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A NEW GENUS AND SUBFAMILY OF MYCOPHAGOUS BOTHRIDERIDAE (COLEOPTERA: CUCUJOIDEA) FROM THE INDO-AUSTRALIAN REGION, WITH NOTES ON RELATED FAMILIES

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Abstract

Xylariophilus gen. n. contains 3 new species: *X. honoratus* (type species) and *X. bicoloripennis* from Queensland, and *X. comatus* from India. At least *X. honoratus* feeds on the fruiting bodies of ascomycete fungi (Xylariaceae). A new subfamily, Xylariophilinae, is proposed for the genus. A key to the species is given and the presumed larva of *X. honoratus* is described. The relationships of Bothrideridae and Cerylonidae are discussed and a key is given to the subfamilies of both groups. Anommatinae is transferred from Cerylonidae to Bothrideridae. A taxon-character matrix is given for the 4 subfamilies of Bothrideridae, 5 subfamilies of Cerylonidae, and the Biphyllidae, Byturidae, Discolomidae, and Sphaerosomatidae (13 taxa) based on 59 adult and 11 larval characters.

Introduction

Members of the cucujoid family Bothrideridae are usually distinguished from Cerylonidae by having ectoparasitic larvae and by a combination of adult characters, including larger size, elongate and subcylindrical to slightly flattened body, more or less expanded and spinose tibial apices, and corporotentorium without a median process. Some groups of Cerylonidae, however, possess bothriderid-like features (expanded tibial apices and elongate form of *Anommatus* Wesmael and *Metacerylon* Grouvelle), while the diagnostic larval characters of Bothrideridae do not apply to the recently discovered larva of *Teredolaemus leae* (Grouvelle), a mycophagous commensal in the tunnels of ambrosia beetles (Platypodidae) (Lawrence 1985, in press). The new genus of free-living, mycophagous Bothrideridae described below further obscures the differences between these 2 taxa and calls for a reexamination of their relationships (*see* Discussion).

Abbreviations: Collections: ANIC—Australian National Insect Collection; BM—British Museum (Natural History); BPBM—Bernice P. Bishop Museum; CAS—California Academy of Sciences; IZP—Institute of Zoology, Polish Academy of Sciences; NMNH—National Museum of Natural History (Smithsonian Institution); QM—Queensland Museum; ZSIC—Zoological Survey of India. Measurements: PL/PW, the ratio of the median length of pronotum to its greatest width; EL/EW, the ratio of the length of the elytra along the suture to their combined greatest width; and EL/PL, the ratio of the median elytral length to the median pronotal length.

Xylariophilus gen. n.

Type species—Xylariophilus honoratus sp.n.

Description (Figs 1-13)

Body (Figs 1-4) slightly elongate, moderately convex; surfaces somewhat shiny, bicoloured or tricoloured, densely clothed with moderately long, fine hairs. Length 1.4-2.0 mm. Without external differences between the sexes.

Head (Figs 4-5) slightly declined, narrower than prothorax, slightly transverse. Frons and vertex simple; transverse occipital ridge and stridulatory file absent. Frontoclypeal suture distinct, slightly concave. Eyes moderately large, coarsely facetted; temples very short and shelf-like. Antennae 11-segmented (often appearing 10-segmented), their insertions dorsolateral and completely exposed; scape moderately large; pedicel narrower and slightly elongate; segment 3 subequal to and narrower than scape; segments 4-8 short and subequal; segment 9 slightly wider than 8 and strongly transverse; segments 10 and 11 closely associated, forming an abrupt, compact, slightly elongate club; segment 10 glabrous except at apex; segment 11 densely pubescent. Shallow antennal groove formed between eye and mandibular articulation on each side, the groove not extending beyond posterior edge of eye. Pregular region with transverse impression located just behind mouthparts and extending laterally to meet temple on each side. Labrum (Fig. 6) strongly transverse, truncate, slightly sclerotised at apex; tormae with long, narrow posterior arms and broader, curved mesal arms which extend posteromesally and terminate at the cibarial filter; labral rods heavily sclerotised, gradually enlarged anteriorly and club-like; epipharyngeal armature as in Fig. 6. Mandible (Fig. 7) with 3 apical teeth, a fringed prostheca, and well-developed mola. Maxilla (Fig. 8) with narrow, elongate lacinia bearing 2 apical spines and a broad galea, densely pubescent at apex; maxillary palps with segments 2 and 3 subequal and apical segment longest, fusiform, gradually narrowed apically. Labium (Fig. 9) with trapezoidal mentum bearing triangular raised area in middle; ligula slightly expanded and truncate; labial

palps broadly fusiform, subtruncate apically. Tentorium (Fig. 5) with straight, narrow corporotentorium bearing a short median process and subparallel anterior arms, which do not closely approach one another at midline.

Pronotum transverse, between 0.70 and 0.85 X as long as wide, widest at middle; sides very weakly to moderately rounded; lateral edges complete with narrow margins, which are not serrulate; anterior and posterior angles obtuse and not produced; anterior and posterior edges broadly rounded, the former sometimes and the latter always bisinuate, the latter with a very narrow margin; disc moderately convex and simple, without ridges or impressions. Scutellum well-developed, rounded posteriorly.

Elytra slightly elongate, about 1.4 to 1.5 X as long as their greatest combined width, completely concealing abdomen from above, with broadly rounded apices; sides very weakly rounded; each elytron with 10 more or less complete rows of punctures, with or without additional rows of smaller punctures in the intervals; punctures and intervals pubescent; epipleura extending almost to apex, well-developed to about middle.

Prosternum (Figs 4, 10) in front of coxae more than 2 X the length of prosternal process, slightly convex, not tumid or carinate; prosternal process narrow, parallel-sided and rounded at apex, which is neither expanded nor elevated. Procoxae rounded externally, with well-developed internal extensions; coxal cavities internally and externally open, the notal projections behind the coxae short and acute. Notosternal sutures complete to anterior edge of sternum; hypomera without cavities.

Pterothorax (Figs 4, 11). Mesosternum simple, neither carinate nor impressed; mesocoxae narrowly separated and narrowly open laterally (not closed by meeting of mesosternum and metasternum). Sternal fitting between mesocoxae consisting of a single metasternal knob. Metasternum transverse, moderately convex, flattened in middle, without femoral lines but with very narrow anterior margin bordering mesocoxal cavities; median impressed line short to moderately long (between 0.3 and 0.6 X sternal length); metacoxae moderately widely separated. Metendosternite with short, broad stalk, long, narrow arms, strongly curved, narrow laminae, and widely separated anterior tendons (arising near base of each lamina).

Hindwing (Fig. 13) without radial cell or median vein, with indistinct radio-medial crossvein and medio-cubital loop, and with a single anal vein (sometimes indistinct). Subcubital fleck divided. Jugal lobe present.

Legs (Fig. 11). Trochanterofemoral attachment of the heteromeroid type (strongly oblique so that base of femur is in contact or almost in contact with coxa); femora slightly swollen near middle; tibiae slightly expanded at apex, which bears a row of spines and 2 short, subequal tibial spurs. Tarsal formula 4-4-4 in both sexes; segments simple; claws simple; empodium reduced.

Abdomen (Figs 4, 12) about as long as wide at base, with ventrites freely articulated; ventrite 1 (sternite 3) longest, without femoral lines; intercoxal process moderately long, subtriangular with rounded apex; ventrites 2-5 (sternites 4-7) subequal, with internal apodemes at anterior angles; ventrite 5 (sternite 7) not crenulate. Abdomen with 7 pairs of spiracles.

Aedeagus (Figs 14-17) symmetrical, of cucujoid type; tegmen moderately long, with articulated, setose parameres and a very long and narrow anterior ventral strut; median lobe long and narrow, straight or slightly curved, with short, paired anterior struts. Sternite 8 in female with long spiculum gastrale at base. Ovipositor with divided coxites and well-developed, moderately sclerotised, apically attached, narrow styli. Spermatheca coiled.

Distribution

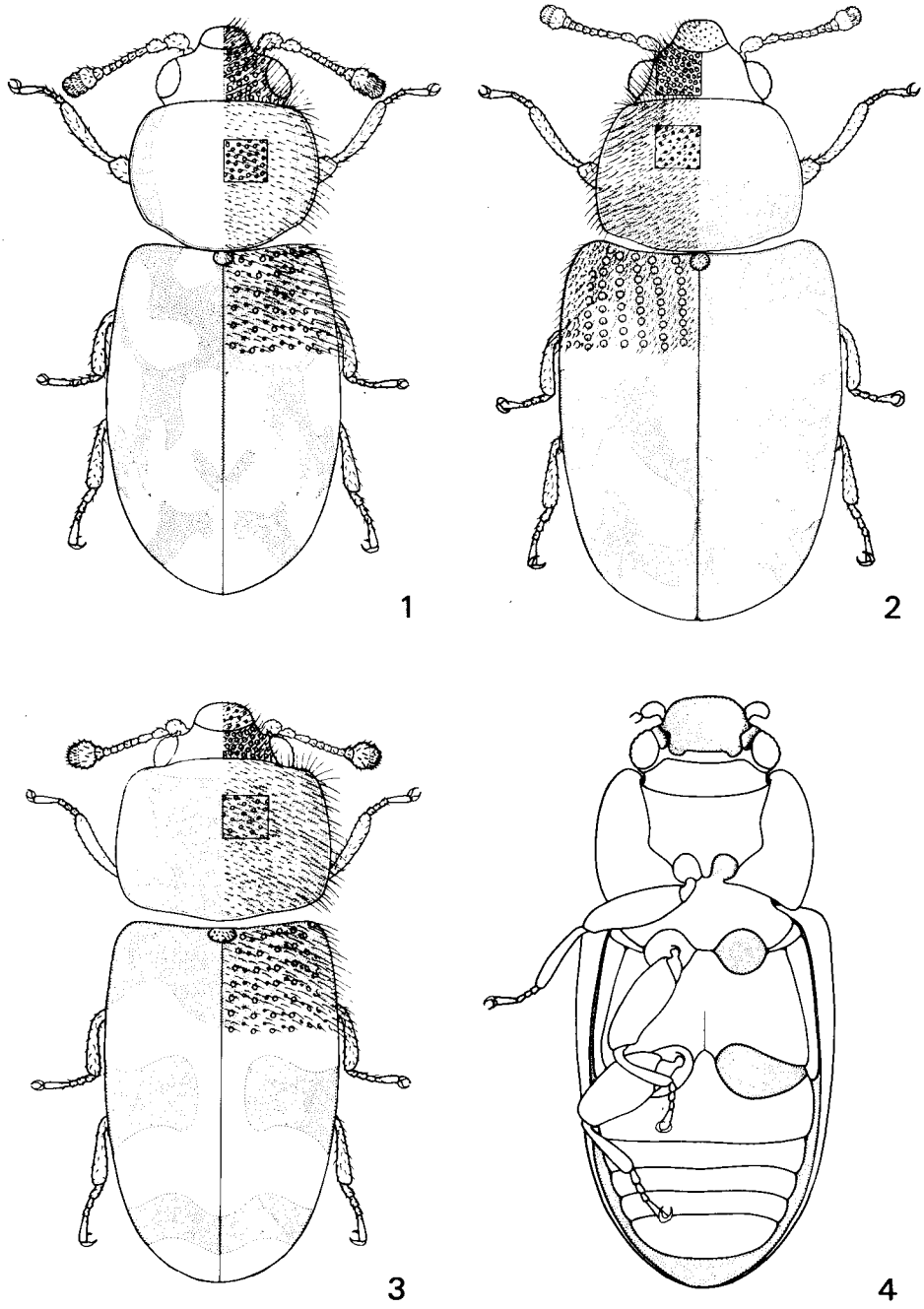
Eastern coast of Queensland, Australia, and India.

Biology

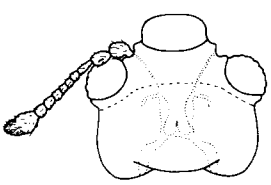
One species (*X. honoratus*) has been found feeding on the surfaces of *Hypoxylon cyclopicum* Spegazzini, *H. jecorinum* Berkeley and Ravenel, *Kretzschmaria cetrarioides* (Welwitsch and Currey) Saccardo, and *Xylaria anisopleura* (Montagne) Fries (Ascomycetes: Xylariaceae) at night, and the presumed larva of this same species was found feeding on *H. cyclopicum*. Adults of the other 2 species were found under bark and in rotten wood and leaf litter; it is probable that these are also associated with ascomycete fungi.

Etymology

From the genus *Xylaria*, type of the family of Ascomycetes upon which at least *H. honoratus* feeds, and a latinisation of the Greek adjective philos, beloved.



FIGS **1-4**—*Xylariophilus* spp. adults: **(1)** *X. bicoloripennis* sp.n., dorsal view; **(2)** *X. comatus* sp.n., dorsal view; **(3-4)** *X. honoratus* sp.n.: **(3)** dorsal view; **(4)** ventral view, mouthparts and left legs removed.



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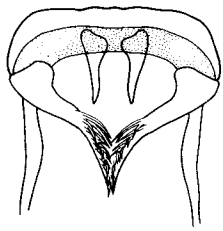

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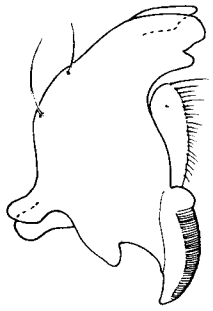

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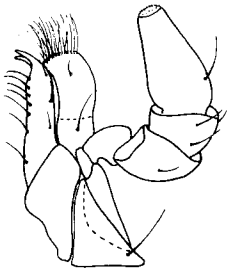

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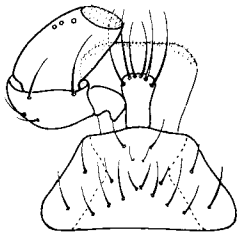

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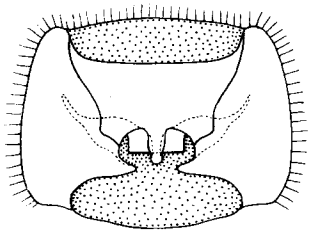

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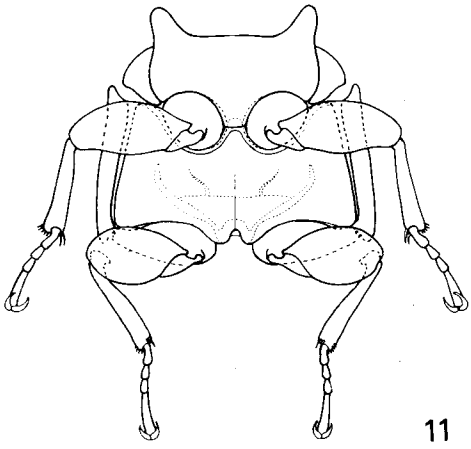

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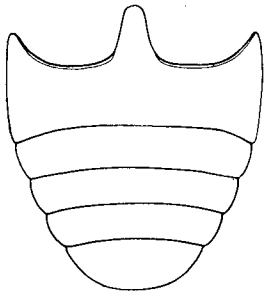

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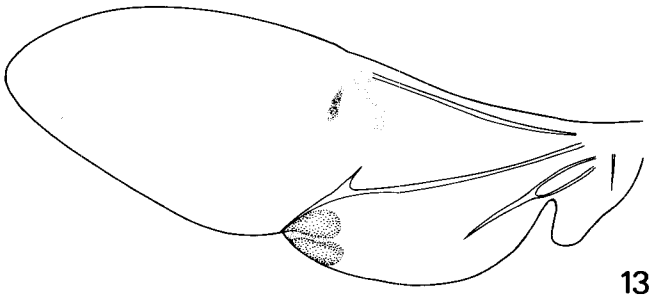
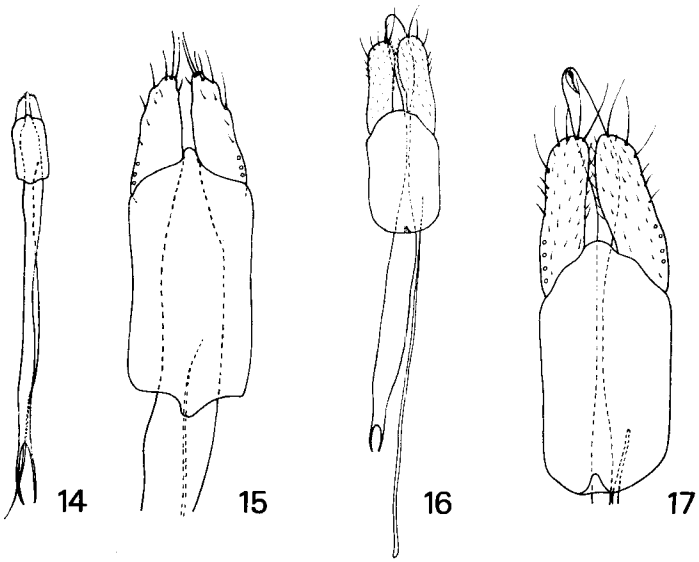
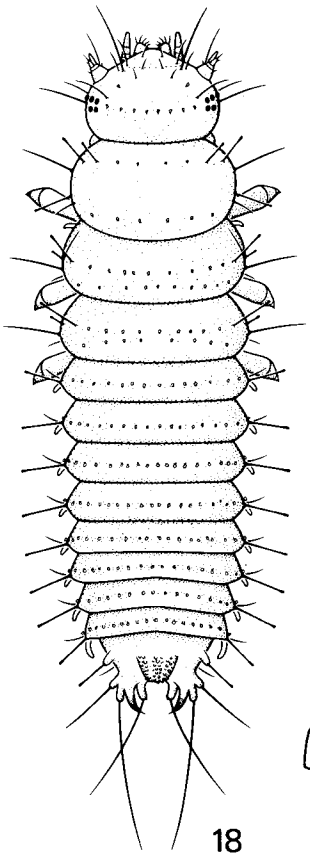
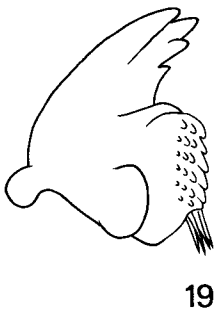
FIGS 5-12—*Xylariophilus honoratus* sp.n. adults: **(5)** head, dorsal view, showing internal tentorium and ventral transverse impression; **(6)** labrum-epipharynx, dorsal view, showing labral rods and arms of tormae; **(7)** left mandible, dorsal view; **(8)** left maxilla, ventral view; **(9)** labium, ventral view, with left palp removed; **(10)** prothorax, ventral view, with both legs removed, showing internal extension of coxal cavities; **(11)** mesothorax and metathorax, ventral view, showing internal metendosternite (metendosternal laminae not shown); **(12)** abdomen, ventral view.

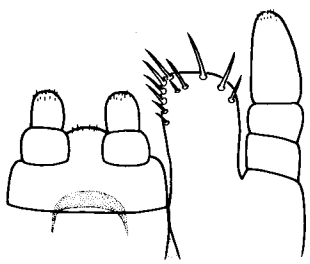


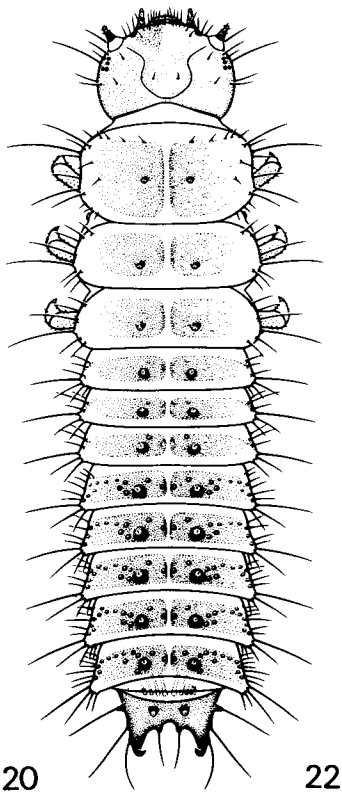


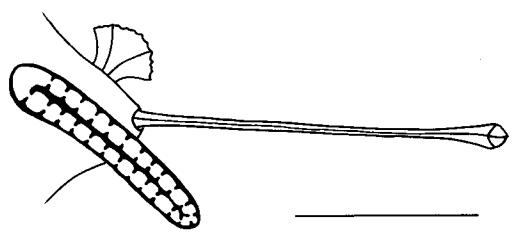
FIGS **13-17**—*Xylariophilus* spp. adults: **(13-15)** *X. honoratus* sp.n.: **(13)** hindwing; **(14)** aedeagus, dorsal view; **(15)** apical (posterior) part of aedeagus, dorsal view; **(16-17)** *X. bicoloripennis* sp.n.: **(16)** aedeagus, dorsal view; **(17)** apical (posterior) part of aedeagus, dorsal view.

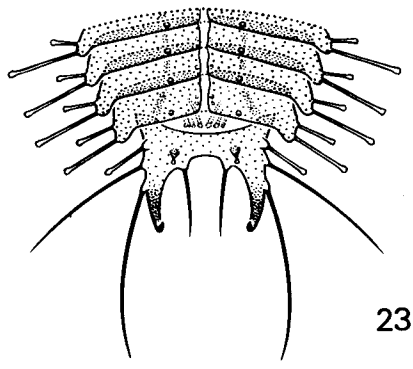




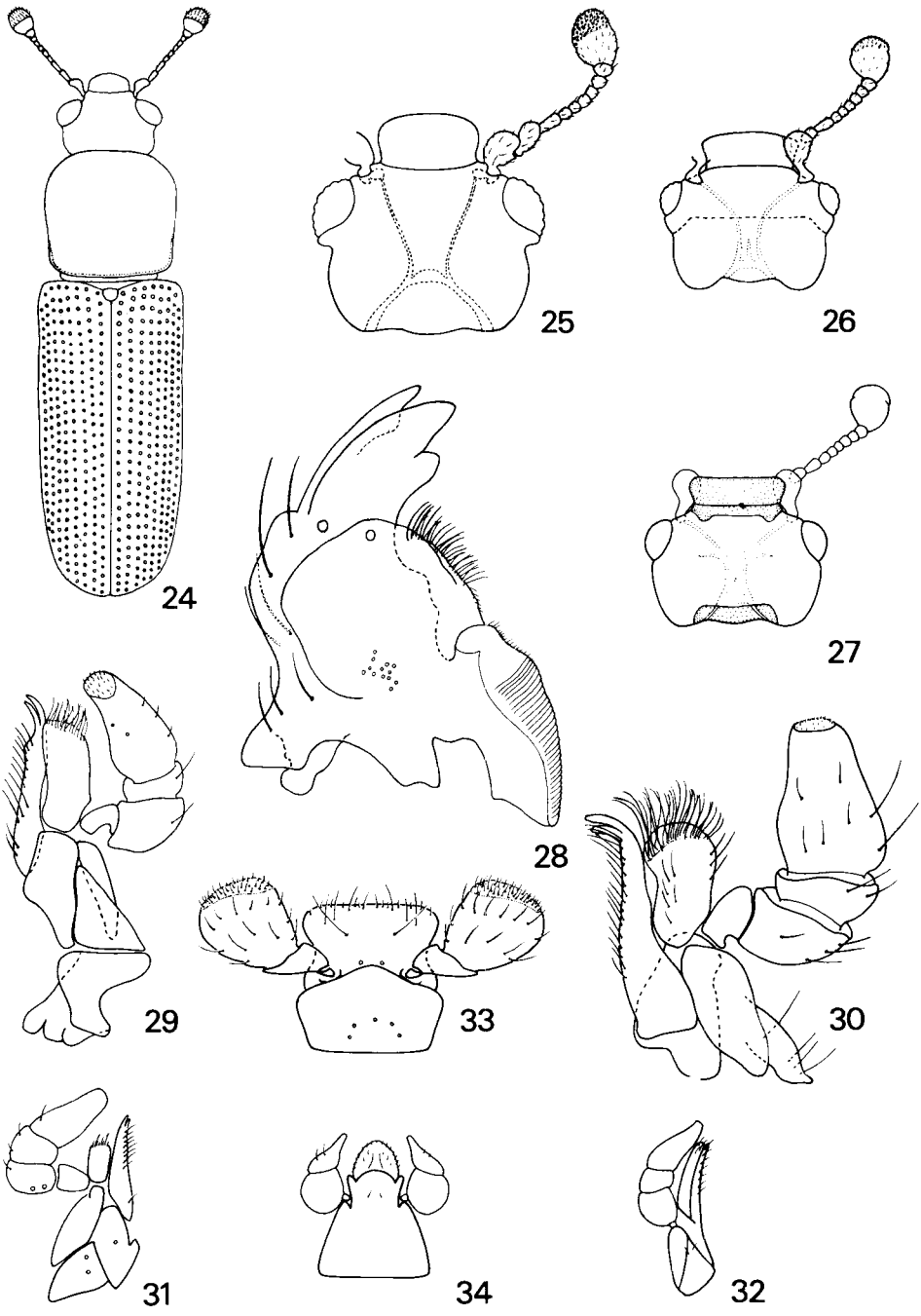




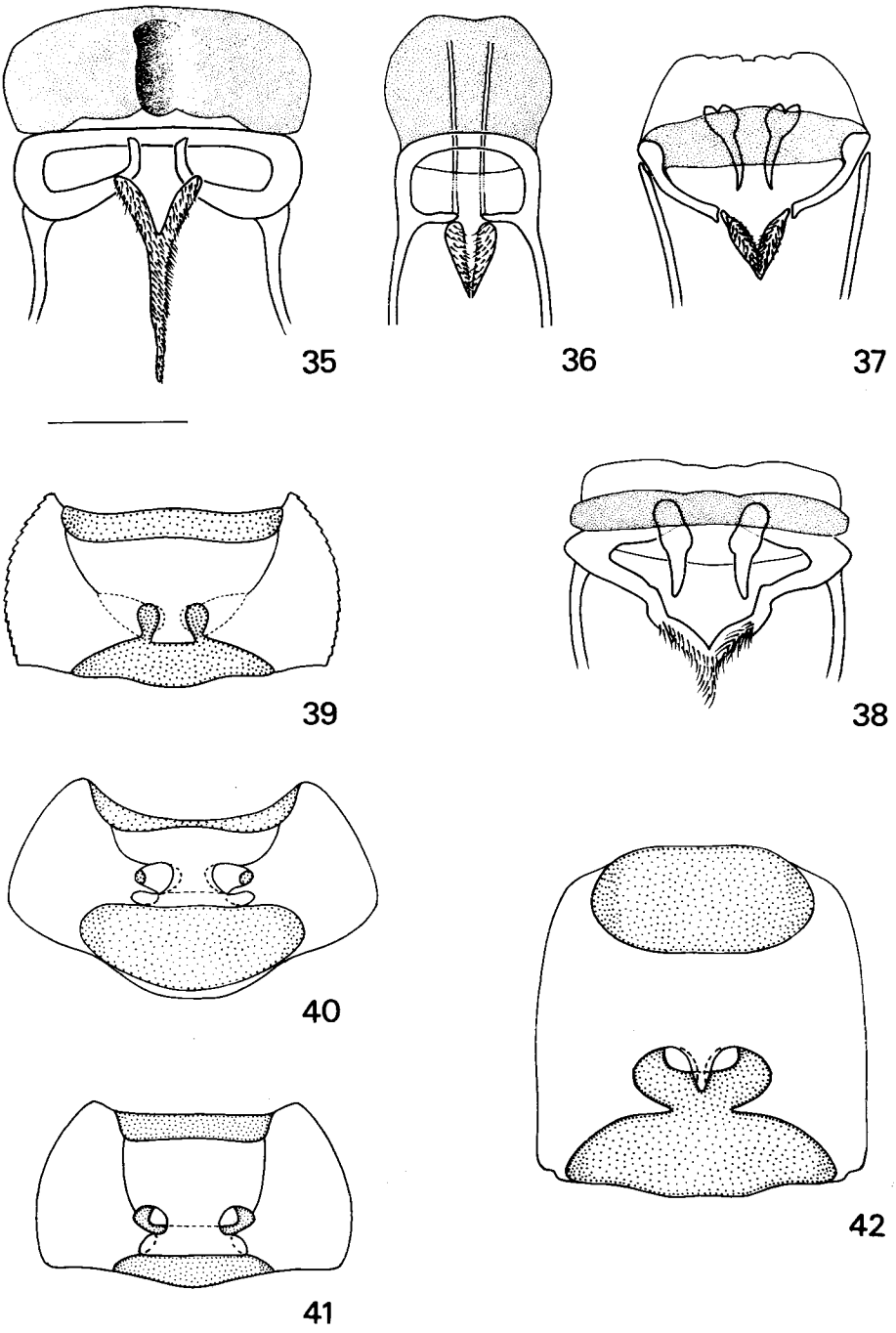




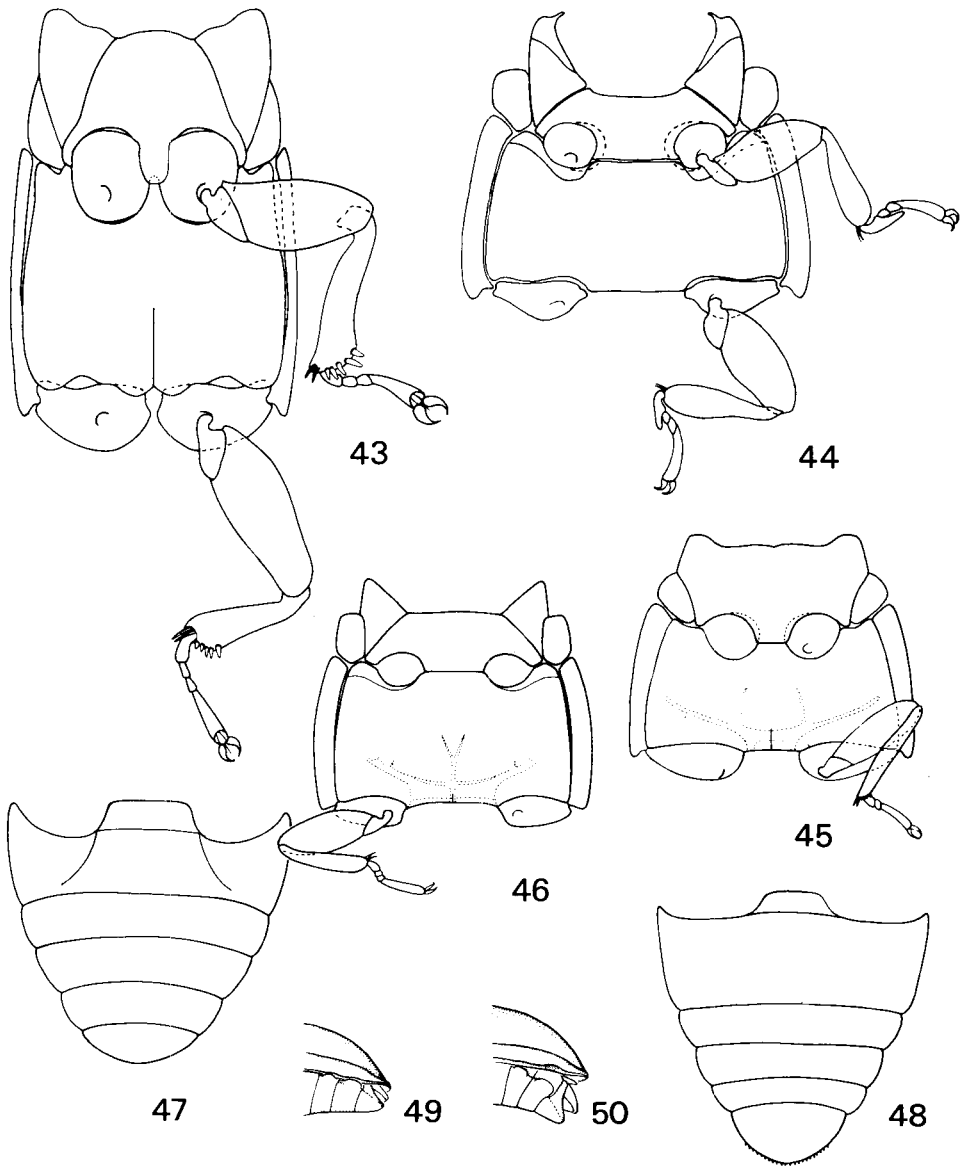
FIGS **18-23**—Larvae: **(18-21)** *Xylariophilus honoratus* sp.n.: **(18)** dorsal view; **(19)** right mandible, ventral view; **(20)** left maxilla and labium, ventral view, showing hypopharyngeal sclerome lying behind (above) labium; **(21)** lateral portion of 6th abdominal segment, ventral view, showing elongate accessory openings forming part of long spiracular tube, an elongate frayed seta, and a short, scale-like seta; **(22-23)** *Teredolaemus leae* (Grouvelle): **(22)** late instar, dorsal view; **(23)** early instar, posterior part of abdomen, dorsal view. Line = 0.03 mm.



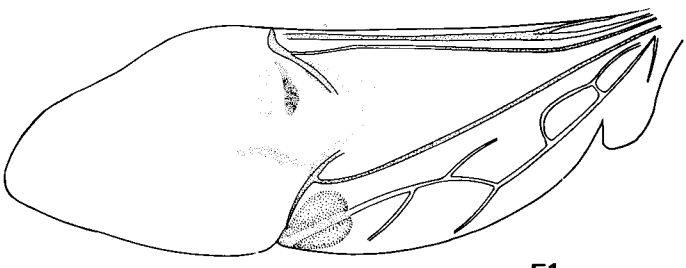
FIGS **24-34**—Adults: **(24-25)** *Teredolaemus unicolor* Grouvelle: **(24)** dorsal view; **(25)** head, dorsal view, showing internal tentorium; **(26)** *Euxestus translucidus* (Motschulsky), head, dorsal view, showing internal tentorium and ventral transverse impression; **(27)** *Ceryleuxestus brasiliensis* Sen Gupta and Crowson, head, ventral view, with mouthparts removed, showing internal tentorium; **(28)** *T. unicolor*, left mandible, dorsal view; **(29)** *E. translucidus*, left maxilla, ventral view; **(30)** *T. unicolor*, left maxilla, ventral view; **(31)** *C. brasiliensis*, maxilla; **(32)** *Ostomopsis* sp., maxilla; **(33)** *Sphaerosoma pilosum* (Panzer), labium, ventral view; **(34)** *Ostomopsis* sp., labium, ventral view. Figs 27, 31, 32, 34 redrawn from Sen Gupta and Crowson, 1973.



FIGS 35-42—(35-38) Labrum-epipharynx: (35) *Sosylus* sp., ventral view, showing epipharyngeal impression and arms of tormae; (36-38) dorsal view: (36) *Cerylon distans* Lawrence and Stephan, showing very narrow labral rods and arms of tormae; (37-38) showing labral rods and arms of tormae: (37) *Hypodacne tasmaniae* (Lea); (38) *T. leae*; (39-42) prothorax, ventral view, with both coxae removed: (39) *Ostomopsis* sp., showing internal extent of coxal cavity on each side (redrawn from Sen Gupta and Crowson, 1973); (40) *E. translucidus*; (41) *Ceryleuxestus brasiliensis*; (42) *T. unicolor*.



FIGS **43-50**—**(43-44)** Meso-metathorax, ventral view, with right legs removed: **(43)** *T. unicolor*; **(44)** *E. translucidus*; **(45)** *Ostomopsis* sp., meso-metathorax, with mesothoracic legs and right metathoracic leg removed, showing internal metendosternite; **(46-47)** *C. brasiliensis*: **(46)** meso-metathorax, ventral view, with mesothoracic legs and left metathoracic leg removed, showing internal metendosternite; **(47)** abdomen, ventral view; **(48)** *Ostomopsis* sp., abdomen, ventral view, showing crenulate outer edge of 5th ventrite; **(49-50)** *Micruloma minuta* (Carter), abdominal apex, lateral view; **(49)** showing lateral interlocking lobes of ventrites 3 and 4 engaged; **(50)** showing lobes disengaged from epipleural impressions. Figs 45-46 redrawn from Sen Gupta and Crowson, 1973.



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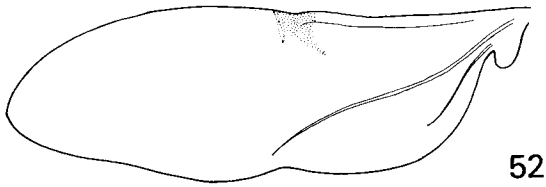

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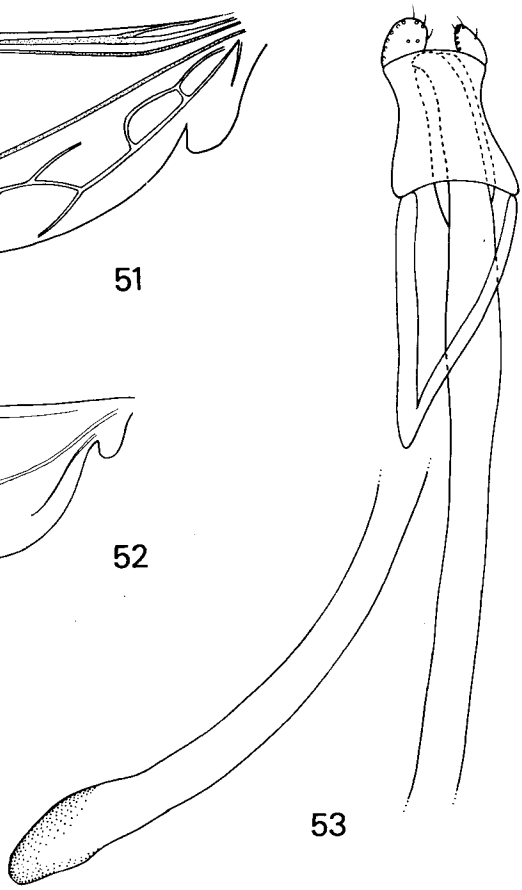

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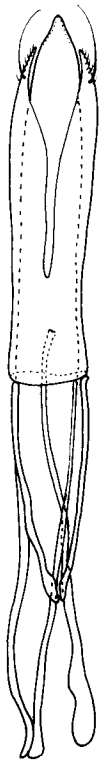

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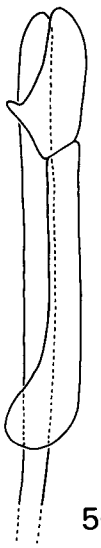

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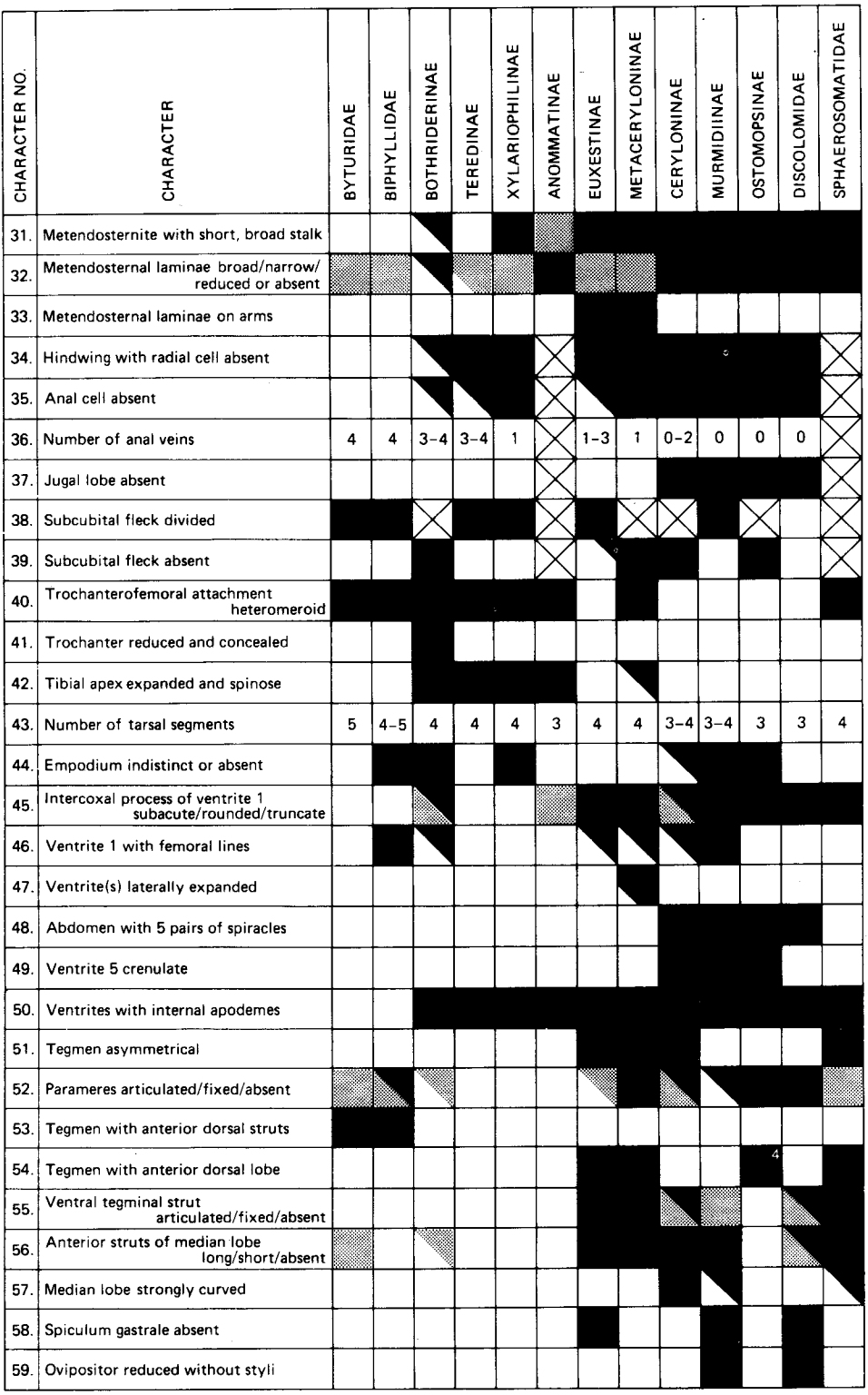
FIGS **51-56**—Adults: **(51-52)** hindwing: **(51)** *T. leae;* **(52)** *C. brasiliensis;* **(53-54)** aedeagus, dorsal view; **(53)** *E. translucidus*; **(54)** *Biphyllus* sp., **(55-56)** diagrammatic lateral view: **(55)** bothriderine type of aedeagus, showing articulated parameres and anterior tegminal strut lying beneath median lobe; **(56)** euxestine aedeagus, with broad, asymmetrical, anterior tegminal lobe lying above median lobe.

FIG. 57—Character-Taxon Matrix for Bothrideridae and Related Groups.

CHARACTER NO.	CHARACTER	BYTURIDAE	BIPHYLLIDAE	BOTHRIDERINAE	TEREDINAE	XYLARIOPHILINAE	ANOMMATINAE	EUXESTINAE	METACERYLONINAE	CERYLONINAE	MURMIDIINAE	OSTOMOPSINAE	DISCOLOMIDAE	SPHAEROSOMATIDAE
1.	Transverse occipital ridge present													
2.	Frontoclypeal suture present									1				
3.	Transverse pregular impression present													
4.	Antennal grooves absent/short/long													
5.	Corporotentorium without median process			2									2	
6.	Anterior tentorial arms meeting			3										
7.	Number of antennal segments	11	11	9-11	11	11	10-11	8-11	9-11	6-11	8-11	10	8-10	
8.	Number of antennal club segments	3	2-3	2-3	2-3	2	1-2	1-3	1	1-3	1-2	1	1	
9.	Antennal club compact													
10.	Apex of labrum truncate/rounded/subacute													
11.	Epipharyngeal impression present													
12.	Mesal arms of tormae perpendicular													
13.	Labral rods slender or absent/intermediate/broad and club-like													
14.	Lacinia without apical spines													
15.	Apical segment of maxillary palp aciculate													
16.	Apical segment of maxillary palp securiform													
17.	Lateral edges of pronotum serrulate													
18.	Hypomera with antennal cavities													
19.	Prosternal process expanded apically													
20.	Procoxae broadly separated													
21.	Procoxal cavities internally closed													
22.	Procoxal cavities externally closed													
23.	Procoxae externally globular													
24.	Procoxal cavities without lateral extensions													
25.	Scutellary striole absent													
26.	Mesocoxae broadly separated													
27.	Mesometasternal junction a straight line													
28.	Mesocoxal cavities laterally closed													
29.	Metasternum with femoral lines													
30.	Metacoxae broadly separated													


CHARACTER NO.
CHARACTER
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BOTHRIDERINAE
TEREDINAE
XYLARIOPHILINAE
ANOMMATINAE
EUXESTINAE
METACERYLONINAE
CERYLONINAE
MURMIDIINAE
OSTOMOPSINAE
DISCOLOMIDAE
SPHAEROSOMATIDAE
31. Metendosternite with short, broad stalk
32. Metendosternal laminae broad/narrow/ reduced or absent
33. Metendosternal laminae on arms
34. Hindwing with radial cell absent
35. Anal cell absent
36. Number of anal veins
4 4 3-4 3-4 1 1-3 1 0-2 0 0 0
37. Jugal lobe absent
38. Subcubital fleck divided
39. Subcubital fleck absent
40. Trochanterofemoral attachment heteromeroid
41. Trochanter reduced and concealed
42. Tibial apex expanded and spinose
43. Number of tarsal segments
5 4-5 4 4 4 3 4 4 3-4 3-4 3 3 4
44. Empodium indistinct or absent
45. Intercoxal process of ventrite 1 subacute/rounded/truncate
46. Ventrite 1 with femoral lines
47. Ventrite(s) laterally expanded
48. Abdomen with 5 pairs of spiracles
49. Ventrite 5 crenulate
50. Ventrites with internal apodemes
51. Tegmen asymmetrical
52. Parameres articulated/fixed/absent
53. Tegmen with anterior dorsal struts
54. Tegmen with anterior dorsal lobe
55. Ventral tegminal strut articulated/fixed/absent
56. Anterior struts of median lobe long/short/absent
57. Median lobe strongly curved
58. Spiculum gastrale absent
59. Ovipositor reduced without styli

CHARACTER NO.	CHARACTER	BYTURIDAE	BIPHYLLIDAE	BOTHRIDERINAE	TEREDINAE	XYLARIOPHILINAE	ANOMMATINAE	EUXESTINAE	METACERYLONINAE	CERYLONINAE	MURMIDIINAE	OSTOMOPSINAE	DISCOLOMIDAE	SPHAEROSOMATIDAE
60.	LARVA. 2-segmented, sensorium basal/ 2-segmented, sensorium apical													
61.	LARVA. Antennae short/mod./long													
62.	LARVA. Number of stemmata per side	6	6	0	6	6	0	0-2		0	0		3	5
63.	LARVA. Mandible without mola													
64.	LARVA. Prostheca reduced–absent/ brush or setae													
65.	LARVA. Mala truncate/ intermediate/falciform									5				
66.	LARVA. Hypostomal rods absent													
67.	LARVA. Urogomphi present													
68.	LARVA. Urogomphi short–simple/ hooked/straight–complex													
69.	LARVA. Spiracles annular/annular–biforous/"biforous"													
70.	LARVA. Spiracles on tubes													

Comments

This genus possesses most of the diagnostic features of the bothriderid subfamily Teredinae, including the form of the antennae and maxillae, the proximity of all coxae, the type of mesometasternal fitting (single knob), the heteromeroid (strongly oblique) type of trochanterofemoral articulation, the expanded and spinose tibial apices, and the form of the aedeagus (symmetrical, with articulated parameres and a narrow, ventral, tegminal strut); however, it differs from all teredines in the shorter and broader body form, which is densely setose, distinct antennal grooves, corporotentorium with a median process, simpler mandibles (without a plate-like dorsal process, Fig. 28), laterally open mesocoxal cavities (Fig. 11); reduced metendosternite and wing venation, and no distinct empodium. It is considered sufficiently distinct from all other teredine genera to warrant its placement in a new subfamily, Xylariophilinae, subfam. n. The presence of a median process on the corporotentorium tends to link *Xylariophilus* with members of the Cerylonidae, which may be superficially similar and also exhibit a reduction in metendosternite and wing venation. Most cerylonids, however, have at least the mesocoxae and often all coxae more widely separated, the trochanterofemoral articulation of the normal type (straight or slightly oblique), and the aedeagus either asymmetrical of without articulated parameres. Other distinguishing characters may be found in the subfamily key (*see* Discussion) and in Fig. 57.

Key to species of *Xylariophilus*

1. Apical segment of antennal club distinctly longer than basal segment and apparently subdivided into 2 parts (Fig. 1); pronotum reddish brown with black areas on lateral portions of disc; elytra whitish yellow with a pattern of well defined black markings. Australia . . . . . **X. bicoloripennis** sp.n.

Apical segment of antennal club not larger than basal one and not subdivided; pronotum blackish brown with reddish brown marking anteriorly; elytra yellowish brown or reddish brown with a pattern of black markings, the edges of which are not as well defined 2

2. Anterior edge of pronotum slightly sinuate on each side near eyes; less than one-fourth of pronotal disc reddish brown; elytra with interstitial punctures well-developed, often more than half as large as punctures forming major rows; median impressed line of metasternum less than half as long as median length of sternum; small species (less than 1.85 mm). Australia **X. honoratus** sp.n.

Anterior edge of pronotum uniformly curved; at least anterior half of pronotal disc reddish brown; elytra without distinct interstitial punctures; median impressed line on metasternum more than half as long as median length of sternum; larger species (1.93 mm). India .. .. **X. comatus** sp.n.

Xylariophilus bicoloripennis sp.n. (Figs 1, 16-17)

Types—QUEENSLAND: *holotype*, Lamington National Park (near O'Reilly's), 2-4.iii.80, under bark of rotten logs, J. F. Lawrence (ANIC, No. 88); *paratypes*: 10, same data as holotype; 2, same locality and dates, ANIC Berlesate 673, leaf litter, J. F. Lawrence, (ANIC and ZSIC).

Adult

Length 1.63-1.70 mm (1.68 ± 0.03) (n = 8). Head reddish brown; pronotum reddish brown with a longitudinal black marking on each side extending from anterior to posterior angle and occupying about one-seventh of the width. Elytra whitish yellow with distinct black markings forming a complex pattern as shown in Fig. 1. Upper surfaces somewhat shiny, densely clothed with long, fine hairs.

Head coarsely and densely punctate, with interspaces about as wide as a puncture diameter; punctation of clypeus finer and sparser. Antennal club with basal segment much shorter than apical one, which appears to be subdivided (because of the uneven distribution of pubescence). *Pronotum* about 0.78 X as long as wide (PL/PW = 0.72-0.86); sides moderately rounded, distinctly converging anteriorly and posteriorly; anterior edge uniformly curved; posterior edge arcuate, sinuate on each side just mesad of posterior angles, which are slightly obtuse but not rounded. Punctation finer and denser than on head, with interspaces about as wide as a puncture diameter. Scutellum transverse. *Elytra* about 1.49 X as long as greatest combined width (EL/EW = 1.45-1.52) and about 2.38 X as long as pronotum (EL/PL = 2.25-2.50); sides very slightly curved. Punctures in intervals well-developed, almost as large as those forming puncture rows. Metasternum about 0.6 X as long as wide; median impressed line 0.5 X as long as median length of sternum. *Aedeagus* as in Figs 16-17.

Xylariophilus comatus sp.n. (Fig. 2)

Types—INDIA: *holotype*, Arunachal Pradesh, Namdapha Survey, 21.iv.81, under bark, S. Biswas, (ZSIC); *paratype*, same data as holotype, (ZSIC).

Adult

Length of holotype 1.93 mm. Head deep brown; pronotum reddish brown with posterior four-ninths and anterolateral angles black. Elytra yellowish brown with black markings forming 3 irregular bands as in Fig. 2. Upper surfaces slightly shining, densely clothed with long, fine hairs.

Head coarsely and sparsely punctate, with interspaces about as wide as a puncture diameter. Antennal club with basal segment about as long as apical one, which is uniformly pubescent and not subdivided. *Pronotum* 0.73 X as long as wide; sides moderately rounded, distinctly converging anteriorly; anterior edge uniformly curved; posterior edge arcuate, sinuate on each side just mesad of posterior angles which are obtuse and somewhat rounded. Punctation finer and sparser than on head with interspaces distinctly wider than punctures. Scutellum about as long as wide. *Elytra* 1.51 X as long as greatest combined width and 2.50 X as long as pronotum; sides slightly curved. Interstitial punctures apparently absent. Metasternum 0.57 X as long as wide; median impressed line 0.61 X as long as median length of sternum. *Aedeagus* not studied.

Xylariophilus honoratus sp.n. (Figs 3, 14-15)

Types—QUEENSLAND: *holotype*, ♀, Claudie River, near Iron Range, 19-25.vii.78, Lot No. 78-67, ex *Hypoxylon cyclopicum*, J. F. Lawrence, (ANIC, No. 87); *paratypes* 21, same data as holotype; 16, same locality and dates, Lot 78-113, ex *Hypoxylon jecorinum*; 1, same locality and dates, Lot 78-62, ex *Xylaria anisopleura*; 1, same locality and dates, Lot 78-131, ex *Kretzschmaria cetrarioides* (ANIC, BM, BPBM, CAS, IZP, NMHN, QM and ZSIC).

Adult

Length 1.48-1.88 mm (1.73 ± 0.12) (n = 11). Head deep brown; pronotum black or blackish brown with anterior fifth or sixth reddish brown; elytra yellowish brown to reddish brown with black markings usually forming 3 characteristic bands (Fig. 3), the middle one broken at the suture and the posterior one sometimes absent. Upper surfaces somewhat shining, densely clothed with long, fine hairs.

Head coarsely and densely punctate, with interspaces narrower than puncture diameters; punctation of clypeus finer. Antenna with basal club segment slightly larger than apical one, which is uniformly pubescent and undivided. *Pronotum* about 0.74 X as long as wide (PL/PW = 0.71-0.77); sides very weakly rounded and sometimes almost parallel, only slightly converging anteriorly; anterior edge slightly sinuate on each side near eyes; posterior edge arcuate, slightly sinuate on either side of midline; posterior angles obtuse and somewhat rounded. Punctation slightly finer than on head, with interspaces usually wider than punctures. Scutellum transverse. *Elytra* about 1.43 X as long as greatest combined width (EL/EW = 1.40-1.47) and about 2.25 X as long as pronotum (EL/PL = 2.16-2.34). Interstitial punctures well-developed and almost as large as those forming puncture rows. Metasternum about 0.60 X as long as wide; median impressed line 0.30 X as long as median length of sternum. *Aedeagus* as in Figs 14-15.

Presumed larva of Xylariophilus honoratus *sp.n.* (Figs 18-21)

Length 3 mm. Body (Fig. 18) elongate, more or less parallel-sided, slightly flattened and lightly pigmented. Upper surfaces granulate, asperate and tuberculate. Vestiture consisting of short to long, simple setae, long, expanded setae, and short, scale-like setae.

Head protracted and prognathous, moderately broad, transverse, and slightly flattened, clothed with both short and long, simple setae and a transverse row of scale-like setae. Epicranial suture not apparent; median endocarina absent. Number of stemmata on each side 6 (5 well-developed lenses forming 2 vertical rows, 3 anterior and 2 posterior, plus a smaller eye spot at the ventral end of the posterior row). Antennae short, about 0.16 X as long as head width (appearing longer because of well-developed basal membrane); 3-segmented; segment 1 very short and ring-like; segment 2 slightly longer but strongly transverse; segment 3 about 2.5 X as long as segment 2 and much narrower; sensorium on segment 2 slightly longer than segment 3 and lying ventral to it. Frontoclypeal suture absent; labrum free. Mandibles (Fig. 19) symmetrical, tridentate, with an additional tooth on incisor edge, and with a large accessory ventral process. Mola well-developed and asperate, with asperities extending onto ventral surface and with a brush of hairs at base; prostheca reduced and closely adpressed to mola. Ventral mouthparts retracted. Maxilla (Fig. 20) with transverse cardo, elongate stipes and well-developed articulating area; maxillary palp 3-segmented, segments 1 and 2 transverse and subequal, segment 3 as long as 1 and 2 together; mala truncate, setose. Labium (Fig. 20) with short, broad, rounded ligula and 2-segmented labial palps, which are separated by less than basal width of one. Hypopharyngeal sclerome present. Hypostomal rods moderately long and diverging, but not very heavily sclerotised. Ventral epicranial ridges absent. Gula transverse.

Thorax and Abdomen. Thoracic and abdominal terga covered with granules, tubercles, and sharp asperities. Thorax relatively large, about 0.67 X as long as abdomen, without well-developed lateral tergal processes. Protergum with anterior and posterior transverse rows of scale-like setae, a few more on disc between 2 rows, and 3 pairs of long, expanded setae on each side (2 anterior and 1 posterior); meso- and metatergum each with an anterior transverse row of scale-like setae, a few more behind this, and 1 long, expanded seta on each side; lateral portions of thorax with few additional long, simple setae. Legs moderately stout, widely separated, with unisetose tarsungulus. Abdominal terga 1-8 expanded laterally forming short processes, each of which bears a long, expanded seta and a short, scale-like seta (Fig. 21); surface of each tergum with a single transverse row of scale-like setae. Tergum 9 bearing a distinct median boss, covered with scale-like setae, tubercles, and asperities, a pair of dorsolateral processes, each bearing a long, expanded seta, a pair of short, strongly upturned urogomphi, sclerotised at apex, and 3 additional pairs of processes near the base of each urogomphus, each process bearing a long, simple seta; base of tergum 9 without transverse row of internal rods. Sternum 9 simple; segment 10 oval, ventrally oriented. Spiracles (Fig. 21) annular-biforous, but of a peculiar type with accessory openings much longer than main opening and occupying one side of a long spiracular tube.

Material examined—A single specimen collected in the fruiting body of *Hypoxylon cyclopicum* on the Claudie River, near Iron Range, North Queensland, 19-25 July 1978 (J. F. Lawrence, Lot 78-67), in the company of a number of adults.

Comments

The larva differs considerably from the lightly sclerotised, grub-like, and degenerate ectoparasitic larvae described for the bothriderine genera *Dastarcus* Walker (Piel 1938), *Bothrideres* Erichson, *Lithophorus* Sharp, and *Deretaphrus* Newman (Craighead 1920), *Sosylus* Erichson (Browne 1962; Roberts 1980), and *Asosylus* Grouvelle (Roberts 1980). The known larval types most closely resembling this one are those of *Anommatus duodecimstriatus* (Müller), described by d'Aguilar (1937) and Dajoz (1968) and presently included in Cerylonidae (Sen Gupta and Crowson 1973), *Sphaerosoma algiricum* Reitter, described by Peyerimhoff (1913) and included by Crowson (1981) and Lawrence (1982) in the monotypic family Sphaerosomatidae, *Teredolaemus leae*, described by Lawrence (1985, in press)

(Figs 22-23), and the same or a related species of *Teredolaemus* Sharp, described by Sen Gupta and Crowson (1971), who apparently misidentified the first instar (Figs 9a-f) as that of *Xenoscelinus australiensis* Sen Gupta and Crowson and a later instar (Figs 10a-d) as that of *Cryptophilus integer* Heer, both members of the family Languriidae. Larvae of all 3 genera have very short, 3-segmented antennae, mandibles with a well-developed mola and reduced prostheca, short to moderately long hypostomal rods, hooked urogomphi, and annular-biforous or apparently biforous spiracles; while all but *Anommatus* have 5 or 6 stemmata on each side and well-developed spiracular tubes. The *Anommatus* larva differs from that of *Xylariophilus* in lacking stemmata, and having lateral tergal processes on terga 6 to 9 and a more complex 9th tergum. The larva of *Sphaerosoma algiricum* differs from that of *X. honoratus* in having a different type of sculpture and vestiture, one less stemma on each side, and a median process on the 8th tergum. The *Teredolaemus* larvae have less highly modified spiracles, which are of a typical annular-biforous type located on shorter spiracular tubes, and also differ in having longer urogomphi and a series of deep pockets located between terga 8 and 9. Also similar are the described larvae of the Cerylonidae-Euxestinae, representing the genera *Elytrotetrantus* John (Jeannel and Paulian 1945), *Euxestus* Wollaston (Lawrence in press; Sen Gupta and Crowson 1973) and *Hypodacne* Leconte (Nititskii and Belov 1979; Sen Gupta and Crowson 1973). These all differ from the *Xylariophilus* larva, however, in having 2 or fewer stemmata on each side, long, straight, diverging urogomphi, somewhat longer antennae, and no hypostomal rods. Larvae of some Languriidae (Cryptophilinae and Xenoscelinae) resemble those of *Xylariophilus* and related forms in general body form and surface sculpture, but they differ in having a well-developed prostheca and only a single tarsungular seta.

Discussion

The history of the Bothrideridae and Cerylonidae is complex and confusing. Most species currently placed in the 2 taxa have been variously combined into several subgroups of the family Colydiidae (Euxestini, Cerylonini, Lapethini, Murmidiini, Mychocerini, Teredini, Deretaphrini, Dastarcini, and Bothriderini) by most beetle taxonomists (Erichson 1845; Lacordaire 1854; Sharp 1894, 1895; Grouvelle 1908; van Emden 1928; Hetschko 1930; Heinze 1943, 1944; Pope 1961; Dajoz 1977), but they differ from true colydiids in having completely exposed antennal bases (not concealed from above by frontal ridges), a cucujoid type of aedeagus (with a ring-like tegmen more or less surrounding the median lobe), and larvae which are typically "clavicorn" (with a pygopod-like 10th segment and mandibles with a hyaline prostheca and/or an accessory ventral process) and have only one tarsungular seta. When Sen Gupta and Crowson (1973) united the first 5 tribes with the genera *Metacerylon*, *Anommatus*, *Abromus* Reitter, *Ostomopsis* Scott, and several new taxa to form the cucujoid (clavicorn) family Cerylonidae, they retained members of the bothriderine complex (last 4 tribes above) in the tenebrionoid (heteromeran) family Colydiidae. Lawrence (1980, 1985, in press) transferred the latter group to Cucujoidea (= Clavicornia), where they comprise the family Bothrideridae, first recognised by Craighead (1920). Although typical Cerylonidae (Ceryloninae) are easily distinguished from bothriderids by the lack of a frontoclypeal suture, the presence of aciculate maxillary palps (with the apical segment shorter and much narrower than the penultimate one), the simple tibial apices, and the type of abdominal apex (with crenulate edge on ventrite 5) and aedeagus (asymmetrical and lying on one side), these differentiating features tend to break down with the addition to the former group of such diverse taxa as *Anommatus*, *Metacerylon* and *Ostomopsis*, as well as the murmidiines and euxestines. This combined with the discovery of *Xylariophilus* and additional larval types mentioned above would appear to call for a reexamination of the limits of both Cerylonidae and Bothrideridae, which in turn would require a cladistic analysis of the entire "cerylonid series" of Crowson (1955), as well as other taxa, like Biphyllidae and Byturidae, which are likely sister groups for the entire complex. We feel that such an analysis is premature at this time for the following reasons: (1) a manuscript on the classification of the entire Cucujoidea (Clavicornia) is nearing completion by T. Sen Gupta and R. A. Crowson; (2) work in progress by S. A. Slipinski on Bothrideridae and Cerylonidae may well alter the constitution of these families, and (3) important related taxa like the

Endomychidae are poorly understood and require complete revision. As a partial solution, we present a character-taxon matrix for the subgroups of Bothrideridae and Cerylonidae, plus certain related families, and will suggest new limits and a new subfamilial classification of the Bothrideridae.

The matrix in Fig. 57 consists of 13 family group taxa and 70 characters, 11 of which are based on larvae. The constitution of the various taxa are as follows. Biphyllidae, Byturidae, and Discolomidae are used in the sense of Crowson (1955), while Anommatinae, Euxestinae, Metaceryloninae, Ceryloninae, Murmidiinae, and Ostomopsinae are equivalent to the Anommatini, Euxestini, Metacerylonini, Ceryloninae, Murmidiini, and Ostomopsini, respectively, of Sen Gupta and Crowson (1973) (Lawrence and Stephan 1975). *Micruloma* Carter, described in Tenebrionidae, also belongs to Metaceryloninae (Kaszab 1978). Xylariophilinae is based on *Xylariophilus*, while Sphaerosomatidae includes only the genus *Sphaerosoma* Leach (Crowson 1981). Bothriderinae is comprised of the tribes Deretaphrini and Bothriderini, as recognised by most authors (Pope 1961; Dajoz 1977), and corresponds to Hetschko's (1930) Dastarcini, Bothriderini, and Deretaphrini, excluding those genera removed by later workers (summarised by Lawrence 1980), and also excluding *Sysolus* Grouvelle and *Sosylopsis* Grouvelle. This group, which is not generally recognised, is defined by the unique type of trochanter, which is reduced and more or less concealed within an excavation at the base of the femur, and by the distinctive type of ectoparasitic larva. The Teredinae includes *Teredus* Shuckardt, *Teredolaemus* Sharp, *Teredomorphus* Heinze, and *Oxylaemus* Erichson (Pope 1961; Lawrence 1985) plus *Sysolus*. This last genus is very distinctive and recently has been placed in a distinct tribe Sysolini (Slipinski and Pal 1985). *Sosylopsis*, which Dajoz (1980b) placed in a new tribe, Sosylopsini, because of the well-developed trochanters, combined with the widely separated metacoxae characteristic of Bothriderinae-Bothriderini, has not been examined and is excluded from consideration. The tribe Orvoeniini, based on the Indonesian genus *Orvoenia* Dajoz (1980a), is said to be intermediate between Teredini and Metacerylonini (Cerylonidae), but the figures and description indicate that it is almost certainly a nitidulid near the genus *Megauchenia* Macleay. The families Discolomidae and Sphaerosomatidae are included in the matrix because of larval similarities to Murmidiinae and Xylariophilinae, respectively.

In Fig. 57, a white square indicates plesiomorphy, a black one apomorphy, and a grey one an intermediate condition; in some cases, however, the character polarity is doubtful, and in others both grey and black squares represent apomorphic conditions derived independently from the plesiomorphic one. Partially shaded squares indicate variability within taxa, while an X indicates that the character is inapplicable to that taxon. Five meristic characters (7, 8, 36, 43, 59) have not been coded. In the list below, character states are separated by slashes and the presumed plesiomorphic state is listed first.

1) Transverse occipital ridge absent/present. This feature has almost certainly evolved independently in Biphyllidae, Murmidiinae and some Ceryloninae (Lapethini).

2) Frontoclypeal suture absent/present (Fig. 5). Note 1: the absence of a frontoclypeal suture in Biphyllidae, Byturidae and some apparently related cucujoids, such as Languriidae (including Cryptophilinae), suggests that the suture has arisen within this complex. Its absence in Cerylonidae, however, certainly represents a reversal associated with the profound modifications of the mouthparts in this group.

3) Transverse pregular impression absent/present. This impression is seldom well defined and may be an artifact produced by the enlargement of the posterior portion of the head, especially the gular area.

4) Antennal grooves absent/short, lying between eye and mandibular articulation on each side/long, extending below and behind each eye. It is not certain whether the first or second character state is plesiomorphic.

5) Corporotentorium with median process present (Figs 5, 26-27)/absent. This feature is certainly apomorphic within Cucujoidea, but it appears to be a basic feature in this lineage and apparently has been secondarily lost in Bothriderinae, Teredinae

and some Biphyllidae. If Discolomidae, Sphaerosomatidae, and other families in the "cerylonid series" are also considered to be part of this lineage, then the median process has been lost in these taxa as well. Note 2: in Discolomidae and some Bothriderinae, the corporotentorium is absent.

6) Anterior tentorial arms well separated/meeting at midline. This feature also occurs in Endomychidae. Note 3: in some Bothriderini, the 2 halves of the tentorium are fused at the base.

7) Number of antennal segments. The plesiomorphic state is 11, but reduction in number of segments has probably occurred a number of times.

8) Number of antennal club segments. The plesiomorphic state is 3, and reduction to produce a club of 1 or 2 segments has probably occurred more than once by the compaction of club segments. In some groups, like Teredinae and Xylariophilinae, the last segment becomes closely associated with the penultimate segment and appears to take over the sensory function entirely, so that there appears to be a single segment with a glabrous base and pubescent apex.

9) Antennal club loose/compact.

10) Apex of labrum truncate/rounded/subacute. The relative plesiomorphy of the first 2 states is in doubt.

11) Epipharyngal impression absent/present (Fig. 35). This and other features of the labrum-epipharynx need to be examined in more detail for more taxa.

12) Mesal arms of tormae oblique, projecting posteromesally (Figs 6, 37-38)/more or less perpendicular to lateral arms, projecting mesally (Figs 35-36).

13) Labral rods slender (Fig. 36) or absent/intermediate (slightly enlarged anteriorly) (Fig. 37)/broad and club-like (Figs 6, 38).

14) Lacinia with (Fig. 32)/without apical teeth or spines.

15) Apical segment of maxillary palp more or less subulate (Figs 8, 29-31)/aciculate (shorter than and much narrower than penultimate segment). In *Ostomopsis* and the Murmidiinae, the maxillary palps are said to be aciculate (Sen Gupta and Crowson 1973), but they do not satisfy the definition used here.

16) Apical segment of maxillary palp more or less subulate/securiform (Fig. 33).

17) Lateral edges of pronotum smooth/serrulate (Fig. 39).

18) Pronotal hypomera without/with anterolateral antennal cavities. These sometimes extend onto the dorsal surface of the pronotum (*Murmidius* Leach).

19) Prosternal process not expanded/expanded apically (Figs 39-41).

20) Procoxae narrowly separated (Figs 10, 42)/broadly separated (Figs 39-41).

21) Procoxal cavities internally open (Figs 10, 39, 41-42)/internally closed (Fig. 40). Sen Gupta and Crowson (1973) consider the murmidiines to have internally closed procoxal cavities; although there is an internal process partly blocking the opening, it is not complete.

22) Procoxal cavities externally open (Figs 10, 39, 42)/externally closed (Figs 40-41).

23) Visible portion of procoxae transverse/globular (Fig. 4). In Biphyllidae, the procoxae are only slightly transverse, unlike some more primitive cucujoids. In forms with apparently globular procoxae, there is a well-developed internal portion which is not visible.

24) Procoxal cavities with/without external lateral extensions.

25) Elytra with/without scutellary striole. An X has been used when punctures are never arranged in rows or striae.

26) Mesocoxae narrowly separated (Figs 11, 43)/broadly separated (Figs 44-46).

27) Mesometasternal fitting (mesal junction between mesosternum and metasternum) consisting of a metasternal knob (Figs 11, 43)/a straight line (Figs 44-46). The loss of the ball and socket joint between the mesosternum and metasternum appears to be correlated with the lateral movement of the mesocoxae.

28) Mesocoxal cavities laterally "open", partly closed by mesepimeron (Fig. 11)/laterally closed by meeting of mesosternum and metasternum (Figs 43-46). The cavities are narrowly open in *Xylariophilus*, while the closure in some Teredinae (*Sysolus*) may be a relatively narrow one.

29) Metasternum without/with femoral lines (Figs 44, 46).

30) Metacoxae narrowly separated (Figs 11, 43)/broadly separated (Figs 44-46).

31) Metendosternite with stalk longer than broad/about as long as broad/broader than long (Figs 1, 45-46).

32) Metendosternite with laminae well-developed and broad/well-developed but narrow and sometimes curved/highly reduced and sometimes absent.

33) Metendosternite with laminae originating near bases of lateral arms and-or very close to anterior tendons/out on lateral arms and well separated from anterior tendons. In some Botheriderinae, both the anterior tendons and the reduced laminae are located out on the arms.

34) Hindwing with radial cell present/absent.

35) Hindwing with anal cell present (Fig. 51)/absent.

36) Number of anal veins in hindwing. The plesiomorphic state is 4.

37) Hindwing with jugal lobe present (Figs 13, 51-52)/absent. This lobe at the base of the wing is often lost in dissection.

38) Hindwing with subcubital fleck undivided/divided (Figs 13, 51). A divided subcubital fleck is not necessarily bisected by a vein.

39) Hindwing with subcubital fleck present (Fig. 51)/absent (Fig. 52). This structure is often called a binding patch, which is functionally correct.

40) Trochanterofemoral attachment of the "normal" type, not strongly oblique (Figs 44-46)/of the "heteromeroid" type, strongly oblique so that femur is in contact or almost in contact with coxa (Figs 11, 43). The character polarity here is not at all certain. A strongly oblique or heteromeroid type of attachment may be plesiomorphic in this group of families, although the extreme condition in Bothriderinae (*see* character 41) is autapomorphic.

41) Trochanter normally developed, easily visible/highly reduced and concealed within notch at base of femur.

42) Tibial apex not expanded and spinose/expanded and spinose (Figs 11, 43).

43) Number of tarsal segments. The plesiomorphic condition is 5.

44) Empodium well-developed and easily visible/absent or indistinct and not usually visible.

45) Intercoxal process of ventrite 1 subacute or narrowly rounded (Fig. 12)/broadly rounded/truncate (Figs 47-48).

46) Ventrite 1 without/with femoral lines (Fig. 47).

47) Ventrite 4 or ventrites 3 and 4 without lateral expansions/each with a pair of lateral expansions, which fit into depressions on the elytral epipleura (Figs 49-50).

48) Abdomen with 7 pairs of spiracles/5 pairs of spiracles.

49) Ventrite 5 with exposed edge smooth/crenulate (Fig. 48).

50) Ventrites without internal apodemes/each with a pair of anterolateral internal apodemes. These vary in their degree of development in the taxa concerned, but they appear to be completely absent in Biphyllidae and Byturidae.

51) Tegmen symmetrical/asymmetrical (Fig. 53).

52) Parameters articulated (Figs 14-17)/fixed/absent.

53) Tegmen without/with paired anterior dorsal and ventral struts (forming a "double" tegmen (Fig. 54).

54) Tegmen without/with an anterior dorsal lobe lying above the median lobe (Figs 53, 56). Note 4: the narrow anterior dorsal strut in *Ostomopsis* is almost certainly not homologous with the broad and asymmetrical lobe of Euxestinae and Metaceryloninae.

55) Anterior ventral tegminal strut articulated (Figs 14-17, 55)/fixed/absent. The presence of an anterior ventral strut is apparently primitive in Cucujoidea, and it appears that an articulated strut is plesiomorphic at least within this complex.

56) Anterior struts of median lobe long/short/absent.

57) Median lobe relatively straight/strongly curved.

58) Spiculum gastrale present/absent.

59) Ovipositor well-developed, with styli/reduced, without styli.

60) LARVA. Antenna with 3 distinct segments and sensorium on segment 2/with 2 segments and sensorium on segment 1/with 2 segments and sensorium at apex of segment 2.

61) LARVA. Antennae short (less than 0.2 X head width)/moderately long (between 0.2 and 0.5 X head width)/very long (more than 0.5 X head width). It is likely that the moderate condition is plesiomorphic and that both very short and very long larval antennae are apomorphic.

62) LARVA Number of stemmata on each side. The plesiomorphic state is 6.

63) LARVA. Mandible with (Fig. 19)/without a mola.

64) LARVA. Mandibular prostheca consisting of a well-developed hyaline lobe/reduced or absent, sometimes adpressed to distal edge of mola (Fig. 19)/consisting of a brush of hairs or reduced to 1 or 2 setae.

65) LARVA. Maxillary mala truncate (Fig. 20)/obliquely truncate or narrowly rounded at apex/falciform. Note 5: styliform in Ceryloninae. The polarity here is uncertain.

66) LARVA. Hypostomal rods present/absent.

67) LARVA. Urogomphi absent/present. The polarity here is not at all certain. If the lack of urogomphi is plesiomorphic, then they have developed independently in Biphyllidae, Byturidae, Bothrideridae (perhaps more than once) and euxestine Cerylonidae, as well as Sphaerosomatidae.

68) LARVA. Urogomphi short, simple, upturned/short to moderately long, hooked at apex and accompanied by 2 or more accessory processes or tubercles at base (Figs 18, 22-23)/long and straight or very slightly curved, bearing 2 or more pairs of accessory processes.

69) LARVA. Spiracles annular/annular-biforous/"biforous" (Fig. 21). The spiracles of *Xylariophilus*, *Sphaerosoma*, and some Euxestinae are actually of the annular-biforous type, in which the accessory openings have become much longer than the main opening. Unlike the truly biforous spiracles of many Elateriformia, these lack an ecdysial scar. It is probable that the annular-biforous condition is plesiomorphic, with the annular and the "biforous" types representing alternative apomorphisms.

70) LARVA. Spiracles not placed/placed at the ends of tubular processes (Fig. 21). These are relatively short in Teredinae and Euxestinae, but very long in Xylariophilinae and Sphaerosomatidae.

The matrix shows that the relationships among the taxa comprising the Bothrideridae and Cerylonidae are complex and that no clear separation of the 2

groups is possible. Within the first family, the Bothriderinae appear to form a well defined unit based on apomorphic features, such as the nature of the trochanter, the presence of a characteristic impression on the epipharynx, the ectoparasitic and probably hypermetamorphic larval type, and the occurrence of a pupal cocoon. The last character, however, is doubtful, since the wax cocoon in *Sosylus* and *Asosylus* differs from and may not be homologous with the silken cocoon found in *Deretaphrus* and the Bothriderini. Most characters shared by the Teredinae and Xylariophilinae, such as the externally open procoxal cavities, narrowly separated mesocoxae, normally developed trochanters, subcubital fleck in the hindwing, and non-ectoparasitic type of larva, are plesiomorphies, while the reduction of the radial cell in the wing is a synapomorphy which precludes the derivation of Bothriderinae from either group. If the median process on the corporotentorium is indeed an ancestral feature in this complex of families, then its absence in Teredinae and Bothriderinae may represent a synapomorphy. Several features of *Sysolus*, namely the loose, 3-segmented antennal club, large and club-like labral rods, narrowly closed mesocoxal cavities, and broad metendosternal laminae, do not occur in other Teredinae, and it is possible that Sysolini should be elevated to subfamily rank.

The Anommatinae have been uncomfortably housed in several families, including Colydiidae (Hetschko 1930), Merophysiidae (Crowson 1955), and Cerylonidae (Sen Gupta and Crowson 1973), while Dajoz (1977) treated them as a distinct family. Males appear to be rare in the group and few workers have examined the aedeagal structure; however Binaghi (1941) showed that the aedeagi of 3 alpine species of *Anommatus* had articulated parameres, a narrow, ventral tegminal strut, and a median lobe with long anterior struts. This type of aedeagus, which is characteristic of *Xylariophilus*, teredines, and bothriderines, but not euxestine Cerylonidae, combined with other features, such as the expanded and spinose tibial apices, support the transfer of Anommatinae from Cerylonidae to Bothrideridae.

Among the remaining Cerylonidae, the largest and most well defined group is the Ceryloninae, adults of which can always be distinguished by the lack of a frontoclypeal suture and the presence of aciculate maxillary palps. The larvae, which have been described for *Cerylon* Latreille (Sen Gupta and Crowson 1973; Lawrence in press), *Lapethus* Casey (Slipinski 1984; Lawrence in press), and *Philothermus* Aubé (Sen Gupta and Crowson 1973), are also easily distinguished from any other cucujoid by the highly modified mandibles and maxillae, which are stylet-like and either endognathous or enclosed within a tubular beak.

The Euxestinae and Metaceryloninae are probably sister groups, sharing a unique type of aedeagus (Figs 53, 56) and a metendosternite (Fig. 46) in which the laminae are located out on the lateral arms, well separated from the anterior tendons, which may be approximate or contiguous; the latter also share features with Ceryloninae (absence of subcubital fleck) and Teredinae (expanded and spinose tibial apices), and the discovery of a metacerylonine larva may refute the above hypothesis.

The Murmidiinae and Ostomopsinae, have an aedeagal type (Lawrence and Stephan 1975, Figs 5-7), which is basically more primitive than those of other cerylonids, in that it is symmetrical, with articulated parameres (in some forms) and a ventral tegminal strut. The inclusion of *Ostomopsis* in the family is based on the presence of a median corporotentorial process and a crenulate edge on ventrite 5, both of which are shared with Ceryloninae and Murmidiinae. There is no strong evidence for combining Ostomopsinae and Murmidiinae into a single subfamily, but the discovery of the larva of *Ostomopsis* may shed more light on this. Similarities between the broad and flattened, disc-like larvae of Murmidiinae and Discolomidae have led to suggestions of their close relationship (van Emden 1928; Crowson 1955). The only murmidiine larva known is that of *Murmidius ovalis* (Beck) (Böving and Craighead 1931; Sen Gupta and Crowson 1973; Lawrence in press), while 4 genera of Discolomidae have been characterised on the basis of larval characters: *Aphanocephalus* Wollaston (Fukuda 1969), *Cassidoloma* Kolbe (van Emden 1957), *Discoloma* Erichson (van Emden 1932), and *Notiophygus* Gory (van Emden 1938, 1957). Most of these larval similarities, however, are either superficial ones (general body form, long antennae) or characteristic of several other families in the complex; differences between

the 2 larval types include the 2-segmented antennae in Discolomidae and the hypostomal rods and median endocarina in *Murmidius*. Adult murmidiines differ from disclomids in having a median process on the corporotentorium, antennal cavities on the prothorax, internally and externally open procoxal cavities, femoral lines on the metasternum, a subcubital fleck on the hindwing, and a crenulate edge on ventrite 5.

The larval similarities between Xylariophilinae and Sphaerosomatidae suggest a close relationship between these 2 groups; however, there is little in adult structure to support this. The truncate palpal apices occur in Endomychidae but in no members of the Bothrideridae or Cerylonidae, while the aedeagal type resembles that characteristic of Euxestinae and Metaceryloninae.

The Biphyllidae and Byturidae, which are generally thought to form a monophyletic group (Falcoz 1926), have a type of wing venation (with the subcubital fleck bisected by an anal vein), procoxae (with more or less concealed trochantins), and larval tarsungulus (with a single seta) characteristic of the bothriderid-cerylonid complex, and have an aedeagal type (the so-called "double tegmen" with both dorsal and ventral struts, Fig. 54) which could give rise to all the major types present in the latter group. Furthermore, the habits of many Biphyllidae resemble those of *Xylariophilus*, in that both larvae and adults feed on the fruiting bodies of Xylariaceae. Most Biphyllidae and Byturidae exhibit features which are plesiomorphic in relation to taxa discussed above (loose, 3-segmented antennal club, procoxae slightly transverse, hindwing with radial cell, 5-segmented tarsi), but the condition of the procoxal cavities (internally and externally closed) is synapomorphic. It is likely that the ancestor of the bothriderid-cerylonid complex and probably the entire cerylonid series had features common to these 2 families, but with internally and externally open procoxal cavities. Among the more primitive cucujoid families, the Rhizophagidae have a biphyllid type of wing venation, with an anal vein bisecting the subcubital fleck, and at least some rhizophagids (species of *Hesperobaenus* LeConte and *Bactridium* LeConte) live on the fruiting bodies of Xylariaceae (Lawrence 1977). A bothriderid derived from this ancestor might have had the characters of *Xylariophilus* combined with a more complete type of wing venation and more primitive type of metendosternite (with broad laminae), as occur in *Deretaphrus* and some other Bothriderinae. An attractive scenario involves a free-living, mycophagous ancestor, feeding on the fruiting bodies of Xylariaceae, giving rise to a more specialised tunnel inhabitant, feeding on the ambrosia fungi cultured by platypodids, and this, in turn, producing an ectoparasitic type of bothriderid, attacking platypodids and other wood-boring insects. Such an hypothesis, however, needs further data to support it. The basal connections among the lineages of both Bothrideridae and Cerylonidae remain unresolved, partly because of lack of data from other families in the cerylonid series (Endomychidae, Coccinellidae, Corylophidae, and Lathridiidae) and in consideration of revisionary work in progress (*see* above). The distinguishing features of the subfamilies comprising the 2 groups are given in the following key.

Key to the Subfamilies of Bothrideridae and Cerylonidae

1. *Adult*. Trochanter highly reduced and concealed within notch at base of femur; protibial spurs usually unequal in length, one being enlarged and strongly curved or hooked; elytra almost always with longitudinal ridges or carinae. *Larva*. Surfaces smooth and vestiture consisting of simple setae only; body either very lightly sclerotised and grub-like, often physogastric, with vestiture of scattered fine setae (ectoparasitic type) or minute, somewhat flattened, fusiform, and clothed with posteriorly projecting, stout setae (triungulin type); antennae short and 2-segmented; stemmata absent; mandibular mola absent; spiracles annular. Usually found in the tunnels of wood-boring insects
.. .. **BOTHRIDERIDAE (Bothriderinae)**

   Adult. Trochanter not reduced, always easily visible; protibial spurs more or less equal in length, neither greatly enlarged nor hooked; elytra almost always without longitudinal ridges or carinae. *Larva*. Upper surfaces granulate or tuberculate, often with

paired tergal processes; vestiture often including modified setae (expanded or frayed (Figs 18, 21, 23), occasionally barbed); without other characters in combination 2

2. *Adult.* Frontoclypeal suture absent; maxillary palps aciculate, with apical segment shorter and much narrower than penultimate segment; mouthparts sometimes highly modified and enclosed within tubular, piercing beak. *Larva.* Mandibles and maxillae stylet-like, either endognathous or enclosed within tubular, piercing beak .. .. **CERYLONIDAE (Ceryloninae)**

Adult. Frontoclypeal suture present; maxillary palps not aciculate, with apical segment always longer than and usually not much narrower than penultimate segment; mouthparts never of piercing type. *Larva.* Mandibles of normal chewing type, with basal mola. 3

3. *Adult.* Head with transverse occipital ridge; pronotum with anterolateral cavities (sometimes located ventrally on hypomera) for reception of antennal clubs; ventrite 5 with crenulate edge; metasternum with femoral lines; median impressed line of metasternum either absent or extending to anterior edge. *Larva* (*Murmidius*). Body broadly ovate, strongly flattened, and disc-like; vestiture including barbed setae; antennae more than 0.5 X as long as head width; median endocarina present; mandible with distinct, hyaline prostheca .. .. .**CERYLONIDAE (Murmidiinae)**

Adult. Head without transverse occipital ridge; pronotum without anterolateral cavities; if ventrite 5 with crenulate edge, then metasternum without femoral lines and median impressed line short. *Larva.* Body not disc-like, without barbed setae; antennae shorter, never more than 0.5 X as long as head width; median endocarina absent; prostheca absent or reduced and closely adpressed to mola (Fig. 19) 4

4. *Adult.* Lateral edges of pronotum serrulate (Fig. 39); apical segment of labial palp abruptly constricted at apex (Fig. 34); procoxae widely separated, their cavities open internally and externally (Fig. 39); body short and broad, somewhat flattened, and densely setose. *Larva* unknown .. .. **CERYLONIDAE (Ostomopsinae)**

Adult. If lateraL edges of pronotum serrulate, then body elongate, narrow and subglabrous; apical segment of labial palp not abruptly constricted at apex; if procoxal cavities internally and externally open, then procoxae narrowly separated. 5

5. *Adult.* Procoxae and mesocoxae moderately to very widely separated (Figs 40-41, 44, 46); procoxal cavities externally closed; prosternal process expanded apically (Figs 40-41); intercoxal process of ventrite 1 truncate (Fig. 47); aedeagus with an asymmetrical anterior tegminal lobe lying above the median lobe, which lacks anterior struts (Figs 53, 56); body short and broad or antennal club 1-segmented. *Larva* (Euxestinae). Urogomphi long, diverging, and more or less straight; hypostomal rods absent; abdominal terga 1-8 with long lateral processes or shorter dorsal and lateral processes.. 6

Adult. Procoxae narrowly separated and prosternal process not expanded apically (Figs 10, 42), except in *Teredus*, which is elongate and narrow with a 2-segmented antennal club; mesocoxae narrowly separated (Figs 11, 43); intercoxal process of ventrite 1 usually subacute or narrowly rounded (Fig. 12); aedeagus symmetrical, with an anterior tegminal strut lying below the median lobe, which has well-developed anterior struts (Figs 14-17, 55). *Larva.* Urogomphi shorter, subparallel, dorsally projecting, and distinctly hooked at apex (Figs 18, 22-23); hypostomal rods present; abdominal terga 1-8 without or with very short lateral processes. 7

6. *Adult.* Ventrite 4 or ventrites 3 and 4 usually with paired lateral lobes which fit into elytral depressions (Figs 49-50); body usually more or less flattened, or if strongly convex, then elongate and parallel-sided; hindwing without subcubital fleck (Fig. 52). *Larva* unknown .. .. **CERYLONIDAE (Metaceryloninae)**

   Adult. Ventrites without paired lateral lobes; body more or less oval and moderately to strongly convex; hindwing with subcubital fleck (Fig. 13) .. .. **CERYLONIDAE (Euxestinae)**

7. *Adult.* Eyes absent; hindwings absent; metasternum shorter than ventrite 1; tarsi 3-segmented. *Larva.* Stemmata absent; lateral edges of terga 6-9 more strongly produced than those of anterior terga .. .. **BOTHRIDERIDAE (Anommatinae)**

   Adult. Eyes present; hindwings present; metasternum longer than ventrite 1; tarsi 4-segmented. *Larva.* Stemmata 5 or 6 on each side; lateral edges of terga 6-9 not more strongly produced than those of anterior terga.. 8

8. *Adult.* Mesocoxal cavities closed laterally by meeting of mesosternum and metasternum (Figs 43-46); hindwing with 3 or 4 anal veins (Fig. 51); antennal grooves absent; corporotentorium without median process (Fig. 25); body longer, narrower and subglabrous or sparsely setose (Fig. 24). *Larva.* Thoracic and abdominal terga each with pair of paramedian tubercles (Fig. 22); membrane between terga 8 and 9 with several deep pockets (Fig. 22); tergum 9 without median elevation. Living in tunnels of wood-boring beetles (especially ambrosia beetles) .. .. **BOTHRIDERIDAE (Teredinae)**

   Adult. Mesocoxal cavities not closed laterally by meeting of sterna (partly closed by mesepimeron) (Figs 4, 11); hindwing with 1 anal vein (Fig. 13); antennal grooves present (Fig. 4); corporotentorium with median process (Fig. 5); body shorter, broader, and densely setose (Figs 1-3). *Larva.* Thoracic and abdominal terga without paired tubercles (Fig. 18); membrane between terga 8 and 9 without deep pockets; tergum 9 with large, median elevation (Fig. 18). Associated with rotten wood and fruiting bodies of pyrenomycete fungi (Ascomycetes: Xylariaceae) .. .. **BOTHRIDERIDAE (Xylariophilinae)**

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