T.VII, tergite VII; T.VIII, tergite VIII; T.IX, tergite IX.

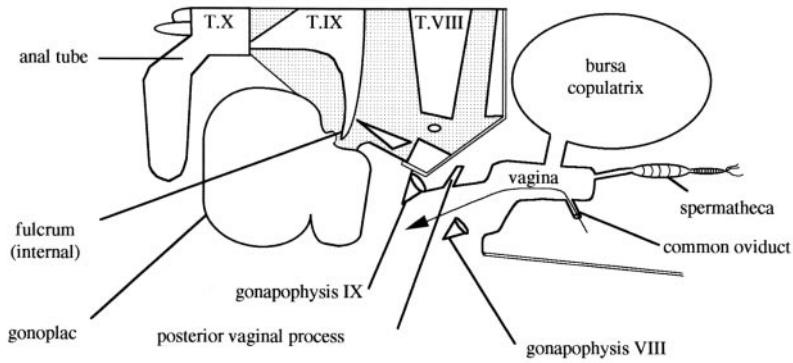
FIG. 19. Anal tube in lateral view, *Megacarna* sp. (Lophopidae); LAn, lobe of the anal tube.

FIG. 20. Anal tube in lateral view, *Virgilia* sp. (Lophopidae); LAn, lobe of the anal tube; MeAn, median extension of the anal tube.

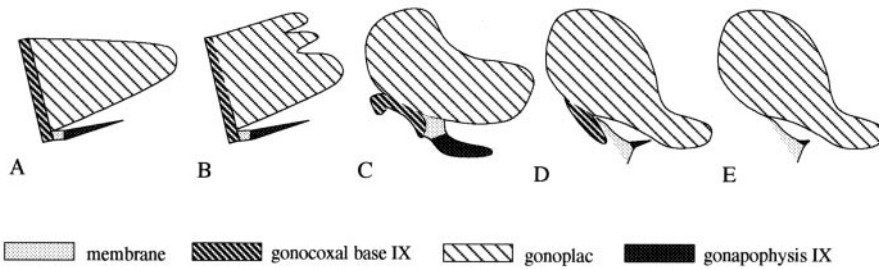
gonocoxae VIII, as observed for the genera *Aluma* and *Aspidonitys*. The gonopophysis VIII are present but reduced in the Lophopidae with the exception of *Silvanana* and *Hesticus*, which present lobate gonopophysis VIII. The gonospiculum, which is a tegumentary pouch between the gonoplocs and the gonopophysis IX, is absent in all Lophopidae with the exception of *Silvanana* and *Hesticus* (Fig. 23).

For the taxa studied here, the ectodermic genital duct represents a monotrysian condition. The gonoporus is the only opening to the outside and it is located between gonopophysis VIII and IX. From the gonoporus to the common oviduct a posterior–anterior morphological developmental axis is defined. All parts located below this axis are said to be ventral, and all parts located above it are dorsal. These references are only

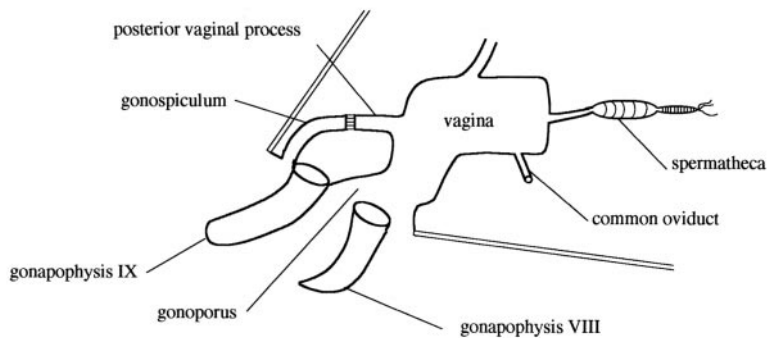
topological. The common oviduct has for its origin segment VII, whereas the vagina, which carries the spermatheca and the bursa copulatrix, finds its origin in segment VIII (Snodgrass, 1933; Bitsch, 1979). The posterior vagina bears dorsally the vaginal process, which is absent for some genera. When this process is present, it is generally anteriorly oriented except for the Eurybrachidae observed. The vaginal wall can be well sclerotized (e.g., *Onycta*) or completely membranous (e.g., *Carriona*). The bursa copulatrix occupies an anterior position in comparison to the vagina process. The wall of this bursa can be ornamented with a small cuticular growth limited or not by a circular ring (Soulier-Perkins and Bourgoïn, 1998). For seven genera studied, the bursa was not ornamented with cuticular growth.



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FIG. 21. Schematic drawing of the female genitalia of the Lophopidae.

FIG. 22. Schematic drawing of the gonoplacs, the gonocoxal base IX and the gonapophysis IX; (A) *Ricania* and *Pochazia* (Ricaniidae), (B) *Hesticus* and *Silvanana*, (C) *Aspidonitys* (Eurybrachidae), (D) *Loxocephala* (Eurybrachidae), and (E) Lophopidae with the exception of *Hesticus* and *Silvanana*.

FIG. 23. Schematic drawing of the gonospiculum and vaginal process in a typical Fulgoromorpha.

Male Characters

The ninth abdominal segment or pygofer is shaped as a ring more or less closed on its upper part. Posteriorly the diaphragm closes it. This fine membrane closes the general cavity and represents the anterior wall of the genital atrium, which is the space where the external male genitalia rest. Dorsally, the pygofer bears the anal tube or urites X and XI, which are variable. The connective is present in all the taxa studied (Fig. 24) except for the genus *Carriona*. This connective is divided into different parts. The first is the ventral support of the connective, which appears as an anterior pouch of the diaphragm (in comparison to the aedeagus). This ventral support is followed by the corpus connectivi. The tectiductus followed by the tectiform structure is also the result of a diaphragm pouch, which here is posterior to the aedeagus. The corpus connectivi and the tectiform structure appear welded, but a central space is kept and named the foramen. The ductus ejaculatorius crosses this foramen and becomes the ductus seminis. This ductus seminis rests on the brachi connectivi, which is an extension of the corpus connectivi. Within the Lophopidae, this last structure is poorly developed. In a lateral view, the tectiform structure is generally shaped as a spatula except in a few genera, which present a triangular-shaped structure.

The phallic complex is composed of a succession of interlocked sclerotized and membranous structures (Fig. 24). It seems to be protected dorsally by the anal tube and laterally by the gonostyli. It is composed of two distinct structures, the periandrium and the aedeagus s.l., which itself is divided into the aedeagus s.s., and the endosoma. Inside the aedeagus s.l. run the ductus seminis, which generally opens ventrally in the Lophopidae. The periandrium is divided in two parts, the phallotheca and the endotheca, which are respectively, external and internal, as described by Snodgrass (1935). Within the taxa studied the periandrium can also be divided into dorsal and ventral parts when observed laterally. The dorsal part is often more developed than the ventral part and can become very complex, as in the genus *Zophiuma* (Fig. 25). For practical reasons we distinguish the dorsal part from the ventral part although they are the same morphological entity. The periandrium can more or less sometimes preclude direct observation of the aedeagus s.l. The aedeagus s.l. is sclerotized and basally attached to the

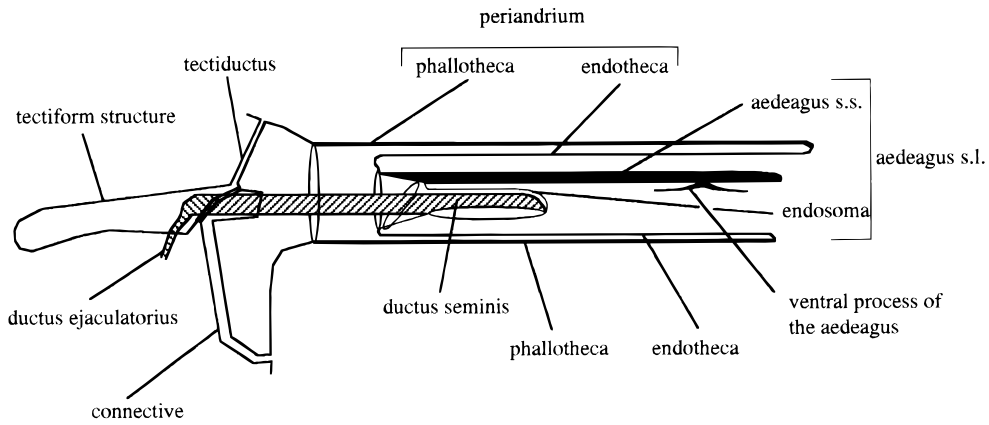
endotheca. Dorsolaterally it is well developed except in the genera *Carriona*, *Hesticus*, and *Silvanana*. In other Lophopidae, the aedeagus is elongate basally bifid, producing a paired structure symmetric in a vertical plan. The aedeagus bears some ventral processes that can be anterior or posterior. Beyond the insertion point of the processes, the aedeagus is sometimes elongate dorsally and variable in shape. The gonostyli are well developed. They are paired and symmetric in a sagittal plan. Each generally bears a small spine on its dorsolateral part. They are posterior to the diaphragm except for their apodemes, which are located in the general cavity.

RESULTS

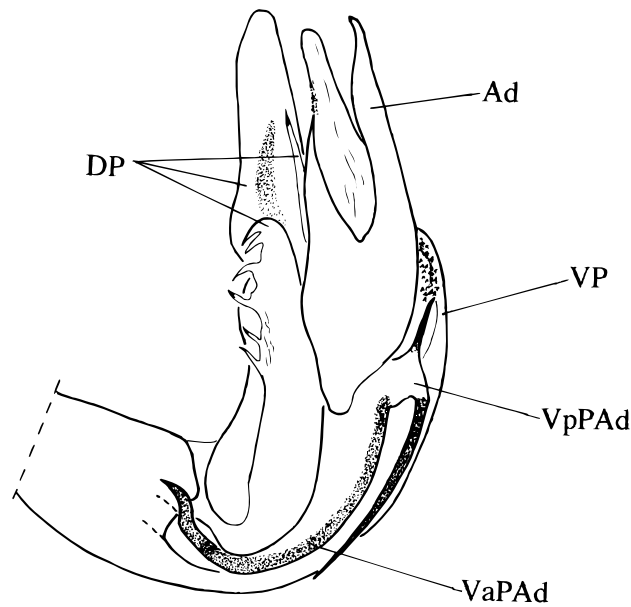
After analysis, nine cladograms were obtained with a length of 152 steps, a consistency index (CI) of 0.526, and a retention index (RI) equal to 0.783. The strict consensus of these nine trees shows the same length, CI, and RI as those of the cladograms described above. The polytomies observed are the result of the presence of nonsupported branches (Nixon and Carpenter, 1996). Consequently, the strict consensus is the only cladogram strictly supported (Figs. 26A–26C). This phylogeny shows that the ingroup is not a monophyletic lineage because two of the three South American genera, *Hesticus* and *Silvanana*, were always located among the outgroups on the cladograms (Figs. 26A–26C). The systematic position for these two genera is therefore uncertain. They cannot yet be included in another family of Fulgoromorpha. A cladistic analysis of each of the 19 remaining Fulgoromorphan families must be performed first. A new family could be described for these two genera, but not before determining that these genera are in no way members of an existing family.

The Outgroups

The section of the tree designated to the outgroup (including *Hesticus* and *Silvanana*) changes topology as a function of the order in which the outgroup data are entered (Figs. 26A–26C). The topology of the ingroup Lophopidae, however, remains the same. Barriol and



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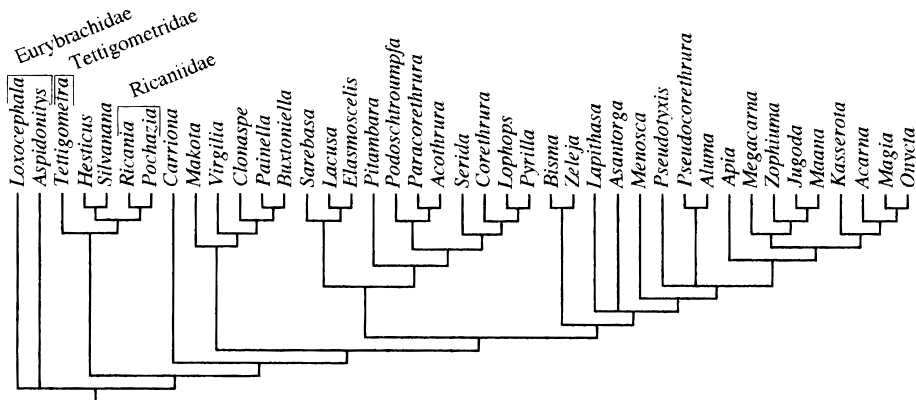
FIG. 24. Schematic drawing of the male genitalia of the Lophopidae.

FIG. 25. Phallic complex in lateral view, *Zophiuma* sp. (Lophopidae); Ad, aedeagus s.l., DP, dorsal part of the periandrium; VaPAd, ventral anterior process of the aedeagus; VP, ventral part of the periandrium; and VpPAd, ventral posterior process of the aedeagus.

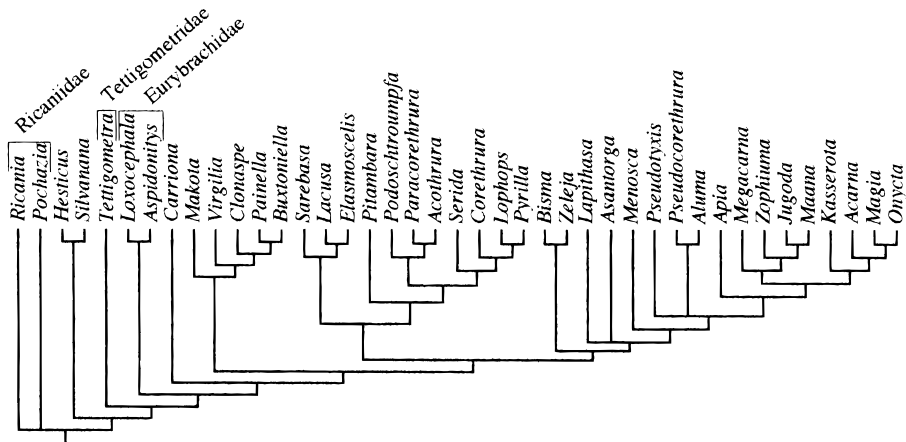
Tassy (1996, 1998) recommended producing a strict consensus (Fig. 27) of all trees obtained by outgroup permutations (Fig. 26). This consensus is longer with 185 steps. Its CI and RI are 0.42 and 0.68, respectively.

Two scenarios (Figs. 26B and 26C) suggest that the Eurybrachidae is the sister group to the Lophopidae.

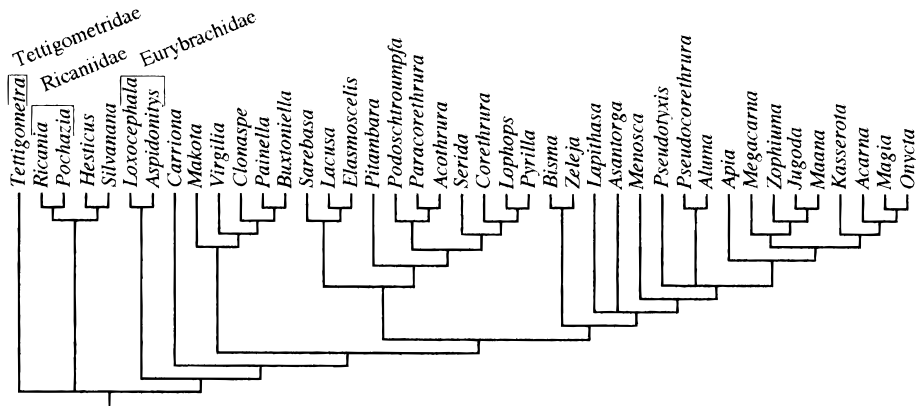
Discovering that *Hesticus* and *Silvanana* should really be considered as outgroup taxa, we ran a new heuristic



A



B



C

FIG. 26. Strict consensus of the nine cladograms obtained with five taxa in the outgroup (*Tettigometra*, *Loxocephala*, *Aspidonityx*, *Ricania*, and *Pochazia*); (A) cladogram topology observed when outgroup *Loxocephala* or *Aspidonityx* is entered first in the matrix; (B) cladogram topology observed when outgroup *Ricania* or *Pochazia* is entered first in the matrix, and (C) cladogram topology observed when outgroup *Tettigometra* is entered first in the matrix.

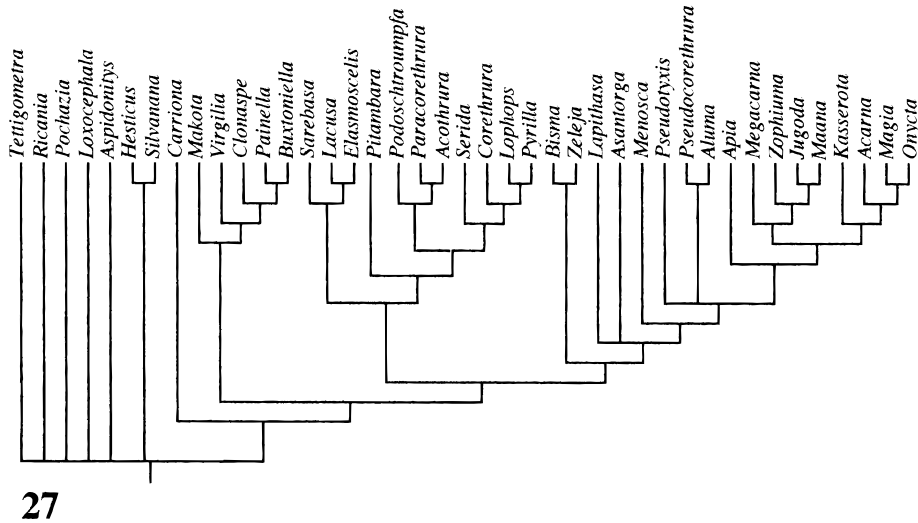


FIG. 27. Strict consensus of all trees obtained by outgroup permutations.

research in PAUP. Again nine cladograms were obtained and only the strict consensus is supported. Its length, CI, and RI are 152 steps, 0.526, and 0.783, respectively (Fig. 28). The Bremer index for each resolved node is presented in Fig. 29. This time, even if we change the order in which the outgroup taxa are entered into the matrix, the topology of the cladogram obtained remains stable. The monophyletic lineage presents the same topology as that observed previously but the organization between taxa in the outgroup is unique. For this reason this cladogram will be kept for the following studies.

The Ingroup

Within the Lophopidae, four main monophyletic groups will be discussed: Carriona⁺, Makota⁺, Bisma⁺, and Sarebasa⁺. The Lophopidae and these four groups are supported by a number of synapomorphies (Fig. 28).

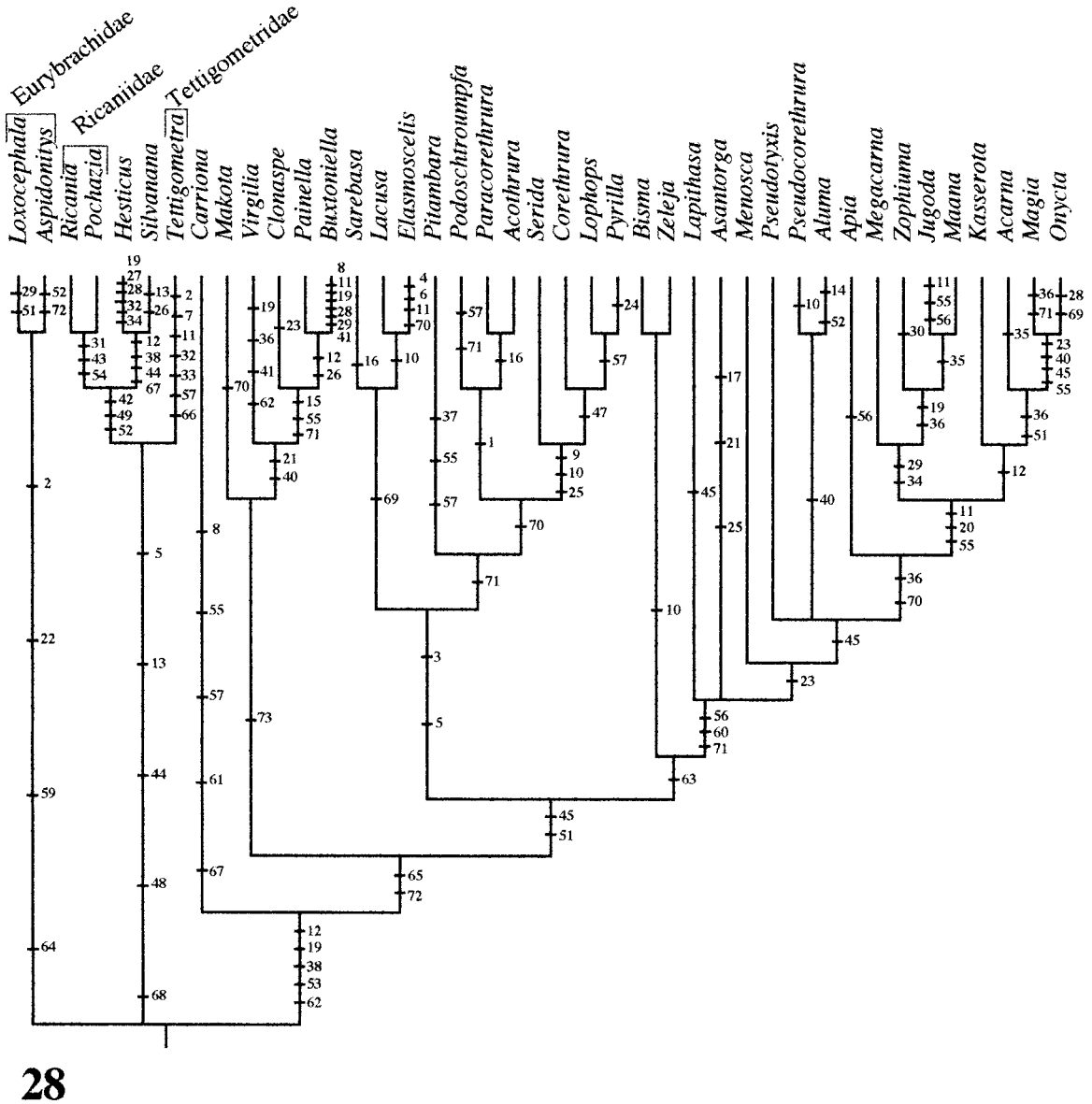
The genus *Carriona*, which is the only representative of the group Carriona⁺, with three species, is characterized by five synapomorphies. This genus is the only one for which the corpus connectivi is absent (character 61). Its ocelli are absent (character 8). The females of this genus have a posterior vaginal process absent (character 57) and on their bursa copulatrix no ornamentations are observable (character 55). The males present an edeagus that is not developed dorsally (character 67).

The Makota⁺ group is composed of five genera (*Makota*, (*Virgilia*, (*Clonasphe*, (*Painella*, *Buxtoniella*))))). The males of all these genera bear gonostyli not flattened laterally (character 73).

The Bisma⁺ group, composed of many genera (Fig. 28), is also characterized by one synapomorphy: the males have a periandrium with numerous folds (character 63). Note, however, that no male specimens of *Zeleja*, *Aluma*, or *Pseudocorethrura* were available for study.

The fourth group, Sarebasa⁺, also with many genera, has two synapomorphies: apex of the hind tibia bearing numerous small spines (character 3) and the first segment of the hind tarsus bearing a pad of microsetae (character 5).

We must not forget that the groups formed by Sarebasa⁺ + Bisma⁺ and Sarebasa⁺ + Bisma⁺ + Makota⁺ are equally monophyletic. Each of the two groups is supported by two synapomorphies. For the monophyletic lineage Sarebasa⁺ + Bisma⁺, both synapomorphies are linked to the female genitalia, the size of the upper lobe for the bilobate gonopods is reduced—not larger than 1.5 times the lower lobe (character 45), and the sacculiform structure is present (character 51). The group Sarebasa⁺ + Bisma⁺ + Makota⁺ is supported by two synapomorphies linked to the male genitalia, the ventral endosoma is absent (character 65), and the gonostyli are not attached to each other (character 72).



28

FIG. 28. Strict consensus of the nine cladograms obtained with seven taxa in the outgroup (*Tettigometra*, *Loxocephala*, *Aspidonitys*, *Ricania*, *Pochazia*, *Hesticus*, and *Silvanana*). Each character number correspond to a nonambiguous synapomorphy.

Character Transformation Scenarios

The location of homoplasy on the cladogram depends on the chosen character optimizations (Acctran, Deltran, or Minf) (Kitchin, 1992). For this phylogeny 13 characters present different possible optimizations. For 4 of them, only one optimization is considered plausible.

Character 39 All lophopid females have an anal

tube prolonged posteriorly as a pair of lobes, whereas the Eurybrachidae have an anal tube prolonged posteriorly but without any lobe and compressed laterally. Females of Ricaniidae, Tettigometridae, *Hesticus*, and *Silvanana* have small anal tubes without posterior prolongation. Three optimizations are possible (Fig. 30). Because elongate and ornamented anal tubes with lobes have been observed only in Lophopidae, we reject the Minf optimization, thus leaving only the second

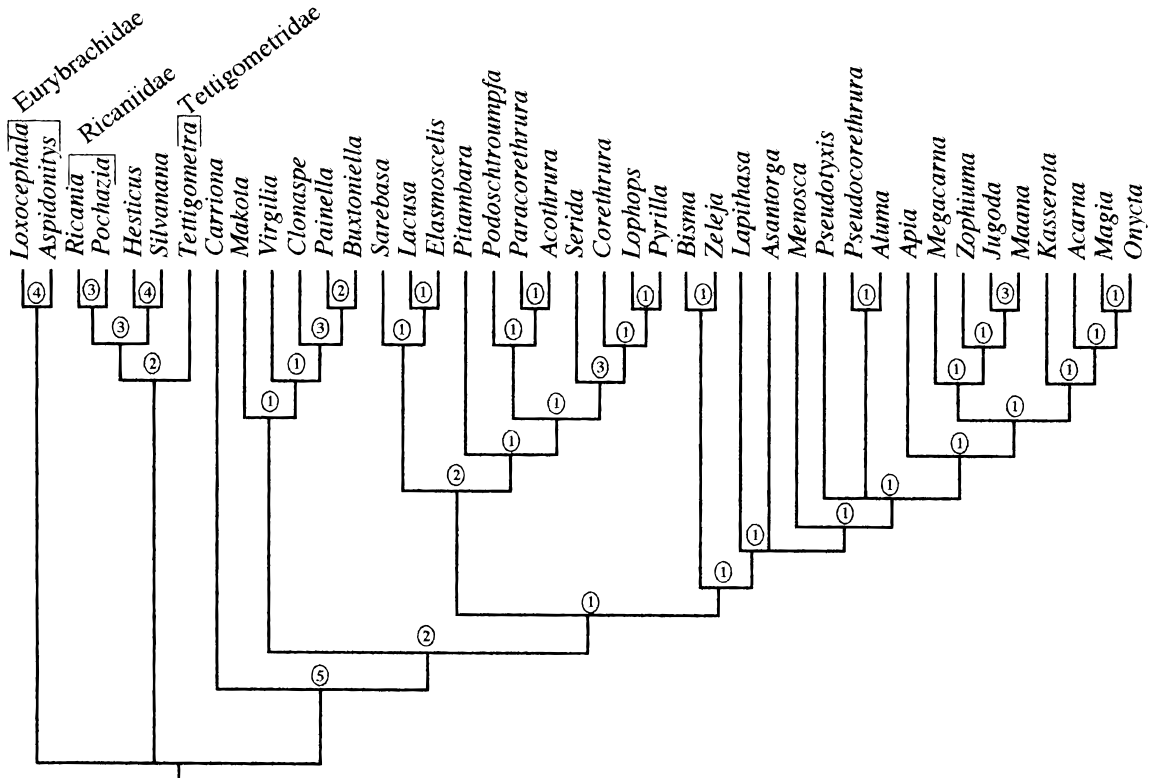


FIG. 29. Strict consensus of the nine cladograms with the decay index indicated for each node resolved.

and third optimizations as plausible. A fourth optimization however, is possible if it is true that the Eurybrachidae is the sister group of the Lophopidae. The common ancestor of the Eurybrachidae and Lophopidae derived a simple elongated anal tube (not observed in any extant taxa), which subsequently swelled apically into two lobes in ancestral Lophopidae and compressed laterally in ancestral Eurybrachidae.

Character 46. Two optimizations are possible here (see Fig. 31). The gonocoxal base was lost independently in the Lophopidae and Tettigometridae (Acctran and Deltran) or was derived independently at least twice in Ricaniidae + *Hesticus* + *Silvanana* and in the Eurybrachidae (Minf). Within the female genitalia of the insects presenting a gonocoxae IX (gonocoxal base IX + gonoplac), the gonocoxal base IX is considered to be part of the ground plan (Snodgrass, 1933). Thus the optimization given by Acctran and Deltran is most plausible.

Character 47. For this character four optimizations are possible (see Fig. 32). With the optimization given

by Acctran and Deltran, the gonapophysis IX, present in the ancestral Fulgoromorpha, would have disappeared or become strongly reduced in the families Tettigometridae and Lophopidae. The peculiar shape of the gonapophysis of *Aspidonityx* is characteristic of this genus. The three other optimizations (Minf and 2 manual) suggest that the ancestral condition of gonapophysis IX is to be reduced or absent. As showed by Bourgoïn (1993), the Fulgoromorpha generally possess some development of gonapophysis IX. According to his observations, therefore, only the optimization given by Acctran and Deltran is plausible.

Character 58. Within the upper Fulgoromorpha [sensu Bourgoïn (1993), all families but Cixiidae, Dephacidae, Kinnaridae, and Meenoplidae], the female genitalia present a bridge between the gonospiculum and the vaginal process (see Fig. 33). This bridge was absent in the examined Tettigometridae and in all Lophopidae. The Tettigometridae does not have this bridge because of the absence of posterior vaginal process, whereas for the Lophopidae this bridge is absent

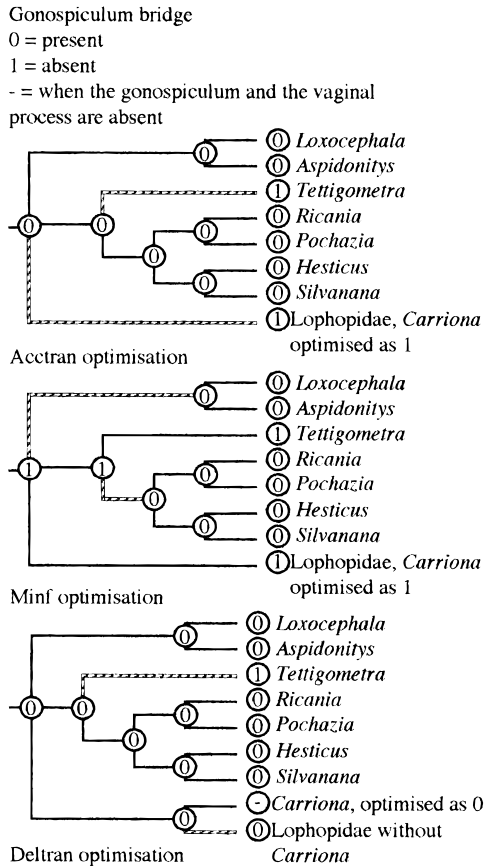


FIG. 33. Possible optimizations for character 58.

and appeared within the Eurybrachidae and at the base of the group *Hesticus* + *Silvanana* + *Ricaniidae*. The ingroup and the outgroup are considered as upper Fulgoromorpha. This bridge must be in their ground plan (Bourgoin, 1993). The optimization Minf is therefore rejected, leaving only the Acctran optimization as plausible.

Impact of Male and Female Characters upon the Phylogeny

To investigate the impact of sex-linked characters on our phylogeny, cladograms are generated after first the female and then the male characters are subtracted. By comparing the resultant cladograms with the cladogram obtained using all the characters available (Fig. 28), this allows us to see how female and male characters affected our phylogeny.

Cladogram Obtained without the Use of Female Characters

Twenty-one characters concern the females directly; if we withdraw them from the original matrix, 52 characters will be used in the new parsimony analysis. After a heuristic search, 1968 cladograms are retained with a length, CI, and RI equal to 97, 0.51, and 0.78, respectively. On the strict consensus tree obtained (Fig. 34), *Carriona* is still the sister group of all the other Lophopidae. *Sarebasa*⁺ and *Makota*⁺ remain monophyletic when the *Bisma*⁺ group does not appear any more as a monophyletic lineage. The phylogeny of the family (Fig. 28) is strongly disrupted basally. Some apical groups are no longer resolved and some new polytomies are observed (e.g., the three clades including *Megacarna*, *Sarebasa*, and *Serida*). The phylogeny of this family appears to be disrupted on two different levels, apically between a small number of genera and basally in the resolution between the four monophyletic groups *Sarebasa*⁺, *Makota*⁺, *Bisma*⁺, and *Carriona*⁺.

Cladogram Obtained without the Use of Male Characters

When we withdraw the 14 characters linked to the males, the new parsimony analysis will be done with 59 characters. The heuristic search gives seven cladograms. Each of them presents a tree length, CI, and RI equal to 120, 0.53, and 0.77, respectively. The strict consensus tree (Fig. 35) shows that the Lophopidae remain a monophyletic lineage. *Sarebasa*⁺ is also still a monophyletic group but is partially resolved. *Carriona* no longer appears as the sister group of all other Lophopidae; *Virgilia* now occupies this position. *Makota*⁺ and *Bisma*⁺ do not appear as monophyletic groups.

When we compare these two gender-based phylogenies, some differences are observed. Neither the absence of female characters nor the absence of the male characters disrupts the monophyly of *Sarebasa*⁺, which is supported by two autapomorphies located on the hind legs. Without male characters in the phylogeny, the four groups (*Sarebasa*⁺, *Carriona*⁺, *Makota*⁺, and *Bisma*⁺), previously observed and taken as a whole, remain despite some polytomies within them. When female characters are absent, some polytomies observed on the tree are located basally among the four

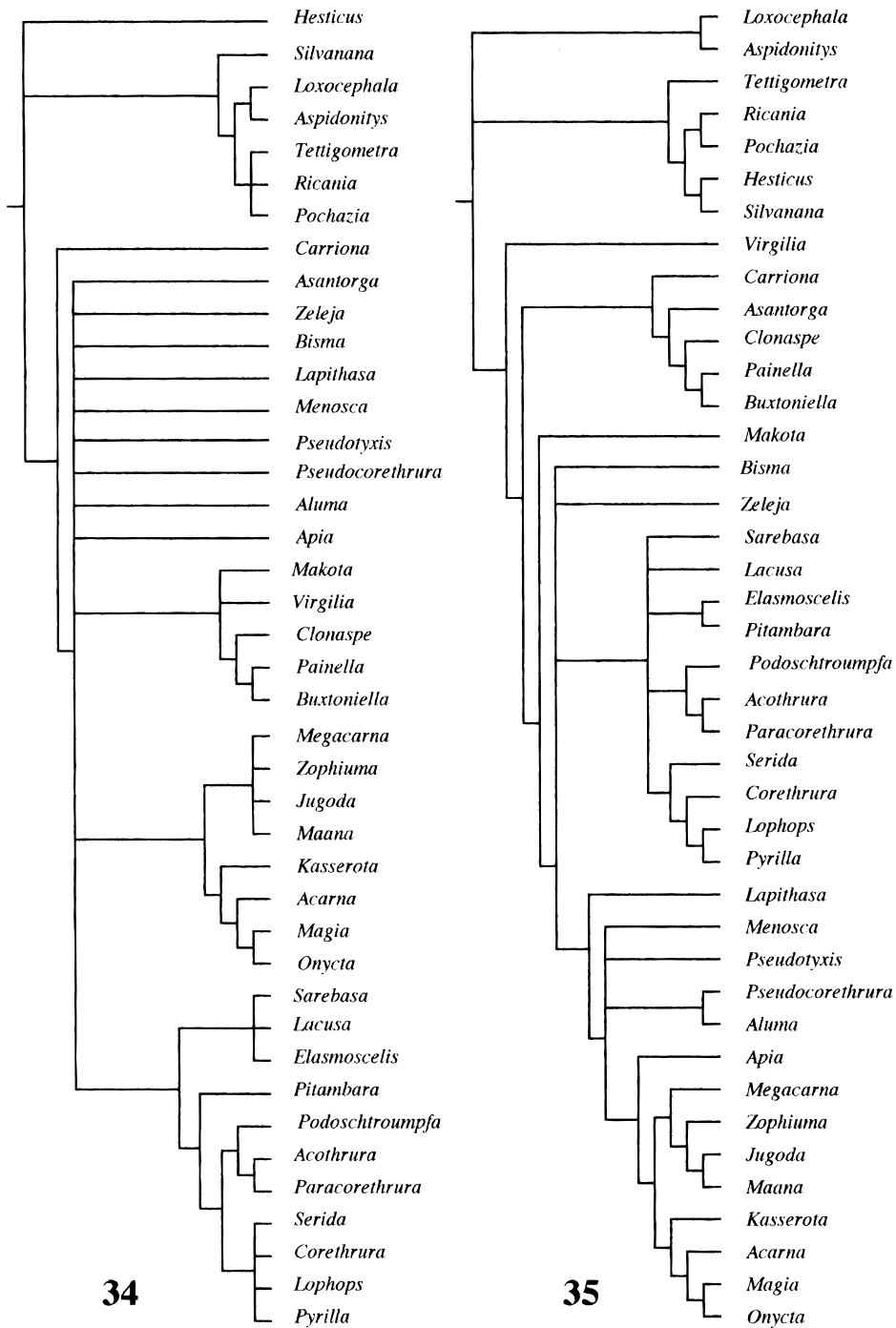


FIG. 34. Strict consensus of the trees obtained when all the characters linked to the females are withdrawn from the original matrix.

FIG. 35. Strict consensus of the trees obtained when all the characters linked to the males are withdrawn from the original matrix.

groups. The Bisma⁺ group is strongly disrupted and only the eight terminal taxa remain as a monophyletic lineage. Very apically this phylogeny is disrupted and the resolution between three to four genera collapse. From these observations, it appears that the female characters carry a phylogenetic signal on the basal evolution of the Lophopidae while the male characters bring information higher in the cladogram, and then again the female characters are informative and are implicated in the apical resolution of this cladogram. Alternatively, male and female characters bring information at different levels of the resolved cladogram.

It is hypothesized that there is a sexual conflict between males and females over the control of fertilization (Eberhard, 1985; Alexander *et al.*, 1997; Sculier-Perkins and Bourgoïn, 1998). We can expect that morphological changes will occur in the genitalia and will be linked to these characters, giving some benefit over the control of fertilization for the carrier. These differences in morphology should be observable in the females, then in the males, and so on over time.

Very apically on the Lophopidae cladogram the female characters are informative. If these observed characters are the result within the female of the sexual conflict over the control of fertilization, we may observe some convergence in these characters and a high level of homoplasy. When we observe the distribution of the female and male characters according to their consistency index, we notice that 5 of the 21 female characters present a CI lower than 0.5, whereas for the male characters only 1 of the 12 is lower than 0.5. The level of homoplasy is higher for the female characters than for the male characters. The alternation of informative characters linked to the sexes observed in the phylogeny of the Lophopidae supports the hypothesis of sexual conflict between male and female over the control of fertilization.

CONCLUSIONS

The Lophopidae can be considered as a monophyletic group after the taxa *Hesticus* and *Silvanana* are withdrawn. This family is recognizable by two autapomorphies, both linked to the females. This study enables us to present for the first time the phylogeny of the Lophopidae. The phylogeny was used together

with more general studies on Fulgoromorpha to choose the most plausible histories of equally parsimonious optimizations of four characters. The evolution of the female and male characters of this family supports the hypothesis of sexual conflict between males and females over the control of fertilization in which there is a coevolutionary arms race between sexes, driving the evolution of sexual morphological traits (Arnqvist and Rowe, 1995). The disruptions inflicted to the phylogeny by withdrawing either the female characters or the male characters yielded two conclusions. (1) A phylogeny can be used to trace along in time how a sexual selection has been working on the evolution of a monophyletic lineage and which type of sexual selection is responsible for these morphological changes. (2) Also, for an accurate phylogeny, it is important to include both male and female characters along with all the other available characters and, if possible, the holomorph.

APPENDIX 1: CHARACTER LIST FOR THE MATRIX OF TABLE 1

1. Regular line of brown spots of profemur: (0) absent; (1) present
2. Lateral and external spines of hind tibia: (0) present, 2 or 3; (1) present, 4 or more; (2) absent
3. Apical spines of hind tibia: (0) large and never more than 12; (1) small and generally numerous
4. Pad of microsetae on the apex of hind tibia: (0) absent; (1) present
5. Apical spines of the first segment of the hind tarsus: (0) organized in a line; (1) form a triangular zone; (2) organized in two lots separated by a pad of microsetae
6. Shape of the pad of microsetae on the apex of hind tibia: (0) striated lengthways; (1) not striated; (–) for the taxa without pad of microsetae
7. Apical spines on the second segment of the hind tarsus: (0) present and one on each side; (1) absent
8. Lateral ocelli: (0) present; (1) absent
9. Frontal disc hollowed longitudinally: (0) no; (1) yes
10. Median carina of the frons: (0) present (sometimes faint); (1) absent

TABLE 1
Data Matrix for Lophopidae and Five Outgroup Taxa: Two Eurybrachidae, *Loxocephala* sp. Schaum and *Aspidonitys* sp. Lallemand; One Tettigometridae, *Tettigometra* sp. Latreille; and Two Ricaniidae: *Ricania* sp. Germar and *Pochazia* sp. Amyot and Seville

	—	—	—	—	—	—	—	—	—	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3											
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7										
<i>Tettigometra</i>	0	2	0	0	0	—	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0									
<i>Loxocephala</i>	0	1	0	0	1	—	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	—	0	0	0	0	0									
<i>Ricania</i>	0	0	0	0	0	—	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0									
<i>Pochazia</i>	0	0	0	0	0	—	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0									
<i>Aspidonitys</i>	0	1	0	0	1	—	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0									
<i>Hesticus</i>	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	1	1	0	0	0	0	0	1	0	0	0									
<i>Silvanana</i>	0	0	0	0	0	—	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0									
<i>Carriona</i>	0	0	0	0	1	—	1	1	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	1	0	0	0	0									
<i>Lophops</i>	0	0	1	0	2	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0								
<i>Serida</i>	0	0	1	0	2	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0								
<i>Corethrura</i>	0	0	1	0	2	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0								
<i>Pyrila</i>	0	0	1	0	2	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0								
<i>Paracorethrura</i>	1	0	1	0	2	0	1	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	0	1	0	0	0	0								
<i>Acothrura</i>	1	0	1	0	2	0	1	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	0	0	1	0	0	0	0							
<i>Lacusa</i>	0	0	1	0	2	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0								
<i>Sarebasa</i>	0	0	1	0	2	0	1	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	0	1	0	0	0	0								
<i>Elasmoscelis</i>	0	0	1	1	2	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0								
<i>Pitambara</i>	0	0	1	0	2	0	1	0	0	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1							
<i>Podoschtroumpfa</i>	1	0	1	0	2	0	1	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	0	0	1	0	0	0	0							
<i>Jugoda</i>	0	0	0	0	1	—	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0						
<i>Lapithasa</i>	0	0	0	0	1	—	1	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	0	0	1	0	0	0	0							
<i>Apia</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0						
<i>Menosca</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0							
<i>Makota</i>	0	0	0	0	1	—	1	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	0	0	1	0	0	0	0							
<i>Virgllia</i>	0	0	0	0	1	—	1	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	0	0	1	0	0	0	2	0						
<i>Painells</i>	0	0	0	0	1	—	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0						
<i>Clonaspe</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0						
<i>Buxtoniella</i>	0	0	0	0	1	—	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	—	—	0	—	0	—	0	0	0	0	0							
<i>Magia</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	—	0	1	1	0	0			
<i>Zophiuma</i>	0	0	0	0	1	—	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	2	0			
<i>Kasserota</i>	0	0	0	0	1	—	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	—	0	1	0	1	0		
<i>Megacarna</i>	0	0	0	0	1	—	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0		
<i>Acarna</i>	0	0	0	0	1	—	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	—	0	1	0	0	0	
<i>Onycta</i>	0	0	0	0	1	—	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
<i>Pseudotyxis</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0			
<i>Maana</i>	0	0	0	0	1	—	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0		
<i>Bisma greeni</i>	0	0	0	0	1	—	1	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	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
<i>Pseudocorethrura</i>	0	0	0	0	1	—	1	0	0	0	0	1	0	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	1	0	0	0	1	0	0	
<i>Aluma</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	1	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	0/1	0	0	0	0
<i>Asantorga</i>	0	0	0	0	1	—	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0
<i>Zejeja</i>	0	0	0	0	1	—	1	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	0	0	0	0	0	0	0	0	0	0	0	0	0

11. Lateral carinae of the frons: (0) present and continuous from the frons–vertex suture to the frontoclypeal suture; (1) present but incomplete

12. Median height of the frons compared to its maximal width: (0) higher than wide; (1) wider than high

13. Lateral margins of the frons shaped as a flattened arc of a circle: (0) yes (Fig. 11); (1) no

14. Sublateral carinae of the frons: (0) not swollen or absent; (1) swollen

15. Transverse colored stripes on the frons: (0) absent; (1) present

16. Regular disposed brown patches between the lateral margins and the sublateral carinae of the frons: (0) no; (1) yes

TABLE 1—Continued

	3	3	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7	7	7	7	
	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	
<i>Tettigometra</i>	0	0	—	0	1	0	0	—	1	1	0	1	2	1	1	0	1	0	0	1	1	—	0	0	0	0	0	0	0	0	0	—	—	—	0	0	
<i>Loxocephala</i>	0	1	—	0	1	0	2	0	0	0	1	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	—	—	—	0	0	
<i>Ricania</i>	0	0	—	0	0	1	0	—	0	0	0	0	0	1	0	0	0	1	0	—	0	1	0	0	0	0	0	0	1	0	0	—	—	—	0	0	
<i>Pochazia</i>	0	0	—	0	0	1	0	—	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	—	—	—	0	0	
<i>Aspidonitys</i>	0	1	—	0	1	0	2	0	0	3	1	1	2	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	—	—	—	1	0	
<i>Hesticus</i>	1	0	—	0	0	0	1	—	0	0	0	0	1	1	0	0	1	2	0	0	0	1	?	0	0	0	0	0	1	1	0	—	—	—	0	0	
<i>Silvanana</i>	1	0	—	0	0	0	1	—	0	0	0	0	1	1	0	0	1	2	0	0	0	1	?	0	0	0	0	0	1	1	0	—	—	—	0	0	
<i>Carriona</i>	1	2	0	0	1	0	2	0	1	1	1	1	2	1	1	1	1	2	0	1	—	—	0	1	1	0	0	0	1	1	1	—	—	—	0	0	
<i>Lophops</i>	1	2	2	0	1	0	2	1	1	2	1	1	2	0	1	1	1	0	0	1	—	—	0	0	1	0	0	1	1	0	1	1	1	0	1	0	
<i>Serida</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	0	0	1	1	0	1	1	1	0	1	0	
<i>Corethrura</i>	1	2	2	0	1	0	2	1	1	2	1	1	2	0	1	1	1	?	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Pyrila</i>	1	2	2	0	1	0	2	1	1	2	1	1	2	0	1	1	1	0	0	1	—	—	0	0	1	0	0	1	1	0	1	1	1	0	1	0	
<i>Paracorethrura</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Acothrura</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	0	0	1	1	0	1	1	1	0	1	0	
<i>Lacusa</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	0	1	1	0	
<i>Sarebasa</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	0	0	1	?	0	1	0	0	1	1	0	
<i>Elasmoscelis</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	1	1	1	0	
<i>Pitambara</i>	1	2	2/3'	0	1	0	2	1	1	1	1	1	2	0	1	1	1	2	0	1	—	—	0	0	1	0	0	1	1	0	1	1	0	0	1	0	
<i>Podoschtroumpfa</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	1	—	—	0	0	1	0	0	1	1	0	1	1	1	1	1	0	
<i>Jugoda</i>	1	2	3	0	1	0	2	1	1	1	1	1	2	1	1	1	1	0	1	0	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1	0	
<i>Lapithasa</i>	1	2	2	0	1	0	2	2	1	1	1	1	2	0	1	1	1	0	1	0	1	1	1	0	1	1	0	1	1	0	1	1	0	2	1	0	
<i>Apia</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	0	1	1	1	0	0	0	1	1	1	0	1	1	0	1	1	0	1	1	1	2	1	0	
<i>Menosca</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	0	1	0	2	1	0
<i>Makota</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	1	1	1	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1
<i>Virglia</i>	1	2	1	1	1	0	2	0	1	1	1	1	2	1	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1	0	1	1	1	
<i>Painella</i>	1	2	1	0	1	0	2	0	1	1	1	1	2	1	1	1	1	2	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	3	1	1	
<i>Clonaspe</i>	1	2	1	0	1	0	2	0	1	1	1	1	2	1	1	1	1	2	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	3	1	1	
<i>Buxtoniella</i>	1	2	1	1	1	0	2	0	1	1	1	1	2	1	1	1	1	2	0	0	1	1	1	0	0	1	1	0	1	1	0	1	1	0	3	1	1
<i>Magia</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	0	1	1	1	0	0	0	1	1	1	0	1	1	0	1	1	0	1	1	1	1	2	1	0
<i>Zophiuma</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	1	1	1	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	0	1	2	2	1	0
<i>Kasserota</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	0	1	1	1	2	1	0	
<i>Megacarna</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	0	1	1	2	2	1	0	
<i>Acarna</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	0	1	1	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	1	2	1	0		
<i>Onycta</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	0	1	1	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	1	2	1	0		
<i>Pseudotyxis</i>	1	2	2	0	1	0	2	0	1	1	1	1	2	?	1	1	1	0	1	0	1	0	1	1	0	1	?	0	1	1	0	1	0	2	1	0	
<i>Maana</i>	1	2	3	0	1	0	2	1	1	1	1	1	2	1	1	1	1	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	1	2	1	0	
<i>Bisma greeni</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	2	0	1	1	0	
<i>Pseudocorethrura</i>	1	2	0	0	1	0	2	0	1	1	1	1	2	0	1	1	1	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Aluma</i>	1	2	0	0	1	0	2	0	1	1	1	1	2	0	0	1	1	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Asantorga</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Zelega</i>	1	2	2	0	1	0	2	1	1	1	1	1	2	?	1	1	1	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

Note. Missing data are indicated by question marks; nonapplicable characters are indicated by dashes. The data matrix represents, 41 taxa and 73 characters.

17. Sensorial protuberances on the frons: (0) absent; (1) present

18. Median carina of the clypeus: (0) present; (1) absent

19. Lateral carinae of the clypeus: (0) present; (1) absent

20. Ocellar carinae: (0) absent; (1) present

21. Genal carinae: (0) absent; (1) present

22. Apex of the labium: (0) cut perpendicularly to its longitudinal axis (Fig. 14A) (1) bevel-edged (Fig. 14B)

23. Length of the labium: (0) short, not reaching the metatrochanters; (1) long, extending beyond metatrochanters

24. In dorsal view, length of vertex, and frons longer than 1/4 of insect's total length: (0) no; (1) yes
25. In lateral view, the base of the frons continue the vertex: (0) no (Fig. 15A); (1) yes (Fig. 15B)
26. Angle between the clypeal tangent and the vertex plan: (0) more than 40° (Fig. 16B); (1) less than 22° (Fig. 16A)
27. Length of the pedicel of the antenna compared to its diameter: (0) not longer than 2 times its diameter; (1) 3 times longer than its diameter
28. Foramen of the antenna separated from the compound eye base: (0) yes; (1) no
29. Costal vein on the tegmina: (0) present, at least basally; (1) absent; (–) not recognizable
30. Position of the cubital vein on the tegmina: (0) clearly distinct from the cubital fold; (1) parallel and very close to the cubital fold; (–) venation not recognizable
31. Length of the cubital fold on the tegmina: (0) extending to 2/3 of the tegmina length; (1) extending nearly to the apex of the tegmina
32. On the tegmina, costal vein distinct to the costal margin: (0) only from the base of the wing to half the distance to the nodal area; (1) from the base of the wing to the nodal area especially; (–) venation not recognizable
33. Median carina on the posterior wing: (0) not curved; (1) curved
34. Surface of the tegmina: (0) at least 80% colored; (1) at least 60% transparent
35. Ocellus of color on the tegmina: (0) absent; (1) present
36. Mesothoracic median carina: (0) simple or absent; (1) paired but welded anteriorly; (2) paired and completely independent
37. Anterior margin of the prothorax: (0) rounded; (1) pointed anteriorly
38. Distance between the external margin of the compound eyes compared to the prothorax maximal width: (0) equal; (1) inferior
39. Anal tube: (0) small and not prolonged posteriorly; (1) prolonged posteriorly and squeezed laterally; (2) prolonged posteriorly by a pair of lobes
40. Shape of the anal lobes: (0) partially welded and lightly squeezed ventrally; (1) small lobes dorsally oriented; (2) large lobes dorsally and ventrally oriented; (3) large lobes extending laterally and covering the gonoplares; (–) female without any lobes
41. Median and ventral extension of the posterior apex of the anal tube: (0) absent; (1) present
42. Insertion of the gonoplares: (0) attached by a large base well sclerotized; (1) attached by a narrow base partially sclerotized or membranous
43. Strong teeth on the external margin of the gonoplares: (0) absent; (1) present
44. Shape of the gonoplares: (0) one lobe and shaped as a triangle; (1) multilobate; (2) bilobate, the second lobe can be very reduced
45. Size of the upper lobe for the bilobate gonoplares: (0) large, much larger than the lower lobe; (1) reduced, not larger than 1.5 times the lower lobe
46. Gonocoxal base IX: (0) present but reduced; (1) absent
47. Gonapophysis IX: (0) relatively developed, elongated, and slender; (1) reduced or absent; (2) reduced to a median membranous lobe; (3) type *Aspidonitys*
48. Gonocoxae VIII: (0) present and shaped as two large plates; (1) present but reduced
49. Gonapophysis VIII: (0) well developed; (1) reduced
50. The gonapophysis ornamentation: (0) present and shaped like teeth; (1) present and shaped like lobes; (2) absent
51. Sacculiform structure: (0) present; (1) absent
52. Endogonocoxal process: (0) present; (1) absent or extremely reduced
53. Gonospiculum: (0) present; (1) absent
54. Number of chambers in the bursa copulatrix: (0) 2; (1) 1
55. Bursa copulatrix ornamentation: (0) small cuticular growth present but not limited by a circular ring; (1) small cuticular growth present and limited by a circular ring; (2) small cuticular growth absent
56. Vagina sclerotization at spermatheca attachment: (0) membranous; (1) strongly sclerotized
57. Posterior vaginal process: (0) present; (1) absent
58. Gonospiculum bridge: (0) present; (1) absent; (–) when the gonospiculum and the posterior vaginal process are absent
59. Orientation of the posterior vaginal process: (0) posteriorly; (1) anteriorly; (–) taxa for whom the posterior vaginal process is absent
60. Lateral part of the anal tube: (0) not extended latero-ventrally; (1) extended latero-ventrally
61. Corpus connectivi: (0) present; (1) absent

62. Shape of the tectiform structure in lateral view: (0) triangular; (1) spatulate
63. Shape of the dorsal periandrium: (0) less than 3 folds in each side; (1) complex, more than 3 folds on each side
64. Visibility of the aedeagus s.l.: (0) not directly observable—only the processes extend beyond the periandrium; (1) directly observable—the periandrium is widely open
65. Ventral endosoma: (0) present; (1) absent
66. Bursa of the endosoma: (0) present; (1) strongly reduced to absent
67. Dorsal development of the aedeagus: (0) yes; (1) no
68. Ventral development of the aedeagus: (0) yes; (1) no
69. Ventral anterior process of the aedeagus s.s.: (0) absent; (1) present and simple; (2) present and divided in two apically
70. Ventral posterior process of the aedeagus s.s.: (0) absent; (1) present and simple; (2) present and divided in two
71. Apical extension of the aedeagus s.s.: (0) absent; (1) present and spine shaped; (2) present and complex apically; (3) present and rounded apically
72. Gonostyli: (0) partially attached to each other; (1) not attached to each other
73. Shape of the gonostyli: (0) flattened laterally; (1) not flattened laterally.

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Note added in proof. Changes in the nomenclature of a group, and especially changes made at the supra-specific level, have many consequences. It would seem difficult to accept such changes without having first conducted phylogenetic research into the problem, which is why I object to the changes made by Liang (2000) to the classification of the Lophopidae. Liang proposes three new generic synonymies: *Corethrura* Hope, 1843 and *Serida* Walker, 1857 with *Lophops* Spinola, 1839 and *Sarebasa* Distant, 1909 with *Lacusa* Stål, 1862. As shown by the phylogenetic analysis in this paper, the characters clearly allow separation of

these taxa which, if we follow Liang's proposition, would lead us to recognise a polyphyletic genus *Lacusa* sensu Liang. It is for this reason that I propose to revert to the original classification with five distinct genera: *Lophops*, *Corethrura*, *Lacusa*, *Serida*, and *Sarebasa* and to reject Liang's synonymies. Liang also states that "*Lophops* is distributed in Africa, Asia and Australia. Its sister genus is probably *Pyrilla* Walker." It would be interesting to know what support he has for this statement, as it confirms the phylogeny presented above, where *Lophops* and *Pyrilla* appear as sister groups, and my provisional results presented at the 9th International Auchenorrhyncha Congress, 1997. Last, I should like to correct an error in Liang's article concerning the holotype of *Podoschtroumpfa magna* Soulier-Perkins. I have not, as of yet, sent the holotype to the Berenice P. Bishop Museum, so it could not have been "[examined]," as written by the author.

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