

Phylogenetic position of Decliniidae (Coleoptera:  
Scirtoidea) and comments on the classification of  
Elateriformia (*sensu lato*)

by J. F. Lawrence, N. B. Nikitsky and A. G. Kirejtshuk

Division of Entomology, CSIRO, G.P.O. Box 1700, Canberra, ACT 2601, Australia

Zoological Museum, Moscow State University, Herzen Street 6, Moscow K-9, 103009 Russia

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg, 199034 Russia.

Reprinted from:

**Biology, Phylogeny, and Classification of Coleoptera**  
Papers Celebrating the 80th Birthday of Roy A. Crowson

Eds. J. Pakaluk and S.A. Ślipiński

1995, Muzeum i Instytut Zoologii PAN, Warszawa  
ISBN 83-85192-34-4

# Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (*sensu lato*)

J. F. LAWRENCE  
N. B. NIKITSKY  
A. G. KIREJTSHUK

**Abstract.** The genus *Declinia* (Decliniidae) is redescribed and figured, based on adult females only. Phylogenetic relationships of the family Decliniidae are discussed, based in part on the results of a cladistic analysis involving 34 genera representing 28 currently recognized families of Scirtoidea (=Eucinetoidae) plus Dascilloidea and Elateriformia of Crowson (1960) and four outgroups representing Staphylinoidae, Myxophaga and Archostemata. The family is placed in the superfamily Scirtoidea within a redefined series Elateriformia.

## Introduction

The description of *Declinia relictata* (Nikitsky *et al.* 1994), a new genus and species representing a new beetle family, Decliniidae, from the Russian Far East, is one of the more important recent events in the study of Coleoptera phylogeny. The fact that such a distinctive taxon can still be found in the Palearctic Region is unusual enough, but its apparent relict status and affinity to basal Polyphaga invite comparison with the archostematan *Crowsoniella relictata* Pace, another enigmatic Palearctic form discovered in relatively recent times (Pace 1976, Crowson 1976). Although *Declinia* has been described and illustrated, the paper cited above appeared in a new journal not widely accessible at present. This fact and the availability of new morphological data and additional illustrations justify a redescription at this time. Also, the placement of the new family is discussed in more detail, based on comparisons with a range of

J. Pakaluk and S.A. Ślipiński (eds.): *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson.*

© 1995, Muzeum i Instytut Zoologii PAN, Warszawa. ISBN 83-85192-34-4.

other beetle taxa and a cladistic analysis of 34 representative genera plus 4 possible outgroups using 122 characters.

**TERMINOLOGY AND MEASUREMENTS.**— Wing vein terminology follows that of Kukalová-Peck and Lawrence (1993). In describing the ommatidia, the phrase "not of exocone type" is used to indicate that a corneal lens is absent but a crystalline lens may be present (eucone) or absent (acone); these last two states are indistinguishable unless specimens have been fixed to preserve the crystalline lens. Measurements: BL = body length (total length, excluding head, or PL + EL); PL = median pronotal length; PW = greatest pronotal width; EL = greatest elytral length; EW = greatest elytral width.

**PHYLOGENETICS.**— Cladistic analyses were carried out using PAUP 3.1 (Swofford 1991). Extensive use was made of DELTA (Dallwitz *et al.* 1993) for the coding and handling of taxonomic data; the tonex option of confor was used to produce matrices suitable for PAUP, and intkey was used to interrogate the data and check for errors. A topologically constrained permutation tail probability (TPTP) test (Faith 1991) was carried out on minimum trees produced by PAUP in order to assess whether the data support the two major clades at a statistically significant level.

### ***Declinia* Nikitsky, Lawrence, Kirejtshuk and Gratshev, 1994**

*Declinia* Nikitsky *et al.* 1994: 4. Type species, by monotypy: *D. relictia* Nikitsky *et al.* 1994: 5, Figs. 1–13.

**REDESCRIPTION.**— Body slightly more than twice as long as wide, broader posteriorly; moderately convex dorsally, relatively flat ventrally; GD/EW = 0.60. Length = 3.5–5.5 mm.

Head (Figs. 1–2) hypognathous, about 0.6 times as long as wide, frons and vertex convex; head abruptly constricted behind eyes forming short tempora (about 0.2 times as long as longitudinal eye diameter), hind edges of tempora sharp and fitting closely to anterior edge of pronotum and thus concealing short neck, continuing mesally as transverse occipital carina, which tends to fade out at middle; frontoclypeal suture fine but distinct, slightly arcuate; frontal ridges sharp but not protruding, so that antennal insertions are exposed. Eyes well-developed, widely separated, entire, not protruding laterally, finely, weakly faceted, without interfacetal setae; ommatidia not of exocone type. Antennal grooves well-developed, narrow, deep, extending well below eyes, housing first 5 antennomeres. Gular sutures widely separated; gula strongly transverse, about 0.25 times as long as wide; submentum strongly transverse, separated from gula by suture; corporotentorium moderately broad; laminatentoria absent.

Antennae (Figs. 2, 9) short, extending posteriorly just beyond base of pronotum; scape about 1.2 times as long as broad, wider apically; pedicel about 0.7

times as long as and narrower than scape, about as long as broad; antennomeres 3–5 elongate and relatively narrow, 3 distinctly longer than 4, 4 slightly longer than 5; antennomeres 6–11 broader, forming slightly asymmetrical, 6-segmented club; antennomeres 6–10 as long as wide or slightly transverse and serrate, expanded portions with apical surface bearing group of several compound sensilla coeloconica (Snodgrass 1935), each consisting of a circular cavity bearing a central compound structure surrounded by a ring of simple microtrichia (Figs. 9–11); antennomere 11 slightly elongate, and broadly rounded at apex. Labrum about 0.6 times as long as wide, strongly rounded laterally and very weakly emarginate at apex; upper surface distinctly convex and setose; epipharynx with a quadrate anterior field of uniformly distributed, flattened sensilla, flanked on either side by field of mesally directed microtrichia.

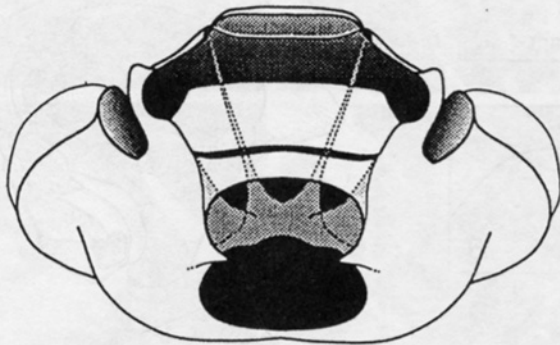
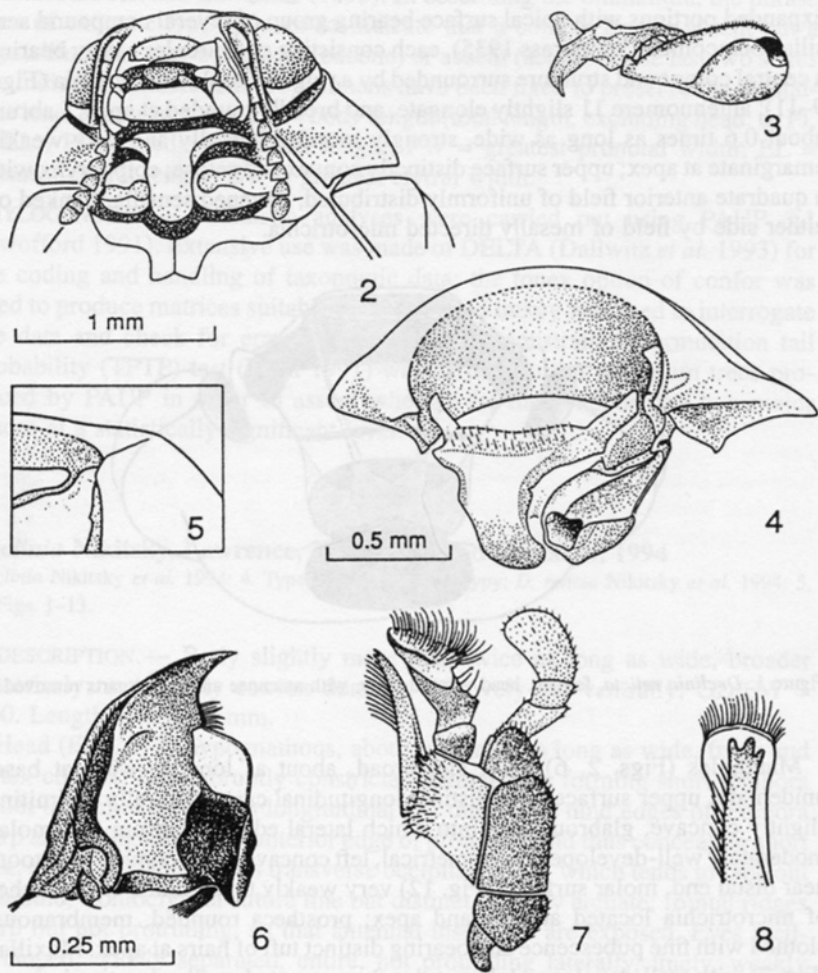


Figure 1. *Declinia relicta*, female, head, ventral view, with antennae and mouthparts removed.

Mandibles (Figs. 2, 6) short and broad, about as long as wide at base, unidentate; upper surface with distinct longitudinal carina laterally delimiting slightly concave, glabrous area into which lateral edge of labrum fits; molae moderately well-developed, asymmetrical, left concave, right convex with tooth near distal end, molar surfaces (Fig. 12) very weakly tuberculate, with patches of microtrichia located at base and apex; prostheca rounded, membranous, clothed with fine pubescence and bearing distinct tuft of hairs at apex. Maxillae (Fig. 7) with well-developed lobes; galea 2-segmented, well sclerotized except at apex, which is membranous and densely setose; apical segment asymmetrical with external process near base and with apex oblique; lacinia much narrower than galea, evenly sclerotized, with hairs along inner edge and 3 curved teeth at apex (Fig. 8). Maxillary palpomere 4 more or less cylindrical and apically truncate. Labium with ligula broad, cleft, with mesal sclerite between lobes.

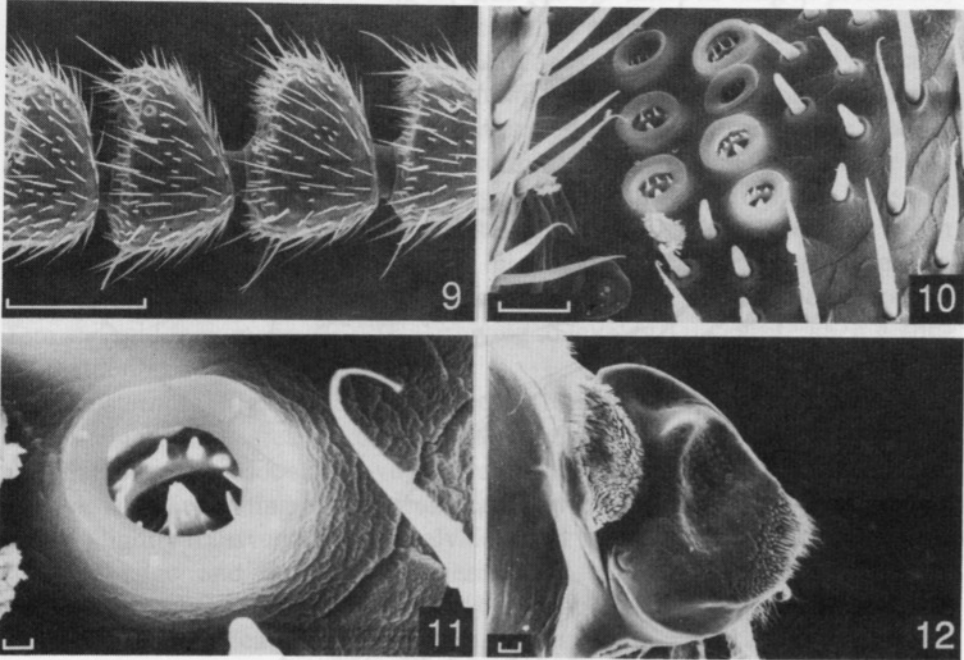


Apical palpomere almost squarely truncate. Mentum (Fig. 2) well developed, sclerotized, rounded anteriorly, concealing mouthparts from below.



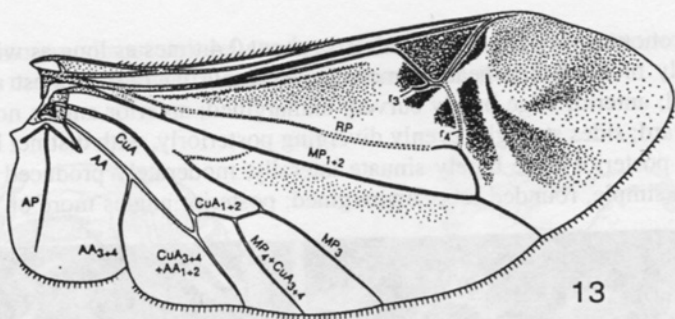
Figures 2-8. *Declinia relicta*, female. (2) Head and prothorax, anterolateroventral view, with forelegs removed, showing position of antennae at rest. (3) Procoxa and pleurotrochantin, ventral view. (4) Prothorax, anterolateroventral view, with right coxa and left leg removed. (5) Detail of junction of sternum, pleuron and notum at anterior edge of prothorax. (6) Left mandible, dorsal view. (7) Left maxilla, ventral view. (8) Detail of apices of lacinia and galea, mesal view, showing sclerotized hooks on lacinia. Scale lines: 2 = 1 mm, 3-4 = 0.5 mm, 6-8 = 0.25 mm.

Pronotum very strongly transverse, about 0.4 times as long as wide, considerably broader than head, somewhat explanate laterally, widest at posterior thiorl; anterior edge barely curved, unmarginated; anterior angles not produced forward; sides strongly, evenly diverging posteriorly, with distinct lateral carinae; posterior edge barely sinuate laterally, moderately produced mesally to form simple, rounded lobe, unmarginated; posterior angles more or less right.

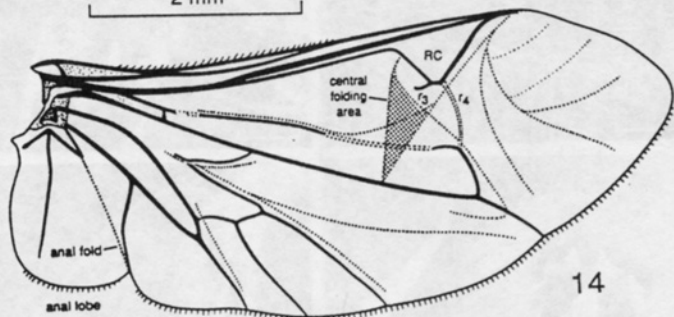


Figures 9–12. *Declinia relicta*, female. (9) Antennomeres 7–10, lateral view. (10) Apical portion of antennomere 8, showing group of sensilla coeloconica. (11) Single sensillum. (12) Left mandibular mola and portion of prosthema, mesoventral view. Scale lines: 9 = 0.1 mm; 10, 12 = 0.01 mm; 11 = 0.001 mm.

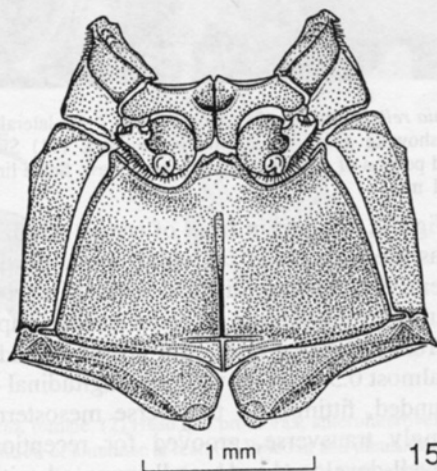
Prosternum (Figs. 2, 4) short in front of coxae, width at mid point of coxa about 0.4 times as great as mid coxal width; mesal portion slightly produced anteriorly and ventrally, forming distinct, vertical head rest, lateral portions abruptly narrowing beyond middle of coxal cavity, impressed, not reaching pronotal hypomeron; prosternal intercoxal process broad, about equal to mid coxal width and almost 0.5 times as wide as longitudinal diameter of procoxa, apex broadly rounded, fitting into transverse mesosternal cavity. Procoxae (Figs. 2–4) strongly transverse, grooved for reception of femoral base; pleurotrochantin well-developed and broadly exposed, with short pleural flange extending anteriorly in between sternum and notum to reach anterior edge of prothorax (Figs. 4–5). Hypomeron slightly impressed mesally and posteriorly, combining with impressions on sternum and coxa to form housing for antennal



13



14



15

Figures 13–15. *Declinia relicta*, female. 13–14. Hind wing: (13) showing pigmentation; (14) showing folds. (15) Pterothorax, ventral view, with legs removed. Scale lines: 13–14 = 2 mm, 15 = 1 mm.

club and foreleg; notal projections behind coxae absent, but posterior projections forming part of very weakly developed interlocking device with mesothorax. Procoxal cavities broadly open internally and externally.

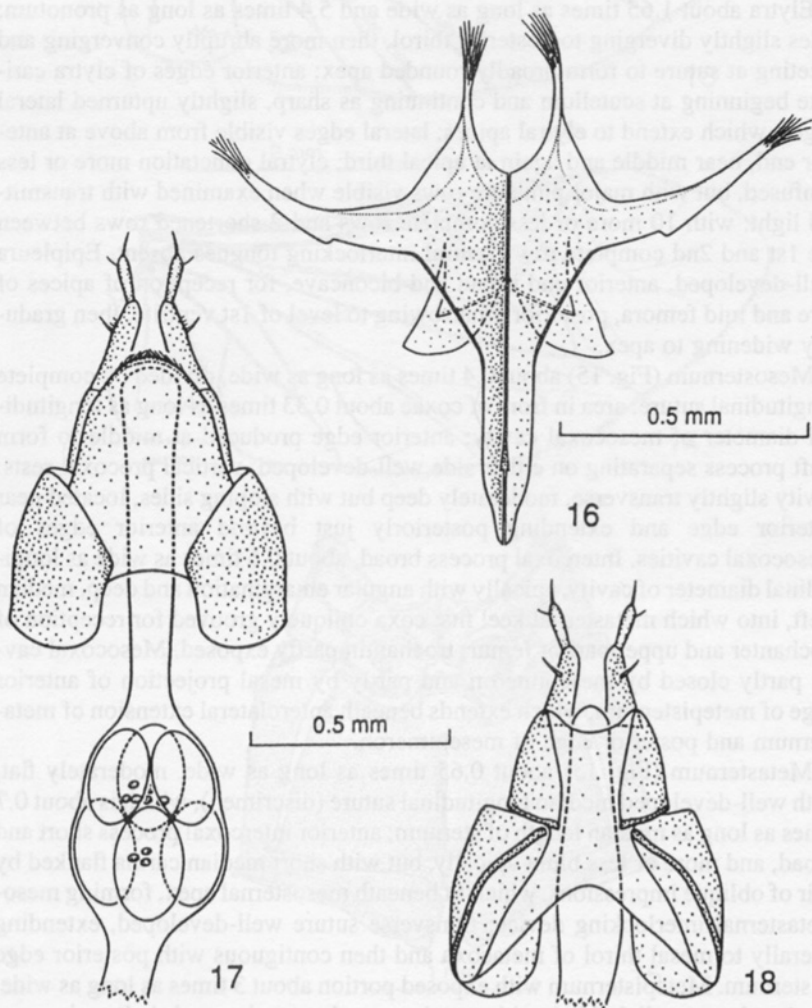
Scutellum somewhat cordate, with straight, simple anterior edge, strongly rounded sides and subacute apex. Scutum deeply, moderately broadly emarginate anteriorly.

Elytra about 1.65 times as long as wide and 5.4 times as long as pronotum; sides slightly diverging to posterior third, then more abruptly converging and meeting at suture to form broadly rounded apex; anterior edges of elytra carinate beginning at scutellum and continuing as sharp, slightly upturned lateral edges, which extend to elytral apices; lateral edges visible from above at anterior end, near middle and again at apical third; elytral punctation more or less confused, but with major puncture rows visible when examined with transmitted light; with 10 more or less complete rows and 2 shortened rows between the 1st and 2nd complete row; ventral interlocking tongues absent. Epipleura well-developed, anterior end broad and biconcave, for reception of apices of fore and mid femora, posteriorly narrowing to level of 1st ventrite, then gradually widening to apex.

Mesosternum (Fig. 15) about 0.4 times as long as wide, divided by complete longitudinal suture; area in front of coxae about 0.33 times as long as longitudinal diameter of mesocoxal cavity; anterior edge produced at middle to form cleft process separating on either side well-developed, vertical procoxal rests; cavity slightly transverse, moderately deep but with sloping sides, located near anterior edge and extending posteriorly just beyond anterior edges of mesocoxal cavities. Intercoxal process broad, about 0.6 times as wide as longitudinal diameter of cavity, apically with angular emargination and deep, median cleft, into which metasternal keel fits; coxa obliquely grooved for reception of trochanter and upper part of femur; trochantin partly exposed. Mesocoxal cavity partly closed by mesepimeron and partly by mesal projection of anterior edge of metepisternum, which extends beneath anterolateral extension of metasternum and posterior edge of mesepimeron.

Metasternum (Fig. 15) about 0.65 times as long as wide, moderately flat, with well-developed median longitudinal suture (discrimen), which is about 0.7 times as long as median length of sternum; anterior intercoxal process short and broad, and more or less blunt apically, but with short median carina flanked by pair of oblique impressions, which fit beneath mesosternal apex, forming mesometasternal interlocking device; transverse suture well-developed, extending laterally to mesal third of metacoxa and then contiguous with posterior edge of sternum. Metepisternum with exposed portion about 3 times as long as wide, more or less parallel-sided, with anterior mesal extension and shallow impression for housing part of mid femur. Metepimeron a slender, transverse sclerite partly concealed beneath edge of metepisternum. Metacoxae almost contiguous, separated by narrow intercoxal process of first ventrite; coxal plates well devel-

oped, broad mesally, somewhat abruptly tapering at mesal 3rd and more or less parallel-sided laterally. Metendosternite (Fig. 16) with moderately narrow stem, long, curved arms, well-developed ventrolateral processes, which are apically acute, and short, broad, deeply emarginate anterior process, with anterior tendons well separated.



Figures 16–18. *Declinia relicta*, female. (16) Metendosternite, posterodorsal view. (17) Pregenital segments, ovipositor and rectum, dorsal view. (18) Ovipositor and vagina, ventral view. Scale lines = 0.5 mm.



Hind wing (Figs. 13–14) well developed, about 2.2 times as long as wide, with membrane about 0.25 times as long as entire wing; posterior edge deeply incised, forming anal lobe; radial cell short and broad, forming a more or less equilateral triangle; cross-veins r3 and r4 originating close to one another, the former short, oblique at its base but abruptly curved apically towards base of wing, the latter very weakly sclerotized; pigment patches surrounding radial cell and r4; RP variable in the two wings examined and in that figured by Nikitsky *et al.* (1994), sometimes with a very short apical section only, but usually with moderately well-developed (although weakly pigmented) basal section including the basal attachment to RA and a short cross-vein connecting it with MP<sub>1+2</sub>. Base of MP and medial bridge weakly sclerotized; MP<sub>1+2</sub> flattened and somewhat ribbon-like with weakened area near apex (not shown in figure). Medial area (between MP<sub>1+2</sub> and anal fold) with 4 apical veins; CuA very long, forked at apex, CuA<sub>1+2</sub> fusing with MP4; AA<sub>3+4</sub> abruptly diverging towards base of wing and reaching anal fold; wedge cell absent. Wing folding very similar to that in Scirtoidea (Bostrychiformia B of Forbes 1926), with well-developed triangular area between the radial cell and MP<sub>1+2</sub> and apical folding differing from that of typical byrrhoids (Dryopiformia A of Forbes 1926).

Legs relatively short with large, obliquely attached trochanters; femora subequal in length to tibiae but considerably thicker, internal edge forming sharp carina; anterior surfaces of forelegs and posterior surfaces of mid and hind legs slightly concave, external edges of fore and mid femora angularly broadened just before middle; tibiae slender and straight, fitting into femoral concavities; external apical angles rounded, not produced, spurs small, about half as long as first tarsomere. Tarsi about 0.33 times as long as tibiae; tarsomeres 1–4 expanded and produced below to form setose pad, tarsomere 4 distinctly bilobed; apical tarsomere shorter than 1–4 combined; claws simple.

Abdomen a little longer than wide at base; ventrite 1 shorter than rest, with pair of large transverse basal impressions for reception of hind legs; ventrites 1–3 connate, 4 and 5 freely movable; all ventrites with outer edges slightly produced to form distinctly concave laterosternites; tergites moderately heavily sclerotized; spiracles on segment 8 reduced and non-functional. Tergite 8 about 0.75 times as long as wide, somewhat trapezoidal with slightly emarginate apex and deeply emarginate base; sternite 8 0.7 times as long as wide, broadly rounded at apex, biemarginate at base, with short lateral struts. Ovipositor (Figs. 17–18) about 1.5 times as long as wide, moderately sclerotized; proctiger broadly rounded and densely setose at apex, more lightly sclerotized mesally than laterally; paraprocts separated by membranous area almost equal to width of one of them; valvifers about as long as and distinctly broader than coxites, with sinuate baculi; coxites divided, basal section broad and subtriangular with transverse basal baculum, apical section much narrower, distinctly articulated and palpiform, slightly narrowed apically and with 2 lateral setae (one stout, the other fine) at about apical 3rd; styli well-developed, slightly more than half



as long as apical section of coxite. Genital tract (Fig. 19) with moderately large bursa lying well anterior to common oviduct and bearing curved sclerite at its base; accessory gland attached near base of bursa.

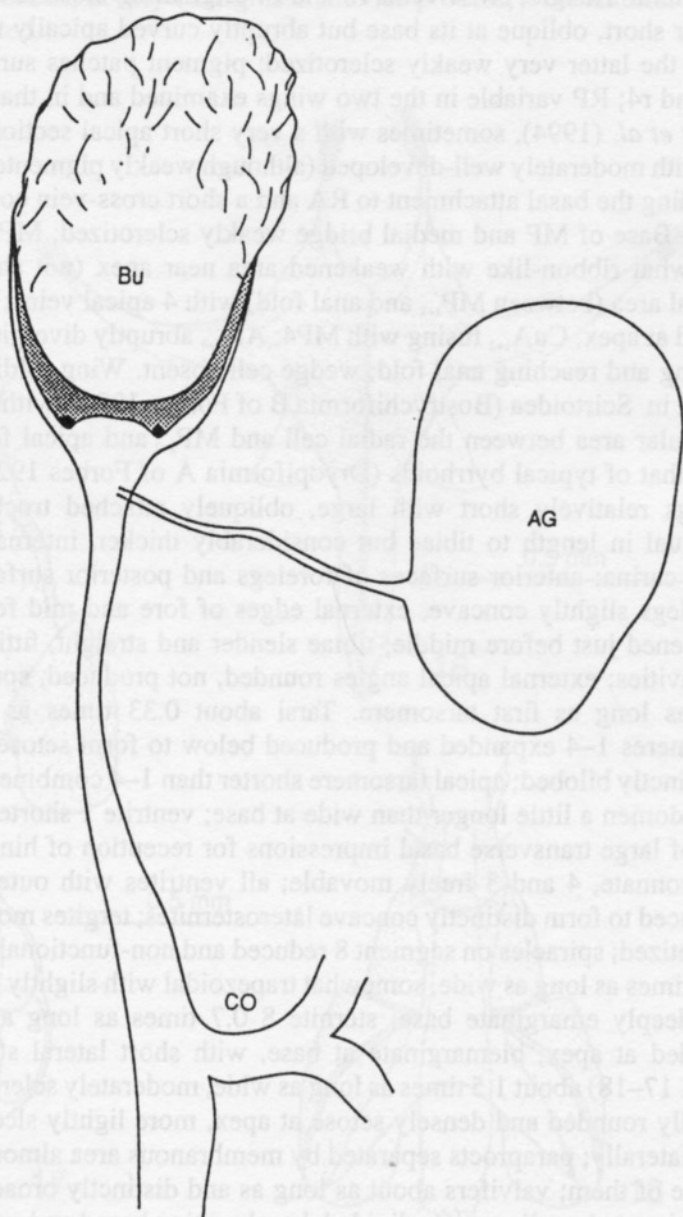


Figure 19. *Declinia relictica*, female, internal reproductive tract. AG = accessory gland, Bu = bursa copulatrix, CO = common oviduct.

**DISTRIBUTION.**—*Declinia relictata* has been collected from several localities in the Russian Far East, from the Khasan District of the Maritime Province, south of Vladivostok (ca. 43°N, 131°E) north to the floodplain of the Arman River, near Magadan (ca. 59°N, 151°E) and inland as far as the confluence of the Amgun, Suluk and Kuyuk Rivers in Khabarovsk Province (ca. 51°N, 134°E).

**BIOLOGY.**—Most specimens examined by Nikitsky *et al.* (1994) were collected in window screen traps (flight intercept traps) in forest communities. The beetles inhabit a variety of forest types, but appear to have a preference for humid habitats with still water and bogs. Dominant trees in the Magadan Region include *Larix*, *Betula*, and *Alnus*, although deforested landscapes are common. In the Ussuriysk District (110–120 km north of Vladivostok), where a number of specimens were collected, there is a mixed forest with a dominance of *Syringia*, *Juglans*, *Alnus*, with some *Fraxinus*, *Betula* and *Pinus* and *Quercus* on elevated terrains.

A female dissected by one of us (JFL) had only pollen grains in the gut, indicating that the species is presumably pollinophagous during at least part of the adult stage. The pollen grains were of at least two types, monocolpate and tricolpate. In this same specimen, there were approximately 60 eggs in the abdomen; these were from 0.30 to 0.45 mm long and 1.33 to 1.75 times as long as wide.

### Phylogenetic Relationships

Although the placement of *Declinia* within the Coleoptera was made more difficult by the absence of males and immature stages, sufficient characters were available to associate the genus with an apparently monophyletic assemblage and to eliminate it from all of the families currently comprising that lineage.

In comparing Decliniidae with other families of Coleoptera, the well-developed hind wings provide a particularly useful suite of characters, which was used extensively by Forbes (1926) and Crowson (1955) and recently analyzed by Kukalová-Peck and Lawrence (1993). Major features of the *Declinia* hind wing include: (1) a relatively short membrane; (2) a short, broad radial cell forming an equilateral triangle; (3) well-developed RP and basal cross-vein rmp; (4) moderately well-developed triangular central folding area, which reaches but does not cross; (5) a weakened area in MP<sub>1+2</sub>; (6) medial area (between MP<sub>1+2</sub> and anal fold) with 4 veins reaching posterior edge; (7) long CuA, which forks apically and fuses with MP<sub>4</sub>; (8) distinct incision in posterior edge, forming anal lobe; (9) absence of a wedge cell, and (10) confluence of AA<sub>3+4</sub> and the anal fold. In the Forbes system, the wing folding pattern would fall into category Bostrychiformia B. This type of wing immediately eliminates the

group from Archostemata, Adephaga or Myxophaga, which have a distinctive hinge on the medial bar ( $MP_{1,2}$ ) and a different type of radial cell (not framed posteriorly by  $RA_{3,4}$ ). Members of these three suborders also differ in the absence of cervical sclerites and the presence of an external propleuron (although a trace of the latter remains in *Declinia*). Within the fourth suborder, Polyphaga, *Declinia* is eliminated from both Staphyliniformia and Scarabaeiformia (the hydrophiloid lineage of Kukalová-Peck and Lawrence 1993) by the absence of the uniquely specialized haplogastran wing type (Forbes 1926). Additional features distinguishing Decliniidae from Staphyliniformia are the presence of a transverse metasternal suture and lack of a staphylinoid type of metendosternite; they are further distinguished from scarabaeiforms by the presence of a transverse metasternal suture and excavate metacoxae, and the absence of large, projecting procoxae. The primitive bostrichiform type of wing venation and folding also exclude the *Declinia* from the large, derived polyphagan series Cucujiformia; other features excluding them from cucujiforms are the excavate hind coxae, transverse metasternal suture (represented by a trace in some cucujoids) and lack of a hylecoetoid type of metendosternite (Crowson 1955). Other key features of Cucujiformia, such as the open rhabdome (Caveney 1986) and cryptonephridic Malpighian tubules (Poll 1932) were inaccessible in the specimens studied.

Among members of the Bostrichiformia (Crowson 1960), Decliniidae may be distinguished from Derodontidae by lacking the highly derived type of wing and metendosternite, as well as the 3-segmented antennal club and paired ocelli. The wing in *Declinia* is more similar to that in Nosodendridae, but the radial cell is not strongly oblique; the head is not prognathous, the labrum is well-developed, the antennal club is not large and 3-segmented, the ommatidia are not exocone, and the tibiae are not expanded and flattened. Most Dermestidae have wings similar to those of *Declinia*, although in *Dermestes* they are more elongate and dascillid-like; dermestids also differ from *Declinia* in the concealed or barely exposed protrochantin, cryptonephridial rod on the rectum, relatively long tarsi, and lack of a mandibular mola and transverse metasternal suture. Furthermore, *Dermestes* differs in having exocone ommatidia, while most other dermestids have a median ocellus. Wings of the Bostrichoidea (*sensu* Crowson 1961) also resemble those of *Declinia*, but members of that group differ in having exocone ommatidia, no mola (except in *Endecatomois*), globular to conical procoxae with concealed trochantins, a cryptonephridial rod on the rectum and no transverse metasternal suture.

The remaining Polyphaga constitute the Dascilliformia as originally defined by Crowson (1955). Unfortunately, the higher classification of the group has undergone a number of changes since that time, and the limits of the various superfamilies are still in dispute. An historical summary might help to clarify the concepts used in the discussions to follow. Crowson's Dascilliformia included the superfamilies Dascilloidea (with Eucinetidae, Clambidae, Helodidae

and Dascillidae), Byrrhoidea (Byrrhidae), Dryopoidea (Psephenidae, Euryponidae, Ptilodactylidae, Chelonariidae, Heteroceridae, Limnichidae, Dryopidae and Elmidae), Rhipiceroida (Rhipiceridae and Callirhipidae), Buprestoidea (Buprestidae), Elateroidea (Cebriionidae, Elateridae, Trixagidae, Cerophytidae, Perothopidae and Eucnemidae) and Cantharoidea (Brachypsectridae, Homalisidae, Karumiidae, Drilidae, Phengodidae, Telegeusidae, Lampyridae, Cantharidae and Lycidae). In 1960, Eucinetidae, Clambidae and Helodidae were placed by Crowson in Eucinetoida, Dascilloidea (with Dascillidae only) was placed with Scarabaeoidea in another series Scarabaeiformia, and the remaining taxa were assigned to a new series Elateriformia. In 1971, Crowson (1971a) moved both Rhipiceridae and Karumiidae to Dascilloidea and (1971b) placed Eucinetoida in a separate series Eucinetiformia; in 1972 he added the families Cneoglossidae, Plastoceridae and Omethidae to Cantharoidea; and in 1973 he proposed another superfamily, Artematopoidea, to include Artematopidae, Callirhipidae and Brachypsectridae. Another two dryopoid families, Eulichadidae and Lutrochidae, were recognized in Kasap and Crowson (1975), but Lutrochidae was later considered to be a subfamily of Dryopidae (Crowson 1978). This entire complex, including Eucinetoida and Scarabaeoidea, was given the term "elateriform lineage" by Lawrence and Newton (1982) and infraorder Elateromorpha by Ponomarenko and Zherikhin (1980). Lawrence (1988) redefined Elateriformia to exclude Eucinetoida and Scarabaeoidea and include Dascilloidea (*sensu* Crowson 1971a). The elateriform families were placed in four superfamilies: Dascilloidea (Dascillidae, including Karumiidae, and Rhipiceridae), Byrrhoidea (Buprestidae, Byrrhidae, Dryopidae, Lutrochidae, Elmidae, Heteroceridae and Limnichidae), Psephenoidea (Psephenidae, Callirhipidae, Eulichadidae, Cneoglossidae, Ptilodactylidae and Chelonariidae), and Elateroidea (Artematopidae, Brachypsectridae and Rhinorhipidae, a new family, plus the former Elateroidea and Cantharoidea). Lawrence and Britton (1991) resurrected Buprestoidea and combined Psephenoidea and Byrrhoidea into a single superfamily. Matters have been further complicated by the following nomenclatural changes: Scirtidae (= Helodidae), Scirtoidea (= Eucinetoida), Artematopodidae (= Artematopidae or Euryponidae), Omalysidae (= Homalisidae or Omalysidae), Throscidae (= Trixagidae) (*see* Pope 1976, Lawrence and Newton 1995). For the purposes of the following discussion, Elateriformia is used in the sense of Crowson (1960, 1973), Elateroidea in the sense of Crowson (1955), and Cantharoidea in the sense of Crowson (1955) but with the exclusion of Brachypsectridae, unless otherwise noted.

The most primitive wing type in this complex is that which most closely resembles those of the most basal bostrichiform taxa (except Derodontidae), in which there is a well-developed triangular folding area in the middle of the wing. It occurs in *Declinia*, Eucinetidae and Scirtidae, and with modifications associated with reduction in Clambidae or with elongation of the basal part of the wing in Artematopodidae, Dascilloidea and basal Buprestidae (Schizo-

podinae). Two other polyphagan wing types were described by Forbes (1926): the normal or diversicorn type and the dryopiform type. In the first the medial area has become elongated and the apical area or membrane of the wing is reduced, so that there is little reduction in wing length with folding, the radial cell is usually elongate and straight, and cross-vein r3 is often long and transversely oriented. These wings differ from the elongate dascilloid wing (or that of *Dermestes*) in that the two pivotal folds beyond the radial cell meet at a point on the anterior wing margin. In the second type, the membrane is relatively long and the wing length may be greatly reduced with folding, the radial cell is often oblique or reduced, and the pivotal folds meet at a point behind the anterior wing margin. The diversicorn wing type is characteristic of most Buprestidae (but not the primitive Schizopodinae), Callirhipidae and Eulichadidae, Rhinorhipidae, Brachypsectridae, Elateroidea and Cantharoidea; whereas the dryopoid type is found in most of the families placed in Dryopoidea by Crowson (1955), namely Byrrhidae, Dryopidae, Lutrochidae, Elmidae, Limnichidae, Heteroceridae, Psephenidae, Ptilodactylidae, and Chelonariidae. Both types also occur in Cucujiformia.

The following are some additional features in the adult female which distinguish all groups of Dascilloidea and Elateriformia from *Declinia*:

Dascilloidea: (1) head with long occipital region and no transverse occipital ridge or subgenal ridges, (2) ommatidia exocone, (3) mandible without mola, (4) lacinia without hooks, (5) ligula deeply bilobed, (6) procoxae narrowly separated, (7) pronotal projection relatively long and acute, (8) mesosternal cavity weak or absent, (9) metepisternum short and broad, (10) metacoxal plates weak at least laterally, (11) metendosternite with very short lateral arms, (12) tarsi with membranous appendages, (13) fewer than 3 ventrites connate, (14) spiracles on segment 8 functional.

Buprestidae: (1) head with long occipital region and no transverse occipital ridge or subgenal ridges, (2) mandible without mola, (3) lacinia without hooks, (4) metepisternum short and broad, (5) metacoxal plates weak at least laterally, (6) metendosternite with very short lateral arms, (7) tarsi with membranous appendages, (8) fewer than 3 ventrites connate, (9) spiracles on segment 8 functional.

Byrrhidae: (1) head with long occipital region and no transverse occipital ridge or subgenal ridges, (2) ommatidia exocone, (3) elytral epipleura abruptly narrowed, (4) tibiae all strongly expanded, (5) fewer than 3 ventrites connate, (6) spiracles on segment 8 functional.

Dryopidae-Lutrochidae: (1) head with long occipital region and no transverse occipital ridge or subgenal ridges, (2) eyes with interfacetal setae, (3) frontoclypeal suture weak or absent, (4) tarsi long, slender, simple, (5) spiracles on segment 8 functional.

Elmidae: (1) head without transverse occipital ridge or subgenal ridges, (2) ommatidia exocone, (3) subantennal grooves absent, (4) lacinia without hooks,



(5) tarsi long, slender and simple, (6) spiracles on segment 8 functional, (7) long, narrow spiculum ventrale present.

Limnichidae: (1) head without subgenal ridges, (2) ommatidia exocone, (3) lacinia without hooks, (4) subantennal grooves absent, (5) tarsi long, slender and simple, (6) spiracles on segment 8 functional, (7) ovipositor laterally compressed.

Heteroceridae: (1) head prognathous, (2) head with long occipital region and without transverse occipital ridge or subgenal ridges, (3) ommatidia exocone, (4) subantennal grooves absent, (5) lacinia without hooks, (6) prosternum very long in front of coxae, with chin piece, (7) procoxae narrowly separated, (8) epipleura abruptly narrowed, (9) mesosternal cavity weak or absent, (10) metacoxal plates weak or absent, (11) tarsi long, slender, simple, (12) spiracles on segment 8 functional, (13) ovipositor highly reduced.

Psephenidae: (1) subgenal ridges absent, (2) ommatidia exocone, (3) frontoclypeal suture absent, (4) mandible without mola, (5) lacinia without hooks, (6) mesosternal cavity weak or absent, (7) metaxocal plates weak or absent, (8) tarsi not lobed.

Cneoglossidae: (1) subgenal ridges absent, (2) frontoclypeal suture absent, (3) mandible without mola, (4) lacinia without hooks, (5) procoxae conical and projecting, (6) mesosternal cavity weak or absent, (7) mesocoxae narrowly separated, (8) transverse metasternal suture absent, (9) metacoxal plates weak or absent, (10) metendosternite with very short arms and no ventrolateral processes, (11) tarsi not lobed.

Ptilodactylidae: (1) subgenal ridges absent, (2) ommatidia exocone, (3) lacinia without hooks, (4) ligula deeply emarginate, (5) procoxae narrowly separated, (6) mesocoxae narrowly separated, (7) transverse metasternal suture absent.

Chelonariidae: (1) head opisthognathous, (2) subgenal ridges absent, (3) ommatidia exocone, (4) frontoclypeal suture absent, (5) subantennal grooves absent, (6) mandible without mola, (7) lacinia without hooks, (8) ligula deeply emarginate, (9) prosternum highly reduced, (10) procoxae narrowly separated, (11) transverse metasternal suture absent, (12) tarsi with membranous appendages on tarsomere 3, tarsomere 4 reduced.

Callirhipidae: (1) subgenal ridges absent, (2) ommatidia exocone, (3) frontoclypeal suture absent, (4) subantennal grooves absent, (5) mandible without mola, (6) lacinia without hooks, (7) maxillary lobes reduced, (8) ligula deeply emarginate, (9) procoxae narrowly separated, (10) mesosternal cavity weak or absent, (11) mesocoxae narrowly separated, (12) transverse metasternal suture absent, (13) metendosternite with short lateral arms and no ventrolateral processes, (14) tarsi without lobes, (15) spiracles on segment 8 functional.

Eulichadidae: (1) transverse occipital ridge and subgenal ridges absent, (2) ommatidia exocone, (3) frontoclypeal suture absent, (4) subantennal grooves absent, (5) lacinia without hooks, (6) procoxae narrowly separated, (7) pronotal



projections long and acute, (8) mesocoxae narrowly separated, (9) transverse metasternal suture absent, (10) metendosternite with very short lateral arms and no ventrolateral processes, (11) tarsi without lobes, (12) spiracles on segment 8 functional.

Rhinorhipidae: (1) head opisthognathous, (2) occipital area long, (3) transverse occipital ridge and subgenal ridges absent, (4) ommatidia exocone, (5) frontoclypeal suture absent, (6) subantennal grooves absent, (7) labrum concealed, (8) mandible without mola, (9) lacinia without hooks, (10) ligula deeply emarginate, (12) procoxae conical and projecting, narrowly separated, (13) mesosternal cavity weak or absent, (14) mesocoxae narrowly separated, (15) transverse metasternal suture absent, (16) metepisternum short and broad, (17) metacoxal plates weak, (18) tarsi without lobes, (19) spiracles on segment 8 functional.

Artematopodidae: (1) transverse occipital ridge and subgenal ridges absent, (2) ommatidia exocone, (3) frontoclypeal suture absent, (4) mandible without mola, (5) lacinia without hooks, (6) mesosternal cavity weak, (7) elytral apex with interlocking tongue, (8) transverse metasternal suture absent, (9) metendosternite with short lateral arms and no ventrolateral processes, (10) tarsi with membranous appendages, (11) 5 ventrites connate, (12) spiracles on segment 8 functional.

Brachypsectridae: (1) transverse occipital ridge and subgenal ridges absent, (2) ommatidia exocone, (3) frontoclypeal suture absent, (4) subantennal grooves absent, (5) mandible reduced, without mola, (6) maxillary lobes reduced, lacinia without hooks, (7) hind angles of pronotum produced and acute, (8) prosternum very long in front of coxae, with chin piece, (9) pronotal projections long and acute, (10) mesosternal cavity large and deep, (11) mesocoxae narrowly separated, (12) transverse metasternal suture absent, (13) metendosternite with short lateral arms and no ventrolateral processes, (14) tarsi without lobes, (15) fewer than 3 ventrites connate, (16) spiracles on segment 8 functional.

Elateroidea: (1) ommatidia exocone, except in Eucnemidae, (2) subgenal ridges absent, (3) frontoclypeal suture absent, (4) mandible without mola, (5) lacinia without hooks, (6) hind angles of pronotum produced and acute, (7) promesothoracic clicking mechanism present, (8) procoxae externally globular with concealed trochantins, (9) mesosternal cavity usually very large and deep, (10) transverse metasternal suture absent, (11) metendosternite with short lateral arms and no ventrolateral processes, (12) 4 to 5 ventrites connate, (13) spiracles on segment 8 functional.

Cantharoidea: (1) ommatidia exocone, (2) subgenal ridges absent, (3) mandible slender and falciform, without mola, (4) lacinia without hooks, (5) subantennal grooves absent, (6) corporotentorium absent, (7) procoxae conical and projecting, (8) mesosternal cavity weak or absent, (9) metasternal transverse suture absent, (10) metendosternite with short lateral arms and no ventro-

lateral processes, (11) fewer than 3 ventrites connate, (12) sternite 2 visible, (13) spiracles on segment 8 functional.

Having eliminated everything but the Scirtoidea (=Eucinetoidae), it remains to compare *Declinia* with the families Eucinetidae, Clambidae and Scirtidae. Superficially, *D. relictata* resembles members of the last group, because of the broad, somewhat flattened body with a large head and short prothorax. In contrast, members of the first two families have a very different appearance from *Declinia*, eucinetids because of the small, anteriorly narrowed head, ovate, streamlined body narrowed posteriorly, greatly enlarged metacoxal plates and spinose mid and hind legs, and clambids because of the minute, strongly compacted, globose body and distinct 2-segmented antennal club. A more detailed examination of the head and prothorax of *Declinia* reveals a number of features lacking in all scirtoids.

Members of all three families have a very strongly declined, somewhat opisthognathous head which rests against the large, projecting, subcontiguous procoxae and may reach the mesosternum or metasternum (in some Clambidae); the prosternum is highly reduced and concealed by the head and procoxae. In Scirtidae and Clambidae, the vertex is more or less inserted beneath the anterior edge of the pronotum. In Eucinetidae the head is strongly constricted posteriorly, forming very short tempora and a short neck; however the neck is concealed because the transverse occipital ridge abuts on the anterior edge of the pronotum. In *Declinia*, the head is somewhat declined but not opisthognathous, and it rests on the well-developed prosternum and not on the coxae, which are transverse and widely separated by the prosternal process (Figs. 2, 4). Posteriorly, the head is similar to that in eucinetids, with short tempora, a concealed neck region and a transverse occipital ridge abutting on the pronotum. Another apparent synapomorphy of *Declinia* and Eucinetidae is the enlarged rectal sac bearing 6 cuticular rings (Fig. 17).

As mentioned above, the hind wing in *Declinia* is of a primitive polyphagan type called Bostrichiform B by Forbes, but it is most similar to the wings of various scirtoids. The presence of the relatively large, equilaterally triangular radial cell, the points at which the cross-veins r3 and r4 meet the cell, the presence of an anal lobe, the weakness in MP<sub>1+2</sub>, the presence of a large central triangular area, and the apical folding are all characteristic of Scirtoidea (with reductions in some Clambidae). The *Declinia* wing has plesiomorphic features, including the well-developed basal portion of RP, the rp–mp cross-vein, the distinct cross-vein between MP<sub>1+2</sub> and MP<sub>3</sub>, the very long base of CuA (and thus the long first cubital cell), the fusion of CuA<sub>1+2</sub> and MP<sub>4</sub>, and the extension of MP<sub>4</sub> to the wing margin. Other features, such as the loss of AP<sub>4</sub> and the nature of the pigmentation surrounding the radial cell, r3 and r4 also occur in Eucinetidae.

Two plesiomorphic features of *Declinia* are only rarely encountered in Polyphaga. These are the presence of a well-developed anterior propleural flange

and the partial closure of the mesocoxal cavities by the metepisternum. The anterior pleural flange actually separates the notum from the sternum at the anterior edge of the prothorax, a condition which is unique in Polyphaga but characteristic of most Archostemata, Myxophaga and Adepaga (Hlavac 1975). The meeting of the metepisternum and mesocoxal cavity is very narrow and partly concealed by portions of the mesepimeron and metasternum (in Fig. 15 the sclerites are partly disarticulated). Some other plesiomorphies of *Declinia* include (1) non-exocone ommatidia, (2) well-developed labrum, (3) relatively large mandibles with distinct molae, (4) well-developed maxillary lobes with curved teeth on the lacinia, (5) prothorax with complete lateral carinae and poorly developed interlocking device, (6) transverse procoxae, (7) distinct transverse metasternal suture, and (8) well-developed metacoxal plates.

Most Scirtidae differ from *Declinia* in having the third abdominal ventrite free from the second, but there is one exception: the New Zealand genus *Amplectopus*. The genus was placed in Chelonariidae by Kasap and Crowson (1975), but the type of hind wing, metendosternite and male genitalia are definitely of the scirtid type, and the last of these is certainly unique in Coleoptera (see Nyholm 1972). *Amplectopus* also resembles *Declinia* in having a distinct 5-segmented antennal club and defensive compaction mechanisms involving leg modifications and cavities for receiving legs and antennae. However, the club segments in *Amplectopus* lack the sensilla coeloconica mentioned above and have unique basal modifications, while the compaction mechanisms are of a different type. Both taxa have well-developed antennal grooves, a distinct vertical cavity at the anterior edge of the mesosternum, and leg impressions on the hypomera, mesepisterna, mesepimera, epipleura, metasternum and first ventrite. In *Amplectopus*, the anterior mesosternal impression receives the head, the fore tarsi fit into the expanded tibia, the mid tarsi into a cavity on the metasternum, and the hind tarsi into weak impressions on ventrite 1; in *Declinia*, the mesosternal impression receives the procoxae, the femora, rather than the tibiae, are expanded, and the shortened tarsi all fit into grooves on the trochanters.

### Cladistic analysis

Lawrence (1988) analyzed 25 family-group taxa of Elateriformia plus the superfamily Scirtoidea (as Eucinetoidea) using 112 characters. The taxa used by Lawrence were generally recognized families, except for Eucinetoidea and Cantharoidea, which represented combinations of three and eight families, respectively. Since a number of the taxa were variable for some characters, *ad hoc* decisions were made concerning the plesiomorphic state for each family. Decisions were also made concerning character polarities when a hypothetical ancestor was used in some runs. In present analysis, most of Lawrence's original characters have been retained, a few have been eliminated because of lack

of precision or extreme variability within family group taxa, others have been reformulated, and some new characters have been added. Terminal taxa used are genera representing family groups. An effort was made to include taxa for which both adults and larvae are known and, if possible, exclude those which appear to be members of highly derived or obviously specialized groups within their particular lineages. Two taxa known only as adults (*Amplectopus* and *Paralimnichus*) were added to the matrix primarily because their systematic placement has been in question. Finally, four alternate outgroups were chosen from outside the Scirtoidea plus Elateriformia. By using representative genera and a series of outgroups no *a priori* decisions were made concerning character polarity and plesiomorphic states for family groups.

#### TAXA

Taxa used in the analyses include the following 38 genera, representing 34 family groups (31 currently recognized families plus Decliniidae) with the first four genera used as alternate outgroups: *Ytu* (Torrindicolidae), *Omma* (Ommatidae), *Distocupes* (Cupididae), *Necrophilus* (Agyrtidae), *Eucinetus* (Eucinetidae), *Acalyptomerus* (Clambidae), *Amplectopus* (Scirtidae?), *Veronatus* and *Pseudomicrocara* (Scirtidae), *Declinia* (Decliniidae), *Dascillus* (Dascillidae), *Sandalus* (Rhipiceridae), *Dystaxia* (Buprestidae: Schizopodinae), *Byrrhus* (Byrrhidae), *Lutrochus* (Lutrochidae), *Pelonomus* (Dryopidae), *Lara* (Elmidae: Larainae), *Byrrhinus* (Limnichidae: Limnichinae), *Paralimnichus* (Limnichidae?), *Lanternarius* (Heteroceridae), *Eubrianax* (Psephenidae: Eubrianacinae), *Sclerocyphon* (Psephenidae: Eubriinae), *Cneoglossa* (Cneoglossidae), *Araeopidius* (Ptilodactylidae: Araeopidiinae), *Byrrcryptus* (Ptilodactylidae: Anchyrtarsinae), *Chelonarium* (Chelonariidae), *Callirhipis* (Callirhipidae), *Eulichas* (Eulichadidae), *Rhinorhipus* (Rhinorhipidae), *Eurypogon* (Artematopodidae: Macropogoninae), *Electribius* (Artematopodidae: Electribiinae), *Cerophytum* (Cerophytidae), *Perothops* (Eucnemidae: Perothopinae), *Aulonothroscus* (Throscidae: Throscinae), *Ampedus* (Elateridae: Elaterinae), *Brachypsectra* (Brachypsectridae), *Metriorrhynchus* (Lycidae) and *Pyraconema* (Lampyridae: Lampyrinae). The families represented in the data set are those used by Lawrence (1988) with the following exceptions: (1) four alternate outgroups have been chosen from Myxophaga (*Ytu*), Archostemata (*Omma* and *Distocupes*) and Staphylinoidea (*Necrophilus*); (2) Scirtoidea are represented by one genus each of Eucinetidae and Clambidae and three genera of Scirtidae; (3) *Declinia* is added; (4) most elateriform families are represented by a single genus, but Limnichidae, Psephenidae, Ptilodactylidae and Artematopidae are each represented by two; (5) Plastoceridae and Cebriionidae are excluded; and (6) Cantharoidea is represented by one genus from Lycidae and one from Lampyridae. *Araeopidius* is considered by Lawrence (1991) to form a distinct subfamily of Ptilodactylidae based mainly on larval features. *Paralimnichus* and *Amplecto-*

*pus* have been placed in Chelonariidae (Kasap and Crowson 1975) (*see* below). Schizopodinae has been elevated to family rank by Nelson and Bellamy (1991). The genus *Electricibus* is discussed by Lawrence (1995).

The choice of an outgroup for these analyses was a difficult one, since there is no general agreement on the relationships of the beetle suborders or the major lineages of Polyphaga. Because *Declinia* exhibits a number of very primitive polyphagan features and others indicating a possible relationship to Scirtoidea, which is thought to be a basal polyphagan group, there are few outgroup choices within the suborder which could not be construed as being derived from a *Declinia*-like ancestor. A non-Polyphagan outgroup has the disadvantage of possessing a suite of independently derived features which will greatly increase the incidence of homoplasy. Among the three non-polyphagan suborders, Adephaga appears to have the greatest number of autapomorphies and was eliminated as a possible outgroup. The Archostemata is usually considered to contain the oldest and most primitive beetle taxa; however, the group is often defined very broadly to include a wide range of Mesozoic taxa (Ponomarenko 1969, 1971) which may well include the ancestors of present day Myxophaga (Lawrence and Newton 1982). Also, extant archostematans have a number of autapomorphies which were probably absent in ancestral beetles. Myxophaga seem to be the most suitable candidates, since they share with Adephaga the most primitive wing type (similar in many respects to that in Scirtoidea) but lack the autapomorphies of either Adephaga or Archostemata (Kukalová-Peck and Lawrence 1993). A member of the myxophagan family Torridincolidae was chosen as the preferred outgroup, but two archostematans in the families Ommatidae and Cupedidae were chosen as alternatives. Within the Polyphaga, the Staphyliniformia is generally considered to be one of the major lineages, which is at least as old as the Scirtoidea and probably not derivable from them; the final alternate outgroup was chosen from the staphyliniform family Agyrtidae.

#### CHARACTERS

The present set includes 122 characters: 96 based on cuticular features of the adult (8 in males only, 8 in females only), 3 taken from internal soft anatomy and not available for some taxa, and 23 based on larvae and unavailable for six taxa, including *Declinia*. Characters 22, 36, 37 and 70 were excluded from some analyses, when they became autapomorphic due to the exclusion of certain taxa. Unless otherwise indicated, the following multistate characters were treated as ordered in the analyses: 9–10, 12, 18, 20, 25, 42–45, 52, 58, 72, 78, 88, 93, 101, 103, 106, 119. When the phrase “ordered characters” is used in the discussions below, it refers these 20 characters only.









1. ADULT: head: 1. prognathous to hypognathous, angle of inclination 90 degrees or less; 2. opisthognathous, angle of inclination more than 90 degrees.
2. ADULT: occipital area (distance between posterior edge of eye and posterior edge of head): 1. distinctly longer than greatest eye diameter; 2. shorter than or about equal to greatest eye diameter.
3. ADULT: transverse occipital ridge or carina: 1. absent; 2. present.
4. ADULT: subgenal ridges: 1. absent; 2. present.
5. ADULT: median occipital line or endocarina: 1. present; 2. absent.
6. ADULT: eyes: 1. without interfacetal setae; 2. with interfacetal setae.
7. ADULT: ommatidial lens type: 1. eucone or acone; 2. exocone.
8. ADULT: frontoclypeal suture: 1. absent or weakly developed; 2. well developed.
9. ADULT: antennal sensory elements beginning on: 1. 3rd antennomere; 2. 4th antennomere; 3. 5th or more apical antennomere. Ordered.
10. ADULT: subantennal groove: 1. absent or very weakly developed; 2. well developed but short; 3. well developed and extending below or behind eye. Ordered.
11. ADULT: labrum: 1. almost entirely exposed; 2. completely or almost completely concealed beneath clypeal region, or absent.
12. ADULT: mandibles: 1. short and broad, less than 1.5 times as long as wide at base; 2. moderately elongate, between 1.5 and 3 times as long as wide at base; 3. very narrow and elongate, more than 3 times as long as wide at base. Ordered.
13. ADULT: mandibles: 1. well developed; 2. very small.
14. ADULT: apex of mandible: 1. with more than 1 tooth or lobe; 2. unidentate.
15. ADULT: mandibular mola: 1. present; 2. absent.
16. ADULT: maxillary lobes: 1. well developed; 2. poorly developed.
17. ADULT: lacinia: 1. with 1 or more hook-like spines or teeth at apex; 2. without hook-like spines or teeth at apex.
18. ADULT: apical maxillary palpomere: 1. cylindrical or subulate; 2. slightly expanded and truncate at apex; 3. securiform or subtriangular. Ordered.
19. ADULT: apex of ligula: 1. truncate or rounded, usually finely cleft at midline, sometimes reduced; 2. deeply emarginate, forming 2 diverging lobes.
20. ADULT: corporotentorium: 1. moderately to very broad; 2. narrow; 3. absent. Ordered.
21. ADULT: laminatentoria: 1. absent or weakly developed and well separated; 2. well developed and approximate or sometimes fused at midline.
22. ADULT: cervical sclerites: 1. present; 2. absent.
23. ADULT: lateral pronotal carinae (sharp lateral edges of prothorax): 1. complete; 2. incomplete or absent.
24. ADULT: posterior angles of pronotum: 1. not produced posteriorly and acute; 2. produced posteriorly and acute.

25. ADULT: ratio of length of prosternum in front of coxa to coxal width at midpoint: 1. less than 0.33; 2. greater than 0.33 but less than 0.60; 3. greater than 0.60 but less than 1.10; 4. greater than 1.10 but less than 1.75; 5. greater than 1.75. Ordered.
26. ADULT: anterior edge of prosternum: 1. not produced well in front of hypomera; 2. produced well in front of hypomera, forming chin piece.
27. ADULT: prosternal head rest (impunctate and shiny area, usually internal): 1. absent or very narrow; 2. moderately to very broad.
28. ADULT: prosternal head rest: 1. horizontal to slightly oblique; 2. moderately to strongly oblique or vertical.
29. ADULT: anterior edge of prosternum: 1. without mesal excavation; 2. with mesal excavation.
30. ADULT: mesal portion of posterior edge of pronotum: 1. not or slightly produced and rounded, truncate or barely sinuate; 2. distinctly produced and emarginate; 3. produced and variously notched.
31. ADULT: posterior edge of pronotum: 1. without crenulations; 2. with crenulations.
32. ADULT: procoxae: 1. narrowly to moderately separated (by less than 0.4 times coxal width); 2. widely separated (by more than 0.4 times coxal width).
33. ADULT: pronotal projection (postcoxal extension of hypomeron): 1. long to moderately short and acute; 2. very short and angulate or absent.
34. ADULT: exposed portion of procoxae: 1. conical and projecting; 2. transverse; 3. globular.
35. ADULT: pro-mesothoracic clicking mechanism: 1. absent; 2. present.
36. ADULT: propleuron: 1. separating notum and sternum at anterior edge of prothorax; 2. not separating notum and sternum at anterior edge of prothorax.
37. ADULT: propleuron: 1. extending laterally behind coxa; 2. not extending laterally behind coxa.
38. ADULT: prothoracic trochantinopleuron: 1. at least partly exposed; 2. completely concealed.
39. ADULT: prothoracic trochantinopleuron: 1. well developed; 2. highly reduced and immobile.
40. ADULT: anterior edge of mesosternum at middle: 1. simple, truncate, rounded or acute; 2. cleft or emarginate.
41. ADULT: mesosternal procoxal rests (impunctate, shiny areas): 1. absent, weak, or very small; 2. moderately to well developed.
42. ADULT: mesosternal procoxal rests: 1. absent, more or less horizontal or slightly oblique; 2. moderately to strongly oblique; 3. vertical. Ordered.
43. ADULT: mesosternal cavity: 1. absent or very weak, shallow; 2. moderately large but relatively shallow; 3. moderately to very large and deep. Ordered.

44. ADULT: mesosternal cavity extending posteriorly: 1. not as far as anterior edge of mesocoxal cavity; 2. as far as anterior 4th or 5th of mesocoxal cavity; 3. as far as anterior 3rd of mesocoxal cavity; 4. as far as middle of mesocoxal cavity or beyond. Ordered.
45. ADULT: mesosternal intercoxal process extending posteriorly: 1. as far as anterior 4th of mesocoxal cavity; 2. beyond anterior 4th up to middle of mesocoxal cavity; 3. beyond middle of mesocoxal cavity. Ordered.
46. ADULT: meso-metasternal junction: 1. straight or curved; 2. emarginate or cleft.
47. ADULT: mesosternum: 1. at least partly divided by longitudinal suture; 2. not divided by longitudinal suture.
48. ADULT: mesocoxae: 1. narrowly to moderately separated (by less than 0.4 times coxal width); 2. widely separated (by more than 0.4 times coxal width).
49. ADULT: mesocoxal cavities: 1. closed partly by metepisterna; 2. not closed partly by metepisterna.
50. ADULT: anterior edge of scutellum: 1. straight to convex, simple; 2. emarginate or notched; 3. crenulate.
51. ADULT: posterior edge of scutellum: 1. acute to narrowly rounded; 2. abruptly narrowed to form distinct median projection; 3. broadly rounded.
52. ADULT: number of elytral puncture rows or striae: 1. 12; 2. 11; 3. 10; 4. 9. Ordered.
53. ADULT: ventral interlocking tongue near elytral apex: 1. absent; 2. present.
54. ADULT: elytral epipleura: 1. absent, even or gradually narrowed posteriorly; 2. more or less abruptly narrowed near junction of thorax and abdomen.
55. ADULT: metasternal transverse suture: 1. at least moderately well developed; 2. absent or represented by median remnant only.
56. ADULT: metasternal longitudinal suture (discrimen): 1. moderately to very long (more than 0.6 times sternal length); 2. short (less than 0.6 times sternal length) or absent.
57. ADULT: exposed portion of metepisternum: 1. elongate (more than 2.5 times as long as wide); 2. relatively short and broad (less than 2.5 times as long as wide).
58. ADULT: metacoxal plates: 1. moderately to well developed and more or less uniform; 2. moderately well developed mesally but very weak laterally; 3. weakly developed or absent. Ordered.
59. ADULT: lateral arms of metendosternite: 1. short; 2. moderately to very long.
60. ADULT: ventrolateral processes of metendosternite: 1. absent to weakly developed; 2. strongly developed.
61. ADULT: anterior process of metendosternite: 1. moderately long; 2. short or absent.

62. ADULT: tarsi: 1. without lobed tarsomeres; 2. with only tarsomere 4 lobed below; 3. with lobes on at least 2 tarsomeres.
63. ADULT: tarsi: 1. with membranous appendages absent or present on 1 tarsomere only; 2. with membranous appendages on 2 or more tarsomeres.
64. ADULT: tarsomere 4: 1. not or only slightly reduced; 2. highly reduced (much smaller than tarsomere 3, which is expanded and lobed).
65. ADULT: number of empodial setae: 1. 0, 2 or occasionally 3; 2. 4 or more.
66. ADULT: ratio of length of wing membrane to that of radial bar: 1. less than 0.25; 2. 0.25 to 0.50; 3. greater than 0.50.
67. ADULT: radial cell: 1. elongate (more than twice as long as wide); 2. shorter and broader (less than twice as long as wide); 3. absent.
68. ADULT: radial cell with proximal end: 1. straight or forming obtuse inner posterior angle; 2. forming acute inner posterior angle; 3. absent.
69. ADULT: radial cell: 1. not forming an equilateral triangle; 2. forming a more or less equilateral triangle.
70. ADULT: medial bar ( $MP_{3+4}$ ): 1. without distinct hinge (sometimes with weakened area); 2. with distinct hinge crossed by fold.
71. ADULT: wedge cell (2nd cubito-anal cell): 1. present; 2. absent.
72. ADULT: number of apical veins in medial area (behind  $MP_{1+2}$ ): 1. 5 or 6; 2. 4; 3. 3 or fewer. Ordered.
73. ADULT: hind wing: 1. without posterior incision forming anal lobe; 2. with posterior incision forming anal lobe.
74. ADULT: wing folding type: 1. not of dryopoid type; 2. of dryopoid type (Forbes 1926).
75. ADULT: hind wing folding: 1. not of diversicorn type; 2. of diversicorn type (Forbes 1926).
76. ADULT: abdominal sternite 2: 1. concealed beneath metacoxae; 2. completely exposed.
77. ADULT: intercoxal process of ventrite 1: 1. well developed; 2. highly reduced or absent.
78. ADULT: number of ventrites connate: 1. none or two; 2. three; 3. four or five. Ordered.
79. ADULT: spiracles on segment 8: 1. well developed and functional; 2. reduced and non-functional or absent.
80. ADULT: tergites 8 and 9 in male: 1. without long basolateral struts; 2. with long basolateral struts.
81. ADULT: tergite 10 (proctiger) in male: 1. distinct and free; 2. partly or completely fused to tergite 9.
82. ADULT: tergite 9 in male: 1. not or only slightly emarginate apically; 2. moderately to deeply emarginate apically.
83. ADULT: tergite 9 in male: 1. entire; 2. longitudinally divided by narrow to broad membranous area, so that two hemitergites are formed.
84. ADULT: aedeagus: 1. symmetrical; 2. asymmetrical.



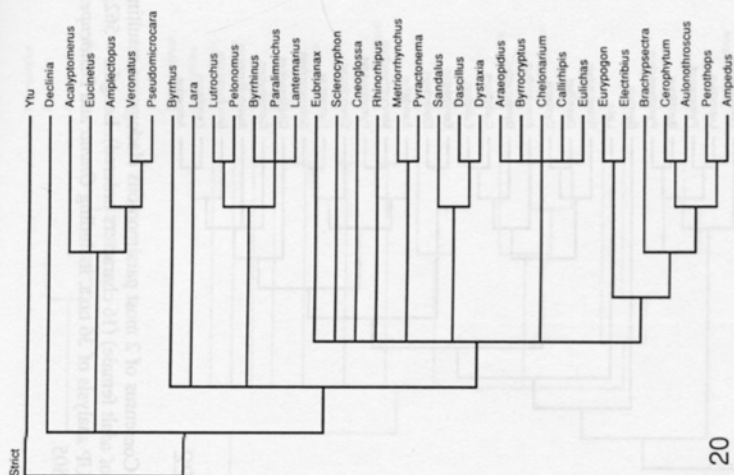
85. ADULT: parameres: 1. more or less articulated to base of aedeagus; 2. fused to base of aedeagus but free from one another; 3. partly or entirely fused together.
86. ADULT: penis: 1. with single lobe (sometimes longitudinally divided or with rod-like ventral sclerotization); 2. with distinct dorsal and ventral lobes.
87. ADULT: penis: 1. not longitudinally divided; 2. longitudinally divided.
88. ADULT: ratio of length to width of ovipositor: 1. less than 1; 2. greater than 1 but less than 3; 3. greater than 3 but less than 6; 4. greater than 6. Ordered.
89. ADULT: styli: 1. well developed and more or less palpiform; 2. highly reduced and button-like or absent.
90. ADULT: coxite: 1. divided (sometimes indistinctly) into basal and apical sections (coxites 1 and 2); 2. undivided.
91. ADULT: coxite: 1. lightly to moderately sclerotized, except for basal baculum, or heavily sclerotized apically and lightly so basally; 2. heavily, more or less uniformly sclerotized.
92. ADULT: coxite: 1. not laterally compressed; 2. laterally compressed.
93. ADULT: ratio of valvifer length to coxite length: 1. less than 1; 2. greater than 1 but less than 1.5; 3. greater than 1.5 but less than 3; 4. greater than 3. Ordered.
94. ADULT: sternite 8 in female: 1. without a narrow, rod-like spiculum ventrale (sometimes with a short, broad anterior process); 2. with a narrow, rod-like spiculum ventrale.
95. ADULT: sternite 8 in female: 1. without paired anterolateral projections; 2. with paired anterolateral projections.
96. ADULT: testes: 1. not elongate and sessile; 2. elongate and sessile.
97. ADULT: midgut: 1. without regenerative crypts; 2. with regenerative crypts.
98. ADULT: rectum: 1. without large sac lined with 6 cuticular rings; 2. with large sac lined with 6 cuticular rings.
99. ADULT OR LARVA: Malpighian tubules: 1. 6; 2. 4.
100. LARVA: epicranial stem: 1. short or absent; 2. long.
101. LARVA: number of stemmata: 1. 5-6; 2. 2-4; 3. 1 or 0. Ordered.
102. LARVA: stemmata: 1. absent, well separated or forming more than one cluster; 2. forming single cluster.
103. LARVA: head on each side: 1. without stemmata, with a single eyespot lacking a lens, or with more than one stemma; 2. with single well-developed stemma consisting of a lens over two or more clustered eye spots; 3. with single, well-developed stemma consisting of a lens over a single eye spot. Ordered.
104. LARVA: antennae: 1. moderately to very long; 2. very short.
105. LARVA: labrum: 1. free; 2. partly or completely fused to head capsule.



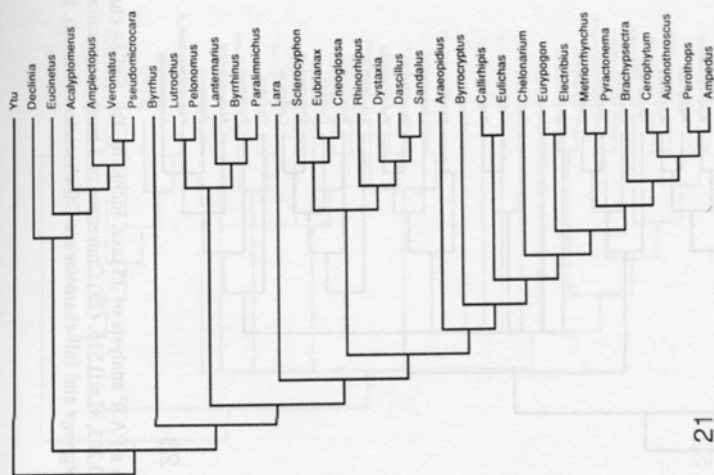
106. LARVA: number of apical mandibular teeth or lobes: 1. 1; 2. 2; 3. more than 2. Ordered.
107. LARVA: mandibular mola: 1. present; 2. absent.
108. LARVA: mandible: 1. with accessory ventral process; 2. without accessory ventral process.
109. LARVA: mandibles: 1. well developed; 2. reduced.
110. LARVA: maxilla: 1. with separate galea and lacinia; 2. with single mala.
111. LARVA: galea or mala: 1. articulated; 2. fixed.
112. LARVA: lacinia: 1. absent or not falciform; 2. falciform.
113. LARVA: number of maxillary palpomeres: 1. 3 or fewer; 2. 4 or more.
114. LARVA: maxillary articulating area: 1. well developed (sometimes concealed behind expanded postmentum); 2. highly reduced or absent.
115. LARVA: maxillolabial sutures: 1. complete; 2. incomplete or absent.
116. LARVA: cardines: 1. well separated; 2. approximate, contiguous or fused together.
117. LARVA: ventral epicranial ridges: 1. absent; 2. present.
118. LARVA: number of pretarsal setae: 1. 2 or occasionally more; 2. 1; 3. 0.
119. LARVA: spiracles: 1. annular or annular-biforous; 2. biforous (with ec-dysial scar); 3. cribriform. Ordered.
120. LARVA: spiracular closing apparatus: 1. present; 2. absent.
121. LARVA: segment 10: 1. posteriorly or terminally oriented; 2. ventrally oriented.
122. LARVA: segment 10: 1. not forming anteriorly-hinged operculum; 2. forming anteriorly-hinged operculum.

## Results and discussion

A default heuristic search (100 repetitions) using PAUP 3.1.1 on the full character set and 34 taxa plus the outgroup *Ytu* produced one most parsimonious tree (length = 751, CI = 0.205, RI = 0.502) illustrated in Fig. 20. The same data set with all characters unordered produced 7 trees (length = 703, CI = 0.219, RI = 0.489); a strict consensus of these cladograms is shown in Fig. 21. A third analysis was carried out using a subset of 84 characters based on external features of the adult female only (since *Declinia* and several other taxa are known from dried adult female specimens only). Two cladograms were produced (length = 562, CI = 0.203, RI = 0.516), the strict consensus of which is illustrated in Fig. 22. Three more analyses were run, each with a different set of outgroups. With *Omma* and *Distocupes*, 3 cladograms resulted (lengths = 777, CI = 0.203, RI = 0.505); with *Necrophilus* 2 were produced (lengths = 753, CI = 0.205, RI = 0.504); and when all four outgroups were used, there

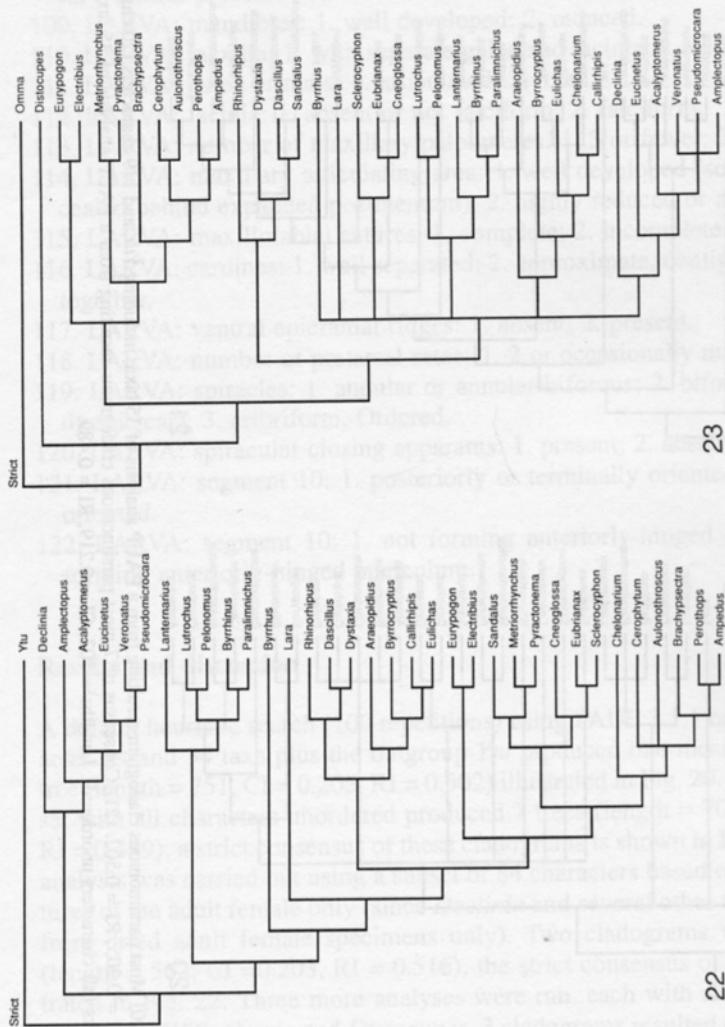


20

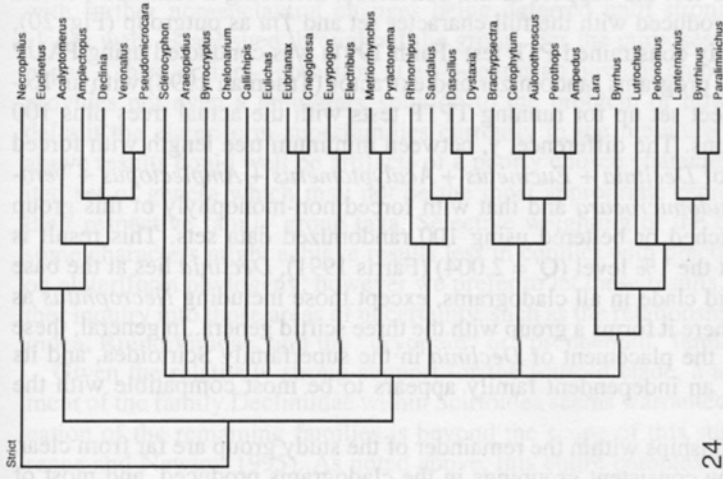
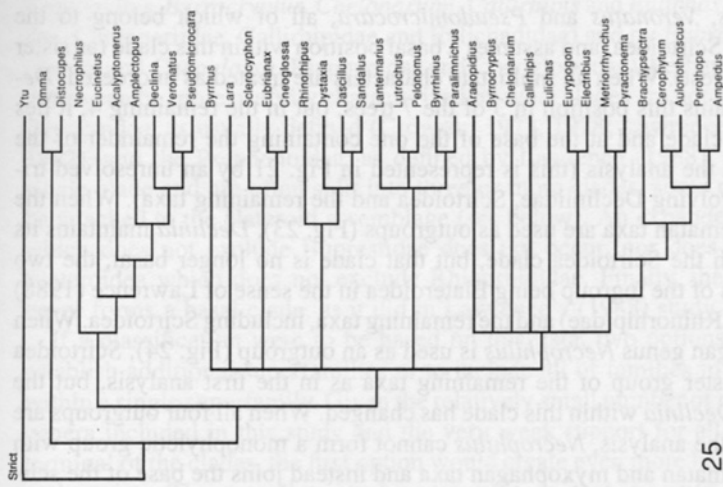


21

Figures 20–21. (20) Most parsimonious cladogram resulting from a PAUP analysis of 35 taxa, including *Ytu*, and 119 characters (20 characters ordered). Length = 751, CI = 0.205, RI = 0.502. (21) Consensus of 7 most parsimonious cladograms resulting from a PAUP analysis of 35 taxa, including *Ytu*, and 119 characters (all characters unordered). Lengths = 703, CI = 0.219, RI = 0.489.



Figures 22–23. (22) Consensus of 2 most parsimonious cladograms resulting from a PAUP analysis of 35 taxa, including *Ytu*, and 84 characters (based on external features of adult female) (16 characters ordered). Lengths = 562, CI = 0.203, RI = 0.516. (23) Consensus of 3 most parsimonious cladograms resulting from a PAUP analysis of 36 taxa, including *Omma* and *Distocupes* as outgroups and full character set (20 characters ordered). Lengths = 777, CI = 0.203, RI = 0.505.



Figures 24–25. (24) Consensus of 8 most parsimonious cladograms resulting from a PAUP analysis of 35 taxa, including *Necrophilus* as outgroups and full character set (20 characters ordered). Lengths = 753, CI = 0.205, RI = 0.504. (25) Consensus of 4 most parsimonious cladograms resulting from a PAUP analysis of 38 taxa, including all four outgroups and full character set (20 characters ordered). Lengths = 841, CI = 0.207, RI = 0.510.

were 4 (lengths = 841, CI = 0.207, RI = 0.510). Strict consensus trees for each are given in Figs. 23–25).

In all cladograms resulting from analyses in which the characters were partly ordered, *Declinia* forms a monophyletic group with *Eucinetus*, *Acalyptomerus*, *Amplectopus*, *Veronatus* and *Pseudomicrocara*, all of which belong to the superfamily Scirtoidea, and assumes a basal position within this clade (as sister taxon to the rest). When all multistate characters are treated as unordered, *Declinia* maintains this position in 3 of the 7 trees, but in the remaining 4, it lies outside this clade and at the base of the one containing the remainder of the taxa used in the analysis (this is represented in Fig. 21 by an unresolved trichotomy involving Decliniidae, Scirtoidea and the remaining taxa). When the two archostematan taxa are used as outgroups (Fig. 23), *Declinia* maintains its position with the Scirtoidea clade, but that clade is no longer basal, the two major clades of the ingroup being Elateroidea in the sense of Lawrence (1988) (but without Rhinorhipidae) and the remaining taxa, including Scirtoidea. When the polyphagan genus *Necrophilus* is used as an outgroup (Fig. 24), Scirtoidea forms the sister group of the remaining taxa as in the first analysis, but the position of *Declinia* within this clade has changed. When all four outgroups are included in the analysis, *Necrophilus* cannot form a monophyletic group with the archostematan and myxophagan taxa and instead joins the base of the scirtoid clade, which again forms the sister group of the remaining taxa.

In order to test the support of the Scirtoidea, including Decliniidae, in the cladogram produced with the full character set and *Ytu* as outgroup (Fig. 20), a topologically constrained PTP test (Faith 1991) was conducted using PAUP 3.1.1 and the programs randomizer and extractor (Trueman 1994) with an Excel spreadsheet set up for running TPTP tests with the actual trees plus 100 randomizations. The difference,  $y$ , between minimum tree length with forced monophyly of *Declinia* + *Eucinetus* + *Acalyptomerus* + *Amplectopus* + *Veronatus* + *Pseudomicrocara* and that with forced non-monophyly of this group was not matched or bettered using 100 randomized data sets. This result is significant at the 1% level ( $Q' = 2.004$ ) (Farris 1991). *Declinia* lies at the base of the scirtoid clade in all cladograms, except those including *Necrophilus* as outgroup, where it forms a group with the three scirtid genera. In general, these data support the placement of *Declinia* in the superfamily Scirtoidea, and its treatment as an independent family appears to be most compatible with the results.

The relationships within the remainder of the study group are far from clear. There are few consistent groupings in the cladograms produced, and most of these are terminal pairs. The only two larger clusters which occur in all cladograms are (1) *Lutrochus* + *Pelonomus* + *Byrrhinus* + *Paralimnichus* + *Lanternarius* (Lutrochidae, Dryopidae, Limnichidae and Heteroceridae) and (2) *Brachypsectra* + *Cerophytum* + *Aulonothroscus* + *Perothops* + *Ampedus* (Brachypsectridae, Cerophytidae, Throscidae, Eucnemidae and Elateridae).



*Byrrhus* (Byrrhidae) and *Lara* (Elmidae) are occasionally attached basally to the first clade, but more often they form independent basal lineages. *Rhinorhipus* often forms a monophyletic group with *Dystaxia*, *Dascillus* and *Sandalus* (Buprestidae plus Dascilloidea) and clades are sometimes formed by *Araeopidius*, *Byrrcryptus*, *Chelonarium*, *Callirhipis* and *Eulichas* (Ptilodactylidae, Chelonariidae, Callirhipidae and Eulichadidae) and by *Eubrianax*, *Sclerocyphon* and *Cneoglossa* (Psephenidae and Cneoglossidae). Perhaps these cladograms can be more usefully characterized by what clades are not included. The Dryopoidea, as usually defined (Crowson 1973, 1978; Lawrence and Newton 1982), and the Psephenoidea, as defined by Lawrence (1988), never form a single clade and are often split into three or more clades, some of which may be attached to the elateroid assemblage (*see below*). An expanded Byrrhoidea which does not exclude Buprestidae does not occur, nor does an expanded Elateroidea which does not exclude Rhinorhipidae. Finally, the Dascilloidea never forms a basal clade, as it did in Lawrence's (1988) study.

If a classification were to be based on this data, two options would be to establish additional superfamilies or to include all of families in this complex within a single superfamily. Given the relatively small number of representative genera included in this study and the very weak support for all but the most terminal of the clades, the first option would create even more havoc than presently exists. The second might be preferable, in that it would allow further studies on phylogenetic relationships of the component taxa to be carried out with further nomenclatural changes being deferred until strongly supported clades were established throughout the group. For the purposes of the present paper, a third option—no action at all—seems an obvious choice, although it provides not even a temporary solution to the problem of how to define or delimit the elateriform superfamilies currently in the literature. Some of the above results could well be artifacts of a poorly chosen character set or a limited set of genera which may not be the most appropriate representatives of their respective family group taxa. Selective weighting or the elimination of some characters might achieve results less in conflict with preconceived ideas on elateriform phylogeny; however we prefer to let these results stimulate further inquiry into those areas of uncertainty, such as the relationships of Dascilloidea, Rhinorhipidae, and the "dryopoid" or "psephenoid" families.

Given the relatively strong support for the scirtoid clade, a tentative placement of the family Decliniidae within Scirtoidea seems warranted. The classification of the remaining families is beyond the scope of this study (*see Lawrence and Newton 1995*). As noted above, this entire complex has had a confusing nomenclatural history, so that there are few superfamilial names with an unambiguous meaning. The families treated in this paper correspond exactly to the series Dascilliformia, as defined by Crowson in his first major work (1960); however that term was more or less eliminated when Crowson (1960, 1971a) included Scirtidae (as Helodidae) in Eucinetiformia, Dascilloidea in

Scarabaeiformia, and the remaining taxa in Elateriformia. The last term has been in constant use for the past 30 years, and we suggest that it be expanded to include both Dascilloidea and Scirtoidea.

### Acknowledgments

The following institutions and individuals are acknowledged for providing specimens of the large number of beetle taxa necessary for this and earlier studies of elateriform Coleoptera: A.A. Allen; American Museum of Natural History, New York (L. Herman); Australian Museum, Sydney (G. Holloway, M. Moulds); Australian National Insect Collection, CSIRO Division of Entomology, Canberra; Bishop Museum, Honolulu (S.I. Miller, G. Nishida, G.A. Samuelson); H.P. Brown; California Academy of Sciences, San Francisco (D.H. Kavanaugh, R. Brett); California Insect Survey and Department of Environmental Science, Policy and Management Entomology (formerly Department of Entomology), University of California, Berkeley (J.T. Doyen, J. Chemsak, J.A. Powell); Canadian National Collections of Insects, Arachnids and Nematodes, Centre for Land and Biological Resources Research (formerly Biosystematics Research Centre), Agriculture Canada (E.C. Becker, J.M. Campbell, L. LeSage, A. Smetana); K.W. Cooper; R.A. Crowson; D. Fedorenko; Field Museum of Natural History, Chicago (H.S. Dybas, A.F. Newton, Jr., M.K. Thayer); T.F. Hlavac; H.F. and A. Howden; M.A. Ivie; P.J. Johnson; C. Kitayama; J. Kukulová-Peck; S. Kurbatov; B.M. Mamaev; Museu de Zoologia da Universidade de São Paulo, São Paulo (C. Costa); Museum of Comparative Zoology, Harvard University, Cambridge (A.F. Newton, Jr., M.K. Thayer; J. Scott); Muséum National d'Histoire Naturelle, Paris (C. Girard); Museum of Victoria, Melbourne (A. Neboiss, K. Walker); National Museum of Natural History, Smithsonian Institution, Washington (D.M. Anderson, T.L. Erwin, J. Pakaluk, P.J. Spangler, T.J. Spilman, N. Vandenberg); The Natural History Museum (formerly British Museum (Natural History)), London (M.J.D. Brendell, P.M. Hammond, C. von Hayek, C.H.C. Lyal); New Zealand Arthropod Collection, Landcare Research (formerly part of DSIR), Auckland (R. Craw, B. Holloway, G. Kuschel, J.C. Watt); S.B. Peck; Queensland Department of Primary Industries, Indooroopilly and Mareeba (B. Cantrell, J. Donaldson, M. Elson-Harris, K. Houston, R. Storey); Queensland Museum, South Brisbane (G. Monteith, E.C. Dahms, G. Thompson); South Australian Museum, Adelaide (E.G. Matthews); J.B. Stribling; G.W. Ulrich; A. Walford-Huggins. We are also grateful to J. Kukulová-Peck and V.G. Gratshev for their comments and assistance in interpreting the wing venation and folding and to S. Caveney for confirming our interpretation of the eye structure. Thanks are given to R.A. Crowson, M.A. Ivie, M. Jäch, A.G. Ponomarenko, S.A. Šlipiński and many of the curators listed above for comments and advice on the possible relationships of

*Declinia relicta*. We are grateful to S.P. Kim for executing the illustrations used in Figs. 2–6 and 13–18 and A. Hastings for those in Figs. 1 and 19; the Microscopy Centre, CSIRO Divisions of Entomology and Plant Industry (C. Beaton) for preparing sections and producing transmission electron micrographs of the *Declinia* eye and for the SEM images used in Figs. 9–12; and the CSIRO Division of Entomology Graphics Unit (S. Smith, C. Hunt) for the preparation and labelling of the plates. Special thanks are given to J.R. Trueman for his assistance in running the PAUP analyses and TPTP test. R.B. Halliday and M. Horak are acknowledged for their critical review of an earlier draft of this manuscript.

## References

- Caveney, S. 1986. The phylogenetic significance of ommatidium structure in the compound eyes of polyphagan beetles. *Canadian Journal of Zoology*, 64: 1787–1819.
- Crowson, R.A. 1955. The natural classification of the families of British Coleoptera. N. Lloyd, London, 187 pp.
- Crowson, R.A. 1960. The phylogeny of Coleoptera. *Annual Review of Entomology*, 5: 111–134.
- Crowson, R.A. 1961. Considerations on the genera *Endecatomois* Mellié and *Euderia* Broun (Coleoptera: Bostrychidae), with descriptions of their larvae. *Proceedings of the Royal Entomological Society of London (B)*, 30: 113–120.
- Crowson, R.A. 1971a. Observations on the superfamily Dascilloidea (Coleoptera: Polyphaga), with the inclusion of Karumiidae and Rhipiceridae. *Zoological Journal of the Linnean Society*, 50: 11–19.
- Crowson, R.A. 1971b. Some problems in the phylogenetic classification of the Coleoptera. *Proceedings of the International Congress of Entomology*, 13(1): 235–237.
- Crowson, R.A. 1972. Review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid*, 21(82): 35–77.
- Crowson, R.A. 1973. On a new superfamily Armatopodea of polyphagan beetles, with the definition of two new fossil genera from the Baltic Amber. *Journal of Natural History*, 7: 225–238.
- Crowson, R.A. 1976. The systematic position and implications of *Crowsoniella*. *Bollettino del Museo Civico di Storia Naturale di Verona*, 2(1975): 459–463.
- Crowson, R.A. 1978. Problems of phylogenetic relationships in Dryopoidea (Coleoptera). *Entomologia Germanica*, 4: 250–257.
- Dallwitz, M.J., Paine, T.A. and Zurcher, E.C. 1993. *Delta User's Guide. A General System for Processing Taxonomic Descriptions*. Fourth Edition. CSIRO, East Melbourne, Victoria, v + 136 pp.
- Faith, D.P. 1991. Cladistic permutation tests for monophyly and nonmonophyly. *Systematic Zoology*, 40: 366–375.
- Farris, J.S. 1991. Excess homoplasy ratios. *Cladistics*, 7: 81–91.
- Forbes, W.T.M. 1926. The wing folding patterns of the Coleoptera. *Journal of the New York Entomological Society*, 34: 42–139.

- Hlavac, T.F. 1975. The prothorax of Coleoptera (except Bostrichiformia-Cucujiformia). Bulletin of the Museum of Comparative Zoology, 147: 137-183.
- Kasap, H. and Crowson, R.A. 1975. A comparative anatomical study of Elateriformia and Dascilloidea (Coleoptera). Transactions of the Royal Entomological Society of London, 126: 441-495.
- Kukalová-Peck, J. and Lawrence, J.F. 1993. Evolution of the hind wing in Coleoptera. Canadian Entomologist, 125: 181-258.
- Lawrence, J.F. 1988. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. Invertebrate Taxonomy, 2: 1-53.
- Lawrence, J.F. 1991. Order Coleoptera, pp. 144-185. In: F.W. Stehr (ed.), Immature Insects. Volume 2. Kendall/Hunt, Dubuque, Iowa.
- Lawrence, J.F. 1995. *Electribius* Crowson: alive and well in Middle America, with notes on *Ctesibius* Champion and the classification of Armatopodidae. (this volume).
- Lawrence, J.F. and Britton, E.B. 1991. Coleoptera (beetles), pp. 543-683. In: CSIRO (ed.), Insects of Australia. 2nd Edition. Volume 2, Melbourne University Press, Carlton, Victoria.
- Lawrence, J.F. and Newton, A.F. Jr. 1982. Evolution and classification of beetles. Annual Review of Ecology and Systematics, 13: 261-290.
- Lawrence, J.F. and Newton, A.F. Jr. 1995. The families and subfamilies of Coleoptera, (with selected genera, notes, references and data on family-group names) (this volume).
- Nelson, G.H. and Bellamy, C.L. 1991. A revision and phylogenetic re-evaluation of the family Schizopodidae (Coleoptera, Buprestoidea). Journal of Natural History, 25: 985-1026.
- Nikitsky, N.B., Lawrence, J.F. Kirejtshuk, A.G. and Gratshev, V.G. 1994. A new beetle family, Decliniidae fam. n., from the Russian Far East and its taxonomic relationships (Coleoptera, Polyphaga). Russian Entomological Journal, 2(5-6)(1993): 3-10.
- Nyholm, T. 1972. Zur Morphologie und Funktion des Helodiden-Aedoeagus (Col.). Entomologica Scandinavica, 3: 81-119.
- Pace, R. 1976. An exceptional endogenous beetle: *Crowsoniella relicta* n. gen. n. sp. of Archostemata Tetraphaleridae from Central Italy. Bollettino del Museo Civico de Storia Naturale di Verona, 2(1975): 445-458.
- Poll, M. 1932. Contribution a l'étude des tubes de Malpighi des Coléoptères. Recueil de l'Institut Zoologique Torley-Rousseau, 4: 47-80.
- Ponomarenko, A.G. 1969. Historical development of the Coleoptera - Archostemata. Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR, 125: 1-240 [in Russian].
- Ponomarenko, A.G. 1971. The geological history and evolution of beetles. Proceedings XIII International Congress of Entomology (Moscow, 2-9 August, 1968), 1: 281.
- Ponomarenko, A.G. and Zherikhin, V.V. 1980. Order Scarabaeida. Coleoptera, or beetles. Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR, 175: 76-84 [in Russian].
- Pope, R.D. 1976. Nomenclatural notes on the British Scirtidae (= Helodidae) (Col.). Entomologist's Monthly Magazine, 111: 186-187.
- Snodgrass, R.E. 1935. Principles of Insect Morphology. McGraw-Hill, New York, ix + 667 pp.
- Swofford, D.L. 1991. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Illinois Natural History Survey, Champaign, Illinois.
- Trueman J.W.H. 1994. Toward a Phylogeny of Odonata. Australian National University, Canberra (PhD. Thesis), xviii + 264 + 7 appendices.