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## A cladistic analysis of the tribe Bactrophorini (Bactrophorinae, Romaleidae)

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### Abstract

The tribe Bactrophorini of the Bactrophorinae is briefly reviewed. Two new genera are erected: *Mayalina*, and *Hylaezentia*. Three new species (*M. cohni*, *M. teapensis* and *M. chajulensis*) of *Mayalina* are described. A key to the genera of the tribe is included.

A cladistic analysis of morphological characters indicates that the Bactrophorini genera fall into two well-supported clades. The first, ("Hyleacrae", after its most basal member) has as its basal branches, the exclusively Amazonian *Hyleacris* and the Amazonian and Central American *Bactrophora*; as its crown group it contains all the remaining Central American genera except *Mezentia*. The Central American genera of the Hyleacrae fall into two lineages: first, the sister genera *Cristobalina* and *Mayalina* (the "Cristobalina genus group") of Mexico, Guatemala, and Honduras, and secondly the "Rhicnoderma genus group", composed of four genera (*Rhicnoderma* Gerstaecker, 1889, *Lempira* (Rehn, 1938) and *Pararhicnoderma* Rowell, 2012, which occur from Southern Mexico south to Panama, plus the Panamanian endemic *Panamacris* Rehn, 1938, which is apparently the sister genus of *Rhicnoderma*).

The second clade of the tribe ("Borae", after its most basal member, *Bora*) contains four exclusively Amazonian genera, plus the fifth and most derived genus, *Mezentia*, which has both Central American and Colombian species. In the Borae there is a second basal genus, *Silacris*, and then a crown group consisting of three very closely related genera, *Mezentia*, *Andeomezentia* and *Hylaezentia*, here referred to as the "Mezentia genus group".

### Key words

grasshoppers, Neotropics, new genera, new species, phylogeny, cladistic analysis

### Preface

In the middle of the 1990s Dr. Christiane Amedegnato (CA) gathered together at the Paris museum (MNHN) all available specimens of the Bactrophorini, soliciting them both from the major museums and from private collections, such as that of CHFR. She worked on this material intermittently over the next 10 y, with the intention of reviewing the tribe. Early in 2010 CHFR wrote to her requesting news of her progress and the return of his specimens. In her reply she indicated that she was seriously ill with cancer, enclosed a variety of computer files documenting some aspects of her work on the Bactrophorini and gave instructions that he should deal with these materials as he felt fit.

Dr. Amedegnato died on 20<sup>th</sup> June, 2010, without having published anything further on the Bactrophorini, and leaving no completed manuscript. Early in September, 2010 CHFR and SP met in the MNHN to review the digital materials and the available specimens and to consider what should be done with them. Unfortunately, CA left us no anatomical drawings or descriptions of the new species

she proposed to erect. Further, it was not practical either to transfer all the specimens (which included, beside the loaned materials mentioned above, the extensive holdings of the MNHN itself, mostly collected by CA, SP and the late M. Descamps) to CHFR's laboratory in Switzerland, nor for him to spend an extended period in Paris to work on the specimens there. We therefore decided against attempting the full scale review of the Bactrophorini which had been CA's original intention.

On the other hand, CA had prepared a morphological character matrix for nearly all the Bactrophorine genera, including all those already published and several new ones which she proposed to erect, in preparation for a cladistic analysis. It is essentially this material we present here, the analysis of her matrix having yielded a well-supported phylogeny. Inevitably, it includes some rather poorly defined taxa: these are the new genera that CA proposed to erect, presumably before publishing the phylogeny, but never did. We think however, that the value of the analysis outweighs this defect.

### Introduction

The Bactrophorini are one of three tribes into which the Neotropical subfamily Bactrophorinae Amedegnato, 1974 is divided: the Taeniophorini Brunner von Wattenwyl, 1893, the Ophthalmolampini Descamps, 1978, and the Bactrophorini Amedegnato, 1974. Early in 2011 the tribe contained only 9 valid genera and 21 valid species. It thus comprises only a small part of the subfamily as a whole (36 valid genera, 195 valid species (Eades *et al.*, accessed September 2010). The subfamily is poorly known and many further species are awaiting description, or probably are still unknown. The majority are arboreal grasshoppers of the Neotropical rain forest, and both their collection and their observation are very difficult.

Amedegnato (1974) gave the Bactrophorinae subfamily rank (originally under the name Trybliophorinae, but the original type genus *Trybliophorus* later transpired to be a Romaleine) and grouped them with the Romaleinae as the family Romaleidae. This allotment of the Bactrophorinae was made primarily on the basis of their male genitalia, which Amedegnato (1977) interpreted as a primitive version of the form characteristic of the rest of the Romaleidae (see also the Discussion below, p. 105); in that work and elsewhere (*e.g.*, Amedegnato & Descamps 1983) she refers to them as the most archaic of all the Cryptosacci [a term coined by Roberts (1943) to denote the more advanced subfamilies of acridoid grasshoppers — it is derived from phallic anatomy]. Molecular systematics, though to date using only mitochondrial ribosomal DNA sequences (Rowell & Flook 1998), confirm that the subfamily are indeed a rather early branch of the Acridoidea, but have not to date succeeded in linking them to the Romaleinae in a single clade corresponding to a family Romaleidae.

The characters thought to link the Bactrophorinae in general to the Romaleinae are the simple form of the cingulum, the aedeagus being either absent or consisting only of undifferentiated ventral and dorsal endophallic sclerites, the lack of a pre-apical diverticulum to the spermatheca, and the presence of an external apical spine on the hind tibia.

**General Description.**—The subfamily Bactrophorinae includes insects ranging from small to large size, usually brachypterous or micropterous, sometimes apterous, with powerful jumping hind legs, often large globular protruding eyes, and long antennae; the second tarsal joint of their hind foot is elongate, as long or nearly as long as the first joint. The tarsi, the hind tibiae, and the lower surfaces of the abdomen are richly provided with sensory hairs. Many species (especially in the tribes Taeniophorini and Ophthalmolampini) are brightly colored, and they probably rely mostly on visual intraspecific communication; they have no stridulatory apparatus and often no tympanum.

The tribe Bactrophorini consists predominantly of arboreal forms adapted for lying along medium-sized twigs; the thoracic sterna are concave to accommodate such a support, and the relatively wide, hair-fringed femora are arranged at rest to disrupt the outline of the animal and allow it to blend with the twig. Some genera (especially *Bactrophora* itself) have elongated rostra, which probably also serve a disruptive function. Females are usually bark colored, males are often similarly colored but in some genera tend to be green with smaller black, white, yellow or red markings. Both sexes are remarkably cryptic in their natural habitat. With one exception (*Mayalina* n.g.) the ovipositor valves are unmodified and apparently indicate oviposition in the ground.

**Bactrophorini diagnosis.**—Size moderate to large. Body form cylindrical, sometimes massive. Head orthognath or moderately prognath (except in *Mayalina*).

Fastigium variable, from extremely elongated (*Bactrophora*) to almost absent (*Rhcnoderma*, *Mezentia*). Lateral carinae of face and frontal ridge well marked. Eyes relatively small for the subfamily (except in *Cristobalina* and *Mayalina*). Interocular space wide, equal to or greater than the width of the frontal ridge between the antennae. Antennae filiform, with 20–25 flagellar segments. Pronotum usually cylindrical or sometimes (*Mezentia*, *Cristobalina*) selliform, very short, often exposing the mesothoracic notum. Disc of pronotum cut by up to 4 sulci. Lateral and medial pronotal carinae absent, except in the females of *Lempira* and *Pararhcnoderma*, where the median carina is somewhat nodular, or in *Cristobalina* & *Mayalina*, where it is cristate and toothed. Posterior margin of pronotum rectangular, slightly excurved in brachypterous genera. Anterior margin of pronotum typically slightly emarginate in midline, with two flanking projections overhanging the vertex. Prosternal process sometimes cylindrical, but typically transverse, anteroposterior compressed, the corners produced, with a tendency to become more or less bifid. Meso- and metasternum slightly concave. Mesosternal space variable.

Fore and middle femora short, robust, sometimes laterally compressed. Hind femora fairly short, not exceeding tip of the abdomen; length of femur divided by its maximum width varies from 3.5 to  $\geq 5.0$ . Hind tibiae noticeably hairy; 6–9 external and internal tibial spines, the inner spines sometimes strongly developed and inwardly curved. Hind tarsi very elongate, cylindrical and hairy.

Brachypterous or apterous; rudimentary elytra present in *Bora* and *Cristobalina*. Elytra if present densely reticulate, wings cycloid, blackish in color except in *Bactrophora*, where they are orange, and

*Mezentia*, where they are sometimes clear, sometimes infumate. Tympanum present or absent. Tenth abdominal tergite often divided, sometimes specialized. Supra-anal plate more or less triangular, divided into two by a transverse furrow, sometimes with a long tongue-shaped posterior process. Male cerci variable, from short and styliiform to complex, depending on the genus. Ovipositor valves robust, except in *Mayalina*. Male subgenital plate normal or long and pointed, sometimes bifid at the tip. Female subgenital plate usually normal, but ornamented with longitudinal ridges in the *Mezentia* genus group.

**Genitalia.**—The phallus is characterised by a particular type of epiphallus, and in some genera (the *Rhcnoderma* genus group) by having the middle and posterior parts of the endophallus in the form of two simple elongate rods.

a/ Epiphallic layer: lateroventral sclerites present or absent. When present, sometimes very large and more or less specialized. Epiphallus bridge shaped, varying from very small (width less than 20% of the length of the middle and posterior parts of the endophallus, *Rhcnoderma* genus group) to considerably larger (50–80%). *Ancorae* very inconspicuous, barely visible, usually poorly differentiated from the anterior processes of the lateral plates. *Lophi* usually digitiform and hooked, sometimes with a tendency to being flattened and fused with the posterior processes of the lateral plates. Oval sclerites sometimes present, varying in size.

b/ Ectophallic layer: cingulum poorly differentiated, sometimes capsular, frequently having an internal mediodorsal ridge; cingular apodemes almost absent or only roughly indicated, never long, always flat and sometimes massive. The rami meet or even fuse ventrally, are simple without any particular elaboration, or have a posteroventral projection from the zone of fusion. *Zygoma* with a mediodorsal projection, varyingly developed, either unitary or bilobed.

The ectophallic sheath covering the ends of the endophallic sclerites varies in form among the various genus groups, and sometimes (*Rhcnoderma* genus group) forms "aedeagal valves" in which the endophallic sclerites play no part. Arch of the cingulum absent, but sometimes there is a yoke (a "pseudoarch") formed from a thickening of the ecto-endophallic fold (*Mezentia* genus group).

c/ Endophallic layer: ejaculatory and spermatophore sacs both voluminous, sometimes bifid. The ejaculatory sac is often provided with tendon-like muscle attachments. The endophallic sclerites sometimes (*Rhcnoderma* genus group) have the form of long fine laterodorsal rods, completely lacking a differentiated posterior part and without a flexure. The apodemes of the endophallic sclerites are of variable size. Gonopore process thick and digitiform.

**Female genitalia.**—Subgenital plate with well-developed Comstock-Kellog pouches. Postvaginal sclerites present, but not very thick, mostly without columellae. Basivalvular sclerites present, but poorly differentiated. Base of the bursa copulatrix generally tubular, the orifice reinforced by a small crescent-shaped sclerite. Spermatheca with no pre-apical diverticulum.

## Taxonomy

The tribe currently comprises 11 genera (*Andeomezentia* Amedegnato & Poulain, 1994, *Bactrophora* Westwood, 1842, *Bora* Amedegnato & Descamps, 1979, *Cristobalina* Rehn, 1938, *Hyleacris* Amedegnato & Descamps, 1979, *Lempira* Rehn, 1938, *Mezentia* Stål,

**Table 1.** *Mayalina* spp. nov. Dimensions (in millimetres). Character abbreviations: L, length of body from frons to tip of abdomen. F, length of hind femur. FW, maximal width of hind femur. IOS, interocular space. FRW, width of frontal ridge (taken at level of antennae). A, length of antennal flagellum. h+p, length of head plus pronotum. Ta1, Ta2, Ta3, lengths of first, second and third tarsal joints of the hind foot. "Foot formula", the relative lengths (as percentage of their total) of first, second and third tarsal joints of the hind foot. Shaded cells are ratios, not dimensions.

Species	Specimen	ANT	IOS	FRW	FRW/ IOS	F	FW	P	h+p	A/h+p	L	Ta1	Ta2	T3	Ta1+2+3	Sex.Dim. Lm/Lf
<i>M. teapensis</i>	Male Holotype	broken	1.75	0.91	0.52	10.57	2.02	3.00	5.20	?	20.05	1.82	1.46	1.85	5.13	0.69
	Foot formula:										0.35	0.28	0.36	1.00		
	Female Allotype	7.40	2.80	1.40	0.50	13.50	2.86	3.82	7.40	1.00	29.20	2.48	1.79	2.17	6.44	
Foot formula:										0.39	0.28	0.34	1.00			
<i>M. cohni</i>	Male Holotype	6.66	1.71	0.83	0.49	9.76	1.91	2.56	5.20	1.28	17.69	1.60	1.22	1.28	4.10	0.81
	Foot formula:										0.39	0.30	0.31	1.00		
	Female Allotype	6.57	2.23	1.13	0.51	11.25	2.20	3.00	6.20	1.06	21.80	1.90	1.28	1.62	4.80	
Foot formula:										0.40	0.27	0.34	1.00			
<i>M. cajulensis</i>	Male Holotype	7.75	1.82	0.95	0.52	10.23	1.85	2.79	5.24	1.48	19.80	1.71	1.30	1.73	4.74	0.81
	Foot formula:										0.36	0.27	0.36	1.00		
	Female Allotype	6.00	2.20	1.11	0.50	11.40	2.37	3.51	6.60	0.91	24.42	1.83	1.38	1.83	5.04	
Foot formula:										0.36	0.27	0.36	1.00			

1878, *Panamacris* Rehn, 1938, *Pararhichnoderma* Rowell, 2012, *Rhichnoderma* Gerstaecker, 1889 and *Silacris* Amedegnato & Descamps, 1979). Together these genera extend from southern Mexico (Vera Cruz, Tabasco, Oaxaca, Chiapas, Guerrero) to Ecuador, Brazil (Paraa) and Amazonian Peru (Loreto); that is, between about 17°N and S latitudes. Only 7 of these genera, *Bactrophora*, *Cristobalina*, *Lempira*, *Mezentia*, *Pararhichnoderma*, *Panamacris* and *Rhichnoderma*, are present in Central America. Of these 7, only *Bactrophora* and *Mezentia* are also found in S. America, the other 5 are confined to Central America.

Dr. Amedegnato proposed to erect 2 new genera, bringing the total for the tribe up to 13. They were 1) *Mayalina*, a Guatemalan and Mexican genus closely related to *Cristobalina*, 2) *Hylaezentia*, an exclusively Amazonian genus closely related to *Mezentia*. 3) She also intended to elevate *Lempira* Rehn, 1938 from its original status as a subgenus of *Rhichnoderma*.

She further proposed to describe numerous new species, belonging to the genera *Bactrophora*, *Lempira*, *Mezentia*, *Rhichnoderma*, *Pararhichnoderma*, *Cristobalina*, *Mayalina* and *Hylaezentia*. Other than the 3 new species of *Mayalina* (below), and 4 species of *Pararhichnoderma* and one of *Lempira* described by Rowell (2012), these are mostly left undescribed in the present work, but may be defined in a later one. Most of the relevant specimens are deposited in the MNHN.

#### Key to the genera of the Bactrophorini

- 1(10) Male cercus wide, complex, flattened and recurved or with an internal fork . . . . . 2
- 2(3) Apterous insects, tympanum absent; inner spines of hind tibia not modified; male cercus short and flat with a small internal apical apophysis . . . . . *Bora* Amedegnato & Descamps
- 3(2) Winged insects; inner spines of hind tibia very strong and recurved . . . . . 4

4(9) Last abdominal tergite of male heavily modified, inflated; male supra-anal plate subrectangular; ventral surface of female subgenital plate ornamented with melanic ridges . . . . . 5

5(8) Male cercus recurved, wide and flat, without internal apophyses . . . . . 6

6(7) Pronotum cylindrical, posterior part of pronotum not modified . . . . . *Hylaezentia* nov.

7(6) Posterior part of pronotum inflated . . . . . *Mezentia* Stål

8(5) Male cercus wide, recurved, with a large internal apophysis . . . . . *Andeomezentia* Amedegnato & Poulain

9(4) Last abdominal tergite of male little modified; male supra-anal plate triangular; male cercus conical with an internal basal apophysis; pronotum regularly cylindrical (Female unknown) . . . . . *Silacris* Amedegnato & Descamps

10(1) Male cercus simple and styliform, long, or short and conical . . . . . 11

11(14) Fastigium of vertex projecting far in front of eyes; male cercus long and recurved . . . . . 12

12(13) Fastigium extremely long; fully winged or brachypterous insects with a tympanum . . . . . *Bactrophora* Westwood

13(12) Fastigium relatively short; brachypterous or apterous insects with no tympanum . . . . . *Hylaeacris* Amedegnato & Descamps

14(11) Fastigium of vertex not projecting far beyond eyes; apterous insects with no tympanum . . . . . 15

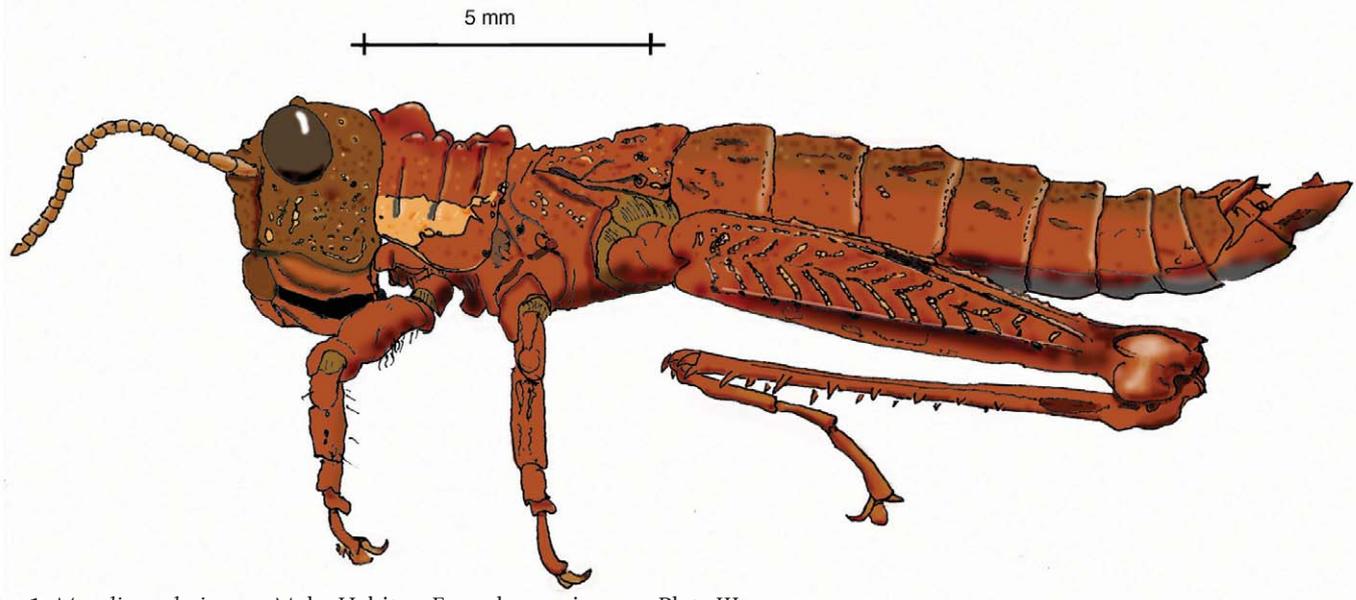


Fig. 1. *Mayalina cohni* n. sp. Male: Habitus. For color version, see Plate III.

15(18) Mesonotum completely covered by pronotum; interocular space twice as wide as frontal ridge; eyes very prominent; medial carina of pronotum partially cristate; prosternal process transverse . . . . . 16

16(17) Ovipositor valves somewhat regressed; prosternal process deeply bifid; medial pronotal carina of female elevated and toothed, highest in the prozona; male subgenital plate bifid apically; completely apterous . . . . . *Mayalina* nov.

17(16) Ovipositor valves normal; prosternal process low, flattened on its front face, entire, not bifid; pronotum selliform; medial pronotal carina present, cristate and elevated at its anterior and especially posterior ends; male subgenital plate not bifid; medial abdominal carina of female toothed. Elytral rudiments present . . . . . *Cristobalina* Rehn

18(15) Mesonotum partly or entirely visible. Elytra completely absent . . . . . 19

19(20) Ventral carinae of the hind femur toothed; rear margin of pronotum slightly inflated. Adults vividly colored in black, orange and green . . . . . *Panamacris* Rehn

20(19) Ventral carinae of hind femur smooth, not toothed; medial pronotal carina of female flat or nodular . . . . . 21

21(22) Mesonotum only partially visible; medial carina of female pronotum cristate at front and especially at rear; male subgenital plate long and narrow; female lacks a small process on medial carina of 2<sup>nd</sup> abdominal segment . . . . . *Lempira* Rehn

22(21) Mesonotum completely visible. Medial carina of pronotum not cristate . . . . . 23

23(24) Subgenital plate of male usually bifid at its tip; 2<sup>nd</sup> abdominal tergite of female bears small process on medial carina (Rowell 2012, Plate 22); lateral lobes of male pronotum marked

with a pale horizontal stripe. Disc of female pronotum often with lumpy processes . . . . . *Pararhicnoderma* Rowell

24(23) Subgenital plate of male always entire not bifid at its tip. Second abdominal segment of female without any elaboration of medial carina; lateral lobes of male pronotum unicolorous, without a pale stripe; first abdominal tergite often ringed by a pale band, vivid in male . . . . . *Rhicnoderma* Gerstaecker

Generic descriptions

4. *Mayalina* gen. nov.

*Etymology*.—Named for the Maya, a modern Central American ethnic group and pre-Columbian Mesoamerican culture, in whose

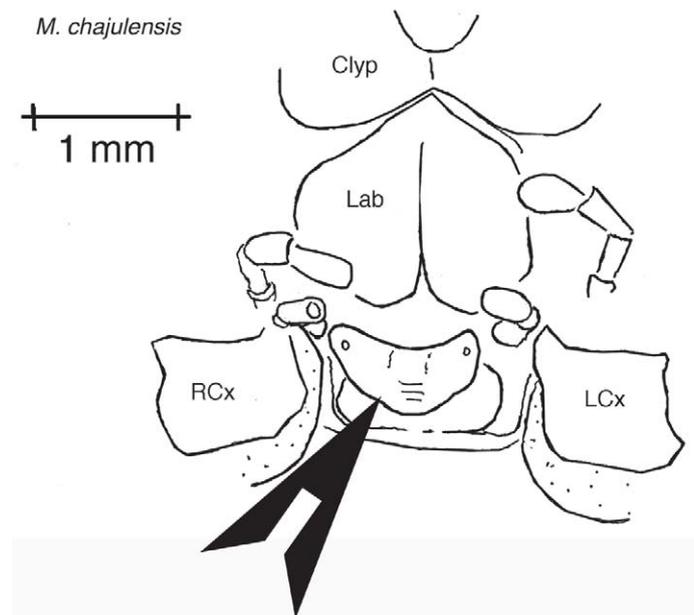


Fig. 2. *Mayalina chajulensis* n. sp. Prosternal process (arrowed), oblique ventral view. RCx, LCx, right and left prothoracic coxae. Lab, labrum. Clyp, Clypeus.

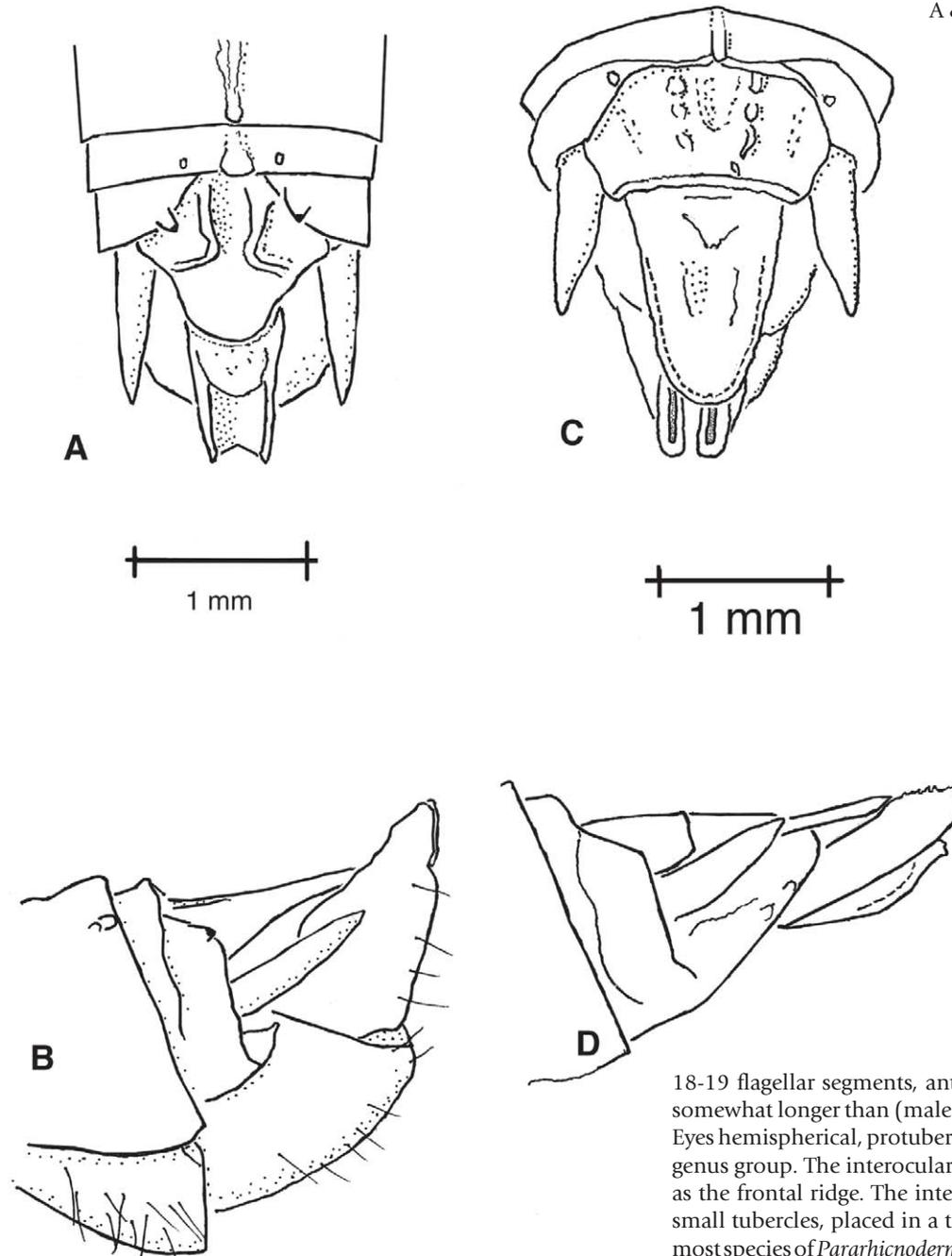
*M. chajulensis*

Fig. 3. *Mayalina chajulensis* n. sp. Male (A & B) and female (C & D) terminalia. A & C dorsal views, B & D lateral views.

territories the genus occurs. Name formed by analogy with the sister genus *Cristobalina* Rehn, 1938.

*Type species.*—*Mayalina cohni*, n. sp.

*Diagnosis.*—In general appearance (Fig. 1, Plate 1) closely similar to *Cristobalina* Rehn, 1938. Both genera are rather small for the tribe, with body length approaching 20 mm in males, up to 30 mm in females (dimensions: see Table 1); noticeably sexually dimorphic in size, male body length about 70% that of female. Integument rugose, richly decorated with small tubercles, especially on head and thorax and dorsal areas of the abdomen.

Antenna filiform, the segments of the flagellum slightly flattened;

18-19 flagellar segments, antennae about as long as (females) or somewhat longer than (males) the head and pronotum combined. Eyes hemispherical, protuberant, more so than in the *Rhicnoderma* genus group. The interocular space is approximately twice as wide as the frontal ridge. The interocular space is decorated with three small tubercles, placed in a transverse line between the eyes, as in most species of *Pararhicnoderma*. Fastigium slopes steeply downward from this point, joining the greatly abbreviated frontal ridge just above the antennal bases. (The fastigium is very similar to that of *Cristobalina* and *Pararhicnoderma*). Frontal ridge dorsal to the medial ocellus short, deeply sulcate, with very prominent fin-like lateral carinae; below the medial ocellus subobsolete, diverging slightly towards the clypeal suture. Lateral carinae of frons strong, diverging downwards, the face being thus markedly trapezoidal in frontal view. Labrum and all mouthparts rotated backwards through nearly 90°, lying almost horizontally below the genae.

The metazona of the pronotum is short, but completely or almost completely covers the mesonotum, in the latter case leaving only a narrow strip exposed. Lateral carinae of pronotum absent, medial carina of the pronotum nodular and to some degree cristate, with a prominent projection in the prozona and one or two lower

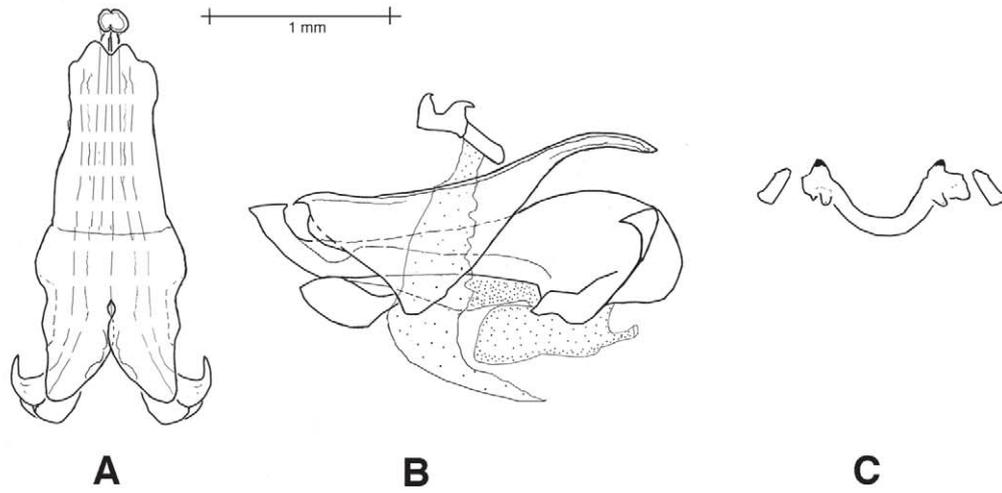
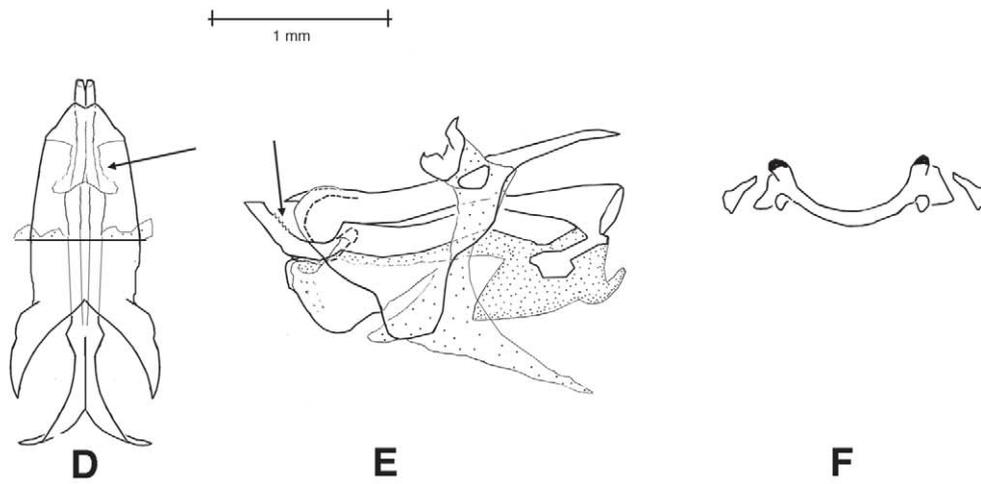
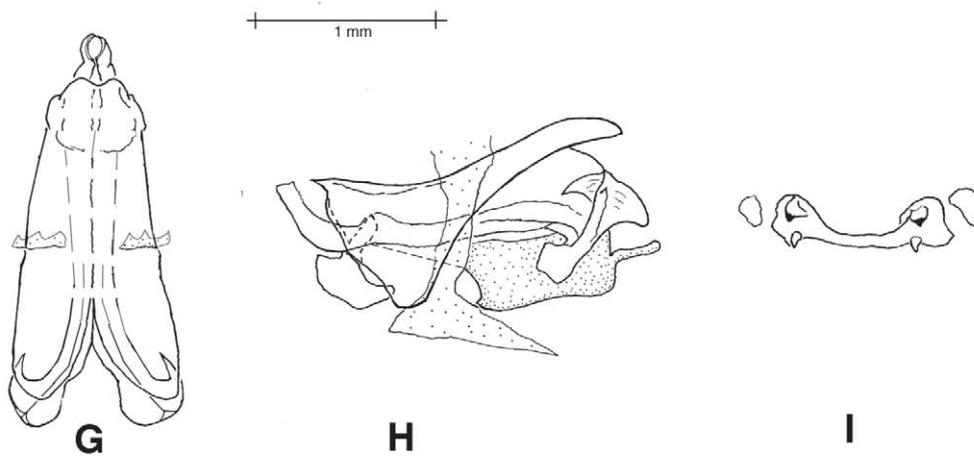
*Mayalina cohni* n.sp.*M. teapensis* n.sp.*M. chajulensis*, n.sp.

Fig. 4. *Mayalina* spp. Phalli of *M. cohni* n. sp., *M. teapensis* n. sp. and *M. chajulensis* n. sp. A,D,G, phallic complexes, dorsal views, with epiphalli removed. B, E, H, phallic complexes, lateral view. C, E, I, epiphalli, dorsal view. Arrows in D & E mark structures mentioned in the text.

ones at the rear of the metazona. Disc of pronotum crossed by only one sulcus, which appears to correspond to the third sulcus of other bactrophorine genera. The first and fourth pronotal sulci are visible on the lateral lobes, but do not attain the disc. Anterior margin of pronotum with a midline embayment flanked by two short pointed lobes overhanging the vertex. Posterior margin of pronotum straight or slightly concave. Apterous and atympanate. Prosternal process deeply bifid, ending in two well-separated points (Fig. 2). Mesosternal interspace open, approximately as wide as long, metasternal interspace almost closed, transverse, and curved towards the rear in the midline. Thoracic sterna slightly concave.

Fore- and midfemora somewhat inflated, rugose. Hind femora slender, slightly shorter than abdomen. All hind femoral carinae are decorated with nodules, and the dorsal medial carina is shallowly but distinctly toothed, ending at the knee in a short blunt point. Ventral lobes of knee rounded. Outer lateral face of hind femur with a heavy "herring bone" pattern of nodular ridges marking the attachments of the fast extensor tibiae muscles (Fig 1, Plate 1). Hind tibia with eight external spines, including an apical spine, and 9 internal spines. Internal tibial spurs slightly more robust than the external spurs. Hind foot long, all three tarsal segments subequal, the second segment being slightly shorter than the other two. Foot formula within the following ranges: 0.35-0.40:0.27-0.30:0.34-0.36.

Abdominal segments with a prominent medial carina, more strongly developed towards posterior margin of segments, sometimes forming a blunt process. Male subgenital plate smoothly rounded basally, pointed and shallowly bifid apically (Fig. 3A, B). Male furcula small and indistinct (Fig. 3A). Supra-anal plate elongate-triangular, with smoothly rounded lingulate tip. Cerci simple, straight and styliform, pointed.

Female subgenital plate with simple smooth posterior margins, slanting in towards the egg guide. Ovipositor valves (Fig. 3C, D) short, barely or not exceeding the supra-anal plate, with smooth or very slightly serrate rounded margins. Upper surface of dorsal valves deeply furrowed.

Phallus (Fig. 4). Epiphallus (Fig. 4 C,E,I) a wide thin bridge-like structure, with small hooked ancorae and bluntly pointed lophi; it is curved forwards in the midline, bow-shaped in dorsal view. Width of epiphallus about 50% of length of entire phallic complex, noticeably larger than in the Rhicoderma group. Oval sclerites present, quite large. Ventrolateral sclerites probably absent (see below). The ectophallus is robust and dominates the structure of the phallus; cingular apodemes short and flat, pointed or rounded at the tips (Fig. 4A,D,G). The cingular rami are wide and almost encapsulate the endophallus; they meet in the ventral midline but do not fuse there. In the dorsal midline the cingulum is smooth and flattened and ends posteriorly in a projecting forked zygoma, which slightly overhangs the aedeagal valves. The lateral posterior margins of the cingulum are complexly infolded and abut the endophallus at the level of its very reduced flexure (arrowed in Fig. 4D). The endophallic apodemes are short, laterally flattened and widely divergent. The gonopore process is robust and spatulate, the ejaculatory and spermatophore sacs relatively large. The mid part of the endophallus consists of two narrow laterally flattened bars; at their posterior ends they form a poorly developed flexure, and end in upwardly curved aedeagal sclerites which project behind the zygoma. In some species the dorsal margin of the aedeagal sclerites is finely toothed (arrowed in Fig. 4E). Ventral to them are another pair of sclerotised "aedeagal valves", which however seem to be entirely derived from ectophallic sheath; their position inside (*i.e.*, medial to) the ectophallic rami suggests they cannot be derived from lateroventral sclerites of epiphallic origin. The dorsal edge of these

valves fuses with the lower margin of the (endophallic) aedeagal sclerites.

In the three species examined to date, the phallus shows rather little variation.

**Coloration.**—Chiefly monochrome brown, mostly devoid of distinct pattern. Males often with a poorly defined pale stripe on lateral lobes of pronotum, weakly present on genae below the eyes, tapering rearwards and slanting upwards and backwards on the lobes towards the metanotum. There is usually a small dark spot on the outer dorsal area of the hind femur, at about midlength, and the inner surface of the hind femur is black or dark brown basally. Many of the tubercles which ornament the cuticle are of a lighter color than the rest of the integument, giving the insect a speckled appearance. The underside of the thoracic and abdominal segments is usually black or dark brown, especially in females.

*Mayalina* differs from *Cristobalina* in the following characters:

1. The mouthparts are not in the normal (orthognath) position, but instead are rotated backwards, forming almost a right angle with the face. The outer surface of the labrum thus comes to lie almost horizontally below the head, and is not visible in frontal view.
2. The ovipositor valves of the female are somewhat regressed, and covered completely or almost completely by the supra-anal plate.
3. The male subgenital plate is weakly bifid at its tip (Fig. 3A,B).
4. Prosternal process deeply bifid, forming two well-separated pointed lobes (Fig. 2).
5. Medial carina of the pronotum is prominently crested and toothed, highest in the prozona. (This differentiates it from *Cristobalina* and *Lempira* where crestring is higher in the metazona.)
6. Medial carina of female abdominal segments prominent, ending in posteriorly rounded knobs, but not prolonged into acute teeth on the posterior segmental margins as in *Cristobalina*.
7. The pronotum in lateral view is much less sellate in form.
8. There are no elytral rudiments.

The combination of the rotated mouthparts and the completely bifid prosternal process is unique and makes the genus very readily identifiable.

*Mayalina* is currently known from three localities, one from near Teapa on the Tabasco/Chiapas border (Mexico) (UMMZ), one from El Sumidero, central Chiapas (Mexico) (UMMZ), and one from Chajul in the adjoining region of northern Guatemala (MNHN). Only a single pair is available from each locality; there is thus no way to assess the variability found in each, but the differences in phallic structure (Fig. 8) make it likely that three separate species are represented. They differ little in their external characters.

## Species descriptions

### 1. *Mayalina cohni* n. sp.

**Holotype male.**—MEXICO: Chiapas: El Sumidero, 13.5 miles N. of Tuxtla Gutierrez (*sic* = Gutierrez), 13. October 1961. (Hubbell, Cantrall, Cohn: their site number 159). UMMZ.

**Allotype female.**— Same data as holotype.

**Etymology.**—Named for one of the original collectors of the genus, the eminent orthopterist Dr. Theodore Cohn.

The smallest of the three known species of the genus, male less than 18 mm long, female less than 22 mm (see Table of dimensions). The general color is a dull reddish brown, the male has a paler stripe on the pronotal lobe (see Fig. 1, Plate 1). The inner face

of the hind femur is blackish proximally, and there is a small dark spot on the outer dorsal face at about half length.

The dorsal margin of the aedeagal sclerites is ornamented with small teeth (arrowed in Fig. 4E). The SAP completely covers the ovipositor valves in dorsal view.

### 2. *Mayalina teapensis* n. sp.

*Holotype male*.—MEXICO: Chiapas/Tabasco border: 8 mi W. of Teapa on Pichucalco rd. (150'), 9. Sept. 1959 1961. (Cantrall, I.J. & Cohn, T.J.: their site number 90). UMMZ Michigan.

*Allotype female*.—MEXICO: Tabasco: 3 mi NE. of Teapa, 27 October 1961. (Hubbell, S.P., & Cohn, T.J.: their site number 180). UMMZ Michigan.

*Etymology*.—Derived from the name of the type locality.

The phallus (Fig. 4A) differs from that of the other 2 known species in having the cingular apodemes pointed rather than rounded, and in the reduced structure of the terminal flanges of the endophallic apodemes. The aedeagal sclerites are smooth, devoid of small teeth on their dorsal edges. Sexual dimorphism more pronounced than in the other 2 known species, the female is relatively larger,  $L_m/L_f = 0.69$ , as opposed to 0.81 for the other spp. The female is also more brightly colored than in other species, with dull orange stripes running behind the eyes from the lower edge of each gena to meet on the disc of the pronotum. The ovipositor valves protrude slightly beyond the tip of the SAP.

### 3. *Mayalina chajulensis* n. sp.

*Holotype male*.—GUATEMALA: Prov. El Quiche: Selva Lacandona, Chajul, 6-13 November 1986. (Amedegnato, C. & Poulain, S.). MNHN.

*Allotype female*.—Same data as holotype.

*Etymology*.—Derived from the name of the type locality.

Male furcula better developed than in other spp. (Fig. 3A). Epiphallus (Fig. 4I) straighter, less bowed, than in other spp. Dorsal edges of aedeagal endophallic sclerites ornamented with a very few small teeth, many fewer than in *M. cohni*. Ends of cingular apodemes broadly rounded.

The ovipositor valves protrude slightly beyond the tip of the SAP (Fig. 3C).

### 5. *Hylaezentia* gen. nov.

*Etymology*.—Compounded from the "Hylea", the Amazonian floodplain forest, and *Mezentia*, the oldest genus of this clade.

*Type species*.—*Mezentia acanthopyga* Rehn, 1938.

*Diagnosis*.—Closely similar to *Mezentia* and *Andeomezentia*. The following characters apply to all three genera:

1. Brachypterous, tympanate insects of medium to large size.
2. Prosternal process roughly cylindrical, blunt, not transverse.
3. Inner spines of hind tibia very strong and recurved.
4. Last abdominal tergite of male heavily modified, inflated, the

outer corners often produced transversely, the posterior margin decorated with multiple black spines.

5. Male supra-anal plate triangular or subrectangular.

6. Male subgenital plate sharply tapering to a rounded point, projecting well beyond the supra-anal plate. Female subgenital plate decorated with bosses or ridges.

In *Hylaezentia* the male cercus is recurved, wide and flat, but without an internal apophysis. Pronotum cylindrical, metazona not modified. *Hylaezentia* differs from *Mezentia* most obviously in that the metazona of the pronotum is normal, not inflated, and from *Andeomezentia* in that the male cercus lacks a large internal apophysis. The male subgenital plate is longer and more tapering than in the other two genera, thus explaining Rehn's specific name.

Apart from *H. acanthopyga* (Rehn, 1938) from the Brazilian Amazon, there are several other undescribed species (MNHN), all from the Amazon floodplain, ranging from French Guyana through the Brazilian Amazon to Iquitos, Peru.

### Cladistic analysis

We have no molecular data on the tribe. As in all "phylogenetic" analyses of morphological data, the assumption is made that morphological similarity corresponds to genetic relatedness. However, as most recently discussed by Wood & Harrison (2011) this assumption can be severely weakened by homoplasy, especially when the different lineages evolve in similar ecological niches, as is indeed the case with the Bactrophorini. *Caveat emptor!*

Dr. Amedegnato selected and tabulated the following 67 morphological characters: 1- 36 are somatic, the remaining 31 are phallic. Thirteen of the 67 are parsimony uninformative: these are asterisked in the list below.

Her tabulation was originally generic only, giving no indication of which species she examined. However, the current genera of the Bactrophorini are very homogenous, and it is unlikely that the different species are polymorphic for the characters she selected. As current opinion in phylogenetics strongly favors the use of named species as terminal taxa (see e.g., Prendini 2001), we have substituted representative species of each genus, to which the matrix descriptions completely apply. In the case of South American species previously described from Paris by CA or M. Descamps we have used their generic type species: for Central American genera we have used species of which we had adequate amounts of material to check the characters.

### Characters

- |   |                  |
|---|------------------|
| <b>1. Fastigium of the vertex:</b>  | <b>UNORDERED</b> |
| 0. Projecting normally – <i>Silacris</i> , <i>Bora</i> , outgroup.  |                  |
| 1. Projecting markedly – as in <i>Hyleacris</i> and especially <i>Bactrophora</i> .   |                  |
| 2. Downward sloping and obsolete. <i>Rhcnoderma</i> genus group, <i>Mezentia</i> genus group, <i>Mayalina</i> , <i>Cristobalina</i> . |                  |
| <b>2. Interocular space:</b>  | <b>UNORDERED</b> |
| 0. Same width as frontal ridge. All other genera.   |                  |
| 1. Width more than 2 times that of the frontal ridge. <i>Rhcnoderma</i> genus group.  |                  |
| <b>3. Eyes shape:</b>   | <b>UNORDERED</b> |
| 0. Normal.  |                  |
| 1. Hemispherical, very globose. <i>Cristobalina</i> / <i>Mayalina</i> only.   |                  |

- 4\*. Pronotum shape:** UNORDERED
0. Normal.
  1. Selliform. *Mezentia*, *Cristobalina*.
- 5. Pronotal sulci:** UNORDERED
0. Normal for the group (*i.e.*, 3 plus the sulcus lying immediately behind the anterior border).
  1. Modification of the normal pattern. *Mezentia* & *Andeomezentia*; *Cristobalina*/*Mayalina*; *Rhcnoderma*.
- 6\*. Posterior part of the pronotum:** UNORDERED
0. Unmodified.
  1. Modified behind the 2nd sulcus. Only *Mezentia*.
- 7. Development of the 3<sup>rd</sup> sulcus:** UNORDERED
0. Subnormal or normal.
  1. Obsolete in the midline. *Mezentia*, *Panamacris*, *Cristobalina*/*Mayalina*, *Lempira* & *Pararhcnoderma*.
- 8. Development of the 2<sup>nd</sup> sulcus:** UNORDERED
0. Normal.
  1. Obsolete. *Cristobalina*/*Mayalina*, *Lempira* & *Pararhcnoderma*.
- 9\*. Median carina of the pronotum (Male):** UNORDERED
0. Obsolete.
  1. Nodulose. *Mayalina* only.
- 10. Median carina of the pronotum (Female):** UNORDERED
0. Obsolete.
  1. Gibbose or nodulose in the prozona and metazona. *Mayalina*, *Pararhcnoderma*.
  2. Gibbose or elevated only in the prozona. No examples.
  3. Gibbose or elevated only in the metazona. *Cristobalina*/*Lempira*.
- 11. Mesonotum:** UNORDERED
0. Hidden under the pronotum.
  1. Clearly visible, at least in part. *Panamacris*, *Pararhcnoderma*, *Lempira*, *Rhcnoderma*. Due to very short pronotum.
- 12. State of flight organs:** UNORDERED
0. Present and developed (though often brachypterous).
  1. Absent or very rudimentary. *Bora* and most of the *Hyleacrae*, but not *Bactrophora* or *Hyleacris*.
- 13. Color of the wings:** UNORDERED
0. Transparent. *Mezentia* genus group.
  1. Black. *Hyleacris*, *Silacris*.
  2. Colored. Only *Bactrophora*.
- 14. Shape of mesosternal space:** UNORDERED
0. Roughly quadrangular (normal).
  1. Narrow. *Hyleacris*, *Bactrophora*, *Bora*, *Panamacris*.
  2. Wide. *Cristobalina*/*Mayalina*, *Rhcnoderma*, *Pararhcnoderma*.
- 15. Shape of the prosternal process:** UNORDERED
0. Cylindrical, *e.g.*, *Mezentia* genus group.
  1. Modified (*e.g.*, transverse). *Rhcnoderma* genus group only, *Mayalina*, *Cristobalina*.
- 16\*. Bifurcation of the prosternal spine:** UNORDERED
0. Absent or weak.
  1. Strong. *Mayalina* only.
- 17\*. Ventral carinae of the hind femora:** UNORDERED
0. Normal, smooth.
  1. Serrulated. *Panamacris* only.
- 18\*. External surface of the hind femora:** UNORDERED
0. Smooth.
  1. Rough and granular.
- 19\*. Dorso-internal area of hind femora:** UNORDERED
0. Present. In outgroup Phaeopariinae only.
  1. Absent. All the ingroup.
- 20. Specialisation of internal spines of the hind tibiae:** UNORDERED
0. No.
  1. Yes. *Mezentia* genus group only, & *Epiprora* (outgroup).
- 21. Second tarsal segment of hind tibiae:** UNORDERED
0. Normal (Much shorter than first tarsal segment). In outgroup Phaeopariinae only.
  1. Elongated. All the ingroup.
- 22. Tympanal organ:** UNORDERED
0. Present. All other genera.
  1. Absent. *Hyleacris*, *Bora*, *Rhcnoderma* genus group, *Mayalina*, *Cristobalina*.
- 23. Hind border of the last abdominal tergite of male:** UNORDERED
0. Normal.
  1. Modified, with black thickenings. *Silacris*, *Mezentia* genus group.
- 24. Dilation of the last abdominal tergite of male:** UNORDERED
0. Absent.
  1. Very significant, with marked dentation - *Mezentia* genus group only.
- 25. Female mediodorsal abdominal carina:** UNORDERED
0. Normal, or obsolete.
  1. Specialised behind the 3<sup>rd</sup> tergite. *Cristobalina*, and weakly in *Mayalina*.
  2. Presence of a callosity at the anterior border of the 2<sup>nd</sup> tergite. *Pararhcnoderma* only.
- 26. Shape of male cerci:** UNORDERED
0. Styliform.
  1. Not styliform, weakly or strongly modified. *Silacris*, *Bora*, *Mezentia* genus group.
- 27. Modification of styliform cerci:** UNORDERED
0. No.
  1. Yes. *Bactrophora* & *Hyleacris* only.
- 28. Presence of internal fork in nonstyliform cerci:** UNORDERED
0. No.
  1. Yes. *Silacris*, *Bora* & *Andeomezentia*.

- 29. Shape of the male supra-anal plate:** UNORDERED
0. Normal (triangular).
  1. With a marked linguiform process, *Hyleacris*, *Mezentia* genus group.
- 30. Development of posterolateral angles of the male supra-anal plate:** UNORDERED
0. Weak.
  1. Strong, giving a rectangular plate. *Mezentia* genus group only.
- 31. Presence of black tubercles on the male supra-anal plate:** UNORDERED
0. No.
  1. Yes. *Silacris*, *Bora*, *Mezentia*, *Hylaezentia*.
- 32. Female supra-anal plate:** UNORDERED
0. Normal.
  1. Large, almost hiding ovipositor valves. *Hyleacris* (*Silacris* unknown), *Mayalina* & *Cristobalina*.
- 33. Female subgenital plate:** UNORDERED
0. Normal.
  1. 1-3 melanized bosses or ridges on posterior margin. *Mezentia* genus group.
- 34. Male subgenital plate:** UNORDERED
0. Normal.
  1. Long and acute. *Bactrophora*, *Hyleacris*, *Mayalina*, *Lempira*, *Pararhcnoderma*.
- 35\*. Ovipositor valves:** UNORDERED
0. Normal.
  1. Weak. *Mayalina* (*Silacris* unknown).
- 36. Male chromatic pattern:** UNORDERED
0. Pale lateral pronotal stripe. All other genera.
  1. None. *Mezentia*, *Andeomezentia*, *Christobalina*.
  2. Pale annular abdominal pattern. *Rhcnoderma*.
  3. Other. *Hyleacris*, *Panamacris*.
- Phallic Characters:**
- A. Epiphallus**
- 37. Epiphallus size (width epiphallus / length of phallic complex):** UNORDERED
0. > 0.7 *Bactrophora*.
  1. 0.3 - 0.7 *Hyleacris*, *Silacris*, *Bora*, *Mezentia* genus group, *Mayalina*, *Cristobalina*.
  2. < 0.3 *Panamacris*, *Pararhcnoderma*, *Lempira*, *Rhcnoderma*.
- 38. Nature of the bridge:** UNORDERED
0. Normal.
  1. Very thick or with apodemes. *Bactrophora*, *Lempira*, *Pararhcnoderma*, *Cristobalina*, *Mezentia* genus group.
- 39. State of the anchorae:** UNORDERED
0. Normal. *Mayalina*/*Cristobalina*, outgroups.
  1. Fused with lateral plates. All other genera.
- 40. Lateral plates:** UNORDERED
0. Normal. *Mayalina*/*Cristobalina*, outgroups, *Hyleacris*.
  1. Not distinct from lophi.
- 41. Shape of lophi:** UNORDERED
0. Digitiform without teeth. Outgroup, *Hyleacris*, *Silacris*, *Mezentia* group, *Rhcnoderma* group.
  1. Modified: digitiform with a single tooth. None.
  2. Bifid. *Bactrophora*, *Bora*.
- 42. Oval sclerites:** UNORDERED
0. Present. *Silacris*, *Mayalina*, *Cristobalina*, *Bora*.
  1. Absent or very weak. *Rhcnoderma*, *Lempira*, *Pararhcnoderma*, *Panamacris*.
  2. Large and thick. *Bactrophora*, *Hyleacris*, *Mezentia* genus group.
- 43. Lateroventral sclerites:** UNORDERED
0. Present.
  1. Absent. *Rhcnoderma* g. group, *Panamacris*, *Mayalina*.
- 44. Size of lateroventral sclerites:** UNORDERED
0. Small.
  1. Large. *Mezentia* genus group.
- 45. Posterior projection of lateroventral sclerites:** UNORDERED
0. Absent. All other genera.
  1. Present. *Silacris*, *Andeomezentia*, *Hylaezentia*, *Bora*.
- B. Ectophallus**
- 46. Dorsomedial zone of the cingulum with 1 or 2 lobes:** UNORDERED
0. Yes. Other genera.
  1. No. *Silacris*, *Bora*, *Mezentia* genus group.
- 47. Development of the dorsal lobes:** UNORDERED
0. No. *Epiprora*, *Phaeoparia*, *Mezentia*.
  1. Yes. *Bactrophora*, *Hyleacris*, *Panamacris*, *Cristobalina*, *Pararhcnoderma*, *Lempira*, *Rhcnoderma*, *Mayalina*.
- 48. Dorsal lobes:** UNORDERED
0. One, unique. Other genera.
  1. Two, separated. *Bactrophora* *Mezentia*, *Panamacris*, *Mayalina*, *Cristobalina*, *Pararhcnoderma*, *Lempira*, *Rhcnoderma*.
- 49\*. Presence of a large membranous digitation:** UNORDERED
0. Absent. Other genera.
  1. Present. *Hyleacris* only.
- 50. Internal median crest of the cingulum:** UNORDERED
0. Absent.
  1. Present. *Bactrophora*, *Mezentia*, *Mayalina*, *Cristobalina*, *Pararhcnoderma*, *Lempira*, *Rhcnoderma*.
- 51. Posterodorsal projection of rami:** UNORDERED
0. Present, no dorsal lobes of cingulum. *Hylaezentia*, *Andeomezentia*.
  1. Present, with dorsal lobes. *Hyleacris*, *Mezentia*, *Bora*.
  2. Absent, but dorsal lobes present. *Bactrophora*, *Cristobalina*, *Mayalina* and the *Rhcnoderma* genus group.

- 52. Structure of rami:** UNORDERED
0. Weak. Mezentiae.
  1. Narrow, easily visible, with distinct apex. *Bactrophora*, *Panamacris*, *Cristobalina*, *Pararhcnoderma*, *Lempira*, *Rhcnoderma*, *Mayalina*.
- 53. Posteroventral projection of rami:** UNORDERED
0. Absent. All of Mezentiae, outgroup.
  1. Present. All of Bactrophorae.
- 54. Apex of the ventral projection separated into a sclerite:** UNORDERED
0. No.
  1. Yes. Rhcnoderma and Cristobalina genus groups.
- 55. Ends of rami participate in aedeagal valves:** UNORDERED
0. No.
  1. Yes. All Hyleacrae except *Panamacris* & *Mayalina*.
- 56. Apodemes of cingulum:** UNORDERED
0. Flat and weak.
  1. Strong and thick. *Hyleacris*, *Mayalina* and *Cristobalina* only.
- 57. General shape of the cingulum:** UNORDERED
0. Normal. Other genera.
  1. Capsuliform. *Bactrophora*, Rhcnoderma & Cristobalina genus groups.
- 58. Pseudoarch, thickening of ecto-endophallic fold:** ORDERED
0. Weak.
  1. Strongly developed and very thick. *Mezentia* g. group only.
- 59. Ectophallic part fused with apex of endophallus (dorsal valve of aedeagus):** ORDERED
0. No.
  1. Yes. All Mezentia genus group.
- 60. Aedeagal valve heavily sclerified with strong striations:** UNORDERED
0. No.
  1. Yes. All Rhcnoderma genus group.
- 61\*. Presence of an entirely ectophallic supplementary dorsal valve:** UNORDERED
0. Absent.
  1. Present. *Hyleacris* only.
- C. Endophallus.**
- 62. Size of central region versus apodeme region of endophallic plates:** ORDERED
0. Shorter than normal. Outgroups.
  1. Normal for the group. *Bactrophora*, *Hyleacris*, *Silacris*, Mezentia genus group, *Mayalina*, *Cristobalina*, *Bora*.
  2. Longer than normal. Rhcnoderma genus group.
- 63. Development of endophallic apodemes:** UNORDERED
0. Strongly developed behind the central carina of the apodeme. Outgroup, *Cristobalina* and *Mayalina*.
  1. Normal for the group. All the Bora, including the Mezentia genus group, plus all the more basal Hyleacrae.
  2. Very reduced. Rhcnoderma genus group.
- 64\*. Posterior part of the endophallic sclerite very long:** UNORDERED
0. No.
  1. Yes. *Hyleacris* only.
- 65. Spermatophore sac:** ORDERED
0. Normal. All other genera.
  1. Very wide with 2 lobes. Rhcnoderma genus group.
- 66. Ejaculatory sac:** ORDERED
0. Normal.
  1. Very wide, bilobate. Rhcnoderma genus group.
- 67. Sclerification of the ejaculatory sac:** UNORDERED
0. Absent. all other genera.
  1. Present, posterior. *Hyleacris*.
  2. Present, anterior. *Epiprora*, *Phaeoparia*.

*Outgroups.*—As outgroups CA originally selected two Phaeoparines, *Epiprora hilaris* Gerstaecker, 1889, plus a species that she referred to only as Taxon 14, on the grounds that this tribe, like the Bactrophorini, are primitive Romaleids that lack a stridulatory mechanism. We are unable to locate or identify her "Taxon 14", presumably an undescribed species, and therefore we ran all the analyses twice, omitting Taxon 14 from the outgroup on the second round. There were no changes in tree topology or bootstrap values due to the reduced outgroup. As a single species is a rather minimal outgroup, we added to the matrix another Phaeoparine species, *Phaeoparia phrygana* Jago 1980, to replace "Taxon 14". Once again, there were no significant changes in the resultant trees.

*Character matrix.*—The matrix of 67 characters and 15 species is given in Appendix 1. The entries for *Phaeoparia*, *Panamacris* and *Mayalina* have been completed with new observations by CHFR, the remainder are due to CA. Thirteen of the 67 characters are parsimony uninformative, leaving 54 informative characters. For our analyses all characters were coded as unordered. (CA originally designated about half of the characters as ordered, but left no indication of her reasons. We repeated the analysis using her coding, but there were no significant differences due to the different coding).

*Analysis.*—The matrix was converted into a NEXUS format file using MacClade version 4.06 (Maddison & Maddison 2003) and analysed using PAUP\* version 4 beta 10-X86 (Swofford 2006), using both maximum parsimony and distance criteria. Bootstrap values were calculated for both maximum parsimony and distance criteria, using 100 replicates. Both criteria yielded very similar phylogenies with reasonable bootstrap support for almost all nodes (Fig. 5). Trees were visualized graphically using either MacClade or Tree View X version 5.0 (Page 2004).

More details of the analytic parameters used are given in the captions to Figs 5 and 6, or can be obtained on request from CHFR.

## Bootstrap 50% majority rule consensus trees

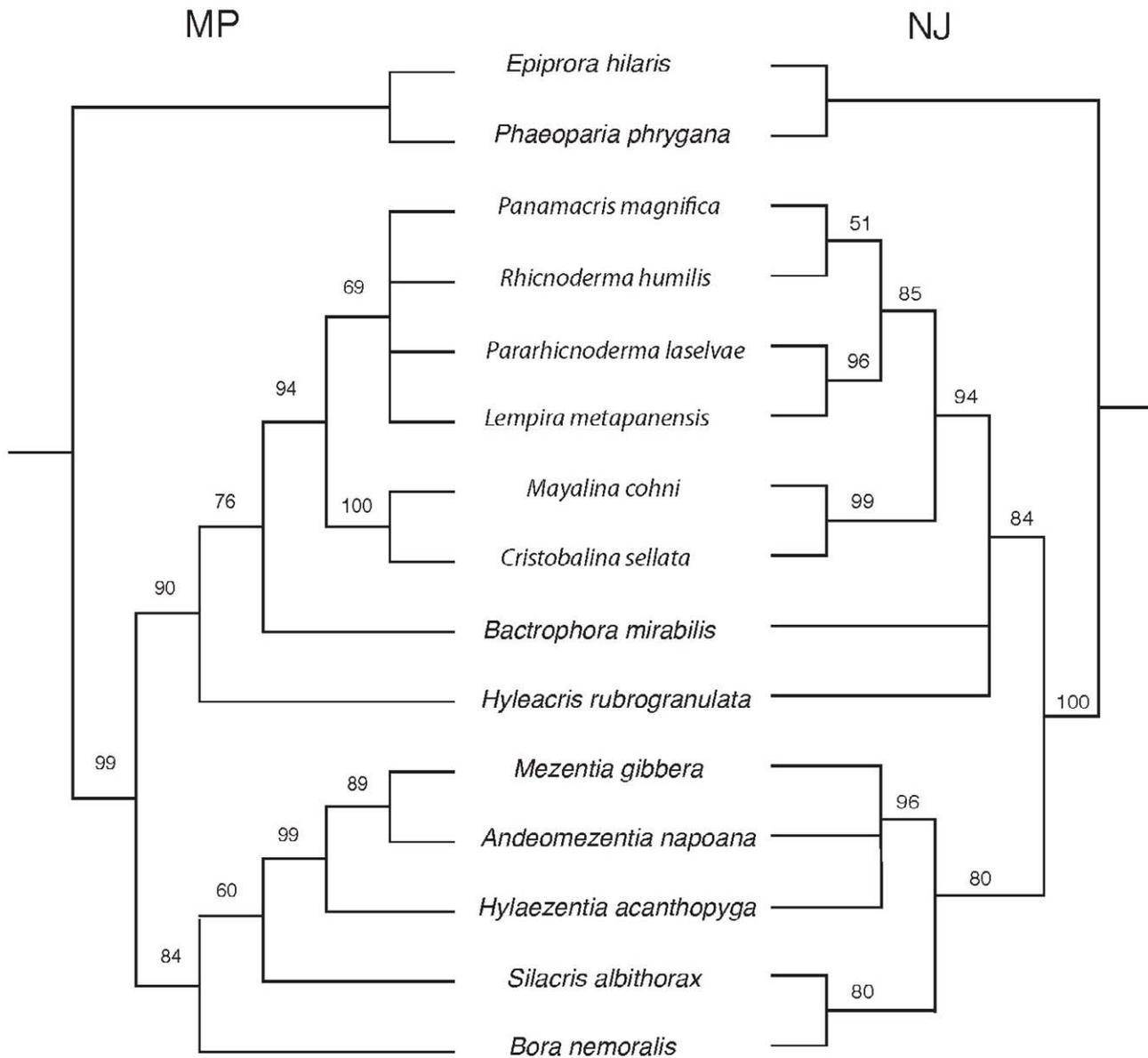


Fig. 5. 50% majority rule bootstrap trees (each derived from 100 bootstrap replicates) under distance (neighbor joining, right hand side of figure) and maximum parsimony criteria (left hand side). The figures at the nodes are bootstrap values. Note that the topology and BS values are very similar in the two trees. PAUP Parameters: Character-status summary: Of 67 total characters: all characters are of type 'unord'. All characters have equal weight. 13 characters are parsimony-uninformative. Number of parsimony-informative characters = 54. Gaps are treated as "missing". Bootstrap method with heuristic search: Number of bootstrap replicates = 100. Optimality criterion = parsimony or distance (minimum evolution). Distance measure = total character difference. Starting tree(s) obtained via stepwise addition. Addition sequence: random. Number of replicates = 10. Number of trees held at each step during stepwise addition = 1. Branch-swapping algorithm: tree-bisection-reconnection (TBR). Steepest descent option not in effect. Initial 'MaxTrees' setting = 1000. Branches collapsed (creating polytomies) if maximum branch length is zero. 'MulTrees' option in effect. Topological constraints not enforced as "missing".

## Results

The most obvious result of the analysis is that the Bactrophorini genera fall into two well-supported clades (Fig 5, Fig. 6; the latter Figure includes the clade terminology described below). The first clade, ("Hyleacrae", after its most basal member) has as its 2 basal

branches the exclusively Amazonian *Hyleacris* and the Amazonian and Central American genus *Bactrophora*; as its crown group it contains all the Central American genera except *Mezentia*. The Central American genera of the Hyleacrae fall into two lineages: first, the northern (Guatemala, Mexico & Honduras) sister genera *Cristobalina* and *Mayalina* (the "Cristobalina genus group"), and secondly the 4

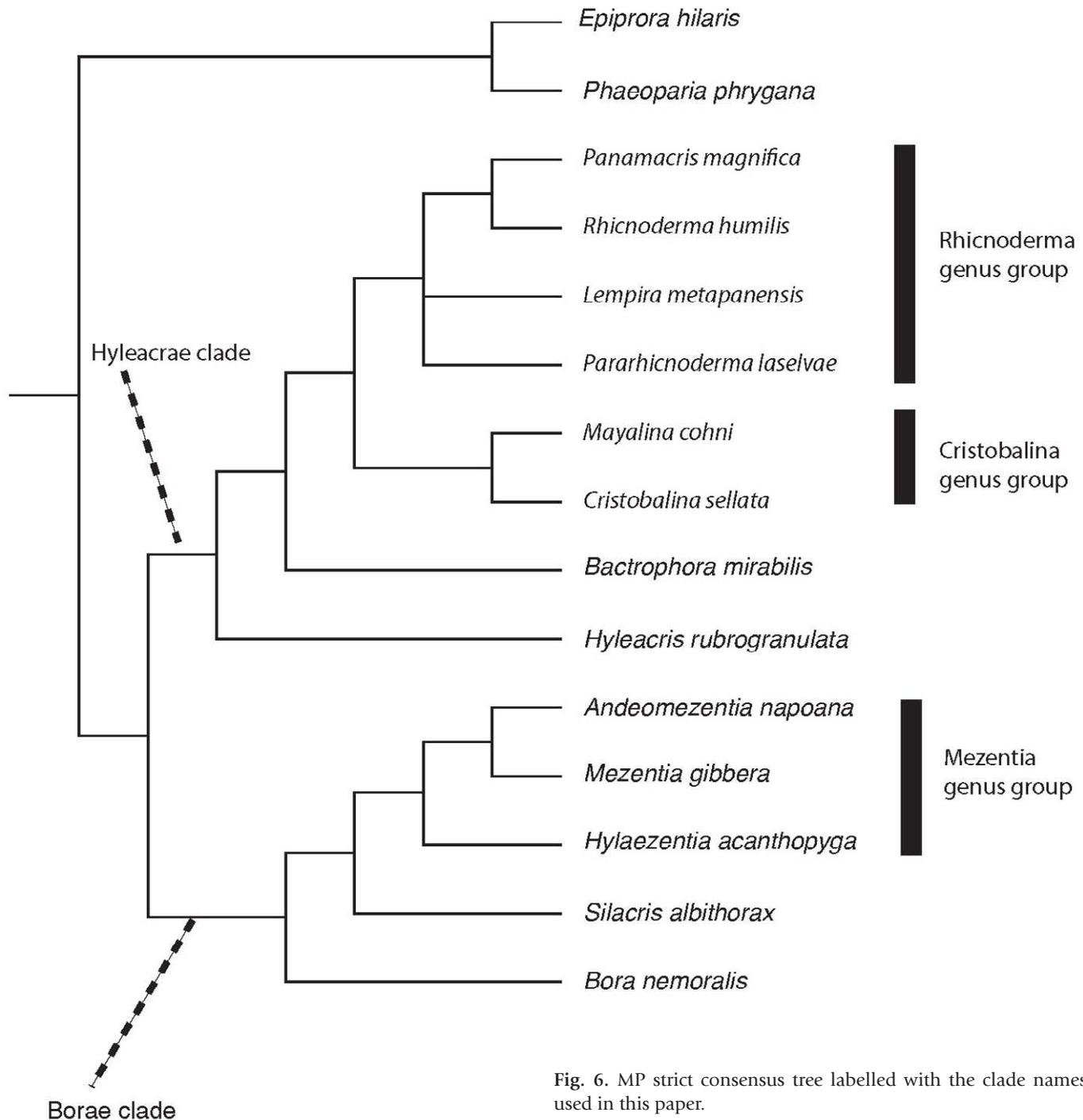


Fig. 6. MP strict consensus tree labelled with the clade names used in this paper.

## 12 Strict consensus of 3 best MP trees.

genera making up the "Rhicnoderma genus group" (*Rhicnoderma s. str.*, *Lempira* and *Pararhicnoderma*, which are present from Southern Mexico south to Panama, plus the Panamanian endemic *Panamacris*, here resolved as the sister genus of *Rhicnoderma*). The second clade (Boraë, after its most basal member *Bora*) contains 4 exclusively Amazonian genera, plus the fifth genus, *Mezentia*, which has both Central American and Colombian species. The two basal genera are *Bora* and *Silacris*, followed by a crown group consisting of three very closely related genera, *Mezentia*, *Andeomezentia* and *Hylaezentia*, here referred to as the "Mezentia genus group".

Tree topology is robust. The distance and parsimony analyses gave very similar results (Fig. 5), and variation in the choice of outgroup taxa (see "Outgroups" above) had no effect.

We repeated the analyses excluding in turn either all the phallic characters or all the somatic characters. The resultant trees (Fig. 7) are very largely compatible, with the phallic characters providing somewhat better resolution, especially of the more basal parts of the tree. The most significant difference is in the position of the Cristobalina genus group. The phallic characters alone resolve this under NJ criteria as the sister group of the Rhicnoderma genus

## NJ 50% consensus bootstrap trees.

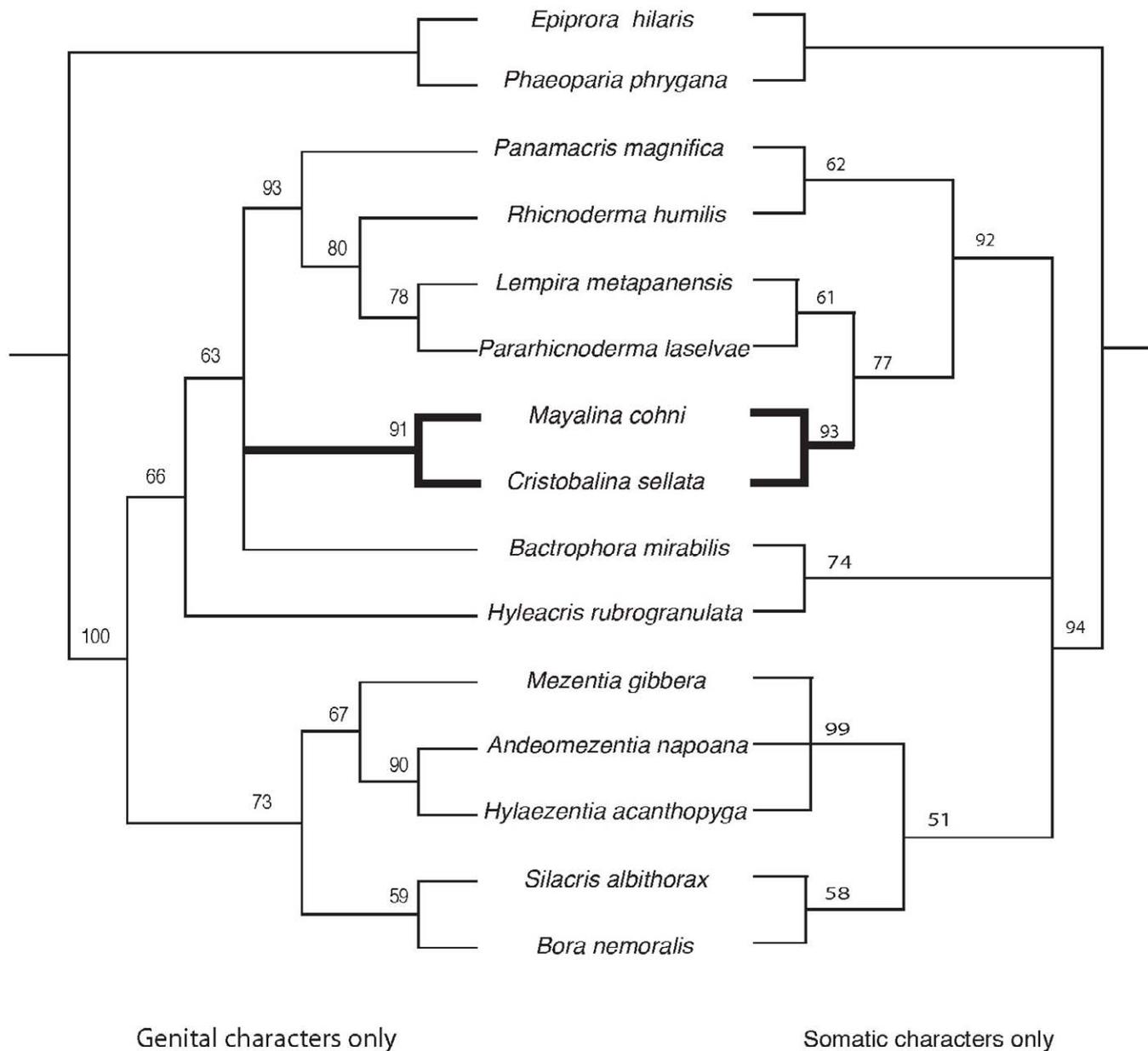


Fig. 7. Neighbor-joining 50% majority rule consensus bootstrap trees produced (A, left hand side) by excluding all somatic characters and using only phallic characters and (B, right hand side) by the reverse procedure, *i.e.*, after excluding all phallic characters from the analysis, leaving only somatic characters. The clade containing the *Cristobalina* genus group (see Fig. 6) in both trees is indicated with heavier lines. Note the good concordance between the two trees, and the fact that the phallic characters produce a slightly more resolved tree. For discussion of the differences, especially in the placement of the *Cristobalina* genus group, see text.

group, or even (in MP trees) of the *Rhicnoderma* genus group plus *Bactrophora*, and thus in a very basal position in the evolution of the Bactrophorini in Central America, whereas the somatic characters alone place it as the sister group to *Pararhicnoderma* plus *Lempira*, in a derived position. The combined character set (*e.g.*, as in Fig. 5) places the *Cristobalina* group as the sister of the *Rhicnoderma* genus group, in a compromise position, as expected. All other differences

are minor, indicating no major conflict between the two datasets; it is noteworthy that both character sets produce exactly the same groupings of the terminal taxa.

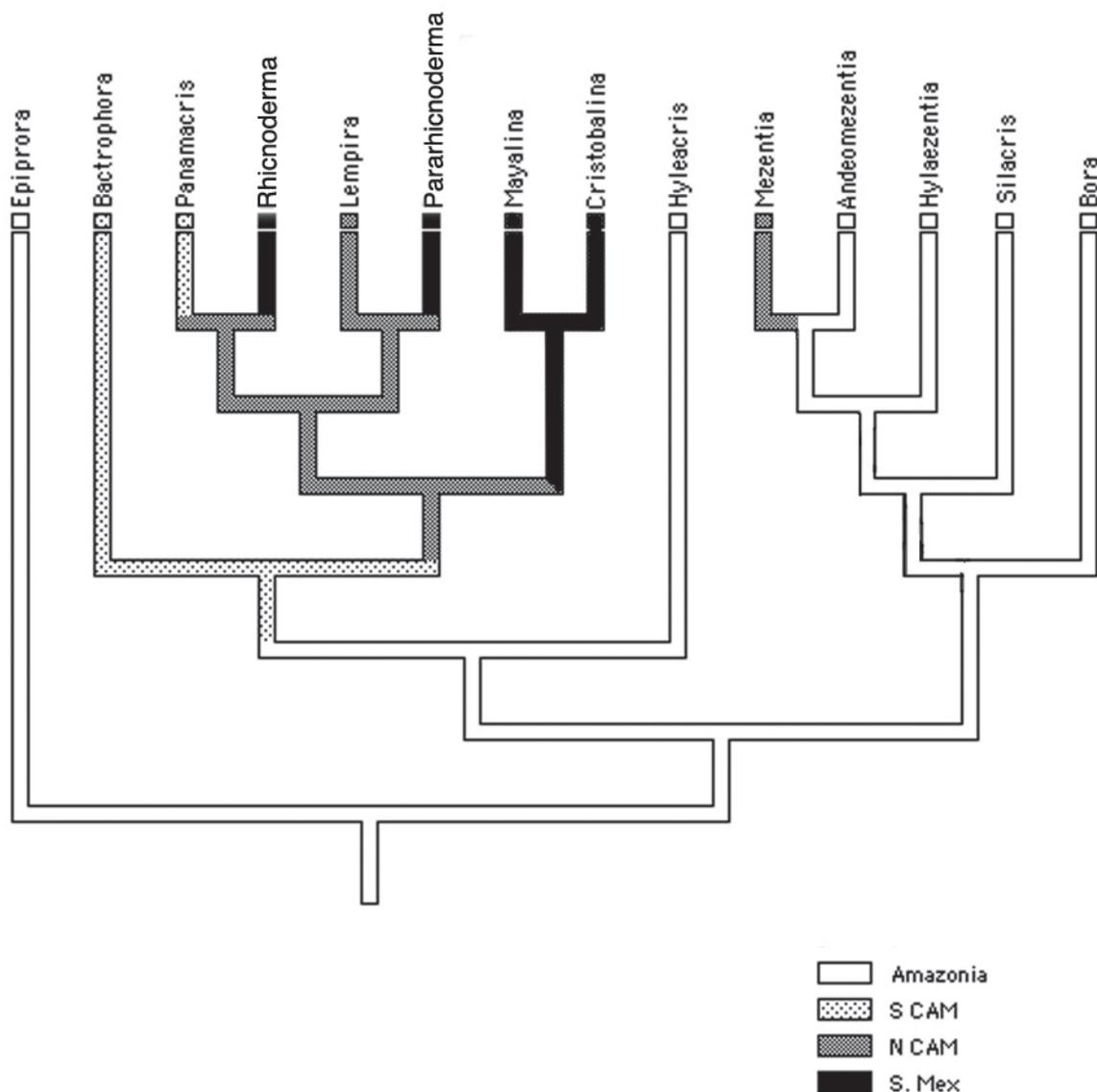


Fig. 8. The northern limit of distribution of each genus superimposed on the phylogeny. No shading, Amazonia; light stipple, S. CAM; heavy stipple, N. CAM; black, Southern Mexico; cross hatching, equivocal. Note that the basal taxa are all Amazonian, the Central American and Mexican genera are all derived. "S. CAM" = Southern Central America, comprising Panama, Costa Rica and Nicaragua; "N. CAM" = Northern Central America, comprising Guatemala, El Salvador and Honduras.

## Discussion

*Phylogeography of the tribe.*— Fig. 8 plots the geographical range of each genus on the phylogeny. It will be seen that the basal members of both clades are exclusively Amazonian, and the most derived are Central American or Mexican. This strongly suggests that in the course of its evolution the tribe has colonized northwards from an originally South American founder population and diversified as it did so. Similarly, the only Central American representative of the Boraie clade, *Mezentia*, is present in Colombia, Panama, Costa Rica, Nicaragua and Honduras, but not further north. The *Cristobalina* genus group, that appears to be the sister group of the *Rhicoderma* genus group, is restricted to Northern Central America and Southern Mexico. It may derive from the original bactrophorine colonists of Central America.

*The place of the tribe within the subfamily.*—Within its subfamily, the tribe Bactrophorini exhibit the most comprehensive structural adaptations to an arboreal way of life, in everything except the structure of the ovipositor (indicating an apparent absence of epiphyllic oviposition in the tribe, with the possible exception of *Mayalina*). They also show marked climatic tolerance, ranging from the Equator to the subtropics. In view of our limited knowledge of the subfamily, it is difficult to speculate on the relationships between its tribes. The Bactrophorini appear to be an ancient group, as suggested by various characters: especially, as previously stressed by CA, the rudimentary nature of the male phallic structures in some genera can be interpreted as a primitive character. However, given that the genitalia are more complex and "normally" developed in the other tribes of the subfamily, a secondary reduction is also quite possible. The most simplified phallic structures are in fact seen in the *Rhicoderma* genus group, here shown to be the most derived of the Hyleacrae, and the more basal members, both of that clade

and of the Borae clade, have more complex phalli, which again strongly suggests secondary reduction in the Rhicnoderma group, and throws doubt on their worth as evidence for the primitive nature of the group.

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## Appendix 1. Character matrix.

Character	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	35					
Genus species																																								
<i>Epiprora hilaris</i>	0	0	0	0	0	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	0	0	1			
<i>Bactrophora mirabilis</i>	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	-	0	0	1	0	1	0	0	0	0	0	0	1	0	-	0	0	0	0	0	0	1			
<i>Hyleacris rubrogranulata</i>	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	-	0	0	1	0	1	1	0	0	0	0	1	1	-	0	0	0	0	0	0	1				
<i>Silacris albithorax</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	0	0	1	0	1	0	1	0	0	1	-	0	1	0	1	?	?	?	0	0				
<i>Mezentia gibbera</i>	2	0	0	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	1	1	1	0	1	1	0	1	-	1	0	1	1	0	1	0	1	0	0			
<i>Andeomezentia napoana</i>	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	-	0	0	1	1	1	0	1	1	0	1	-	1	1	1	0	0	1	0	0	1	0	0		
<i>Hylaezentia acanthopyga</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	1	1	1	0	1	1	0	1	-	1	-	1	1	0	1	0	1	0	0			
<i>Panamacris magnifica</i>	2	1	0	0	0	1	0	0	0	1	1	-	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0		
<i>Mayalina cohni</i>	2	1	1	0	1	0	1	1	1	1	0	1	-	2	1	1	0	1	1	0	1	1	0	0	1	0	0	-	0	0	1	0	1	0	1	0	1	1		
<i>Cristobalina sellata</i>	2	1	1	1	1	0	1	1	0	3	0	1	-	2	1	0	0	1	1	0	1	1	0	0	1	0	0	-	0	0	1	0	0	0	1	0	0	0		
<i>Rhcnodermahumilis</i>	2	1	0	0	0	0	0	0	0	1	1	-	2	1	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0		
<i>Lempira metapanensis</i>	2	1	0	0	0	1	1	0	3	1	1	-	2	1	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	1		
<i>Pararhcnoderma laselvae</i>	2	1	0	0	1	0	1	1	0	1	1	-	2	1	0	0	0	1	0	1	1	0	0	2	0	0	0	-	0	0	0	0	0	0	0	0	0	1		
<i>Bora nemoralis</i>	0	0	0	0	0	0	0	0	0	0	0	1	-	1	0	-	0	0	1	0	1	1	1	0	0	1	-	0	1	0	1	0	0	0	0	0	0			
<i>Phaeoparia phrygana</i>	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	0	0	0	0	0		
Character	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67								
Genus species																																								
<i>Epiprora hilaris</i>	0	0	0	0	0	0	0	0	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	0	0	2		
<i>Bactrophora mirabilis</i>	0	0	1	1	1	2	2	0	0	0	0	1	1	0	1	2	1	1	1	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0		
<i>Hyleacris rubrogranulata</i>	3	1	0	1	0	0	2	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0	1	0	0	1		
<i>Silacris albithorax</i>	0	1	0	1	1	0	0	0	1	1	1	-	-	0	0	0	0	0	-	-	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0		
<i>Mezentia gibbera</i>	1	1	1	1	1	0	2	0	1	0	1	0	1	0	1	1	0	0	-	-	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0		
<i>Andeomezentia napoana</i>	1	1	1	1	1	0	2	0	1	1	1	-	-	0	0	0	0	0	-	-	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0		
<i>Hylaezentia acanthopyga</i>	0	1	1	1	1	0	2	0	1	1	1	-	-	0	0	0	0	0	-	-	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0		
<i>Panamacris magnifica</i>	3	2	0	1	1	0	1	1	-	-	0	1	1	0	0	2	1	1	1	0	0	1	0	0	1	0	0	1	0	2	2	0	1	?	?	0	0	0		
<i>Mayalina cohni</i>	0	1	0	0	0	0	0	1	0	-	0	1	1	0	1	2	1	1	1	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0		
<i>Cristobalina sellata</i>	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	2	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0		
<i>Rhcnoderma humilis</i>	2	2	0	1	1	0	1	1	-	-	0	1	1	0	1	2	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Lempira metapanensis</i>	0	2	1	1	1	0	1	1	-	-	0	1	1	0	1	2	1	1	1	1	0	1	0	0	1	0	2	2	0	1	1	0	0	0	0	0	0	0		
<i>Pararhcnoderma laselvae</i>	0	2	1	1	1	0	1	1	-	-	0	1	1	0	1	2	1	1	1	1	0	1	0	0	1	0	2	2	0	1	1	0	0	0	0	0	0	0		
<i>Bora nemoralis</i>	0	1	0	1	1	2	0	0	1	1	1	-	-	0	0	1	0	0	-	-	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0		
<i>Phaeoparia phrygana</i>	0	0	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	0	0	0	0	2		