REVIEW OF THE LARVAL STAGES OF EPIPOCINAE (INSECTA: COLEOPTERA: ENDOMYCHIDAE)

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Abstract. — The taxonomic history and biology of Epipocinae (= Stenotarsinae) is briefly reviewed. The first larval descriptions are provided for four epipocine genera: Anidrytus Gerstaecker, Epipocus Germar, Periptyctus Blackburn and Stenotarsus Perty. For each genus, a dorsal habitus drawing is presented and important morphological structures are illustrated with scanning electron micrographs. The larval morphologies of Saula Gerstaecker and the presumed larvae of Ephebus Gerstaecker are also discussed. A key to identify larvae of all six genera is provided. Characters of potential phylogenetic importance and their implications for the classification of Epipocinae are briefly discussed.

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Key words. — Coleoptera, Endomychidae, Epipocinae, immature stages.

INTRODUCTION

The Endomychidae are a moderate-sized family of cucujoid beetles with about 120 genera placed in 12 subfamilies (Pakaluk and Ślipiński 1995). Although the larval stages of at least one species of most of these subfamilies have been described, these were usually isolated descriptions of a single species in a genus. This study on the larval stages of Epipocinae (=Stenotarsinae) (see Pakaluk *et al.* 1994) differs in that six genera are treated, five for the first time. We hope that this attempt at a comprehensive study of one subfamily of Endomychidae will eventually improve the higherlevel classification of the family and clarify the placement of endomychids within the cerylonid series.

Endomychidae are generally considered closely related to Coccinellidae, although the former appear to be polyphyletic and the latter have basal clades with uncertain relationships, some of which may include some endomychids (Pakaluk and Ślipiński 1990, Ślipiński and Pakaluk 1992). Although most endomychids are fungivores, the epipocine genus *Saula* feeds on scale insects (Sasaji 1978). While most coccinellids are predators of scale insects or aphids, some, such as bulaeines and halyziines, feed on pollen and mildew, respectively.

The Epipocinae are a widely distributed subfamily of Endomychidae with about 25 genera and 400 species described, although few species are represented in the Holarctic Region. In this paper six genera are treated with about 275 species all told. This represents only about 25% of the generic diversity for the subfamily, while these gen-

era contain almost 75% of its species diversity. If these data presented here are predictive, we may be able to fruitfully utilize these larval character data to elucidate higher-level relationships of epipocines and other endomychids. Two genera previously considered as epipocines, *Monocoryna* Gorham and *Tetrabrachys* Kapur (previously *Mimolithophilus* Arrow), are now placed in cocciduline Coccinellidae.

Of the approximately twenty-five genera of Epipocinae, six are treated in this paper. Saula Gerstaecker, with about 22 species, is distributed in tropical Africa, southeastern Asia and Japan. Stenotarsus Perty is the most speciose epipocine genus with about 175 species. It is widespread, mostly tropical, although absent from Europe. Ephebus Gerstaecker, with about eight species, is uncommon and endemic to the neotropics. Periptyctus Blackburn, with four species described, is endemic to eastern Australia. Anidrytus Gerstaecker is a neotropical genus with about 40 species. Epipocus Germar, with about 25 species, is restricted to the Western Hemisphere, with the majority of species in the neotropics.

MATERIALS AND METHODS

Larval epipocines are fragile, especially those bearing tergal and pleural lobes, so the preparation method that we used was gentler than that normally used. Cold potassium hydroxide solutions were used to relax and clear material. Because the action of ultrasonic cleaners was too

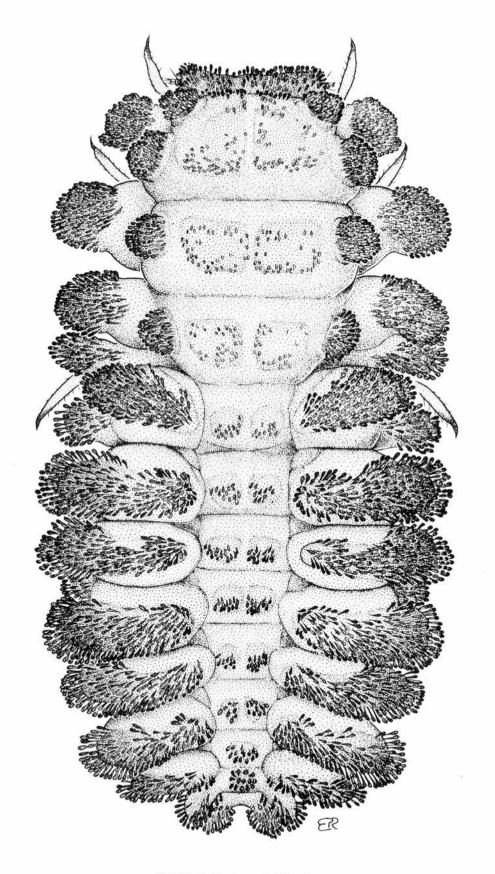
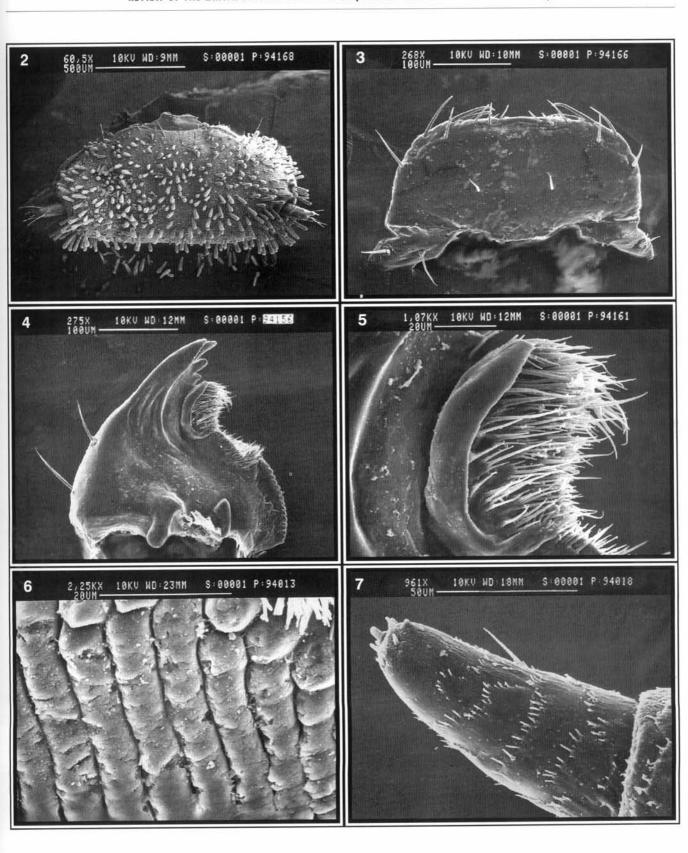


Figure 1. Anidrytus sp., habitus, dorsal.



Figures 2–7. Anidrytus sp.: (2) head, dorsal; (3) labrum, dorsal; (4) right mandible, ventral; (5) right prostheca, ventral; (6) right molar surface, mesal; (7) left maxillary palpus apex, ventral.

severe for these specimens, dirt and debris were removed manually. Slide-mounted preparations were made in canada balsam. Specimens for electron microscopy were sputter coated with gold palladium and viewed using a Cambridge Scientific Instruments S–100 scanning electron microscope.

Morphological interpretations and terminology generally follow Lawrence (1991) and Lawrence et al. (1993). We did not determine whether the terminal lobes on abdominal segment IX of Anidrytus, Ephebus and Epipocus species were tergal or pleural in origin and thus chose to use the term "urogomphi" to mean any pair of terminal sclerotized lobes on abdominal segment IX that are visible dorsally.

The larval identifications were based upon associations with adults in the field. For *Anidrytus*, *Epipocus*, *Stenotarsus* and *Periptyctus* there were multiple collections supporting the generic-level larval identification. The diagnosis of *Ephebus*, however, is based on a single association and should be regarded as tentative. The information used in the key regarding the larval morphology of *Saula* is based entirely on the description of *Saula japonica* Gorham by Sasaji (1978).

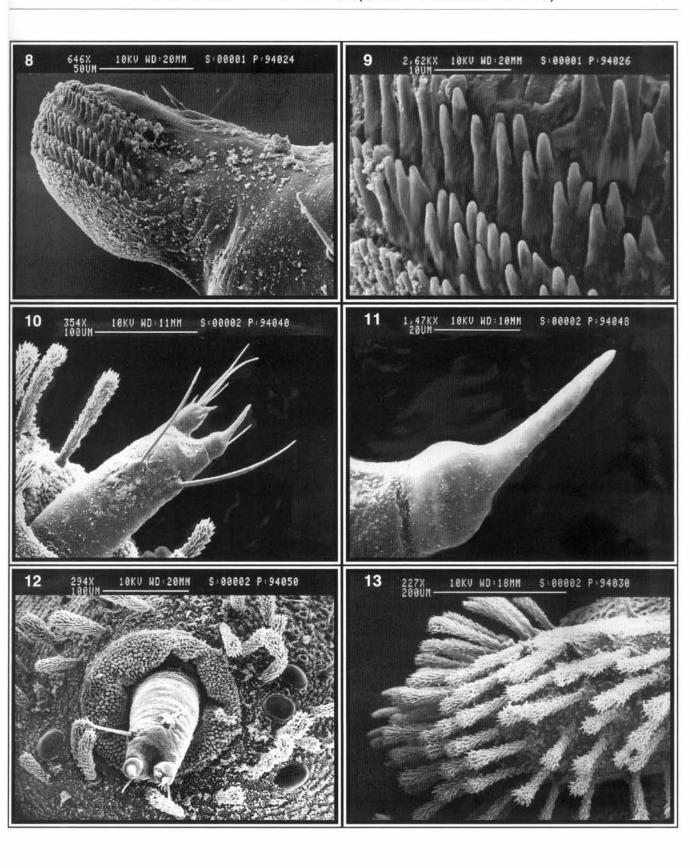
KEY TO KNOWN GENERA OF LARVAL EPIPOCINAE

- 2. Abdominal segments bearing a large lateral tergal and pleural lobe; thoracic segments bearing a large pleural lobe and sometimes also with lateral tergal lobe (Figs 1, 18); each lobe with area of highly modified multiply-barbed dark setae that appear clubbed at lower magnifications (<40×) (Figs 13, 26); apical antennomere longer than wide, longer than 1/2 length of sensorium</p>

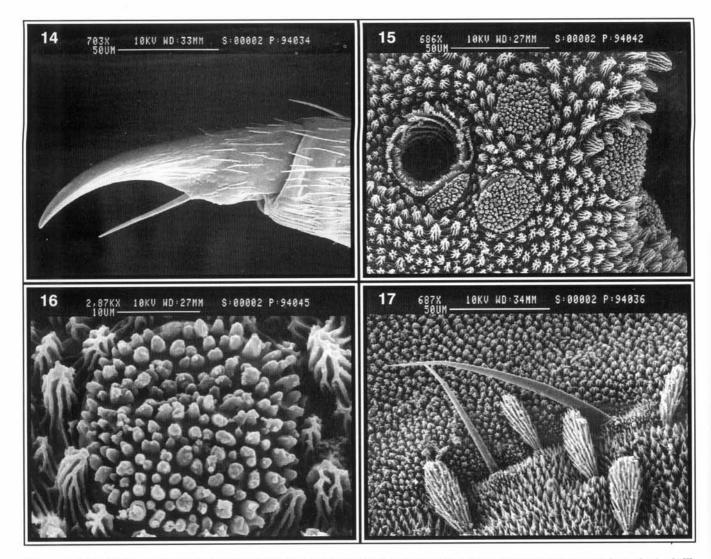
- 3. Mesothorax and metathorax bearing a rounded tergal lobe and pleural lobe laterally; prothorax with two rounded tergal lobes and one rounded pleural lobe; abdominal tergal lobes partially flattened, somewhat lamelliform, and bearing modified setae only in a band along upper and outer surface (Fig. 1) 4
- Mesothorax and metathorax bearing only a large pleural lobe at lateral margin; prothorax with lateral margin produced as one broad, partially divided lobe; abdominal tergal lobes finger-like and bearing modified setae over entire surface (Fig. 18) Epipocus
- Abdominal lateral tergal lobes smaller, directed dorsolaterad, pleural lobes visible in dorsal view; ecdysial line not visible on abdominal segments Ephebus

Anidrytus Gerstaecker (Figs 1–17)

Description. Mature larvae 4.5–5.1 mm long, 2.9–3.4 mm wide. Body broadly ovate (Fig. 1), moderately dorsoventrally flattened; color greyish yellow with darker brown terga, labrum, distal end of tibia, and base of tarsungulus. Surface texture finely granulate. Vestiture consisting of patches of short, stout, multiply-barbed setae



Figures 8–13. Anidrytus sp.: (8) left maxillary mala, ventral; (9) left maxillary malar surface, ventral; (10) left antenna, dorsal; (11) left antennal sensorium, dorsal; (12) left antennal base/stemmata, lateral; (13) modified setae, left tergal lobe, dorsal.



Figures 14–17. Anidrytus sp.: (14) left metatarsungulus, anterior; (15) abdominal spiracle III, lateral; (16) cluster of sensilla near abdominal spiracle III, lateral; (17) abdominal sternal vestiture; ventral.

(Fig. 13) appearing club-shaped at low magnification; clubbed setae dark on dorsal and dorsolateral surfaces of body, pale on ventrolateral and ventral surfaces; venter with some smaller club-shaped setae and longer simple setae (Fig. 17).

Head: Protracted, hypognathous, broad (Fig. 2). Epicranial stem absent, frontal arms U-shaped, bases approximate; endocarinae present, confluent with frontal arms; median endocarina absent. Stemmata, 4 per side, positioned closely around antennal insertion with 2 stemmata closely associated and dorsal to antennal base, 1 stemma posterodorsal, 1 stemma posteroventral (Fig. 12). Antenna short, less than ½ head width, antennomere ratio: AI:AII:AIII=3:5:1; antennal base large, membranous, with granules (Fig. 12), about length of AI; AII with 3 long setae arising at about ¾ length; AIII about twice as long as wide, with 3 long setae arising near apex and 2 short setae arising at about ¾ length (Fig. 10); sensorium large, aris-

ing slightly distally to base of AIII, swollen at base and abruptly narrowed at 1/4 length (Fig 11). Antennal fossa externally closed by head capsule, insertion distant from mandibular articulation point. Frontoclypeal suture present, weakly arcuate. Clypeus transverse, about 1/2 length and same width of labrum. Labrum large, exposed, free, with row of 8 stout curved setae along anterior margin and row of 8 finer setae just posterior to edge (Fig. 3). Mandibles (Fig. 4) symmetrical broad quadridentate, with two large apical teeth and 2 smaller teeth along incisor edge; ventral accessory process present; mola prominent, mesal surface arcuate, with asperites forming discrete transverse rows (Fig. 6); prostheca narrow, hyaline, curved, with dense brush of setae along mesal surface (Fig. 5). Maxillolabial complex retracted; maxilla with elongate stipes and well-developed articulating area, mala with broad rounded apex (Fig. 8) bearing rows of paired asperites on ventral surface (Fig. 9) and short dense setae on lateral surface; maxillary palpomeres 3-segmented, palpomere length ratio: PI:PII:PIII=1:1:2, PII and PIII with transverse rows of asperites (Fig. 7). Labium with mentum and submentum fused; ligula broad, arcuate distally, with pair of apical setae broadly separated; labial palp 1-segmented, arising from enlarged palpifer (see comments on *Epipocus*); bases of palps widely separated.

Thorax and Abdomen: Thoracic terga small (Fig. 1); dorsal verrucae lateral to terga, covered with dark, clublike, multiply-barbed setae. Protergum with 2 small round dorsal verrucae on each side, one near anterolateral angle, other near midpoint of lateral margin. Mesotergum and metatergum each with single small, rounded, lateral verruca near the midpoint of lateral margin. Each thoracic pleural region with a larger lateral lobe covered on apical half with dark, club-shaped setae. Abdomen with small rounded terga; with very large swollen lamella-like lobe projecting dorsolaterally on each side; lobe covered with band of clubbed setae extending along dorsal surface and down distal surface (Fig. 1). Abdominal pleural regions each with smaller conical projection clothed for at least apical half with dense, dark, modified setae. Thoracic and abdominal tergites covered with short, dark, clubbed setae. Thoracic terga divided by narrow pale ecdysial line; abdominal tergites small, with a broader, vaguer separation. Thoracic and abdominal sterna with sparse short multiply-barbed setae; sterna AVII-VIII with transverse row of 4 long fine setae. Legs with stout modified setae on coxa and sparse fine simple setae on trochanter, femur and tibia; tarsungulus slender with single seta (Fig. 14).

Spiracles: annular, not raised on tubes, small, hidden in folds between bases of tergal and pleural lobes. Pleural region around each abdominal spiracle with 10–12 pale oval groups of sensilla (Fig. 15); which have dense covering of warty projections on surface (Fig. 16).

Material. Anidrytus sp. GUYANA: Mazaruni-Potaro District, Kartabo Point, 6.I.1983, W. E. Steiner, (NMNH: 3 adults, 5 mature larvae). EL SALVADOR: Santa Tecla, VI.1958, O.L. Cartwright, (NMNH: 4 adults, 3 pupae).

Comments. All larval specimens examined were damaged, typically missing some of the lateral thoracic or abdominal lobes. While some of the damage apparently occurred after the material was placed in ethanol, it is not clear whether the lobes are easily dehiscent in living individuals.

The material collected in El Salvador did not include any larvae, yet it was helpful to confirm the larval-adult association based upon the Guyanan material. The final larval exuvium, which remains attached at the base of one pupal specimen, closely matches the morphology of the larvae from Guyana.

Ephebus Gerstaecker

Material. Ephebus sp. HONDURAS: Ocotepeque, 11km E Ocotepeque, 1470m, 16.VI.1994, S. Ashe and R. Brooks, Lot #128, ex. fungusy log (SEMC: 1 adult, 2 larvae).

Comments. A full description is not given for Ephebus because the only available larval material is a pair of damaged specimens that were collected together with an adult of an undetermined Ephebus species. There is no additional material to support this tentative identification by association and there was insufficient material for more detailed study.

These larvae are very similar to *Anidrytus* in gross morphology. The prothorax bears three verrucae at the lateral margins and both the mesothorax and metathorax bear a pair of verrucae laterally. These tergal projections of the thorax are small and do not extend beyond the pleural lobes. The lateral lobes of the abdomen are large, somewhat flattened and bear a band of modified setae, as in *Anidrytus*.

Despite the numerous similarities, a few features distinguish the presumed *Ephebus* larvae from *Anidrytus*. The abdominal tergites are not divided by an ecdysial line as in *Anidrytus*. The lateral tergal lobes of the abdomen are slightly smaller than in *Anidrytus* and are directed more dorsad, so they do not extend beyond the apex of the pleural lobes laterally, as is also the case in *Epipocus*.

Epipocus Germar (Figs 18–28)

Description. Mature larvae 4.9–5.2 mm long, 2.9–3.4 mm wide. Body broadly ovate (Fig. 18), moderately dorsoventrally flattened, brown to dark brown. Surface texture finely granulate. Vestiture consisting of patches of short stout dark multiply-barbed setae appearing clubshaped at low magnification (<40x); these modified setae densest on lateral lobes (Fig. 26), on periphery of thoracic tergites and on posterior half of abdominal tergites.

Head: Protracted, hypognathous, broad (Fig. 19). Epicranial stem absent, frontal arms U-shaped. Median endocarina and hypostomal rods absent. Stemmata 4 per side, closely positioned around antennal insertion with 2 stemmata closely associated and anterodorsal to eye, 1 stemma posterodorsal, 1 stemma ventral. Antenna short, less than 1/4 the maximum head width; length ratio of antennomeres: A1:A2:A3=2:5:1; antennal base large swollen membranous, surface granulate; AIII attachment preapical, about same length as sensorium. Antennal fossa closed externally by cranium, insertion widely separated from mandibular articulation. Frontoclypeal suture present, nearly straight. Clypeus transverse, glabrous, dark brown, about 1/2 length of labrum, emarginate apically. Labrum large, exposed, free, glabrous, dark brown; anterior margin arcuate (Fig. 20). Mandibles symmetrical, with five to six teeth extending from the apex down the incisor edge and gradually decreasing in size (Fig. 21); ventral accessory process small (Figs 21, 23); mola prominent, surface with ridges formed by transverse rows of small irregular tubercles (Fig. 23); prostheca membranous, densely setose (Fig. 22). Maxillolabial complex (Fig. 25) retracted; maxilla with elongate stipes and well-developed

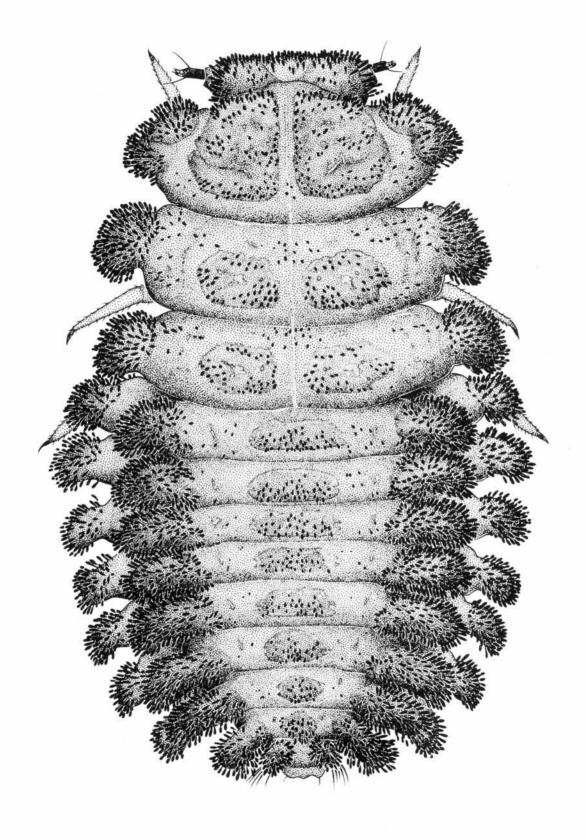
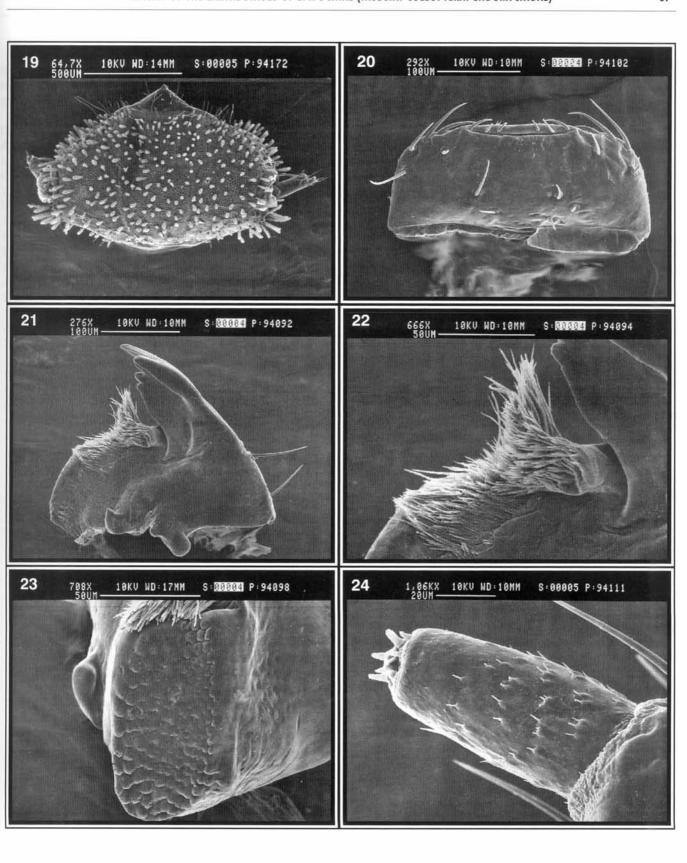
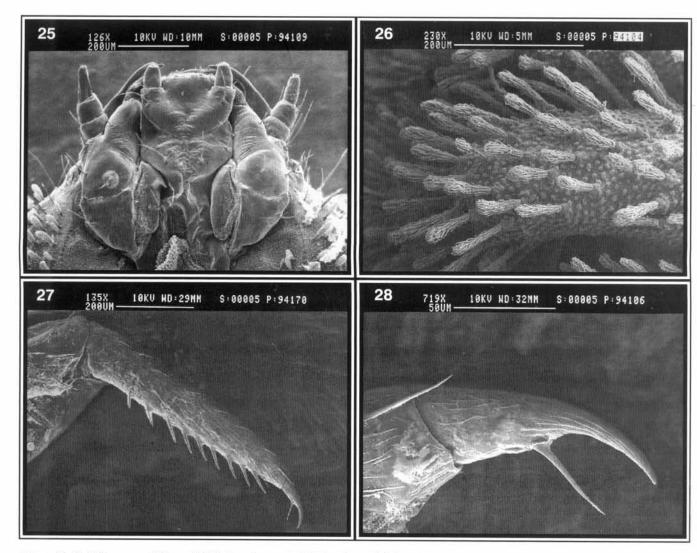


Figure 18. Epipocus sp., habitus, dorsal.



Figures 19–24. Epipocus sp.: (19) head, dorsal; (20) labrum, dorsal; (21) left mandible, ventral; (22) left prostheca, ventral; (23) right molar surface, mesal; (24) left maxillary palpus apex.



Figures 25–28. Epipocus sp.: (25) maxillolabial complex, ventral; (26) vestiture of abdominal tergum III, left side, dorsal; (27) left metathoracic tibia and tarsungulus, anterior; (28) left metatarsungulus, anterior.

articulating area, mala with broad oval obtuse apex bearing rows of paired asperites on the ventral surface and covered with dense setae on the dorsal surface; maxillary palpomere I short, ringlike; palpomeres II and III about equal length, PIII with vague transverse rows of asperites (Fig. 24). Labium with mentum and submentum fused, ligula broadly rounded, undivided; labial palp 1-segmented, arising from enlarged palpifer, apex with about 12 short conical sensilla, bases of palps widely separated.

Thorax and Abdomen: Thoracic segments bearing lateral lobe covered with dark, club-shaped, multiply-barbed setae; tergal plates oval, dark brown, divided by pale ecdysial suture (Fig. 18). Prothoracic lateral lobe broad, with a dorsal pit entering at a shallow angle or a vague transverse sulcus; prothoracic episternum swollen, appearing as tubercle. Mesotergum and metatergum bearing conical lateral lobe, apex of lobe directed laterad, surface granulate with modified setae (Fig. 26). Abdominal tergum bearing conical lateral lobe, apex of lobe directed

laterad to posterolaterad; tergal plates small, oval, undivided. Abdominal pleural regions bearing finger-like posterolateral lobe, similar in size, shape and vestiture to tergal lobes; base of abdominal tergal lobe and corresponding pleural lobe broadly separated leaving spiracle widely exposed; area between tergal and pleural lobes lacking setae. Abdominal segment VIII with urogomphi, similar in position, size, shape, vestiture to pleural lobes of preceding segments. Abdominal sterna with short clubbed setae moderately dense and evenly distributed; sterna II-III with 4 short simple setae, sterna IV-VII with 8-10 simple setae in groups of 2-3, sternum VIII with 4 simple setae at posterior margin. Legs dark, glabrous; coxa naked mesally, with club-shaped setae on outer surfaces and a few simple setae near distal end; trochanter, femur, tibia with simple setae only; tibial setae arranged in longitudinal rows, setae stouter on 2 inner rows (Fig. 27); tarsungulus slender, with single seta extending distally to about apex of claw (Fig. 28).

Spiracles: annular, not raised on tubes; abdominal spiracles located near anterior margin of segment, surrounded by 4–10 pale oval groups of sensilla; 3–5 pale oval groups of sensilla around thoracic spiracle.

Material. Epipocus sp. HONDURAS: Departamento Ocotepeque, 11km E Ocotepeque, 1770m, 16.VI.1994, lot #127, S. Ashe and R. Brooks, (SEMC: 2 adults, 7 pupae, 12 larvae). Departamento Lempira, 13.1km NE and 7.3km E Gracias, lower slopes of Montana Puca, 1320m, 18 June, 1994, S. Ashe, R. Brooks #143, ex. encrusting fungus below log, (SEMC: adults removed, 1 pupa, 14 larvae). MEXICO: Veracruz, 11.7mi S Huatusco, Highway 125, 8.3mi E on Ixhuatlan Rd., 17 July, 1990, 1130m, J.S. Ashe, K.-J. Ahn, R. Leschen, Coll. No. 206, ex. fungusy log (SEMC: adults removed, 3 larvae). 1.4mi S Huatusco, Highway 125, 16 July, 1990, 250m, J.S. Ashe, K.-J. Ahn, R. Leschen, Coll. No. 204, ex. sifting debris (SEMC: adults removed, 1 larva). 11.7mi. S. Huatusco, Highway 125 and 3km E. Ixhuatlan, 17 July, 1990, 1130m, J.S. Ashe, K.-J. Ahn, R. Leschen, Coll. No. 206, ex. sifting trash (SEMC: adults removed, 1 larva).

Comments. The tergal lobes in the larvae of this species may be dehiscent in living individuals. In several specimens that are missing tergal lobes, it appears that the point of attachment at the base of the missing lobe is closed, suggesting that either the missing lobes are the result of abnormal development or that the wound at the base of the missing lobes has healed.

The labial palps appear to be two-segmented due to the presence of a large palpomere-shaped swelling at the base of the apical palpomere. Compound microscopy indicates that this structure lacks a discrete edge basally and mesally where it is continuous with the labium. Therefore, we interpret it to be a palpifer and the labial palps to be one-segmented. This condition also occurs in *Anidrytus* and *Ephebus*.

Periptyctus Blackburn (Figs 29-41)

Description. Mature larvae 4.5–5.0 mm. Body lepismoid (Fig. 29), dorsoventrally flattened. Surface irregularly pitted, rough, with dense minute scale-like to stellate projections (Fig. 41). Dorsal color pattern pale yellowish with broad median dark stripe bearing a pair of more or less distinct pale spots on each body segment, spots sometimes appearing fused on AII–AVI (Fig. 29); lateral lobes darkened on thorax and abdomen; thoracic segments also darkened anterolaterally. Vestiture sparse, some short, stout, hook-like setae especially on lateral lobes (Fig. 40) and some long pale simple setae arranged as follows: 6 on anterior margin of protergum; 1 arising near apex of posterolateral lobes of thoracic terga; 4 on posterolateral margin of abdominal tergum IX; 2 on abdominal sterna VII and VIII.

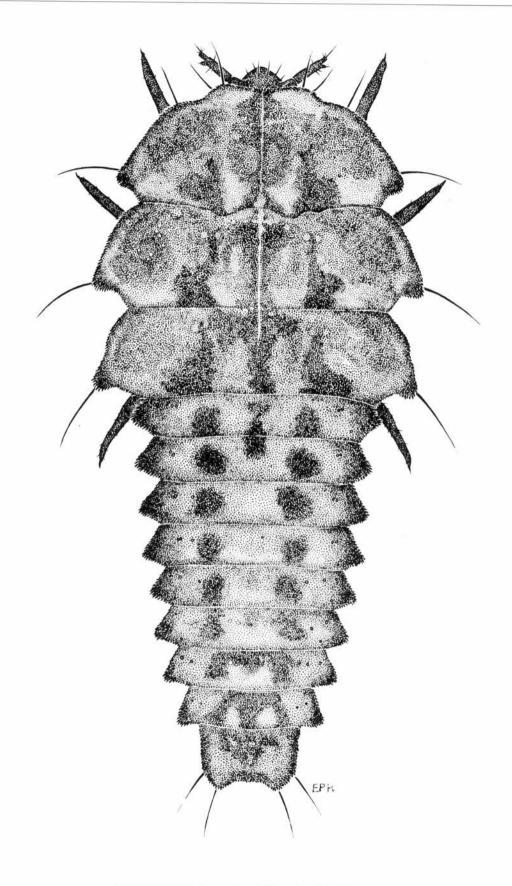
Head: small elongate pyriform (Figs 30, 31), prognathous to weakly declined, longer than wide, not abruptly constricted posterior to stemmata; head capsule emarginate at base dorsally and ventrally, usually protracted,

but retractable into cervical membrane up to stemmata; head partially concealed from above by overlapping prothorax when exerted (Fig. 29), completely hidden in dorsal view when retracted; cervix long, about length of head capsule. Frontoclypeal suture absent, frontoclypeal area depressed anterolaterally. Epicranial stem absent; frontal arms widely separated at base; endocarinae present, coincident with epicranial arms. Stemmata 2 per side, dark, hemispherical, located immediately posterior to antennal insertion (Fig. 36). Antennae well developed, 3-segmented; antennomere length ratios A1:AII:AIII=1:6:1; AIII swollen at apex (Fig. 34); sensorium abruptly narrowed near base, then gradually tapering to acute apex (Fig. 34), length = AIII; antennal fossa closed externally by head capsule, insertion distant from mandibular articulation. Labrum fused to head capsule (Fig. 33). Mandibles endognathous symmetrical broad flat tridentate, two teeth apical, one small tooth on incisor edge, middle tooth largest; prostheca large, rounded with 7 broad tooth-like projections; mola small flat along mesal surface. Ventral mouthparts retracted; maxilla with all basal components fused (Fig. 31), difficult to differentiate; mala (Fig. 32) elongate, flattened, tapering to apex, bearing small apical lobe on outer (lateral) part of apex and with setae and tooth-like unci on mesal portion of apex; palp 3-segmented, palpomere length ratio: PI:PII:PIII=5:4:7; PIII subcylindrical, lacking rows of asperites. Labium fused into single plate basally; palp 2segmented, palpomeres about equal in length, arising from swollen palpifers, bases close; ligula longer than palps, broad, with pair of small tubercles near apex, each tubercle bearing a single short capitate seta; gula short, slightly wider than long, sutures weakly diverging (Fig. 31).

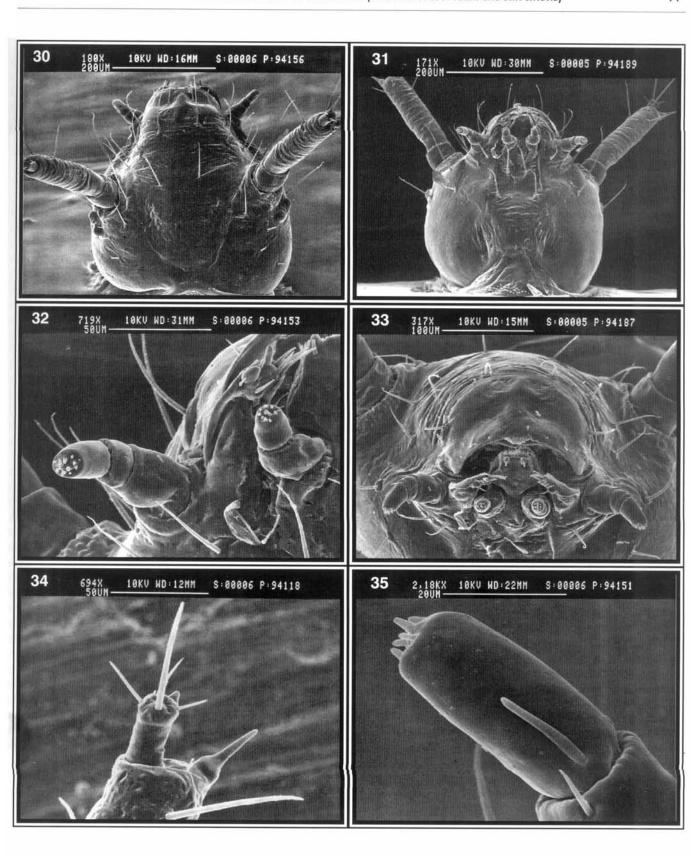
Thorax and Abdomen: Thoracic terga with posterolateral conical process (Fig. 29), prothorax with abruptly swollen broad medial region dorsal to head. Abdominal terga I-VIII about equal in length, with conical lateral process; urogomphi absent; tergum IX large, about twice length of preceding segment, emarginate at apex, with pair of long setae on posterolateral angles. Abdominal segment X tubular, posteroventrally directed, about as long as sterna of preceding segments. Ecdysial line pale distinct narrow on thoracic segments, imperceptible on anterior abdominal segments, vague and narrow on AVI–VIII. Legs pale yellowish, slender; coxa, femur, tibia with short sparse simple setae; trochanter with single long ventral seta; tarsungulus with single seta borne on thumb-like projection (Fig. 37), seta extending distally to about apex of claw.

Spiracles: Spiracles annular, not raised on tubes; thoracic spiracle located centrally on small dark spiracular disk (Fig. 38); abdominal spiracle small, located at posterior edge of small oval disk (Fig. 39), immediately ventral to base of lateral tergal process.

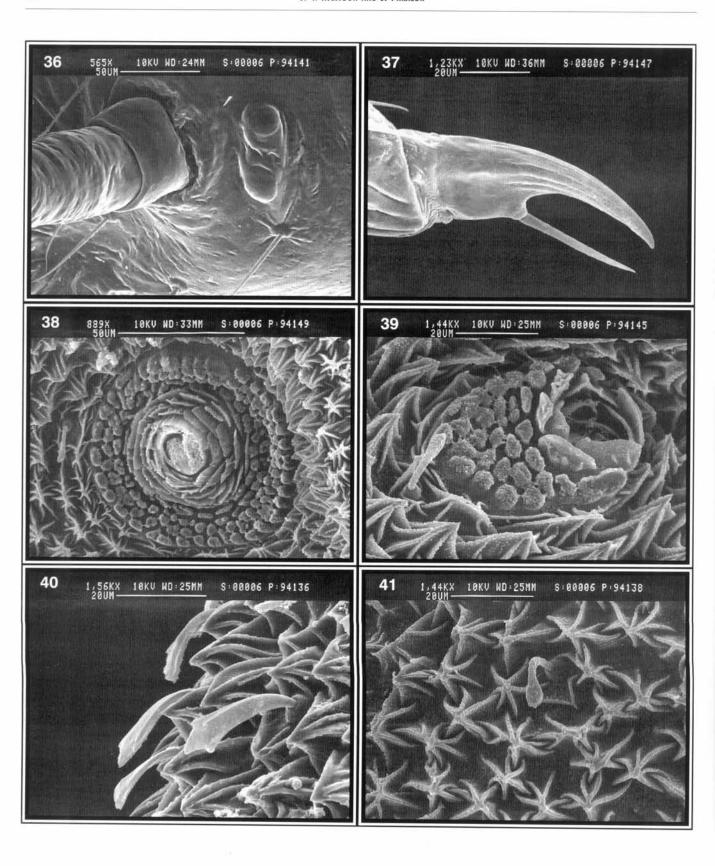
Material. Periptyctus eximus Blackburn. AUS-TRALIA: New South Wales, Dorrigo National Park, 30.22S, 152.44E, 13–15.XI.1990, ex rainforest litter, ANIC Berlesate 1128, T. A. Weir, (ANIC: 2 mature larva, 5 earlier instars).



 ${\bf Figure\ 29.}\ Periptyetus\ eximus, habitus, dorsal, head\ protracted.$



Figures 30–35. Periptyctus eximus: (30) head, dorsal; (31) head, ventral; (32) right maxilla, ventral; (33) head, anterior; (34) antennal apex, right, ventral; (35) apical maxillary palpomere, left, dorsal.



Figures 36–41. *Periptyctus eximus*: (36) stemmata and antennal base, left, lateral; (37) metathoracic tarsungulus, left, anterior; (38) thoracic spiracle, right, lateral; (39) abdominal spiracle III, left, lateral; (40) microsculpture of mesothoracic tergum, dorsal; (41) microsculpture and vestiture of mesothoracic lateral lobe, left, dorsal.

Comments. The material that we examined was from a single berlese sample, but the connection of this type of larvae with adults of *Periptyctus* has been repeated many times for more than one species (J.F. Lawrence, pers. comm.), so it is considered a reliable association and identification.

Stenotarsus Perty (Figs 42–52)

Description. Mature larvae 3 mm, body broadly ovate (Fig. 42), widest at abdominal segment II or III, dorsoventrally flattened. Head chestnut brown. Thoracic terga chestnut brown with a vague pale blotch at anterolateral angles and mesally; meso- and metaterga also with a pair of pale spots, at anterior and posterior margins near midpoint between lateral margin and medial pale region. Abdominal terga I-III and VII-VIII pale; tergum I with slightly darker region opposite the pale spot at posterior margin of metatergum; abdominal terga IV-VI chestnut brown laterally, pale medially; tergum IX chestnut brown. Surface texture finely granular, granules with deep longitudinal grooves and ridges (Figs 51, 52). Vestiture with stout simple setae and complex setae bearing multiple heads clustered in short dense round clusters (Fig. 52) or in an elongate tapering apex (Fig. 51); abdominal segments I-VIII with parascolus laterally (Fig. 42); thoracic segments and AIX with chalaza laterally.

Head: protracted, hypognathous, broadest near stemmata and narrowed greatly anteriorly. Epicranial stem absent, frontal arms U-shaped; endocarinae absent; hypostomal rods absent. Stemmata four per side, positioned on conical lateral extension of head located posterior to antennal base. Two stemmata closely positioned and directed anterodorsad over antennal base; third stemma directed anteroventrad under antennal base and fourth directed posterodorsad from near apex of lateral extension. Antennae well developed (Fig. 43), 3-segmented; about 1/3 head width; antennomere length ratio AI:AII:AIII=2:11:1; AII weakly curved; segment III reduced, mound-like (Fig. 44), about as long as wide; apical sensorium 3 times length of AIII, narrowed asymmetrically at about 1/3 length. Antennal fossa closed externally by cranium, insertion far from mandibular articulation. Frontoclypeal suture weak, deeply arcuate. Clypeus large, glabrous. Labrum free, anterior margin arcuate, with 8 stout curved setae. Mandibles symmetrical, broad, with 10 teeth gradually increasing in size up to tooth VII at apex then gradually decreasing in size down the incisor edge (Fig. 45); ventral accessory process absent; mola large, rounded mesally, with rows of asperites at edges fusing to form ridges and grooves in the middle; prostheca bearing cluster of stout tooth-like projections on distal half and dense setae on basal half (Fig. 46). Maxillolabial complex retracted; maxilla (Fig. 47) with elongate stipes and well developed articulating area, mala flattened; apex broad, with cleft separating a broad apically rounded lobe bearing numerous stout socketed setae at apex and a smaller mesal lobe bearing 2 tooth-like unci and a stout socketed seta; maxillary palpomeres I–II ringlike; palpomere III conical, tapering from broad base to narrow apex (Fig. 48); palpomere length ratio: PI:PII:PIII=3:3:7. Labium with mentum and submentum fused, ligula rounded at apex, with narrow raised median region bearing pair of setae at apex; labial palp 2-segmented, palpomere ratio PI:PII=1:3; apical palpomere conical.

Thorax and abdomen: Thoracic terga expanded laterally (Fig. 42). Abdominal terga with a process extending posterolaterally on each side. Abdominal tergum IX lacking urogomphi. Thoracic terga and abdominal terga I–VIII narrowly divided dorsally by discrete pale ecdysial line. Abdominal pleura I–VII with a weak lateral parascolus; pleuron VIII with lateral chalaza. Abdominal sterna I–VIII with a transverse row of 6–8 long, evenly-spaced setae. Legs well-developed, lightly pigmented, tarsungulus long slender, with one seta (Fig. 49).

Spiracles: Annular, not raised on tubes; abdominal spiracles opening at posterior edge of pale round spiracular disk (Fig. 50) located between the tergal and pleural parascoli, opening surrounded by ring of scale-like projections.

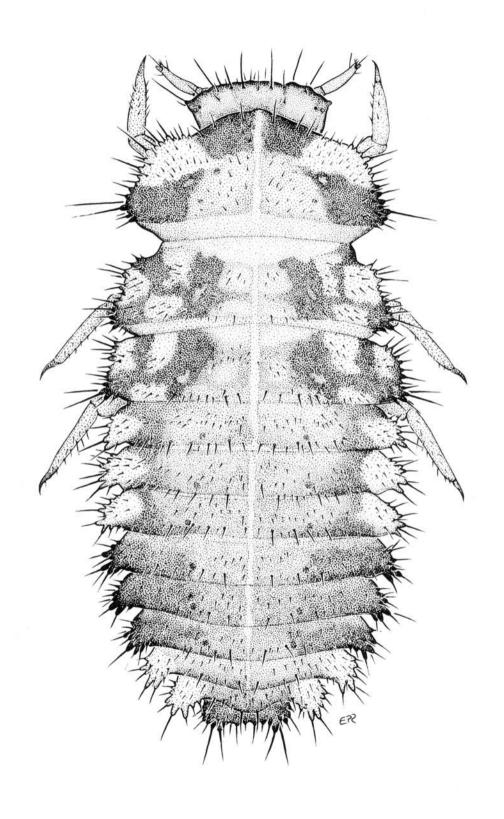
Material. Stenotarsus commodus Blackburn. AUS-TRALIA: Victoria, Acheron Gap, near Warburton, 750m, 28–30.IV.1978, berlesed from frass under logs of Nothofagus, S. and J. Peck, (ANIC: 1 associated adult, 4 mature larvae and 8 early instars). Stenotarsus pisoniae Lea. AUSTRALIA: North Queensland, 31.XII.1979, ex. Stereum sp., 79–52, J.F. Lawrence and D. Frith coll., (ANIC: 2 mature larvae). Stenotarsus sp. PERU: Departamento Loreto, Campamento San Jacinto, 12.VII.1993, 175–215m, R.A.B. Leschen, #90, ex. Poria (SEMC: 2 mature larvae, associated adults removed).

Comments. There may be some variability in color pattern. Among the few specimens that we studied, some of the penultimate larval instars showed a different color pattern than the type described above for mature larvae while others of apparently the same (penultimate) instar had the same coloration. The other pattern observed included a pale head, prothorax, and AII–VIII and a dark mesothorax, metathorax, AI and AIX.

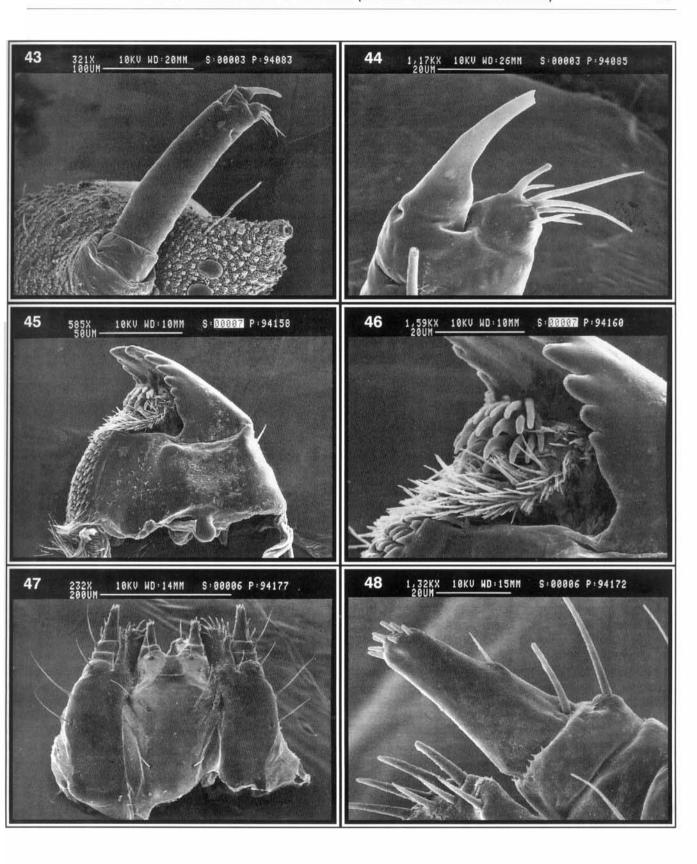
DISCUSSION

As currently defined, the subfamily Epipocinae exhibits great diversity in larval forms. Three distinct informal groupings of Epipocinae are apparent based on larval morphology. The first group is monogeneric, including only the enigmatic genus *Periptyctus* whose larval morphology and biology are peculiar for Epipocinae.

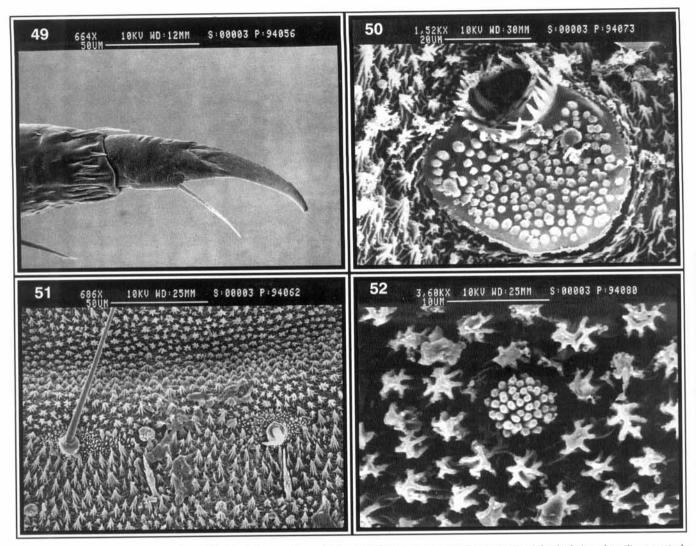
Periptyctus larvae are highly unusual morphologically, differing dramatically from all other known epipocines as illustrated by the characters provided in the above key. Some of these features are apparently unique for the entire family Endomychidae such as concealment of the head from above by prothorax; frontal arms V-shaped and distant at base; mandibles endognathous; fusion of the labrum to the head



 ${\bf Figure~42}. ~Stenotars us~commodus,~habitus,~dorsal.$



Figures 43–48. Stenotarsus commodus: (43) left antenna, anterior; (44) left antennal apex, anterior (apex of sensorium damaged); (45) left mandible, ventral; (46) left prostheca, ventral; (47) maxillolabial complex, ventral; (48) apex left maxillary palpus, ventral.



Figures 49–52. Stenotarsus commodus: (49) left metatarsungulus, anterior; (50) abdominal spiracle III, lateral; (51) abdominal sternal vestiture, ventral; (52) abdominal sternal vestiture, ventral.

capsule; fusion of the cardo and stipes; and fusion of the base of the maxillolabial complex to the head capsule. While these aspects of the morphology are unique for Endomychidae, all of these features occur in other families within the cerylonid series. Some larval Corylophidae and Cerylonidae also exhibit concealment of the head by the prothorax, fusion of various mouthparts and endognathy (Lawrence 1991). The unusual form of frontal arms on the cranium of *Periptyctus* also occurs in some corylophids (Lawrence 1991).

The biology of adult and larval *Periptyctus* is not well studied, yet what is known also seems atypical for the subfamily. Most specimens are found in leaf litter in montane forests of Australia. Although *Saula japonica* inhabits vegetation and is predaceous on scale insect and mites (Sasaji 1978), epipocines are typically found in close association with the macrofungi on which they feed.

While it is possible that *Periptyctus* is a highly derived member of Epipocinae, it seems more likely that the genus is misclassified. Studies of the adult morphology also sug-

gest that the placement of *Periptyctus* in Epipocinae is unsatisfactory (J.F. Lawrence, pers. comm.).

The two remaining groups of epipocine larvae also differ by numerous characters (see key). *Anidrytus*, *Ephebus* and *Epipocus* form one discrete set of taxa (Group II) while *Stenotarsus* and *Saula* form a less cohesive group (Group III). Numerous characters separate these two groups (see key), the most obvious of which pertain to the development of lateral lobes of the abdominal and thoracic terga and pleura. In taxa of Group II, lobe-like projections are present and bear patches of large, multiply-barbed, club-like setae. In Group III, lateral lobe-like projections and patches of specialized setae are absent.

It will not be clear which of these three informal groupings (if any) are monophyletic until a phylogenetic study is conducted on Epipocinae. The wealth of diversity in larval morphology should be quite helpful in this endeavor. The placement of the enigmatic genus *Periptyctus* is likely to require a higher-level analysis to classify satisfactorily.

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REFERENCES

Lawrence, J. F. 1991. Order Coleoptera. In: FW. Stehr (ed.), Immature Insects. Vol. II. Kendall Hunt: Dubuque, Iowa. 974 pp.

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- Lawrence, J. F., A. Hastings, M. Dallwitz and T. Paine. 1993. Beetle larvae of the world: Interactive identification and information retrieval for families and subfamilies. C.S.I.R.O. Information Services, East Melbourne, Victoria, Australia, CD-ROM disk and 52 page manual.
- Pakaluk, J. and S. A. Ślipiński. 1990. Review of Eupsilobiinae (Coleoptera: Endomychidae) with descriptions of new genera and species from South America. Revue suisse de Zoologie, 97: 705–728.
- Pakaluk, J. and S. A. Ślipiński. 1995. Acritosomatinae, a new subfamily of Endomychidae for *Acritosoma* new genus based upon two new species from Mexico and Peru (Coleoptera: Cucujoidea). Genus, 6(3–4): 327–335.
- Pakaluk, J., S. A. Ślipiński and J. F. Lawrence. 1994. Current classification and family-group names in Cucujoidea (Coleoptera). Genus, 5(4): 223–268.
- Sasaji, H. 1978. On the larva of a predaceous endomychid, Saula japonica Gorham (Coleoptera). Kontyû, 46(1): 24–28.
- Ślipiński, S. A. and J. Pakaluk. 1992. Problems in the classification of the cerylonid series of Cucujoidea (Coleoptera), pp. 79–88. *In*: M. Zunino, X. Belles and M. Blas (eds.). Advances in Coleopterology. European Association of Coleopterology, Barcelona.

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