EPURAEOSOMA, A NEW GENUS OF HISTERINAE AND PHYLOGENY OF THE FAMILY HISTERIDAE (COLEOPTERA, HISTEROIDEA)

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Abstract. — *Epuraeosoma* gen. nov. (type species: *E. kapleri* sp. nov.) from Malaysia, Sabah is described, and its taxonomic placement is discussed. The current concept of the phylogeny and classification of Histeridae is critically examined. Based on cladistic analysis of 50 taxa and 29 characters of adult Histeridae a new hypothesis of phylogeny of the family is presented. In the concordance with the proposed phylogeny, the family is divided into three groups: Niponiomorphae (incl. Niponiinae), Abraeomorphae and Histeromorphae. The Abraeomorphae includes: Abraeinae, Saprininae, Dendrophilinae and Trypanaeinae. The Histeromorphae is divided into 4 subfamilies: Histerinae, Onthophilinae, Chlamydopsinae and Hetaeriinae.

✂

INTRODUCTION

Members of the family Histeridae are small or moderately large beetles which due to their rigid and compact body, 2 abdominal tergites exposed and the geniculate, clubbed antennae are generally well recognized by most of entomologists. In fact, this family receives a constant attention from taxonomists world-wide and several important papers have been published in last years (e.g., Kryzhanovskij and Reichardt 1976, Vienna 1980, Johnson *et al.* 1991, Ôhara 1994), including 2 editions of the world catalogue by Mazur (1984, 1997).

In spite of these interests, very little has been published on the phylogeny and classification of the group since the Wenzel (1944) paper distinguishing two major lineages (Histeromorphae and Saprinomorphae) in Histeridae. The classification proposed by Wenzel, and applied to the world histerids by Mazur (1984) has been discussed and refined by Ôhara (1994), who made the first major study of the adult morphology of Histeroidea. The same author (Ôhara 1994) attempted a reconstruction of the Histerid phylogeny applying cladistic methodology. He correctly observed that the Wenzel system was based on a four key characters and as such was not phylogenetical in the cladistic sense, and gave a character state matrix for 13 characters and 12

subfamily level taxa. Ôhara provided cladogram which in his opinion presented the most parsimonious solution to the given data set.

Biology and the immature stages of Histeridae are poorly known. In the most recent treatment of immatures by Newton (1991), there is a brief diagnosis and description of the larvae and a key to 6 subfamilies, including larvae of Trypanaeinae and Trypeticinae, that were previously unknown. The same key is repeated in Hansen (1997). In the present study the larval characters are not included, but some are discussed in the classification section below.

During the routine identifications of various histerids done by the junior author, two remarkable specimens from Malaysia (Sabah) turned out – and none of them could comfortably be placed in any of the existing subfamilies of Histeridae. Both specimens represented unknown genera and their morphology indicated some degree of myrmecophyly. This discovery gave the initial input to our discussions about the phylogeny and classification of Histeridae, brought the senior author into the project, and ultimately led to the present scope of the paper. While already working on this manuscript we learned that one of our new genera is being independently described by Dr. N. Degallier, and we decided to exclude it from this paper, since it was not critical to our studies.

Besides the description of this interesting, new beetle our goal was to discuss and reexamine the Ôhara (1994) data in the light of cladistic parsimony criteria, and to expand the data set to include more taxa and characters with hope that some resolution on the hypothetical phylogeny of the group can be reached. The number of taxa (50) and adult characters (29) included in our studies are by no means exhaustive, although the final character set represents much reduced matrix reached after eliminating all autapomorphies and characters that were discarded because of impossible or unclear coding at the level of our study. The major attempt of our study has been to analyze and reconstruct the basal clades of Histeridae and the interrelationship of the currently recognized subfamilies. We decided to include a number of genera representing all currently recognized subfamilies and tribes (Mazur 1997), and all those available taxa that were known to the junior author to represent transitions between groups (e.g., *Phoxonotus*, *Trypolister* or *Plaesius*). Such a selective approach was necessary to make to project feasible at the moment, but we hope the

conclusions reached in our analyses are sound and can be used as a starting point for further research.

EPURAEOSOMA gen. nov.

Type species: *Epuraeosoma kapleri* sp. nov.
Gender: feminine.

Etymology: the generic name is a combination of the names *Epuraea* (Nitidulidae) and *Platysoma* to call attention to its superficial nitiduloid appearance and its phylogenetic placement.

Diagnosis. This genus posses an elongated, 1-segmented antennal club as the genera of Chlamydopsinae, but the antenna is inserted laterally below the frontal ridge, the scape is not modified and in repose is received in a deep groove along the inner margin of eye and below head (scape is strongly triangular and covers the eye from above in Chlamydopsinae). The apparently hidden labrum, the elongated antennal club, and the shape of the antennal grooves below eyes will immediately distinguish this genus
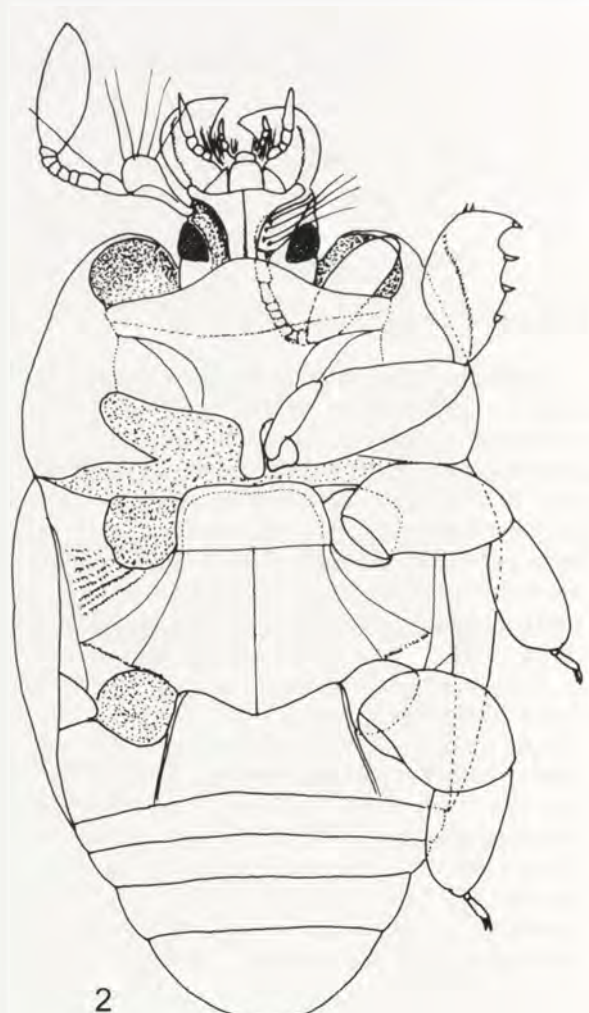
Figures 1, 2. *Epuraeosoma kapleri* sp. nov.: (1) dorsal; (2) ventral
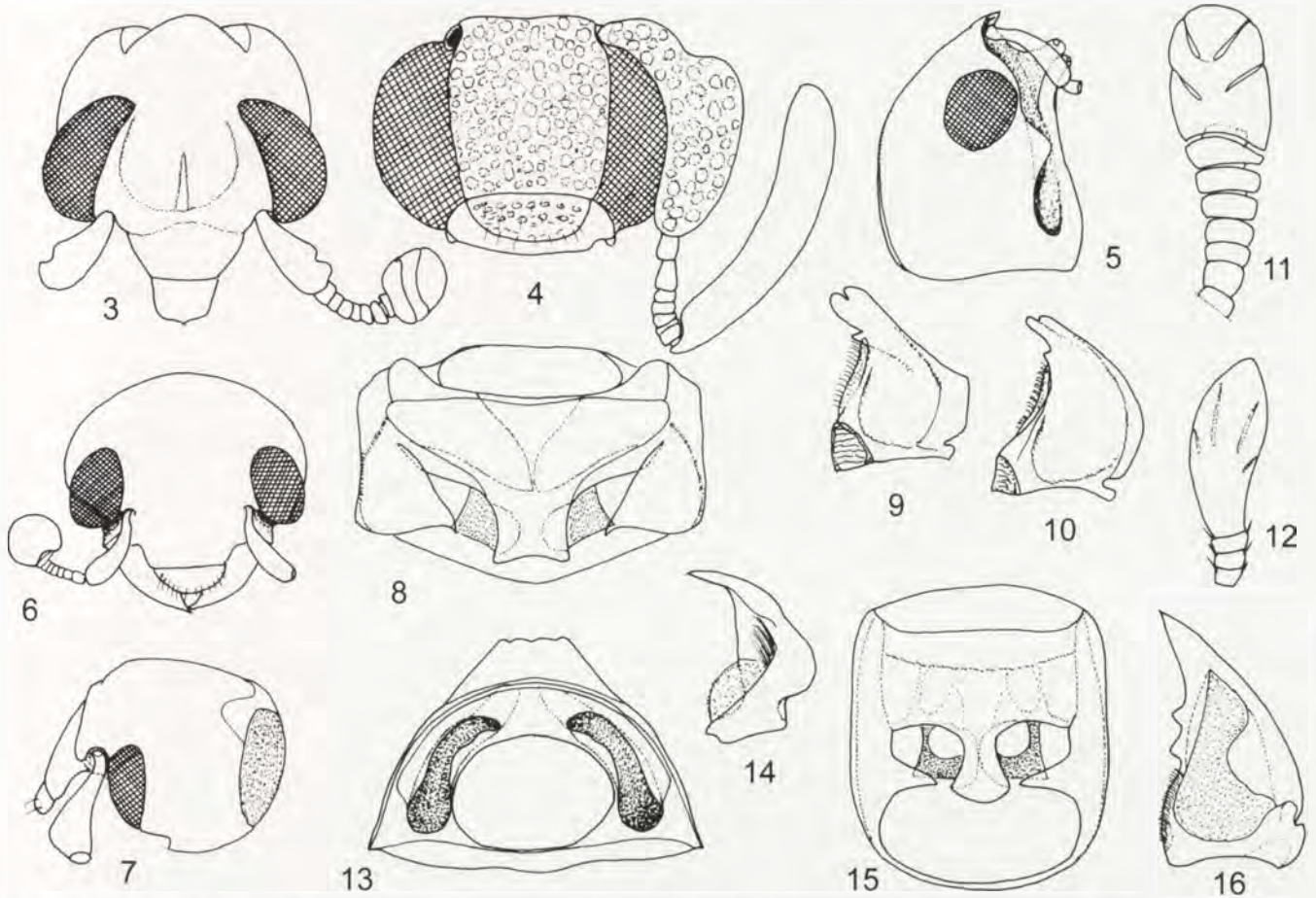
Figures 3–16. 3–7 Head: (3) *Omalodes* sp.; (4) *Chlamydopsis* sp.; (5) *Niponius* sp.; (6) *Trypolister* sp.; (7) *Tribalus* sp. 8, 13. *Chlamydopsis* sp., prothorax: (8) ventral; (13) top view. 9, 10. *Trypanaeus* sp., mandible: (9) oblique inner view; (10) ventral. 11, 12. Terminal antennomeres: (11) *Plaesius* sp.; (12) *Epuraeosoma kapleri* sp. nov. 14. *Chlamydopsis* sp., mandible, ventral. 15, 16. *Niponius* sp.; (15) prothorax, ventral; (16) mandible, ventral

from all known genera of Histerinae, Onthophilinae or Tribalinae. The glabrous labrum, the visible remnants of the V-shaped sutures on the club (Fig. 12) and the prosternal alae covering most of the antennal cavities from below are characterisitc for the Histerinae and place the genus close to the *Platysoma* group.

Description. Female. Body elongate-oval, about 2 times as long as broad (Fig. 1); venter flat, dorsum moderately convex. Vestiture of dorsum consists of whitish, strongly appressed, dense squamiform setae which are evenly distributed on head, pronotum and elytra, forming fringes along occipital ridge and lateral pronotal and elytral edges; venter glabrous; sparse setae along edges and dorsal surfaces of femora and tibiae.

Head slightly prognathous, partially retracted into prothorax up to a strong occipital ridge; dorsum without striae. Labrum apparently hidden and fused to shortened clypeus, asetose; mandible strongly bent, and bearing a single tooth apically, mola not examined; maxillary galea and lacinia not examined; mentum small, almost quadrate, labial palps elongate, approximate at base, terminal palpomere conical, about as long as penultimate one. Antennal insertion about middle length of eye, under distinct frontal

ridge; antennal scape large, bearing 8–10 long bristles dorsally; funicle 7-segmented; antennal club elongate, solidly fused, densely tomentose, with reduced V-shaped sutures visible on cleared club (Fig. 12). Ventral side with median region along the gular suture strongly elevated forming a narrow bridge, internally limiting antennal furrow in which apex of scape, pedicel and most of funicular segments are being received in repose (Fig. 2). Eye coarsely facetted, transverse.

Pronotum transverse, deeply emarginate anteriorly; anterior margin narrowly margined, base and lateral edges unbordered; disk punctate, without striae or impressions.

Scutellum small, triangular.

Elytra densely punctate, truncate apically; each elytron with 6 barely traceable impressed lines, composed of more regular punctures; lateral border (external subhumeral stria) sharp and complete, marginal stria weak, complete; epipleuron convex, punctate and setose.

Propigidium and pigidium almost horizontal, weakly convex, sparsely punctate.

Prosternum of *Platysoma*-type (Fig. 2): median part weakly prominent medially, laterally extended to notopleural suture forming alae covering part of the antennal club cavity
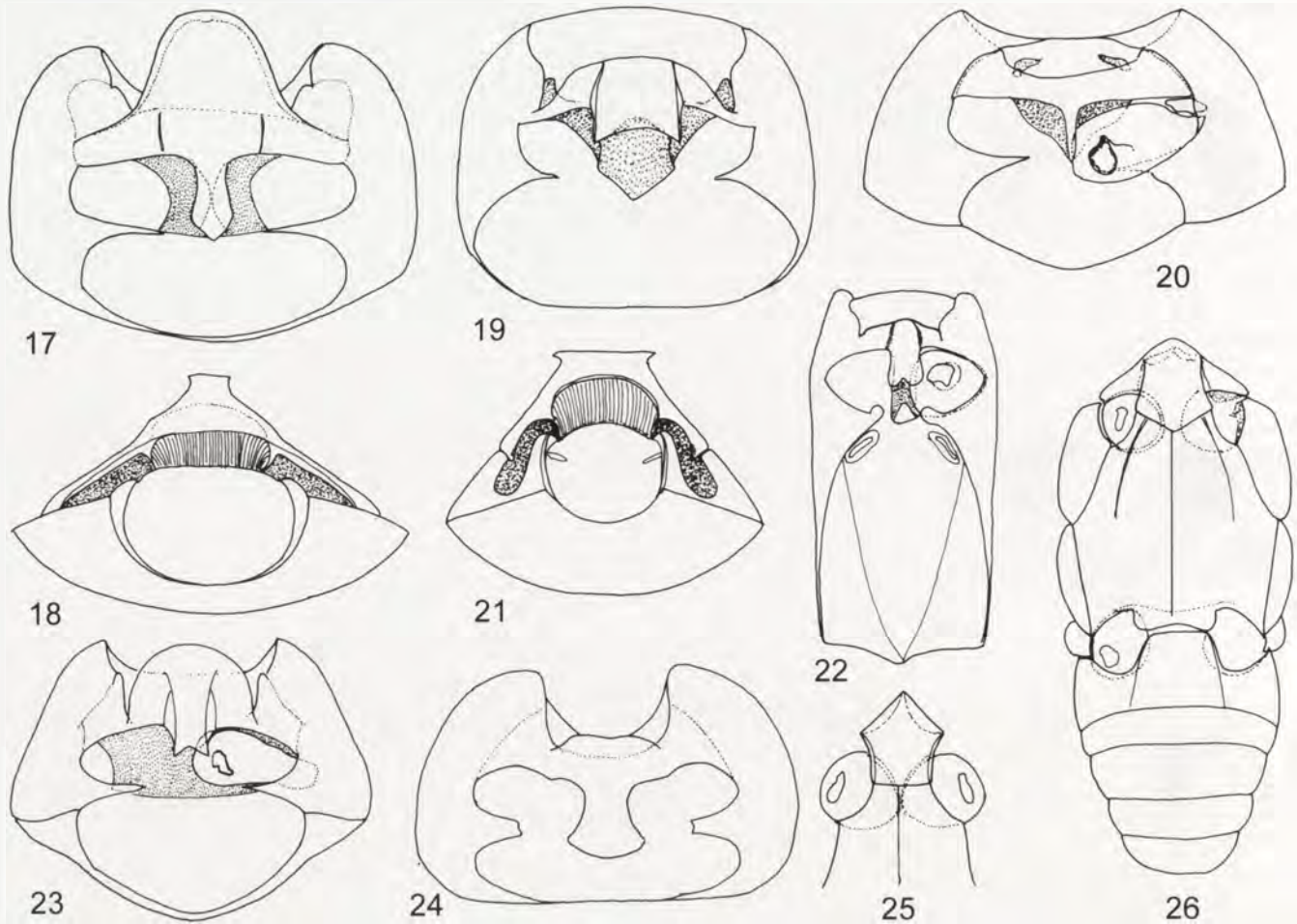
Figures 17–26. 17–24. Prothorax: (17) *Plaesius* sp., ventral; (18) *Plaesius* sp., inner; (19) *Trypolister* sp., ventral; (21) *Onthophilus striatus*, inner; (22) *Trypanaeus* sp., ventral; (23) *Phoxonotus* sp., ventral; (24) *Hololepta plana*, ventral. 25. *Trypanaeus* sp., mexosternum, ventral. 26. *Coptotrophis* sp., pterothorax and abdomen, ventral

from below; antennal club received in clear cavity located at anterior angles of hypomeron; transverse ridge (or stria) very weak, almost obsolete externally; prosternal process very narrow, slightly widened behind coxae, broadly rounded apically; median part of prosternum without striae; lateral marginal stria curved outwardly to meet notopleural suture, a short additional stria placed outside of it.

Mesosternum 3 times as broad as long, barely concave anteriorly; marginal mesosternal stria weak but complete; meso-metasternal suture straight. Metasternum 2 times as long as ventrite 1 with complete longitudinal stria; lateral metasternal stria slightly curved outward, reaches anterior margin of metacoxa; post mesocoxal stria strongly arcuate, delimits the area behind mesocoxa, bearing 3 or 4 additional striae; transverse metasternal stria apparently absent.

Intercoxal process of ventrite 1 distinctly concave medially (Fig. 2); ventrite 1 about two times longer than 2, about as long as 5; lateral stria of ventrite 1 short and almost straight.

Legs: femora thick, especially metafemur; protibia broad with 2 teeth and 2 smaller spines along the external margin,

apical spines unequal, small; meso- and metatibiae with rows of fine microspines along smooth edges; tarsal groove on dorsal side obsolete; tarsi 5-5-5, ventral side of each tarsomere with 2 moderately long setae; claws 2, slender.

Ovipositor moderately long; coxites strongly sclerotized; styli subapical.

Epuraeosoma kapleri sp. nov.

Etymology. Dedicated to Mr. Oldřich Kapler, a Czech histeriologist, who first saw this curious beetle and made it available for our study.

Description. Length 2.9 mm. Color brown with apical parts of elytra, propigidium and pigidium light brown; surfaces shiny. Pronotum 0.4 times as long as wide; elytra 0.7 times as long as wide and 1.8 times as long as pronotum. Pronotum densely and strigosely punctured, in lateral part the strigae appear to form oblique striae or ridges. Elytral punctures 0.3–0.4 times as large as those on pronotal disk, more rounded and less impressed; interspaces densely reticulate.
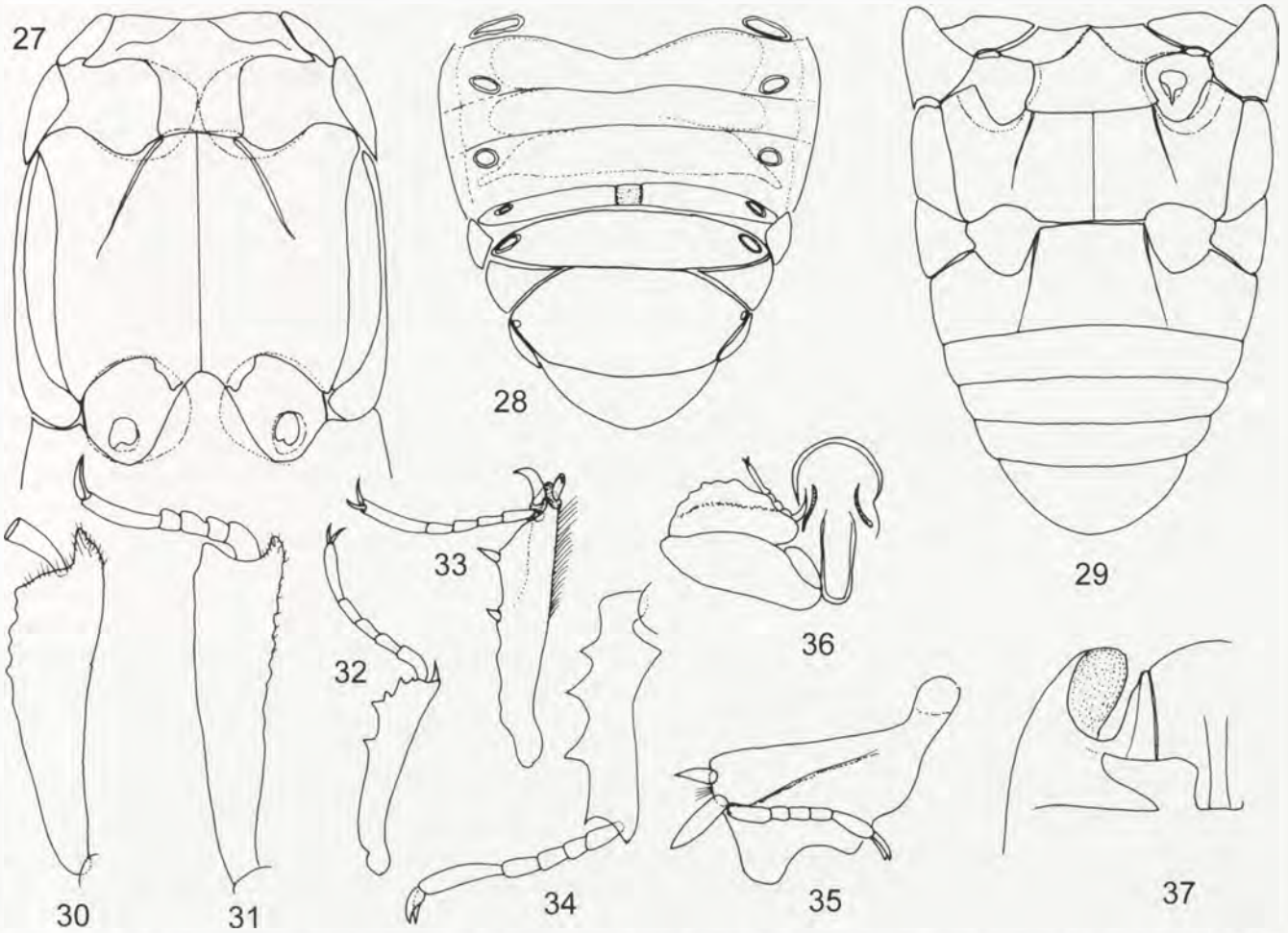
Figures 27–37. 27. *Niponius* sp., pterothorax, ventral. 28. *Plaesius* sp., abdomen, dorsal. 29. *Phoxonotus* sp., pterothorax and abdomen, ventral. 30–32. Metatibia and tarsus: (30) *Trypanaeus* sp.; (31) *Trypolister* sp.; (32) *Niponius* sp. 33–36. Protibia and tarsus: (33) *Niponius* sp.; (34) *Trypanaeus* sp.; (35) *Atholus* sp. 36. *Carcinops troglodytes*, prosternum showing protibial hook being received in the lateral groove. 37. *Acritomorphus silvestris*. lateral part of prothorax, ventral

Holotype female: Malaysia, Sabah, Sipitang, Mendolong, T4/R, 4.v.1988, leg. S. Adebratt (Museum and Institute of Zoology, PAS, Warsaw).

PHYLOGENY OF HISTERIDAE

1. Introduction

The phylogeny of Histeroidea, and brief discussion on the classification of Histerids are included in Hansen's (1997) treatment of Staphyliniformia phylogeny. Hansen provided several characters to define the monophyly of Histeroidea and the included families, establishing a cladistic hypothesis of their relationships — ((Sphaeritidae) + (Synteliidae + Histeridae)). His classification of Histeroidea agrees with that of Lawrence and Newton (1982), who pointed out several important characters for this superfamily. In our studies both Sphaeritidae and Synteliidae were used as outgroups to polarize character states. Their morphology are covered by Crowson (1974), Hlavac (1975), Kryzhanovskij and Reichardt (1976) and Ôhara (1994).

At first we checked the matrix provided by Ôhara (1994) to confirm or refute his cladistic hypothesis about the phylogeny of Histeridae. After we realized his data is incomplete and based on composite characters and taxa, we started to build up our own data matrix. We checked all available information concerning the morphology and characters used in various keys or phylogenetic reconstructions of Histeridae (mostly in Wenzel 1944 and Ôhara 1994). Several characters from the initial set of more than 50, were excluded because of ambiguous definitions or autapomorphy in the terminal taxa. The final taxon-character matrix is presented in Table II. Cladistic analyses were undertaken using Hennig86 (Farris 1988) and Pee-Wee by P. A. Goloboff (1993). All characters were polarized using *Sphaerites* and *Syntelia* as outgroups, and were treated as unordered (nonadditive). During the initial stage of the analysis multiple runs of Hennig86 were done with various options to examine the stability of the trees, the performance of the characters on the trees, and the character coding. The mapping of character states and final cladograms saved

Table I. M. Ôhara (1994) data matrix

	0					5					10		
Ancestor1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ancestor2	0	0	0	0	0	0	0	0	1	0	0	0	0
Niponiinae	1	0	1	1	0	0	0	0	1	0	0	0	0
Chlamydopsinae	1	1	0	0	2	1	0	1	0	0	0	0	0
Onthophilinae	1	1	0	0	2	0	0	0	0	0	0	0	1
Tribalinae	1	1	0	0	1	0	0	0	0	0	0	0	0
Histerinae	1	1	0	0	1	0	0	0	0	0	0	1	0
Hetaeriinae	1	1	0	0	1	0	0	1	0	0	0	0	0
Dendrophilinae	1	1	0	0	3	0	1	0	0	0	0	0	0
Abraeinae	1	1	0	0	4	1	1	0	0	1	0	0	0
Saprininae	1	1	0	0	3	1	1	0	0	0	0	0	0
Trypanaeinae	1	0	0	0	3	1	2	0	1	0	0	0	0
Trypeticinae	1	1	0	0	3	1	1	0	1	0	1	0	0

from Hennig86 or Pee-Wee were produced using CLADOS (Nixon 1992). In the presentations below we often illustrate the Nelson consensus trees from many trees obtained in various analyses – this approach does not mean our faith in consensus trees being "solutions" to our problems, but these are used here mostly to save space in illustrating all trees or to show how much the particular trees vary in their configurations.

2. M. Ôhara (1994) data set – a reanalysis

The character matrix provided by Ôhara (1994) was modified by adding second "ancestor" to accommodate 0/1 state of his character 4, and the numbers were changed to follow "0 ... n" convention used by the computer programs; the transcribed matrix is presented in Table I. The characters used in the Ôhara's matrix are discussed in length in his paper. Below we provide a brief summary, with the convention that the character number assigned in our analysis is followed by his original number in brackets [n]:

0 [0]. Mesosternum between coxae: (0) narrower than mesocoxal cavity; (1) broader than mesocoxal cavity. *Note*: the mesocoxae are approximate in *Niponius*, and certainly broader than mesosternum (Fig. 27).
1 [9]. Head: (0) horizontal in repose; (1) vertical in repose.
2 [7]. Head: (0) without horns; (1) with 2 horns.
3 [8]. Mandibles movement: (0) horizontal; (1) vertical.
4 [5]. Antennal cavities: (0) absent; (1) situated at anterior angles and partially closed by alae; (2) as previous but entirely closed by alae; (3) in front of coxae close to prosternal keel; (4) on anterior angles or in front of procoxae.
5 [1]. Prosternal lobe: (0) present; (1) absent.
6 [11]. Prosternal alae: (0) without antennal cavities; (1) with deep lateral incision; (2) with a slight notch.
7 [3]. Antennal scape: (0) normal; (1) triangular.
8 [4]. Form: (0) round, oval; (1) cylindrical.
9 [6]. Dorsal elytral striae: (0) rarely absent; (1) never present.

10 [10]. Antenna consisting of: (0) 8 segments and a club; (1) 7 segments and a club.
11 [13]. Labrum: (0) with setigerous punctures; (1) without setigerous punctures
12 [16]. Dorsal surface: (0) without costae; (1) with distinct costae.

Both ancestors were used as the outgroups and all the characters were treated as unordered in all procedures. Since the matrix is relatively small we used the implicit enumeration methods ("ie*" option in Hennig86) searching for the shortest trees. The run resulted in 146 equally parsimonious trees of the length 22 (CI 77, RI 75), their Nelson consensus tree is almost non resolved (Fig. 39) except for Niponiinae being the sister group of the remaining subfamilies. The tree with an exact configuration as provided by Ôhara is one of these 146 trees, although one character #4,1[5,1] has to be moved further up on the branch leading to Chamydopsinae etc. (Fig. 38).

Further approximation was used by the successive weighting, reaching at the end 17 "ie*" trees (length 166, CI 91, RI 89), and none of them was identical with the Ôhara's tree, all trees had Trypanaeinae outside of the remaining Histeridae (minus Niponiinae). The Nelsen consensus tree (Fig. 40) of these 17 ie trees is a bit more resolved, but again significantly different from the tree presented by Ôhara. Since Ôhara gave no methodology how his tree was reached or chosen from among other equally parsimonious trees, his hypothesis cannot be treated as "the most parsimonious solution". Additionally the characters and coding of the taxa at the subfamily level (not representing real taxa) have serious flaws due to their composite nature, and that is why we decided to develop our data set to investigate the problem in more depth.

3. Cladistic analysis

Taxa

Most of the specimens used in the analyses represent either type-genera of higher taxa (subfamily, tribe) or taxa for which adult males and/or females were available for dissections. The taxonomic placement of the taxa follow Mazur (1997). The asterisk (*) following the taxon name indicates that at least one specimen was cleared, disarticulated and examined in a glycerine slide. Many additional taxa (mostly from S. Mazur collection) were used to check the character distribution within the groups, but these are not listed below.

Sphaeritidae: *Sphaerites glabratus* (Fabricius)*♀♂;
Synteliidae: *Syntelia histeroides* Lewis;
Histeridae:
   Niponiinae: *Niponius* sp.*♀, Australia, Qld.;
   Trypeticinae: *Trypeticus* spp♀*, Laos and Australia; *Pygocoelis africanus* (Lewis)♀;
   Trypanaeinae: *Trypanaeus ensifer* Marseul* ♂♀; *Coptotrophis* sp.*♀, Ecuador; *Xylonaeus* sp. Brazil;
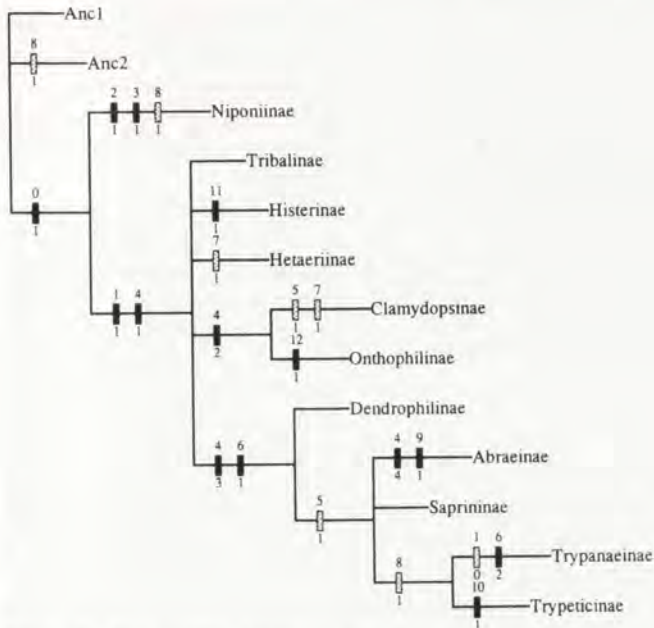
Figure 38. Ôhara (1994) cladogram with characters (Table 1) mapped according to the default optimization of CLADOS. Solid bars represent non-homoplastic characters and open bars homoplastic characters. The numbers above the bars note the character number and the number below the state of the character

Chlamydopsinae:*Eucurtiopsis* sp.* ♀, Malaysia, Sabah; *Chlamydopsis* sp.*♂, Australia;

Onthophilinae: *Onthophilus striatus* (Forster)*♀; *Glymma* sp.*♂, South Africa; *Epiechinus sulcisternus* Bickhardt*♀; *Peploglyptus golbachi* Kanaar*♀; *Vuattuoxinus* sp.*♂, Ivory Coast;

Tribalinae: *Tribalus minimus* (Rossi)*♂♀; *Epierus* sp.*♂, Brazil;

Hetaeriinae: *Hetaerius ferrugineus* (Olivier)*♀; *Satrapes sartorii* (Redtenbacher)*♀;

Histerinae:

Histerini:*Hister* sp.*♀, Poland; *Atholus* sp.*♀, Ivory Coast; *Contipus* sp. Kenya;

Hololeptini: *Hololepta plana* (Sulzer)*♂♀; *Oxysternus* sp.*♂, Cuba;

Platysomatini:*Platysoma oblongum* (Fabricius)*♀♂; *Plaesius* sp.*♂, Thailand;

Omalodini: *Omalodes* sp.*♂, Ecuador;

Exosternini: *Pelorurus* sp.*♂, Ivory Coast; *Adelopygus* sp.*♀, Ivory Coast; *Phelister* sp.*♀, Ecuador; *Yarmister* sp.*♂, Guyana;

Genera *incertae sedis*: *Epuraeosoma* (described above); Gennov*♂ – an undescribed genus from New Guinea;

Saprininae: *Saprinus* sp.*♂, Bulgaria; *Phoxonotus* sp.*♂, Costa Rica; *Phiothis arabicus* Mazur*♂; *Gnathoncus rotundatus* (Kugelann)*♂♀; *Styphrus corpulentus* Motschulsky*♀;

Dendrophilinae:

Anapleini: *Anapleus* sp.*♂, Argentina;

Bacaniini: *Bacanius* sp.*♀, Ecuador;

Dendrophilini: *Dendrophilus pygmaeus*(Linnaeus)*♀♂; *Kissister minimus* (Aube)*♂;

Paromalini: *Paromalus parallelepipedus* (Herbst)*♂♀; *Carcinops pumilio* (Erichson)*♂; *Pachylomalus* sp.*♀, Malaysia;

Abraeinae:

Abraeini: *Chaetabraeus* sp.♂♀, Poland;

Acritini: *Acritus* sp.*♀, Poland; *Halacritus* sp.*♂, Reunion;

Plegaderini: *Plegaderus vulneratus* (Panzer)*♂, Poland;

Teretriini: *Teretrius fabricii* Mazur*♀, Poland; *Trypolister* sp.*♂, Peru;

Acritomorphini:*Acritomorphus silvestris* Mazur♀.

Characters and discussion

0. Protrochantin: (0) exposed; (1) concealed (Fig. 23).

This is one of several synapomorphies for Histeridae + Synteliidae clade listed by Hansen (1997); protrochantin is exposed in *Sphaerites* (Fig. 20).

1. Abdominal tergite 4: (0) simple; (1) with medial slit receiving inflexed sutural edges of both elytra (Fig. 28).

This interlocking mechanism is present in all Histeridae examined, but is strongly reduced in *Hololepta*.

2. Hindcoxae: (0) approximate; (1) distinctly separated.

The hind coxae in Histeridae are at least narrowly separated (Niponiinae, Trypeticinae, Trypanaeinae, Figs 26, 27, 29). The intercoxal process of ventrite 1 is triangular in *Niponius*, while it is broad in the remaining Histerids.

3. Mandibular mola: (0) large; (1) strongly reduced or absent (Figs 14, 16).

Mola is generally present in Histeroidea (Hansen 1997), and it is being lost in several histerid genera or groups (*Chlamydopsis, Niponius, Hetaerius,* Histerini, Hololeptini, Exosternini); mola is strongly reduced in *Platysoma, Paromalus* or *Saprinus*. Hansen (1997) data are used to code the *Syntelia* mola as present.

4. Mandibular apex: (0) single; (1) split, forming double tooth (Figs 9, 10).

Single apical tooth with a variable position of subapical tooth along the incisor edge is a plesiomorphic state among the Histeroidea. Double mandibular apex is found only in Trypeticinae and Trypanaeinae. In *Epierus* and *Tribalus* the mandibular apex appear to be double, but it is apparently caused by the large subapical tooth being very close to the mandibular apex, which is especially visible in *Epierus* where the mandibles are often strongly asymmetric.

5. Lacinia with apical hook: (0) present; (1) absent.

This character is strongly correlated with the presence vs absence of a molar part in the mandible, while even a rudimentary mola is present then there is an apical hook in lacinia; however the strong hook is present in *Niponius* with no trace of the mandibular mola.

6. Antennal insertions: (0) hidden under distinct frontal extension (Fig. 7); (1) visible from above (Fig. 6).

7. Antennal insertion, position: (0) near middle or below

39

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    ┌─0 Ancestor1
├─14┤─1 Ancestor2
    └─2 Niponiinae
        ┌─3 Chlamydopsinae
    ┌─13┤─4 Onthophilinae
    │   ├─5 Tribalinae
    │   ├─6 Histerinae
    │   ├─7 Hetaeriinae
    │   ├─8 Dendrophilinae
    │   ├─9 Abraeinae
    │   ├─10 Saprininae
    │   ├─11 Trypanaeinae
    │   └─12 Trypeticinae
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40

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        ┌─0 Ancestor1
    ├─17┤─1 Ancestor2
    │   └─2 Niponiinae
    │       ┌─11 Trypanaeinae
    └─16┤   ┌─3 Chlamydopsinae
        └─15┤─4 Onthophilinae
        └─14┤─5 Tribalinae
            ├─6 Histerinae
            ├─7 Hetaeriinae
                ┌─8 Dendrophilinae
            └─13┤─9 Abraeinae
                ├─10 Saprininae
                └─12 Trypeticinae
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Figures 39, 40. Strict consensus trees generated from Ôhara (1994) data matrix: (39) of 146 "ie*" trees; (40) of 17 "ie*" trees reached after successive weighting

middle of eye; (1) distinctly above middle; (2) above apical corner of eye (Fig. 4).

The plesiomorphic condition, found in Sphaeritidae and Synteliidae is the placement of an antennifer laterally, under a distinct frontal ridge or extension. This condition has evolved into a state where the antenna is attached more dorsally, above the midlength of an eye (e.g. Onthophilini, Tribalini, Fig. 7); and probably further the frontal ridge become obsolete (*Abraeus, Acritus*) and the insertion is visible from above. The extreme development of this character is found in Chlamydopsines where the antenna is inserted on top of frons (Fig. 4).

8. Prosternum, anterior margin: (0) without traces of lateral notch; (1) with distinct notch laterally (Figs 23, 37).

9. Prosternum, anterior margin: (0) without alae extending on hypomera; (1) extending laterally on hypomeron to form at least weak ridge supporting antenna in repose (Figs 8, 18, 21).

These are the "fundamental" characters in the Histerid classification. In the in-groups, the states "0 & 0" are found only in *Niponius* (Fig. 15); the anterior margin of pronotum is almost straight in the Trypanaeinae *Coptotrophis*, but even in this genus there is a slight notch, indicating the reduction of an emargination, which is clearly seen in *Trypanaeus* (Fig. 22). We believe that two independent modifications of prosternal plate occurred in Histerids: (1) weak elevation of the median part of prosternum forming a chin piece, the antennal funicle is accommodated into a lateral notch, and the club is positioned on prosternum or hypomeron (Figs 23, 37); (2) the prosternal chin piece is usually much stronger and the prosternum extends laterally forming "alae" covering ventrally the antennal cavities to a various degree (Figs. 13, 18, 21). The state (#9,1) is coded in Hololeptini although, especially in *Hololepta*, the alae are greatly reduced (Fig. 24) due to the extremely flattened body.

10. Antennal club position in repose: (0) exposed and pressed against the hypomeron or along prosternum (*Plegaderus*); (1) hidden or partially visible but always

beneath prosternal alae (looking from venter); (2) positioned in an impression or cavity on inner portion of prosternum adjacent to the prosternal keel (Fig. 23).

There is an apparent correlation of the antennal club in repose with the characters # 8 and 9; states (0) and (2) occur mostly in the groups where there is a lateral notch on prosternum, but also in some Histerinae having the prosternal alae weakly developed (e.g., *Hister* or *Plaesius* – Figs 17, 18) or reduced (Hololeptini, Fig. 24). The state (2) is found only in Saprininae but is weakly developed in *Phoxonotus* and absent in *Philothis*.

11. Hind tibia: (0) with apex bearing 2 spines (these may be inconspicuous); (1) with inner corner prolonged and forming a flap or process bearing no spines apically (Figs 30, 31).

This character has not been used so far, but it seems to be very useful in delimiting the *Trypanaeus* lineage, and shows no relationship to *Niponius* (in spite of similar habitat) which has normal spines on the tip of hind tibia (Fig. 32). This character will place the genus *Trypolister* in the *Trypanaeus* group and not in Teretriini. This placement is consistent with *Trypolister* bearing shortened prosternal process (Fig. 19) and a distinct basal piece in a weakly sclerotized male genitalia.

12. Apical spines of protibia: (0) both distinct (usually slightly unequal); (1) one large or moderately large, the second one absent or inconspicuous; (2) both inconspicuous to absent.

The plesiomorphic state (0), protibial apex with both spines long and subequal is found in both outgroups (Figs 33, 35). From this state there has been several, apparently independent, transformations starting with hypertrophy of the outer spine with much reduction of the inner one (Fig. 36) of which the extreme condition is found in Dendrophilinae or most Saprininae; the second trend, possibly correlated with minute body (Abraeinae) or myrmecophily (Chlamydopsinae or Hetaeriinae) is a strong reduction of both spines (2).

13. Prosternal plate: (0) with transverse ridge; (1) without transverse ridge.

The so called "prosternal lobe" has been widely used since Wenzel (1944) implementation to define the group "Histeromorphae". The prominent prosternal lobe (= prosternum of Ôhara) is often demarcated posteriorly by a line (Fig. 17) or ridge, usually named "transverse suture". There is serious doubt the "transverse suture" represents a boundary between the presternum and sternum in the morphological sense because as such is not present in Hydrophiloidea or Scarabaeoidea (Hansen 1997), but if so,

TABLE II. Data matrix used in the cladistic analyses. Characters numbered as in the text "characters and discussion". Note that cladograms on Figs 41–47 are generated without characters # 26–28. Characters not examined are marked with "?".

	0	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
Sphaerites	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
Syntelia	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
Acritomorphus	1	1	1	?	0	?	1	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0	1	2	1	1
Acritus	1	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	1	2	1
Adelopygus	1	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1
Anapleus	1	1	1	0	0	0	1	1	1	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2
Atholus	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1
Bacanius	1	1	1	0	0	0	0	1	1	0	0	0	2	1	0	1	0	0	0	0	1	0	0	0	0	0	1	2	1
Carcinops	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	0	0	2	0	0	1	2	0
Chaetabraeus	1	1	1	0	0	0	1	1	1	0	0	0	2	1	0	1	0	0	0	0	0	0	0	1	0	0	1	2	1
Chlamydopsis	1	1	1	1	0	1	1	2	0	1	1	0	2	0	0	1	0	0	0	1	0	0	0	0	1	1	2	1	1
Coptotrophis	1	1	1	0	1	0	0	0	1	0	0	1	2	1	0	1	0	0	0	1	0	0	0	0	0	1	2	0	1
Dendrophilus	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1
Epiechinus	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	2
Epierus	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	2	0	0	1	1	1	0
Epuraeosoma	1	1	1	?	0	?	0	0	0	1	1	0	0	0	1	1	0	1	0	1	0	0	?	0	0	1	2	1	1
Eucurtiopsis	1	1	1	1	0	1	1	2	0	1	1	0	2	0	0	1	0	0	0	1	0	0	0	0	1	1	2	2	1
Gennov	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	2	0
Glymma	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	2	1	2
Gnathoncus	1	1	1	1	0	1	0	0	1	0	2	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	1	0
Halacritus	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	1	2	2	1
Hetaerius	1	1	1	1	0	1	0	0	0	1	1	0	2	0	0	1	1	0	0	1	0	0	0	1	0	1	2	1	0
Hister	1	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	0
Hololepta	1	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0
Kissister	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	0	0	2	0	0	1	2	1	0
Niponius	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0	0	0	2	0	0
Omalodes	1	1	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0
Onthophilus	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	2
Oxysternus	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	0	1	0
Pachylomalus	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	2	0	0	1	2	1	1
Paromalus	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	2	0	0	1	2	1	1
Pelorurus	1	1	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	1	0
Peploglyptus	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	2	2	2
Phelister	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	1	0
Philothis	1	1	1	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	1	2	1	0
Phoxonotus	1	1	1	1	0	1	0	0	1	0	2	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	1	0
Plaesius	1	1	1	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0
Platysoma	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0
Plegaderus	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	2	2	1
Pygocoelis	1	1	1	0	1	0	1	0	1	0	0	1	2	1	0	1	0	0	0	1	0	0	0	0	0	1	2	0	0
Saprinus	1	1	1	0	0	1	0	0	1	0	2	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	2	1	0
Satrapes	1	1	1	1	0	1	0	0	0	1	1	0	2	0	0	1	1	0	0	1	0	0	0	1	0	1	2	1	0
Styphrus	1	1	1	0	0	1	0	0	1	0	2	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	1	0
Teretrius	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0	1	2	1	1
Tribalus	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	2	1
Trypeticus	1	1	1	0	1	0	0	0	1	0	0	1	2	1	0	1	0	0	1	0	0	0	0	0	0	1	2	0	1
Trypolister	1	1	1	0	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	1	2	1	1
Trypanaeus	1	1	1	0	1	0	0	0	1	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	0	1	2	0	1
Vuattuoxinus	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	?	1	2
Yarmister	1	1	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	0	0

it is a clear plesiomorphic character originated far back in Histeroidea phylogeny.

We think there is another plausible explanation for this character, consistent with the development of the anterior part of prosternum into a protective chin piece. In *Sphaerites* or *Niponius* where there is no trace of the transverse ridge, the prosternum in front of coxae is very short, and the cervical sclerites are attached to a ring located just below the anterior margin (Fig. 20) and head is not retracted into prothorax. In other groups the cervical sclerites are attached much below the anterior margin to an internal ring below the level of antennal cavities (Fig. 21). In these groups the "suture" may correspond to a level of "generalized" anterior margin, overgrown by the prosternal alae protecting ventral part of head and antennae in repose. Assuming the Ôhara's (1994) interpretation of the lobe being present in *Syntelia* is right, then it either independently originated in that genus and several groups of Histeridae or originated once in ancestor of Synteliidae + Histeridae and got independently lost in *Niponius* and other Histerids. The second scenario has been adopted in our studies. After examination of a slide mounted specimen of *Niponius* we rejected Ôhara's (1994) opinion that the lobe is present in *Niponius*; there is a transverse impression along the anterior margin (Fig. 15), but its relative position does not correspond to the suture in other histerids. Also our slide mounted material does not confirm the presence of the ridge in several genera of Dendrophilinae, including our specimens of *Dendrophilus*. On a contrary, in *Chlamydopsis* (Figs 8, 13) there is distinct ridge separating the "prosternal lobe", although this is almost not visible in *Eucurtiopsis*.

14. Labrum: (0) with setigerous punctures; (1) without setigerous punctures.

Ôhara (1994) data are used to assign that the *Syntelia* labrum bears a pair of setae on dorsal surface. We agree with him that the labrum is without sensory setae in Histerinae only, although the state(s) found in Hetaeriinae should be studied in more detail (see figures in Helava *et al.* 1985). The labrum in Chlamydopsinae is heavily sclerotized and sculptured and has many punctures bearing minute setae, but not 2 long ones as in most groups (Fig. 4).

15. Mid coxae: (0) transverse and contiguous below the mesosternal process; (1) distinctly separated or circular while close together.

Niponius has a very distinctive type of mesocoxae (Fig. 27), being transversely oval and contiguous below the mesosternal process; this state is consistent with *Sphaerites* and *Syntelia*. In the remaining examined specimens the mesocoxae are always distinctly separated, except for *Trypanaeus* (Fig. 25) and *Trypeticus*. It is almost certain the approximate coxae in these cases are caused by the extremely narrow, cylindrical body form, and this is supported by their coxae being almost circular, and an existing transitional forms (e.g., *Pygocoelis* or *Coptotrophis*) with narrowly separated (Fig. 26) mid coxae.

16. Ovipositor: (0) sclerotized with coxites scoop like; (1) greatly reduced and desclerotised.

The plesiomorphic state is regarded as one of the apomorphies for Histeroidea (Lawrence and Newton 1982); the state (1) has been confirmed in *Hetaerius, Satrapes, Trypanaeus, Pygocoelis* and *Trypeticus*. The reduction of the ovipositor in Hetaeriinae and *Trypanaeus* group is almost certainly independent.

17. Sutures of antennal club: (0) straight, arcuate or absent; (1) strongly V-shaped (Fig. 11).

The structure of the antennal club in Platysomatini and Hololeptini was studied by De Marzo and Vienna (1982b); they postulated the peculiar sensory pockets were derived between partially fused antennomeres of a club. As such this is treated as apomorphic state, but the value of this character, and independent origin of these structures need further studies.

18. Prosternum with deep lateral groove: (0) absent; (1) present.

This is peculiar character found only in part of Dendrophilinae (Paromalini and Dendrophilini). As it has been demonstrated (Fig. 36) the groove receives the apical hook of protibia in repose forming an interlocking mechanism holding fore legs covering antenna from below.

19. Mesotrochantin: (0) visible; (1) hidden.

It was believed the mesotrochantin is always hidden in Histeridae (Ôhara 1994; Hansen 1997) until SAŚ draw one while executing an illustration of *Phoxonotus* (Fig. 29). After seeing one on the illustration we could confirm its visibility in all examined genera of Saprininae, Onthophilinae (except *Glymma*), *Dendrophilus* and *Anapleus*.

20. Tarsi: (0) 5-5-5; (1) 5-5-4.

The state (1) is found only in Acritini as defined by Wenzel (1944).

21. Antennal club: (0) with simple sensillae; (1) with Reichardt's organ.

Yet, another character related to specialized sensillae (DeMarzo and Vienna 1982a) of unknown value and application. It is used here to define Saprininae, although the structure of the organ and the variability has not been definitively shown to be a sound synapomorphy for the group.

22. Aedeagus: (0) with basal piece shorter than half of apical piece; (1) without basal piece; (2) with basal piece about as long or distinctly longer than apical piece.

The absence of the ring shaped basal piece has been pointed out by Wenzel (1944) as one of the characters of his Abraeinae (incl. Abraeini, Acritini, Plegaderini, Teretriini and Acritomorphini). There are some groups in which the proportion of basal/apical portion of the aedeagus are stable (e.g., Paromalini), but in some vary a lot (e.g., Tribalinae). The states were coded from our specimens or available illustrations (if males were absent in our material).

23. Labrum: (0) articulated with frons; (1) solidly fused with frons.

This character was used by Helava *et al.* (1985) as the only synapomorphy for Hetaeriinae, but its value need further investigation (N. Degallier, personal communication).

24. Antennal scape in repose: (0) positioned along inner

margin of eye and below head; (1) covers eye from above (Fig. 4).

The antenna inserted on top of head with triangular scape covering eye from above is an unique character for Chamydopsinae.

\# 25. Intercoxal process of ventrite 1: (0) narrow and subacute apically (Fig. 27); (1) broad, and never acute (Figs 26, 29).

The outgroups and *Niponius* have the plesiomorphic state, although the hind coxae in the latter are narrowly separated and the process is broader than in *Syntelia* or *Sphaerites*.

Results

Hypotheses tested. (1) The Wenzel (1944) division of Histeridae on Histeromorphae (prosternal lobe present) and Saprinomorphae (prosternal lobe absent) is artificial, because it is based on a presence vs. absence of a plesiomorphic character; (2) the system presented in Ôhara (1994) makes a significant leap forward but needs better definitions and refinements in several details; the major problems are: (a) monophyly of Dendrophilinae, Tribalinae and Saprininae; (b) relationships of Dendrophilinae vs. Abraeinae, and (c) position of Chlamydopsinae, Onthophilinae and Hetaeriinae (all more or less associated with ants and termites).

Strict parsimony and successive weighting. In this step we used Hennig86 to calculate the shortest tree based on unordered characters, and using both Sphaeritidae and Synteliidae as outgroups. Because the matrix was too large for the implicit algorithms (we had to turn off the computer after 2 days of work), we used approximation options in Hennig86 (mhennig* with bb*) to search for the shortest trees. To avoid "a priori" weighting of characters, we followed methods outlined by Farris (1969) and Carpenter (1988) which assigns the weight of the characters according to their fits calculated by the consistency and retention indexes. The procedure was the series of commands "mhen* bb* xsteps w cc" until the tree length did not longer change.

The first run of *mhennig** generated single tree (L 59, CI 50, RI 88) which showed two major groups (Fig. 41) and *Niponius* as a sister group to all remaining Histeridae. The successive weighting resulted in 10 mhennig* trees (L 245, CI 75, Ri 95) with very consistent configurations in the major lineages, showing always three major groups: *Niponius* + (Saprinomorphae + Histeromorphae), which are also clearly shown on their Nelsen consensus tree (Fig. 42). A working definition, proposed here, of these major clades are: Saprinomorphae (prosternum with lateral notch for antennal funicle), Histeromorphae (prosternum with alae at least partially covering antennal groove or cavity from below).

Implied weighting. To check the results obtained by the first group of methods we used the implied weighting method as discussed by Goloboff (1993) and applied in his software Pee-Wee. This algorithm calculates weight of each character according to their homoplasy – and eventually searches for the trees of a maximum total fit (with character fit defined as concave function of homoplasy), rather than trees of

minimum length as in Hennig86. In this procedure we used the following options: HOLD 100 (keeps 100 trees in memory); Hold/20 (maximum 20 trees are kept from each replication of MULT) and MULT20 (20 tree searches with exhaustive branch swapping on randomized input order). These settings turned to be fast enough and effective, which was several times checked using much higher values of MULT, MULT/ and various swappers included in the software. The concavity (CONC) values used with Pee-Wee were 1, 3 (default) and 6, the higher the value of CONC the weight is less strongly against characters with homoplasy.

With the Pee-Wee, we obtained 7 (weak concavity), 239 (default) and 245 (strong concavity) trees respectively. All trees showed the same basal topology (Figs 43, 44), as both consensus trees found by Hennig86. The strong and medium concavity trees (CONC 1 & 3) favor less homoplasy and on their consensus trees the *Abraeus* clade is not supported at all. In our opinion, the Pee-Wee trees, although based on different methodology does support the groupings we found while searching for the shortest trees.

Further testing. Once we reached, what we believed, sound cladistic hypotheses about the relationships of major taxa in Histeridae, we wanted to see how good it was, and if this would behave under further testings. The best test would be to search for congruence with the data generated from larval, behavioral or distributional characters. The first two groups are unavailable to us or too scarce for scoring, while the distributional data are not useful, since most of the genera are pantropical or cosmopolitan in their distributions. We decided to introduce 3 additional, hightly homoplastic characters to our data set, and to repeat all procedures to see how the tree topology is resistant to such addition.

The following characters were added:
\# 26 – antennal club: (0) 3-segmented; (1) 2-segmented; (2) 1-segmented, solidly fused;
\# 27 – procoxae: (0) continuous or very narrowly separated under prosternal process; (1) distinctly separated;
\# 28 – elytra: (0) with punctate or grooved striae; (1) without defined striae, irregularly punctate; (2) with costae.

These characters were at first discarded from the original data set because of high homoplasy and difficult application to some groups. The first one (#26) can only reliably be examined on slide mounted specimens, because on dry specimens the "annuli" which are external whorls of sensillae are usually obscuring or imitating sutures. The second character (# 27) is obviously related to the body shape, the narrower and more cylindrical body, the prosternal process is narrower; there are also some intermediate taxa, which have had to be coded arbitrary. The elytral striae (# 28) are present in outgroups but these are composed of punctures in *Sphaerites* while are partially grooved in *Syntelia*. The costate intervals are generally used to define Onthophilinae, but there exist intermediate, undescribed genus close to *Epierus* with partially costate elytra (S. Mazur, unpublished).
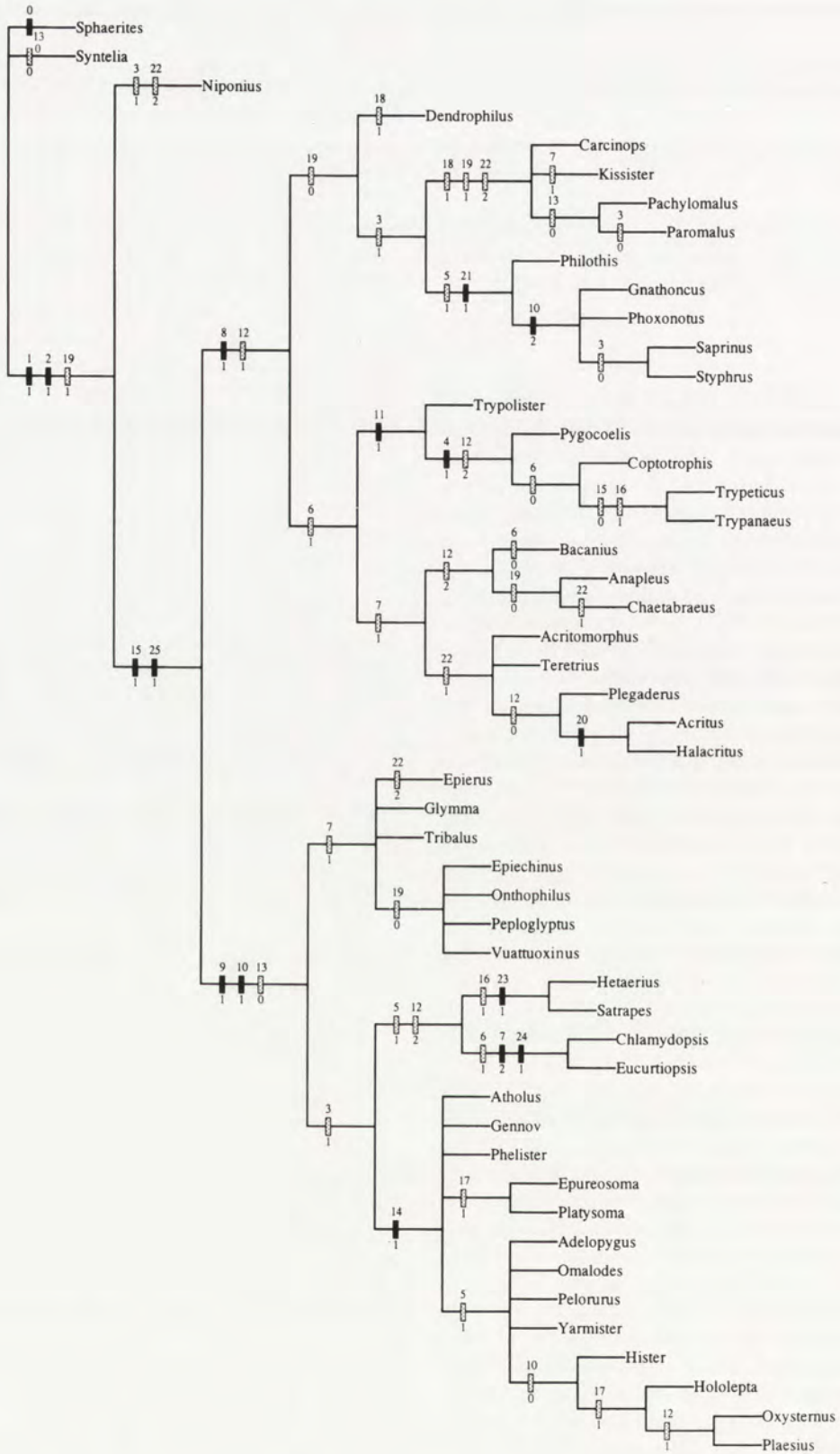
Figure 41. Single mhennig* tree (L 59, CI 50, RI 88) generated from the matrix in Table II (characters 0–25)
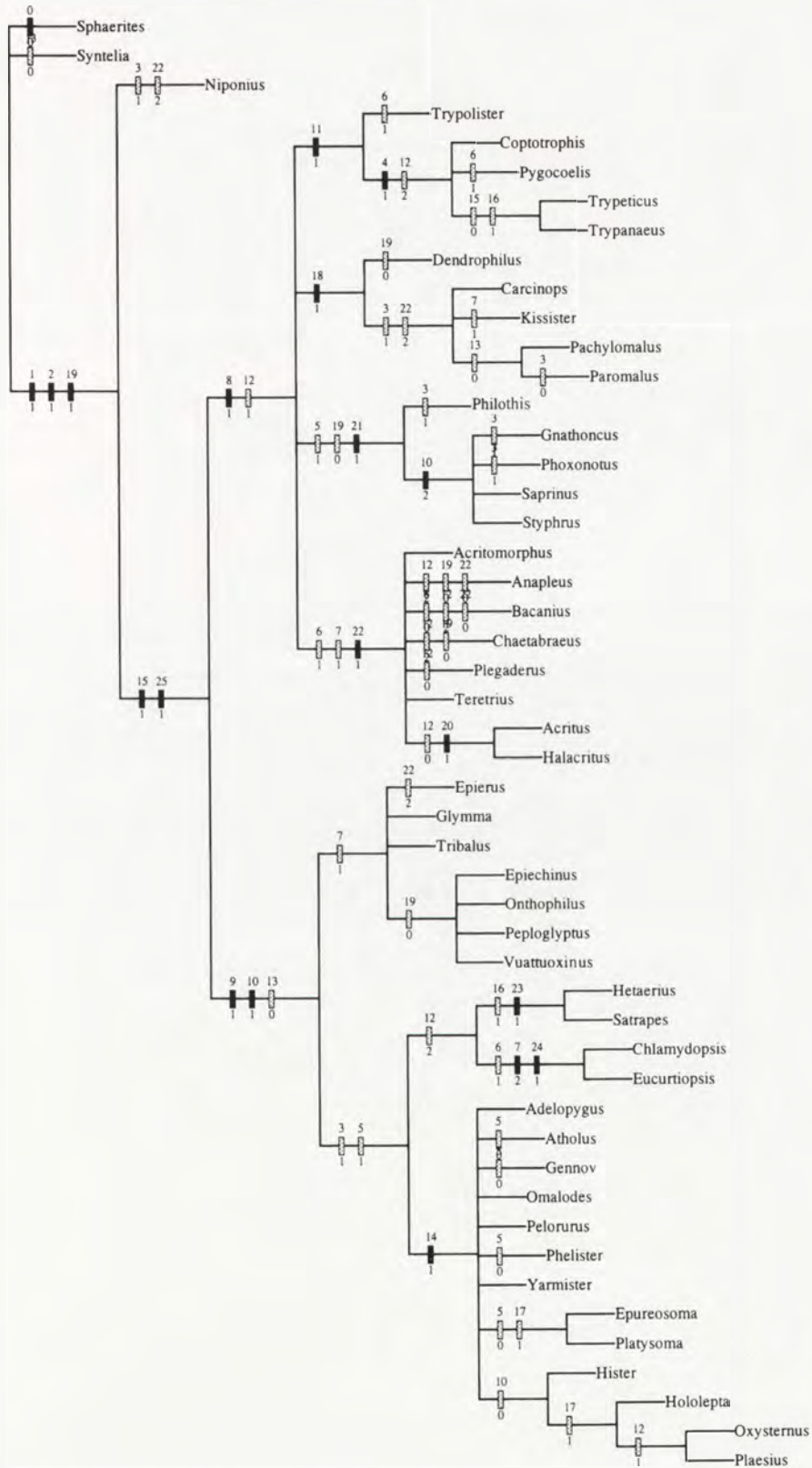
Figure 42. Strict consensus tree from 10 mhennig* trees, reached after successive weighting (L 69, CI 43, RI 84)
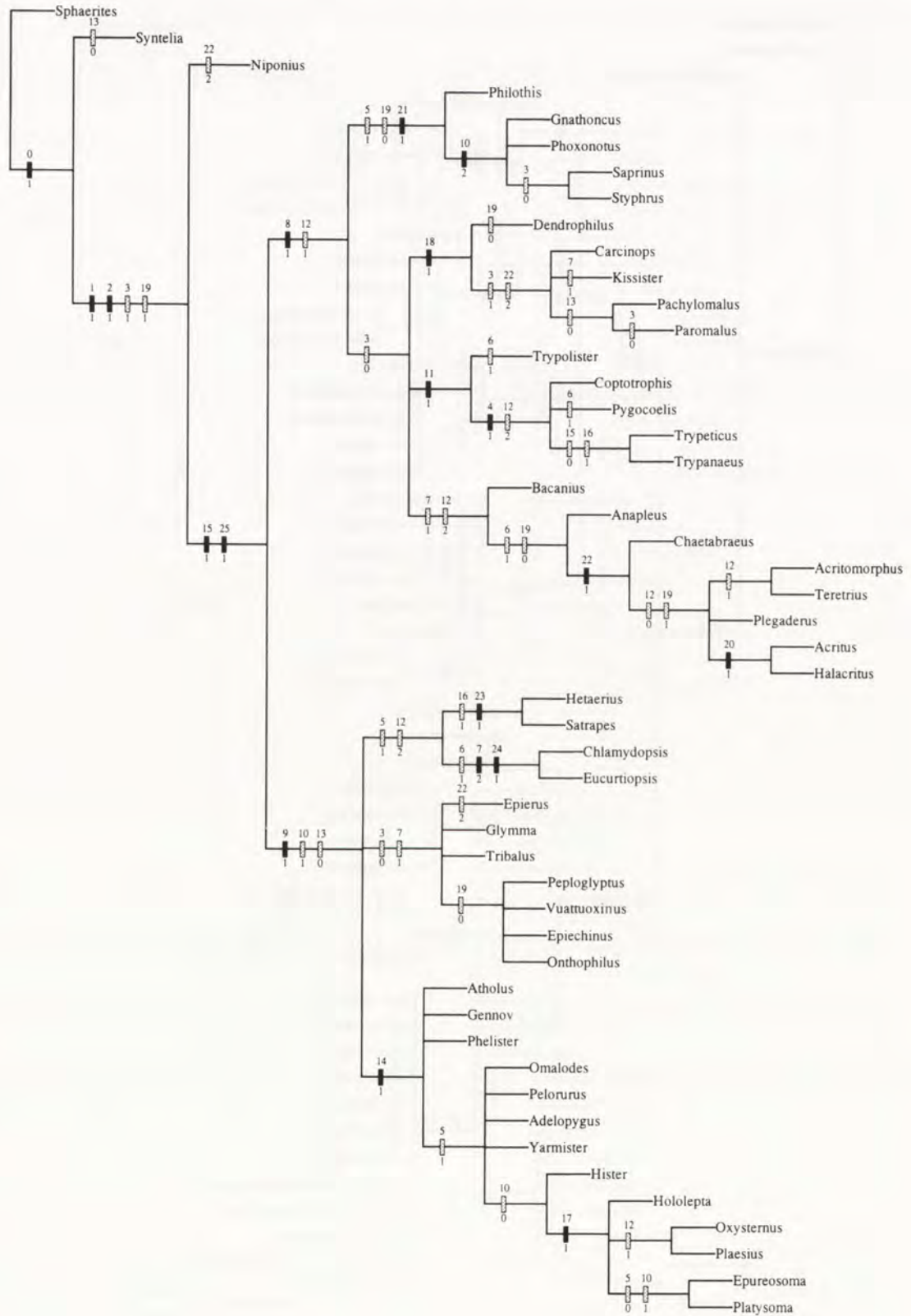
Figure 43. One of 245 Pee-Wee trees generated with CONC=1 (L 61, CI 49, RI 87)
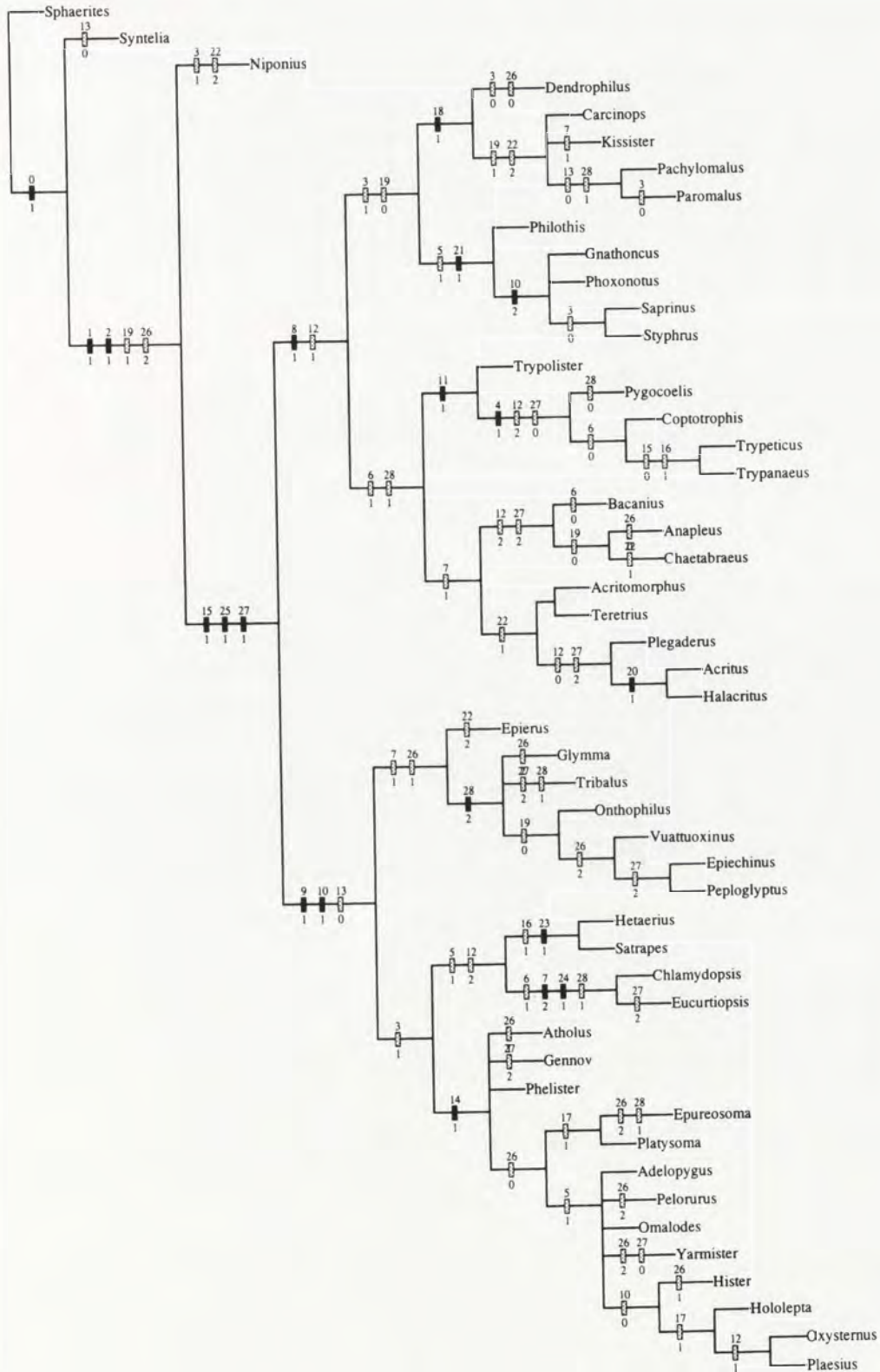
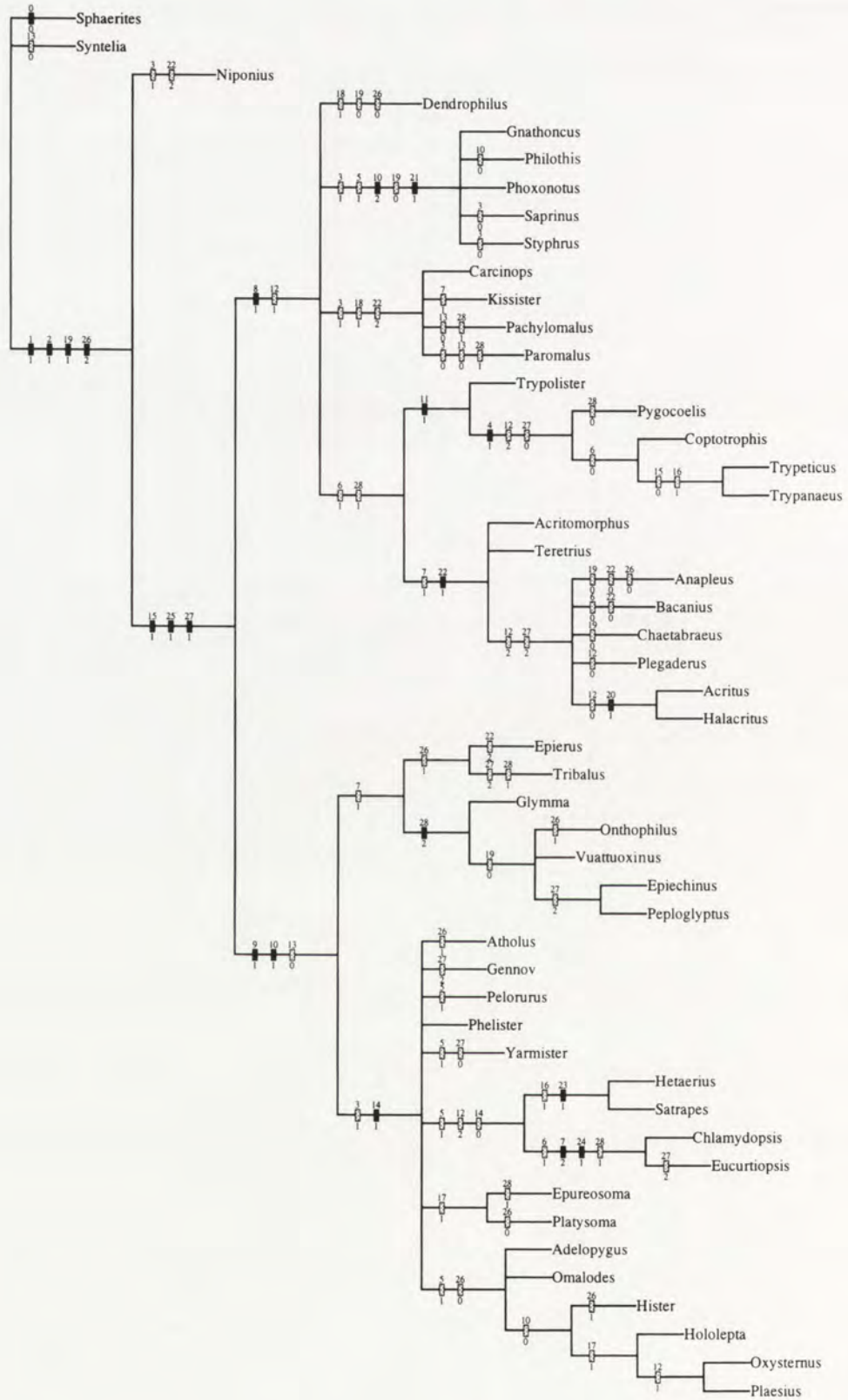Figure 44. One of 7 Pee-Wee trees generated with CONC = 6 (L 87, CI 41, RI 82)

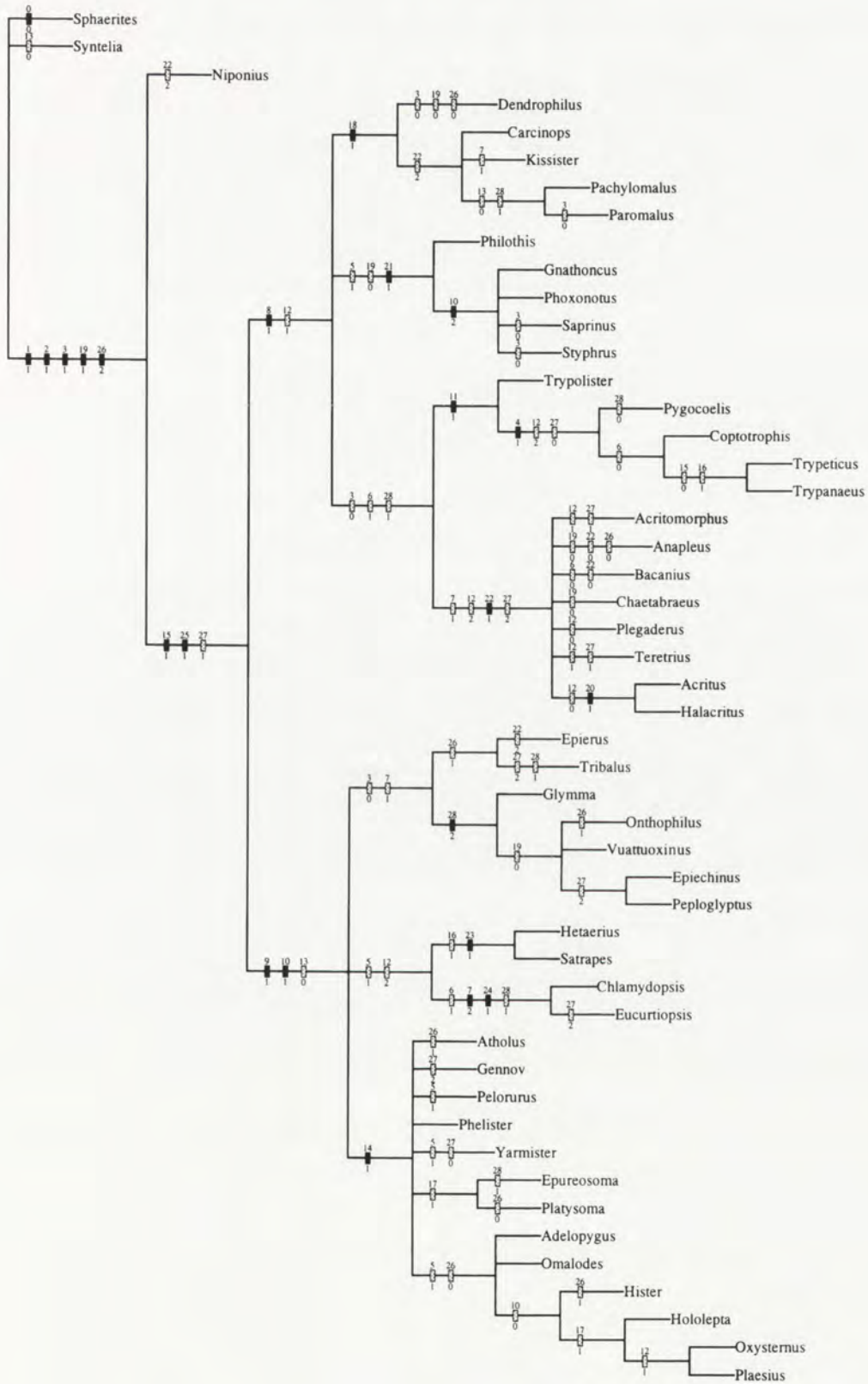Figure 45. Strict consensus of 5 mhennig* trees generated from a complete matrix as in the Table II (L 94, CI 38, RI 80)

Figure 46. Strict consensus of 8 mhennig* trees generated from a complete matrix from the Table II, after a successive weighting (L 93, CI 38, RI 80)
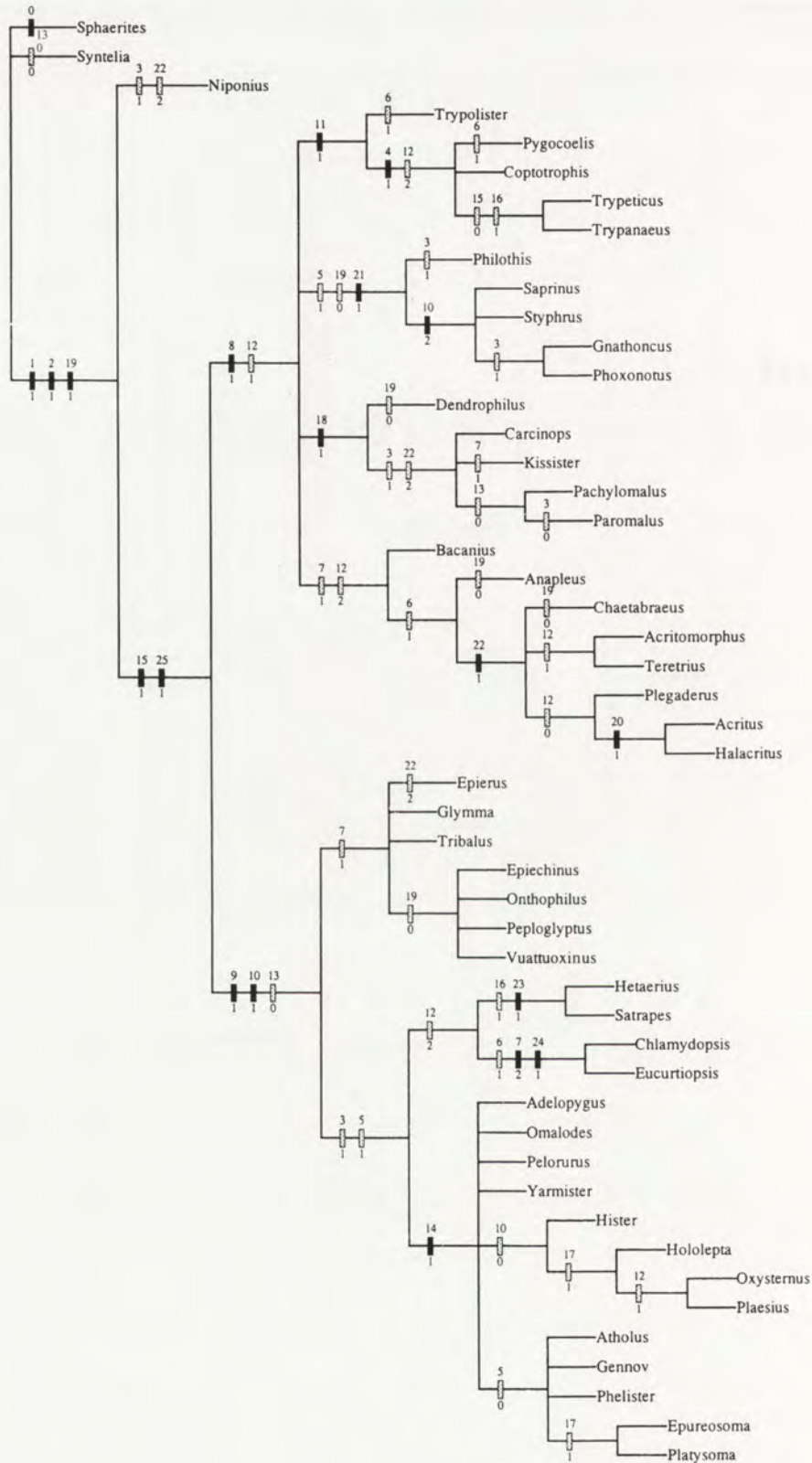
Figure 47. Preferred cladogram; one of 10 mhennig⁹ trees generated from a reduced matrix, after successive weighting (L 60, CI 50, RI 87)

We repeated all Hennig86 and Pee-Wee procedures once again reaching exactly the same major topology as before. The only significant event was the separation of *Dendrophilus* from the rest of Dendrophilinae on some of the trees in the initial run of mhennig*, which is also shown on the consensus tree (Fig. 45). This configuration changed after the successive weighting (Fig. 46) being identical with the results obtained from the restricted matrix.

Preferred cladogram. Our research was mostly aimed on establishing monophyly and the relationships of major clades within Histeridae, with hope to propose subfamily/tribal classification consistent with these findings. We have not hoped for fully resolved trees because of the limitation of the character matrix. We are sure the data set and the procedures applied to obtain the results are in concordance with the parsimonious cladistic methodology. However, more research should be done with inclusion of more taxa on levels here outlined as major branches. Such attempt will allow to use of more characters that were inapplicable on the present level of study.

Having above in mind, we have chosen as our preferred tree, the tree no. 0 of ten mhennig* trees being the result of a successive weithting (Fig. 47). The tree (L 60, CI 50, RI 87), is in a major agreement with all consensus trees obtained by successive weighting and implied weighting methods described above, but does not show any particular relationships in the Saprinomorphae clade. Such choice is done, because there has been a variation in the terminal branches in this group, and although we believe the clades there are well defined and monophyletic their relationships are not conclusive based on our data.

The tree supports three major lineages in Histeridae: *Niponius* (Niponiinae); Saprinomorphae (including Dendrophilinae, excluding Chlamydopsinae) and Histeromorphae (minus Dendrophilinae, plus Chlamydopsinae).

The major change as compared to the Wenzel (1944) and Ôhara (1994) systems is an amalgamation of Abraeinae and Dendrophilinae in spite of the prosternal lobe being visible in some Dendrophilinae. The tree on which the Dendrophilinae are associated with Histeromorphae would be much longer (a minimum 3 steps) and required an independent origin of the prosternal lobe in *Syntelia* and Dendrophilinae + Saprininae and then again its loss in Saprininae plus part of Dendrophilinae. No such tree was found among over 1000 trees generated from our data. No attempt has been made to investigate further status of tribes that used to be recognized in Abraeinae, and these are listed as such in our proposed classification.

Bacanius and *Anapleus* (former Dendrophilinae) are associated with the Abraeinae clade, but this placement is based exclusively on homoplastic data, which may be mostly correlated with the minute and globose body form. Both these taxa are generally more plesiomorphic in their characters as compared to the Abraeinae, e.g., in having median lobe with distinct basal piece, head with narrowly separated gular sutures in *Bacanius* or exposed mesotrochantin and 3-segmented club in *Anapleus*.

We agree with Ôhara about his placement of Trypanaeinae close to Abraeinae, as shown by the "intermediate" genus *Trypolister*, so far classified in Teretriini, although the phylogeny within this complex needs more research, before the sister group relationship between these taxa can definitively be accepted. We prefer to recognize both these lineages as separate subfamilies in our classification. In our opinion the differences between the former Trypeticinae and Trypanaeinae are insignificant and both should be included in a well defined Trypanaeinae.

The major problem which should be further addressed is the constitution of what we recognize as Histeromorphae, especially Histerinae *sensu lato*. The relationship of Tribalinae and Onthophilinae seems to be obvious, but is not easily supported. The raised antennal insertion (# 7,1) is homoplastic, and in spite of their own apomorphies, these clades retain several plesiomorphic characters as compared to Histerinae, e.g., setose labrum, large mandibulal mola and strong lacinial hook or exposed mesotrochantin in most of Onthophilini (except *Glymma*).

The Histerinae, as here recognized, is defined by the absence of the clypeal setae only (# 14,1). Of the previously recognized groups in Histerinae, the Hololeptini and Platysomatini may be jointly defined, because of the peculiar antennal club (# 19,1) but so far there is no potential synapomorphic character for Exosternini, Omalodini or the remaining of Histerini.

There is a serious doubt about the direct relationship of Chlamydopsinae and Hetaeriinae as shown on the cladogram (also pinted out by N. Degallier), since the reduction of the protibial spines (#12,2) show a lot of homoplasy and may be related to their myrmecophilous/ termitophilous habits. Both these groups are thus kept as separate subfamilies.

PROPOSED CLASSIFICATION OF HISTERIDAE

Taking into an account the limitation of our data set and a preliminary character of our analysis we decided, after a long debate with our fellow histeriologists, to propose a scheme which would be consistent with our cladogram but requiring a minimum changes in the existing classification. To accomplish that continue to use informal groups called "–morphae" introduced to Histeridae by Wenzel (1944) to recognize three major clades, which otherwise would require subfamily status, reducing most of the existing subfamilies to the tribal level.

NIPONIOMORPHAE

1. Subfamily: Niponiinae Fowler, 1912

ABRAEOMORPHAE (= Saprinomorphae)

2. Subfamily: Abraeinae MacLeay, 1819
      Tribus ?: Abraeini MacLeay, 1819
            Plegaderini Portevin, 1929
            Teretriini Bickhardt, 1914

Acritini Wenzel, 1944
Acritomorphini Wenzel, 1944
Bacanini Kryzhanovskij et Reichardt, 1976
Anapleini Olexa. 1982
3. Subfamily: Saprininae Blanchard, 1845
4. Subfamily: Dendrophilinae Reitter, 1909
    Syn.: Paromalini Reitter, 1909
5. Subfamily: Trypanaeinae Marseul, 1857
    Syn.: Trypeticinae Bickhardt, 1913

HISTEROMORPHAE

6. Subfamily: Histerinae Gyllenhal, 1808
    Syn.: Hololeptini Hope. 1840
      Platysomatini Bickhardt, 1914
      Exosternini Bickhardt, 1914
      Omalodini Kryzhanovskij, 1972
7. Subfamily: Onthophilinae MacLeay, 1819
    Syn.: Tribalinae Bickhardt, 1914
8. Subfamily: Chlamydopsinae Bickhardt, 1914
9. Subfamily: Hetaeriinae Marseul, 1857

KEY TO THE SUBFAMILIES OF HISTERIDAE

1. Mandibles moving in a plane which is vertical to a longitudinal axis of the head; intercoxal process of ventrite 1 narrow, triangular (Fig. 27); clypeus produced into 2 "horns" anteriorly
    . . . . NIPONIOMORPHAE (=Niponiinae)
–. Mandibles moving in a horizontal plane to a longidudinal axis of the head; intercoxal process of ventrite 1 broad (Fig. 29), truncate or arcuate; clypeus, if modified, with single rostrum or horn 2
2. Prosternum with lateral notch receiving antennal funicle (Figs 19, 22, 37) (ABRAEOMORPHAE) 3
–. Prosternum without lateral notch, with prosternal lobe and alae usually covering antennal cavities in repose (Figs 17, 18, 21) (HISTEROMORPHAE) 6
3. Prosternum with deep basal groove receiving long apical spine of protibia (Fig. 36) . . . . Dendrophilinae
–. Prosternum without basal groove receiving protibial spine 4
4. Inner apex of hind tibia prolonged, without spines (Figs 30, 31); [body elongate with pronotum usually almost as long as elytra, subcylindrical; tibiae with strong teeth on external margin (Fig. 34)] . . . . Trypanaeinae
–. Inner apex of hind tibia truncate, with 2 spines (rarely spines absent); [body very rarely elongate (e.g., *Teretrius*) 5
5. Antennal cavities situated on lateral sides of prosternum, approaching prosternal keel (Fig. 23); antenna with Reichardt's organ (indistinct or absent in *Phoxonotus*); elytra always with striae; antennal insertions always hidden; front coxae very narrowly separated
    . . . . Saprininae
–. Antennal cavities, if defined, on hypomera or along prosternum (Fig. 37); antenna without Reichardt's organ; elytra punctate, rarely with weak impressed striae;

antennal insertions usually exposed; front coxae moderately to broadly separated . . . . Abraeinae
6. Antennal insertion exposed, situated on top of frons (Fig. 4); scape large and covers eye in repose; no antennal grooves long inner margin of eyes . . . Chlamydopsinae
–. Antennal insertion usually hidden and always lateral (Fig. 3); scape received in a groove along inner margin of eye 7
7. Labrum fused to frons; [antennal scape triangular; apical segment of club truncate] . . . . Hetaeriinae
–. Labrum separated from frons [antennal scape normal; apical segment of club rounded] 8
8. Labrum with setigerous punctures; antennal cavities usually entirely covered by prosternal alae from below (Fig. 21); tibiae along outer margin with setae or spines, very rarely denticulate . . . . Onthophilinae
–. Labrum without setigerous punctures; antennal cavities at least partially exposed (Fig. 17), or the cavities not defined (Fig. 24); tibiae usually broad, denticulate or with teeth along external margin . . . . Histerinae

DEFINITIONS OF MAJOR GROUPS OF HISTERIDAE

In this section we briefly discuss the apomorphies (A) and plesiomorphies (P) of the groups recognized in the scheme above. Characters not included in the matrix, but of potential value as synapomorphies are designated (N), and homoplasious ones (H).

HISTERIDAE. Gular sutures fused (A), but narrowly separated sutures are seen in *Dendrophilus* and *Bacanius*; prosternal cavities with internal closing bar (A); protrochantin hidden (A); hind coxae distinctly separated (A); two abdominal tergites exposed (A); tergite 4 with medial slit receiving innner flexures of both elytra and forming an interlocking mechanism (A, Fig. 28). Larvae (Newton 1991) of Histeridae differ from Hydrophilidae (*s. l.*), Syntelidae and Sphaeritidae in having at most single stemma, mentum fused to the head capsule and a maximum 2-segmented urogomphi.

Notes. Hansen (1997) states the procoxal cavities in Histeridae are closed internally, but there is usually no firm connection between the internal bar and the hypomeral process making the closure imperfect.

NIPONIINAE. Clypeus produced into horn like processes (A); labrum partially sclerotized and hidden under clypeus (N, H?); mandibles moving in a plane which is vertical to a longitudinal axis of the head (A); mandible without mola (H); lacinia with strong, inwardly bent hook (A, H?); occiput with longitudinal endocarina (N); head not retracted into prothorax (P); antennal grooves occupy most of head on ventral side, and are clearly separated from inner margin of eyes (A); antennal insertion very far from eye (Fig. 5, N); mid coxae transverse and approximate (P); intercoxal process of ventrite 1 triangular (P). The only described larva of *Niponius* (Gardner 1930) is unique in having ambulatory ampullae and secondary segmentation. It has been reared in India from the scolytid galleries.

ABRAEOMORPHAE. Prosternum with deep slit or notch laterally receiving antennal funicle (A).

Saprininae. Antennal club with Reichardt's organ (A); mandibular mola strongly reduced or absent (H); lacinial hook absent (H); postocciput distinct, forming elongate plates along gular suture (N); antennal cavities situated at inner part of prosternum (A – lost in *Philothis*); prosternal lobe absent (H); mesotrochantin visible (P); apical spines of protibia almost always strongly unequal, the outer one large and hooked (H).

Dendrophilinae. Prosternum with deep basal groove on each side to receive large and bent apical spine of protibia in repose (A); dorsal striae rarely present (N).

Trypanaeinae. Prosternal lobe absent (H); head usually elongate to rostrate (N); labrum usually hidden under clypeus (N, H?); mandible apically bifid (A; absent from *Trypolister*); prosternal process short, not reaching hind margin of procoxae (H); hind tibia without apical spines but with process on inner apical corner (A, Figs 30, 31); ovipositor desclerotized and reduced (H, not confirmed in all genera); median lobe long and weakly sclerotized (N, not examined in all genera); elytra without striae (H). Larva without urogomphi, maxilla eversible, attached to head by long connecting membrane (Newton, 1991).

Abraeinae. Antennal insertions above mid length of eye (H) and almost always visible from above (H); elytra without striae (H); mandible with strong mola and lacinia with apical hook (P); prosternum usually with additional ridge or line along lateral slit (N).

Note. The group includes former Bacaniini and Anapleini of Dendrophilinae as well as the entire Abraeinae.

HISTEROMORPHAE. Prosternal lobe present (P); elytra with striae or costae (N); anterior margin of prosternum extending laterally to form alae covering antennal cavities from below (A); antennal club in repose usually covered from below by prosternal alae (A – lost in some groups ?);

Onthophilinae. Labrum setose (P); antennal insertions above middle length of eye, often exposed (H); antennal cavities entirely hidden from below (N).

Notes. The concept of the group is identical to the traditional Tribalinae (e.g., Wenzel 1944; Kryzhanovskij and Reichardt 1976).

Hetaeriinae. Labrum fused with clypeus (A); antennal club truncate apically (A – but not in *Tarsilister*); antennal scape large and triangular, ovipositor reduced (A or H – but not examined in all genera).

Notes. As already pointed out by Yelamos (1997) monophyly of the group is questionable. Judging from the illustrations in Helava *et al.* (1985) there is a tremendous diversity in the aedeagal and sternal structurs, in the setation of the labrum and antenna. Further research is needed to test the monophyly of the group against the Histerini (especially former Exosternini) and Tribalini, since the clypeus fused to labrum may be a homoplastic character.

Chlamydopsinae. Eyes extremely large and narrowly separated (A); antennal insertion visible and on top of head (A); antennal scape large, covers eye in repose (A); clypeus strongly reduced (N); antennal cavities on prosternum very deep and approximate at middle (A); procoxal cavity relatively narrow, with broad postcoxal process (A); antennal club elongate (N); elytra usually with trichomes or other specialized structures (N).

Notes. This group is sharply defined and certainly monophyletic. The relationship to Hetaeriinae is questionable and needs a confirmation.

Histerinae. Labrum heavily sclerotized and without setae (A); mandibular mola reduced or absent (H); lacinial hook often absent (H).

Notes. Further subdivision of this group needs much more research. Of the currently recognized tribes: Exosternini, Platysomatini, Hololeptini and Omalodini, the Exosternini cannot be cladistically defined (Ôhara and Nakane 1989; Mazur 1990; Yélamos and Kanaar 1997). Omalodini, as compared with Platysomatini and Hololeptini (De Marzo and Vienna 1982b; Mazur 1990) represents plesiomorphic states of the antennal club structure, and cannot be defined as a monophyletic taxon. The above described genus *Epuraeosoma* adds to the diversity of the group, in having strongly reduced clypeus and labrum, non striate elytra and the tarsal groove on protibia absent. It may be placed in the former Platysomatini because of the remnants of the V-staped sutures of the club and large prosternal lobe.

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