Anischia, Perothops and the phylogeny of Elateroidea (Coleoptera: Elateriformia)

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Introduction

Although originally placed in Eucnemidae, Anischia Fleutiaux has been included in Cerophytidae by many workers, based mainly on the absence of metacoxal plates. Fleutiaux (1936) transferred the genus to Elateridae, placing it in a new subfamily. Anischiinae was considered to be incertae sedis within Elateridae by Lawrence and Newton (1995) but recognized as a distinct family by Lawrence et al. (1999). In cladograms produced by Muona (1995) based on 25 elateroid genera and 70 characters (6 larval), Anischia was at or near the base of a clade comprising Elateridae and Throscidae in the sense of Crowson (1955) (including Lissominae and Thylacosterninae). The discovery of a unique, eucnemid-like larva associated with adult Anischia in New Caledonia led us to reconsider the affinities of the genus as part of a reanalysis of the elateroid complex.

Perothops Laporte was placed in a separate subfamily of Eucnemidae (Perothopsitae) by Lacordaire (1857) and the genus is usually included in that family. Perothopidae was also recognized at the family level by Horn (1878), Schenkling (1928), Crowson (1955), Arnett (1963) and a few other workers. Muona (1993) suggested that Perothops might belong to either Eucnemidae or a clade comprising Throscidae (sensu lato) and Elateridae; however he chose to recognize the group as the most basal of eucnemid subfamilies. A number of years ago, one of us (JFL) discovered a large and unusual, eucnemid-like larva in the collections of the National Museum of Natural History in Washington. Although not reared or associated with adult beetles, the size, structure and locality of this soil-inhabiting larva were considered in making the identification (see larval description below).
The purpose of the present paper is to clarify the position of these two unusual genera and determine their relationships to the families Eucnemidae, Cerophytidae, Throscidae and Elateridae.

**Materials and Methods**

**Morphological terms.** – The terms mesoventrite and metaventrite have been used in place of the misapplied terms mesosternite and metasternite following Lawrence 1999 and Lawrence et al. 1999 (see also Beutel & Haas 2000). Wing vein terminology follows that of Kukalová-Peck & Lawrence (1993, 2004).

**Measurements and ratios.** – 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.

**Image enhancement.** – Images in Figs 1–10, 26–28 and 31 were enhanced using Auto-Montage software version 4.00 (Synoptics Ltd., http://www.syn-croscopy.com).


**Character Coding:** – Elateroid relationships have been studied quite intensively, but these studies have yielded conflicting results (Calder et al. 1993; Muona 1995). It was clear to us that a very thorough evaluation of the characters previously used was needed. We hope to have removed all characters that could not be unambiguously coded from the present data set.

The 118 morphological characters and character states are listed in Appendix 1, along with notes on the distribution of these states among the exemplar taxa. The character matrix is included as Table 2.

**Taxon Sampling.** – In addition to Perothops and Anischia, 10 exemplar genera were chosen representing all subfamilies recognized by Muona (1993) except Phlegoninae, three genera representing each of the largest elaterid subfamilies Agrypninae, Dendrometrinae and Elaterinae, five genera representing the disputed elaterid subfamilies Lissominae and Thylacosterninae, and one genus each from the families Cerophytidae and Throscidae. In addition, the genera Brachyspectra and Macropogon were chosen because the families Brachyspectridae and Artematopodidae were considered to be at or near the base of Elateroidea (sensu lato) in Lawrence (1988), Lawrence et al. (1995) and Beutel (1995). In the larval cladogram produced by Beutel (1995), Brachyspectra was basal to the cantharoid complex, and it occupied a similar position in a cladogram based on adults and larvae with Dascilloidea as an outgroup in Lawrence (1988). This taxon was preferred over other more common cantharoid taxa, partly because of its basal position, but also because adult Brachyspectra lack most of the secondary cantharoid features associated with neoteny, short adult life span, and the loss of cuticular strengthening mechanisms in favor of chemical defenses. The three outgroups chosen represent 1) Dascillidae, the most basal member of the series Elateriformia as used by Lawrence 1988 (Dascilliformia of Crowson 1955), Eucinetidae, a member of the Scirtoidea as used by Lawrence 2001 (Eucinetoidea of Crowson 1960) and one of the most basal groups of Polyphaga, and 3) Scarabaeidae, a member of the series Scarabaeiformia.

**Specimens Examined.** – The following list includes those taxa used for the coding of morphological character states and for DNA extraction and representing exemplar genera in the cladistic analyses. Genera are arranged alphabetically with their current family group placement in brackets.


*Anischia* Fleutiaux (Elateridae: Anischiinae or Anischidae). Morphology based on adults of *Anischia* species described below and a larva of *A.


Austrelater Calder & Lawrence (Elateridae: Lissominae?). Morphology based on adults and larvae of A. macphersonensis Calder and descriptions and illustrations in Calder et al. (1993).

Brachypsectra LeConte (Brachypsectridae). Morphology based on adults and larvae of B. fulva LeConte and descriptions and illustrations in Costa et al. (2005).

Cerophytum Latreille & Phytoecerus Costa et al. (Cerophytidae). Morphology based on adults of C. pulsator LeConte and Phytoecerus sp., larvae of C. elateroides (Latreille) and descriptions and illustrations in Costa et al. (2003). Sequence data: Phytoecerus sp., Bolivia, R. Leschen leg. GenBank accession number: EF589369.


Danosoma Thomson (Elateridae: Agrypninae: Agrypnini). Morphology based on adults of D. faciatum (Linnaeus), D. conspersum (Gyllenhal) and D. obtecta (Say), and larvae of D. conspersum, and descriptions and illustrations in Ohira (1962) and Dolin (1978). Sequence data: Danosoma fasciatum (Linnaeus); Finland, P. Martikainen leg. GenBank accession number EF589371.


Drapetes Dejean (Elateridae: Lissominae). Morphology based on adults and larvae of Drapetes geminatus (Say) and descriptions and illustrations of D. biguttatus (Piller) in Burakowski (1973). No sequence data.


Macropogon Motschulsky (Artematopodidae). Morphology based on adults of M. testaceipennis Motschulsky and M. californicus Horn, larvae of M. piceus (LeConte) and descriptions and illustrations in Cooper (1991). No sequence data.


Nematodes Berthold (Eucnemidae: Macraulacinae: Nematodini). Morphology based on adults of N. penetrans (Say) and N. major Bonvouloir, larvae of Nematodes sp. (ACT, Australia), and descriptions and illustrations in Muona (1993, 2000), Leiler (1976) and Mamaev (1976). Sequence data: Nematodes cuneatus (Guerin); Bolivia, C. Thomas leg. GenBank accession number EF589377.

Nyceus Latreille (Eucinetidae). Morphology
based on adults and larvae of *N. infumatus* (LeConte). No sequence data.


*Palaeoxenus* Horn (Eucnemidae: Palaeoxeninae). Adults and larvae of *P. dohrni* (Horn), illustration in Böving & Craighead (1931), and descriptions and illustrations in Muona (1993, 2000). Sequence data: *Palaeoxenus dohrni* (Horn); USA, California, R. Otto leg. GenBank accession number EF589379

*Perothops* Laporte (Eucnemidae: Perothopinae). Adults and larvae of *P. cervinus* Lacordaire, *P. mucida* (Gyllenhal) and *P. witticki* Leconte, a presumed larva of *Perothops* sp. described below, and descriptions and illustrations in Muona (1993, 2000) and Cobos (1964: 430–435). No sequence data.


*Phyllocerus* Lepeletier & Serville (Eucnemidae: Phyllocerinae). Morphology based on adults of *P. flavipennis* Lepeletier & Serville and *P. indigaceum* (Bonvouloir), larva of *Phyllocerus* sp. from Tadzhikistan, and descriptions and illustrations in Ghilarov (1979). No sequence data.

*Pseudomenes* Fleutiaux (Eucnemidae: Pseudomeninae: Pseudomenini). Morphology based on adults and larvae of *P. bakewelli* (Bonvouloir) and descriptions and illustrations in Muona (1993). No sequence data.


*Schizophilus* Bonvouloir (Eucnemidae: Pseudomeninae: Schizophilini). Morphology based on adults and larvae of *Schizophilus subrufus* (Randall) and descriptions and illustrations in Otto & Young (1998). No sequence data.


**Sequence Data.** – Specimens used for DNA extraction were either dried and pinned, or preserved in ethanol. DNA was extracted using the DNeasy Tissue kit (Qiagen) or the Nucleospin DNA Tissue kit (Machiney-Nagel). Variations of methods used at different times were based on availability of materials and preferences of lab technicians or students. Either parts of specimens, typically single legs or flight muscles, or entire specimens were used. In the latter case, specimens were kept intact through the extraction process by gently separating the elytra with a scalpel and puncturing the insides of the thorax to expose muscle tissue, and returned to ethanol when extraction was completed. Using entire specimens allowed for resuspension of a larger volume of good quality DNA.

A 1180 bp fragment of the mitochondrial gene cytochrome oxidase I (COI) was amplified either in one portion with primers Beet+Pat (Table 1), or in two portions using primer combinations Beet+HCO and Jerry+Pat. Jerry+Pat was also used alone to amplify an 800 bp fragment of COI.

PCR reaction mixtures comprised of 2.5 µl 25 mM MgCl₂, 2 µl 10 x PCR buffer with (NH₄)₂SO₄,

<table>
<thead>
<tr>
<th>Primer</th>
<th>Sequence: 5’-3’</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1-J-1718 (Beet)</td>
<td>GGAGGAATTGGAATTGTAGTT</td>
<td>Simon et al. (1994)</td>
</tr>
<tr>
<td>HCO 2198 (HCO)</td>
<td>TAAACTTCAGGGTGACCAAAAAATCA</td>
<td>Lunt et al. (1996)</td>
</tr>
<tr>
<td>C1-J-2183 (Jerry)</td>
<td>CAACATTTATTTGTGTTTGG</td>
<td>Simon et al. (1994)</td>
</tr>
<tr>
<td>L2-N-3014 (Pat)</td>
<td>TCCAATGCACTAATCTGCCATATTA</td>
<td>Simon et al. (1994)</td>
</tr>
</tbody>
</table>
1 µl of both primers of 10 pmol, 1.5 µl 200mM dNTPs, 0.5 units Taq Polymerase (all MBI Fermentas), 0.5-2 µl template DNA, and sterile water up to a total volume of 20 µl.

PCR consisted of (1) an initial 2 min at 95°C, (2) 30 s at 94°C, (3) 30 s at 47°C or 49°C, (4) 2 min at 72°C, (5) steps 2-4 repeated 35 or 40 cycles in total, (6) followed by a final extension step of 10 min at 72°C.

PCR reactions were visualized on 1-1.5% agarose gel using 2-3 µl PCR product. These were cleaned with the GFX PCR DNA and Gel Band Purification kit (Amersham Biosciences) and eluted in 15 µl of sterile water.

Sequencing was done in both directions with the same PCR primers and the Big Dye Terminator 1.0 or 1.1 Cycle Sequencing kit (Applied Biosystems). Sequencing reaction mixtures comprised of 1-2 µl Big Dye, 2-3 µl 2.5 x dilution buffer, 1 µl primer, 0.5-2 µl purified PCR product, and sterile water to a total volume of 10 µl.

Cleaning of cycle sequencing products was performed with Millipore plates and a vacuum pump (Millipore Corporation) or CentriSep Spin Columns (Princeton Separations). Samples were then sequenced with ABI 377 (Applied Biosystems) or MegaBACE 1000 Sequence Analyzer (Amersham Biosciences). Sequencing ambiguities in resulting chromatograms were edited and contiguous sequences were made using Sequencher 4.1.2 software (Gene Codes Corporation) or Sequence Navigator (Applied Biosystems).

Obtaining good quality sequences from rare species can be very difficult. The preservation and age of the samples available to us varied considerably. Because of this, some sequences are much shorter and probably of lesser quality than others.

Systematics

Genus Anischia Fleutiaux
(Figs 1–25)


Redescription of Adult. – Body moderately elongate, about 2.5 times as long as wide, more or less parallel-sided, with elytra slightly expanded basally and tapered apically and prothorax often distinctly curved laterally, so that narrowest point is at pronoto-elytral junction; moderately convex dorsally and ventrally. Color yellowish-brown to black, uniform, except in A. bicolor; vestiture consisting of moderately long, fine, inclined to decumbent hairs, which on pronotum are often transversely oriented towards midline and on elytra are posteriorly oriented. Total length 1.7–3.5 mm. Head strongly transverse, slightly to moderately declined, deeply inserted into prothorax; posterior edge (dorsal rim of occipital foramen) biemarginate, forming median tooth but lacking median endocarina; fine transverse occipital ridge present, continuing below eyes as weak subgenal ridges; eyes large, entire, not protruding, finely faceted; median frontal endocarina absent; frontoclypeal area slightly, gradually declined, with mouthparts anteroventrally oriented; frontoclypeal suture absent; anterior edge of clypeus truncate to concave; antennal insertions exposed and usually separated by less than length of antennomere 1; subantennal grooves short and shallow, without deep pits. Gula reduced, sutures widely separated. Posterior tentorial bridge (corporotentorium) very narrow, slightly arched; tentorial arms expanded mesally and fused at midline forming broad anterior bridge (laminatentorium). Cervical sclerites well developed, each divided into 3 parts. Antennae 11-segmented, extending almost to base of prothorax; antennomeres gradually expanded apically (incrassate or clavate) or more abruptly expanded to form weak, 2- to 5-segmented club; scape slightly inflated, pedicel attached subapically, with sharp tooth just behind (laterad of) attachment; antennomere 3 slightly to distinctly elongate; sensory elements on enlarged preapical antennomeres usually at apex, those on apical one more evenly distributed. Labrum attached beneath edge of clypeus but at least partly visible, strongly transverse, usually rounded anteriorly with distinct median emargination. Mandible short and broad, only slightly longer than wide at base, acutely bidentate; mola reduced, sub-basal, consisting of group of asperities, several of which form a transverse comb-like structure; distinct hyaline area at base of mesal edge; prostheca absent. Maxillary lobes subequal, galea articulated and setose, lacinia narrowed apically, setose and with fine apical hook; terminal maxillary palpmere slightly widened at middle, narrowed apically and obliquely truncate at apex. Labium with truncate ligula; terminal palpmere similar to that of maxillary
Figs 1-10. *Anischia* spp. Adult habitus, dorsal. 1. *A. bicolor*. length = 1.7–2.6 mm. 2. *A. stupenda*; length = 2.5–3.0 mm. 3. *A. kuscheli*; length = 1.75–2.45 mm. 4. *A. monteithi*; length = 2.0–2.4 mm. Figs 5-10. *A. kuscheli* larva. 5. Habitus, dorsal; length = 5 mm. 6. Habitus, ventral. 7. Larval abdominal apex, ventral. 8. Larval head, dorsal. 9. Larval head, ventral. 10. Section of abdomen, ventral, showing goblet-shaped microtrichial patches.
palp. Proventriculus 8-lobed, consisting of setose pads alternating with elongate, hyaline processes lined with saw-like teeth. Pronotum usually widest at about middle, sides barely to strongly rounded, with complete lateral carinae, not visible for their entire lengths from above; anterior angles more or less right; posterior angles acute and more or less produced; hind edge with well-developed interlocking device, including pair of deep sublateral cavities for receiving paired processes on anterior edges of elytra; disc with two pairs of longitudinal carinae extending anteriorly from hind edge, inner carinae longer, arising from basal cavities, slightly to strongly curved and extending to about middle of disc; outer carinae shorter, straight and parallel to lateral carinae or diverging and uniting with lateral carinae. Hypomeron without antennal grooves or cavities but with fine line extending from anterior edge just lateral of notosternal suture to procoxal cavity and then posterolaterally almost to lateral carina; a broader shallow, oblique groove for housing profemur located just behind posterior portion of this line. Prosternum well developed in front of coxae, moderately convex, produced anteriorly to form broad chin-piece; prosternal process posteriorly moderately long, straight, parallel-sided except near lateral edge of cavity, the two lines in some species meeting and forming a single recurved line. Visible portion of metaneusternum very narrow and more or less parallel-sided, anterior edge distant from mesocoxal cavity. Metacoxae slightly oblique, well separated (by more than half the transverse diameter of one), extending laterally almost to epipleuron, but separated from them by posterior protrusions of metaneusternum and metepimeron; coxal plates completely absent. Metendosternite with very broad stalk and long arms, on which anterior tendons are located. Hind wing about 2.4 times as long as wide; apical field about 0.4 times total wing length, with a vague anterior oblique sclerite. Radial cell weakly sclerotized, about 1.6 times as long as wide, with inner posterobasal angle slightly acute; cross-veins r3 and r4 absent. Basal portion of RP very short, radio-medial loop narrow; medial spur straight, not reaching wing margin. Medial field with 3 free veins, none of which reach wing margin; MP3+4 with vague basal cross-vein but no basal spur, not apically forked, joined by CuA; wedge cell absent. Anal notch well developed, deep; AP moderately long, not reaching margin. Legs moderately long and slender, hind legs somewhat longer than anterior pairs. Trochanter very long, almost half as long as femur; trochanterofemoral joint oblique. Tibia relatively slender, only slightly enlarged apically; apex with two tibial spurs of equal length. Tarsomeres simple, 1–4 decreasing in length, and 5 usually as long as previous 3 combined. Tarsal claws simple; empodium weakly developed, not
usually visible beyond apex of tarsomere 5. Abdomen slightly elongate with 5 ventrites; ventrites 1–4 subequal in length, 5 distinctly longer; ventrites 1–3 connate, 4 and 5 movable; ventrite 1 with two postcoxal lines on each side of intercoxal process, one beginning near mesal edge of metacoxal cavity and extending posterolaterally, and the other beginning near lateral edge of cavity, extending mesally following posterior edge of cavity and then abruptly curved posteriorly, the two lines in some species meeting near posterior edge of ventrite and so forming a single curved line. Spiracles on segments I to VIII, located in pleural membrane. Tergites membranous, except for VIII–X, which are lightly sclerotized. Sternite VIII in male with very short median and paired lateral struts. Sternite IX in male with paired lateral struts only; tergites IX and X in male more or less fused together. Sternite and tergite VIII in female lightly sclerotized, except for a median oval, membranous area which extends from near base to apex of sternite; epuliculum ventrale long, slightly, irregularly curved and basally articulated. Aedeagus (Figs 13, 16, 19, 22) with short, asymmetrical, laterally compressed phallobase, about a third the length of parameres, which are fused together at basal half to form a tube; apex of parameres narrowly rounded, truncate or slightly expanded to form lateral tooth. Penis relatively short, body about half as long as parameres, but with paired anterior struts which may extend almost to base of parameral tube; penis usually attached to parameres at point where parameral tube ends and free parameres begin. Ovipositor moderately long and slender; paraprocts with longitudinal bacula 1.5 to 2.5 times as long as coxites, which are moderately sclerotized, narrowed apically and divided into two parts; styli minute and laterally attached. Female genital tract (Figs 24, 25) enlarged anteriorly to form an elongate to almost spherical uterus, to which the common oviduct and spermathecal duct are separately attached; bursa copulatrix absent; spermatheca elongate and cylindrical, finely transversely ridged, with a basal collar and apical invaginated pocket; spermathecal gland attached basally just beyond the collar.

Description of presumed larva. – Material. One larva associated with adults of *Anischia kuscheli* sp. n. New Caledonia: Mt. Rembai, 800m, 21.x.1978, 78/244, 78/245, sifted litter and rotten wood, G. Kuschel (NZAC). The identification is based in part on the length of the larva and the association of *Anischia kuscheli* adults in the same sample. In addition, two species of *Anischia* are very common in this habitat in New Caledonia, and the larva is of a highly derived eucnemid type, which differs in a number of respects from any previously known eucnemid larva.

Length 5 mm. Body elongate, parallel-sided, moderately strongly flattened; dorsal surfaces more heavily sclerotized than ventral ones; color of head uniformly dark reddish-brown; protergum and mesotergum reddish-brown; metatergum and abdominal terga yellowish-brown; ventral surfaces mainly yellow (Figs 5, 6). Surfaces of metatergum, abdominal terga and lateral portions of mesotergum with weakly impressed, fine reticulation; vestiture consisting of a few localized macrosetae, numerous microsetae (some forming transverse rows) and ventral patches of dense spicules and microtrichia (Fig. 10). Head (Figs 8, 9) prognathous and protracted, wedge-like, about as long as wide, widest at base, slightly narrowing anteriorly and broadly truncate at apex; in side view tapering from base to apex; dorsal surface slightly shorter than ventral (so that head is slightly raised), with broad, sinuate basal emargination at each end of which is a small excavation, from which extends a longitudinal furrow ending in a long seta; a second pair of small excavations ventrally, almost at the lateral edge of the head base. One small sterna in front of and lateral to end of each furrow. Epicranial stem and frontal arms absent. Antennae short, 2-segmented, with large sensorium; located in cavities, so that their insertions are concealed from above. Labrum entirely fused to head capsule, with no indication of a clypeo-labral suture. Mandibles movable and opposable (broadly overlapping when closed), broad at base, abruptly narrowed and abruptly curved at basal third, straight apically with a subacute apex and grooved mesal edge. Maxilla without apical lobes; palps 2-segmented. Labium without ligula; palps 1-segmented and widely separated. Postmentum extends to basal edge of head capsule, where it separates two halves of epicranium; maxillae extend almost to base of head, as a very narrow strip of cuticle on either side of postmentum. Thorax: Ratio of segments about 1: 1.15: 1.3. Protergal plate simple, occupying most of dorsum, except for narrow membranous strip anteriorly, extending onto ventral surface but with no distinct lateral edges, largely undivided, with median
ecdysial line at posterior fifth only. Meso- and metathoracic dorsum each with wider anterior strip, narrow posterior strip, not or only slightly extending onto ventral surface and tergal plates completely divided by median ecdysial line. Few macrosetae evident: 1 lateral and 1 lateroventral on each side; microsetae forming transverse rows near anterior and posterior edges of meso- and metatergites. Presternal area delimited only laterally by heavily sclerotized internal rods, which converge posteriorly but do not meet; middle of venter with narrow, transverse spicule patch extending across mesal third; prothoracic legs located at each end of this patch. Mesothoracic spiracle located on lightly pigmented area between prothorax and mesothorax. Anterior edge of mesothoracic venter with a larger, strongly transverse spicule patch with 2 posterior arms forming a π figure. At anterior third, 2 obliquely oval spicule patches extend from near midline antero-laterally, with mesothoracic legs at their ends. Anterior edge of metathoracic venter with larger spicule patch forming a broad V-shaped figure. At the posterior fourth of the venter with pair of comma-shaped patches with the legs at their lateral ends. Legs articulated and more or less similar to one another; each leg with single, short and broad segment, bearing 3 or 4 long, stout setae, and several shorter setae at its apex. Abdominal segments I–VIII subequal in length, each with with relatively large, simple tergite; anterior edge with small median cavity flanked by pair of mesally projecting sclerotized knobs; posterior edge with transverse row of microsetae. Abdominal sterna I–VII each with a large goblet-shaped spicule patch, with stem facing posteriorly and base concave, except for that on VII, which is flat. Sternum VIII with small, semi-circular patch near anterior and posterior edges of meso- and metatergites. Presternal area delimited only laterally by heavily sclerotized internal rods, which converge posteriorly then sides of parameral tube usually merging with lateral carinae; if posteriorly (Fig. 21); antennal club 3–segmented; pronotal punctation coarser and denser; Australia .................. monteithi Lawrence sp. n.

abdomen, its sclerite vertically, slightly obliquely oval; abdominal spiracles with circular sclerite, located laterally in membrane.

Included Species. – The genus currently includes two species from Bolivia, two from Mexico and one from New Guinea, in addition to Afranischia ruandana (Basilewsky), which is here transferred to Anischia (see below). In addition, three new species are described from the Australo-Pacific region, and several more have been seen from Panama, Colombia, Peru, Brazil, the Philippines, New Britain, Solomon Is., Vanuatu and Fiji.

Biology. – Little is known about the habits of Anischia species. A. mexicana Fleutiaux has been collected in Panama from a fungus growing on the surface of logs and in Mexico from a fungus growing on dead, standing tree together with numerous erotylids. Specimens of A. bicolor were found in the fruiting bodies of two polypores, repeatedly on Loweporus roseoalbus (Jungh.) Ryvarden and once on Pycnoporus sanguineus (Linnaeus: Fries) Murrill, infested with Ciidae, while others were taken in sifted litter and rotten wood or by pyrethrum fogging trunks and logs. A single specimen was also collected in flowers of Meryta. Specimens of A. kuscheli, associated with the only known larva, were in sifted white-rotten wood. Both A. kuscheli and A. monteithi have also been collected by pyrethrum fogging logs, and an undescribed Fiji species was beaten from dead branches.

Key to the described species of Anischia occurring in the Old World

1. Greatest distance between inner discal carinae always less than 0.7 times greatest pronotal width; outer discal carinae well removed from lateral carinae; postcoxal lines on each side of ventrite 1 not meeting posteriorly (Fig. 15)........ 2
   – Greatest distance between inner discal carinae always more than 0.75 times greatest pronotal width; outer discal carinae very close to and usually merging with lateral carinae; if postcoxal lines on each side of ventrite 1 not meeting posteriorly, then sides of parameral tube not sinuate .............................................................................................................................................. 3
2 Length 3 mm or less; Australia, New Guinea .. ................................................................. stupenda Fleutiaux
   – Length 3.5 mm; central Africa .. .......................................................... ruandana (Basilewsky)
3. Postcoxal lines on each side of ventrite 1 not meeting posteriorly (Fig. 21); antennal club 3-segmented; pronotal punctation coarser and denser; Australia ................. monteithi Lawrence sp. n.
Figs 11-22. *Anischia bicolor*. 11. Left half of pterothorax in vicinity of mesocoxa, showing postcoxal lines; line = 0.1 mm. 12. Left half of abdominal ventrite 1, showing postcoxal lines; line = 0.1 mm. 13. Aedeagus, ventral; line = 0.1 mm. Figs 14-16. *A. stupenda*. 14. Left half of pterothorax in vicinity of mesocoxa, showing postcoxal lines; line = 0.1 mm. 15. Left half of abdominal ventrite 1, showing postcoxal lines; line = 0.1 mm. 16. Aedeagus, ventral; line = 0.1 mm. Figs 17-19. *A. kuscheli*. 17. Left half of pterothorax in vicinity of mesocoxa, showing postcoxal lines; line = 0.1 mm. 18. Left half of abdominal ventrite 1, showing postcoxal lines; line = 0.1 mm. 19. Aedeagus, ventral; line = 0.1 mm. Figs 20-22. *A. monteithi*. 20. Left half of pterothorax in vicinity of mesocoxa, showing postcoxal lines; line = 0.1 mm. 21. Left half of abdominal ventrite 1, showing postcoxal lines; line = 0.1 mm. 22. Aedeagus, ventral; line = 0.1 mm.
– Postcoxal lines on each side of ventrite 1 meeting posteriorly to form single curved line (Figs 12, 18); antennal club 4- or 5-segmented; pronotal punctuation finer and sparser; New Caledonia

4. Head, pronotal disc and most of hypomera dark brownish-black in color; in sharp contrast to reddish-brown elytra, pterothorax and abdomen; postcoxal lines behind each mesocoxal cavity not meeting posteriorly; postcoxal lines on each side of ventrite 1 meeting at or very close to posterior edge of ventrite (Fig. 12); parameral tube of aedeagus abruptly narrowed apically (Fig. 13) ..............................

.......................................

A. bicolor Lawrence sp. n.

– Head and prothorax reddish-brown in color, only slightly darker than yellowish brown elytra, pterothorax and abdomen; postcoxal lines behind each mesocoxal cavity meeting posteriorly to form a single curved line; postcoxal lines on each side of ventrite 1 meeting well before posterior edge of ventrite (Fig. 18); parameral tube of aedeagus not abruptly narrowed apically (Fig. 19) ..... A. kuscheli Lawrence n. sp.

Anischia bicolor Lawrence, sp. nov.

(Figs 1, 11–13, 23, 24)

Type material. – Holotype, male, NEW CALEDONIA: Pic d’Amoa, north slopes (20º58’ S, 165º17’ E), 500m, 31.i.2002, 8906, pyrethrum trees & logs, G. Monteith (QMB). Paratypes (74 specimens): Aoupinie, (21º11’ S, 165º19’ E), 850m, 20.xi.2000, 9926, pyrethrum, trunks & logs, G. B. Monteith (1, QMB); Aoupinie, top camp (21º11’ S, 165º18’ E), 2-3.xi.2001, 8716, pyrethrum, trees & logs, C. Burwell, G. Monteith, (1, QMB); Ateou (NNE of Kone) (20º37’ S, 165º54’ E), 700m, 27.xi.2001, 8700, pyrethrum, trees & logs, G. Monteith (1, QMB); Col d’Amieu, 6 km NNE (21º33’ S, 165º51’ E), 300m, 13.xi.2000, 9923, pyrethrum, trunks & logs, G. B. Monteith (2, QMB); same locality, 11.xi.2001, 8678, pyrethrum, trees & logs, C. J. Burwell (2, QMB); Col d’Amieu, sawmill (21º35’ S, 165º48’ E), 400m, 11476, flight intercept trap, G. B. Monteith (1, QMB); Col d’Amieu, west slope (21º37’ S, 165º49’ E), 470m, 17.ix.2002, 11180, pyrethrum, logs, G. B. Monteith (1, QMB); same locality, 25.xi.2003, 11427, pyrethrum trees & logs, G. Monteith (8, FMNH, QMB); same locality, 25.xi.2003-27.1.2004, 11475, flight intercept traps, G. Monteith (1, QMB); same locality, 27.i.2004, 11517, pyrethrum log with epiphytes, G. Monteith (1, QMB); Col de Mourirange, 30 km E of Noumea, 300m, 11.viii.1978, S & J. Peck (1, ANIC); Gelima, 5 km. S (21º35’ S, 165º58’ E), 485 m, 15.ix.2002, 11187, pyrethrum trees & logs, G. Monteith, C. Burwell (2, QMB); Kavatch, near Hienghêne, 450m, 28.x.1978, 78/261, sifted litter and rotten wood (4, NZAC); Mandjelia, subsummit (20º24’ S, 164º32’ E), 700m, 6–7.x.2001, 8754, pyrethrum, trees & logs, G. B. Monteith (1, QMB); Col Dzumac road (22º03’ S, 166º28’ E), 700m, 1.xii.2000, 9913, pyrethrum trunks & logs, G. B. Monteith (1, QMB); Monts de Koghis, 420m, 21.i.1979, Meryta flowers, W. C. Gagne, G. M. Nishida, G. A. Samuelson (1, BMH); Mt. Koghis. Track entrance (22º03’ S, 166º02’ E), 700m, 1.xi.2000, 9913, pyrethrum trunks & logs, G. B. Monteith (1, QMB); Mont de Koghis, nr. Noumea, 31.viii.1978, S. & J. Peck (1, ANIC); same locality, 4–6.v.1996, on fruiting bodies of Loweporus roseoalbus,

Figs 23-25. Anischia bicolor. 23. Pterothorax, ventral, both mesocoxae removed; line = 0.1 mm. 24. Internal female tract; line = 0.1 mm. Fig. 25. A. kuscheli. Internal female tract; line = 0.1 mm.
Diagnosis. – The strong contrast between the dark brown or black pronotum and red elytra separates this species from all other Anischia. The two Australian species, A. stupenda and A. monteithi, differ from bicolor in having coarser and denser pronotal punctation, and in both the postcoxal lines on each side of metaventrite and ventrite 1 do not meet posteriorly to form a single curved line. The broadly sympatric A. kuscheli differs from bicolor in the more uniform coloration, less inflated pronotum, the postcoxal lines on each side of metaventrite and ventrite 1 meeting very close to posterior edge of ventrite. Aedeagus about as long as median lengths of last 2 ventrites combined; parameral tube gradually expanded to about middle, then abruptly narrowed to apex, where free portions of each paramere are very narrowly rounded.

Variation. – Measurements in mm (n = 11): TL 1.72–2.60 (2.02 ± 0.19); PL 0.44–0.64 (0.55 ± 0.05); PW 0.60–0.88 (0.71 ± 0.07); EL 1.16–1.76 (1.35 ± 0.13); EW 0.64–0.92 (0.77 ± 0.07). Ratios: BL/EW 2.26–2.67 (2.48); PL/PW 0.69–0.82 (0.77), EL/EW 1.60–1.92 (1.77); EL/PL 2.29–2.78 (2.48).

Remarks. – The unusual dark brown pronotum and contrasting yellowish-red elytra in this species occurs in a large number of small beetles from New Caledonia, forming what appears to be a mimicry complex; included among these are several Staphylinidae, Scydaenidae, Laemophloeidae, Cerylonidae (Ostomopsis), Endomychidae, Corylophidae, Latridiidae, Ciidae and Salpingidae.

Anischia boliviana Fleutiaux, 1896

Anischia boliviana Fleutiaux 1896a: 300. Type data: BOLIVIA: Cochabamba (Germain).

Remarks. – This species differs from most species in the more elongate prothorax, which is widest anteriorly, the sides being very slightly curved and almost parallel. As in A. mexicana, the antennae are gradually thicker apically, without a distinct club, and the apical antennomere is longer than the preceding two combined. Although types have not been examined, specimens tentatively identified as this species have been seen from above the Rio Cauraburi in northern Amazonas, Brazil (MZSP).

Anischia germaini Fleutiaux, 1896

Anischia germaini Fleutiaux 1896a: 301. Type data: BOLIVIA: Cochabamba (Germain).

Remarks. – A. germaini and A. boliviana were both described from Germain material collected at Cochabamba; however the reported differences in the length of the discal carinae suggests that they are not merely the two sexes of one species.
**Anischia kuschei** Lawrence, sp. nov.
(Figs 3, 17–19, 25)


**Diagnosis.** – This species is easily distinguished from *A. bicolor*, the only other species in New Caledonia, by the more slender body, which is more uniformly reddish-brown, the less inflated pronotum, the postcoxal lines on the metaventrite, which are joined posteriorly, and the form of the parameral tube, which is not abruptly narrowed at apex. It may be distinguished from the Australian *A. monteithi* by postcoxal lines on both metaventrite and ventrite 1 being joined posteriorly.

**Description.** – Total length 1.75–2.45 mm. Color reddish-brown except for elytra and legs, which are yellowish-brown; vestiture of moderately long, dense, decumbent, yellow hairs. Antennae with 5-segmented club; ratio of antennomere lengths: 2.4: 1.4: 1.6: 1.4: 1.2: 1.2: 1: 1.2: 1.4: 1.4: 2.4; length/width ratios of antennomeres: 2: 2.33, 2.67, 2.33, 1.5, 1.2, 0.83, 0.86, 1: 1: 1.7. Pronotum about four-fifths as long as wide; disc moderately strongly convex, very finely punctate and shining, with outer discal carinae very close to and merging with lateral carinae and greatest distance between inner discal carinae about 0.75 to 0.8 times greatest pronotal width. Elytra about twice as long as width and 2.75 times as long as pronotum. Postcoxal lines on mesoventrite behind each mesocoxal cavity meeting posteriorly to form continuous angular line. Postcoxal lines on each side of ventrite 1 meeting well before posterior edge of ventrite. Aedeagus slightly longer than median lengths of last 2 ventrites combined; parameral tube gradually expanded to apical third, then narrowed and subacute at apex.

**Variation.** – Measurements in mm (n = 22): TL 1.75–2.45 (2.07 ± 0.17); PL 0.40–0.64 (0.52 ± 0.06); PW 0.54–0.80 (0.66 ± 0.06); EL 1.20–1.64 (1.42 ± 0.11); EW 0.60–0.84 (0.72 ± 0.06). Ratios: BL/EW 2.55–2.90 (2.70); PL/PW 0.74–0.85 (0.78); EL/EW 1.87–2.10 (1.98); EL/PL 2.56–3.00 (2.76).

**Anischia mexicana** Fleutiaux

*Anischia mexicana* Fleutiaux 1896b: 261. Type data: MEXICO: Motzorongo (Becker).

*Anischia crassicornis* Champion 1897: 668. New synonymy. Type data: MEXICO: Motzorongo in Vera Cruz (Flohr); GUATEMALA: Pantaleon (Champion); PANAMA: Bugaba (Champion).

**Remarks.** – Although the type material of *A. mexicana* has not been examined, it is fairly obvious from the descriptions that Champion’s material from Motzorongo, Vera Cruz, Mexico (cited as coming from the Flohr collection) is conspecific with that described by Fleutiaux from the same locality and collection. One of us (JM) has studied syntypes of *A. crassicornis* and seen further specimens from Mexico (Cozumel) and Panama (Canal Zone).

**Anischia monteithi** Lawrence, sp. nov.
(Figs 4, 20–22)


**Diagnosis.** – This species differs from *stupenda* in the longer, narrower prothorax with the inner discal carinae more widely separated and the outer ones less obvious and much closer to the lateral carinae, the 3-segmented antennal club, and the differently shaped parameres. It resembles the New Caledonian *A. kuschei* in general form, but
in that species the metathoracic and abdominal lines on each side meet to form a continuous curve.

**Description.** – Total length 2.0–2.4 mm. BL/EW 2.47–2.76. Color reddish-brown except for elytra and legs, which are yellowish-brown; vestiture of moderately long, dense, decumbent, yellow hairs. Antennae with a well marked, 3-segmented club; ratio of antennomere lengths: 2.67: 2: 1.67: 1: 1.33: 1.33: 2: 2: 2.67; length/width ratios of antennomeres: 1.6, 2, 1.67, 1, 1, 0.9, 0.8, 0.86, 0.86, 1.33. Pronotum about 0.75 times as long as wide; disc moderately convex and more coarsely and densely punctate than in *kuscheli* with longer, slightly curved inner discal carinae, the greatest distance between which is 0.78–0.83 times greatest pronotal width; outer discal carinae very close to lateral carinae but not converging with them. Elytra about 1.9 times as long as wide and 0.6 times as long as pronotum; disc moderately convex and densely punctate. Aedeagus about as long as median lengths of last 3 ventrites combined; parameral tube abruptly expanded at about middle; apex of each paramere narrowly rounded.

**Variation.** – Measurements in mm (n = 9): TL 1.75–2.40 (2.14 ± 0.18); PL 0.68–0.96 (0.84 ± 0.08); PW 0.92–1.24 (1.11 ± 0.10); EL 1.92–2.60 (2.29 ± 0.19); EW 1.00–1.36 (1.22 ± 0.11). Ratios: BL/EW 2.47–2.70 (2.57); PL/PW 0.73–0.80 (0.76); EL/EW 1.80–1.96 (1.88); EL/PL 2.50–2.82 (2.57).

**Anischia ruandana** (Basilewsky)


**Remarks.** – Basilewsky (1955: 155) erected the genus *Afranischia* based mainly on the belief that this species had neither an exposed labrum nor a prosternal chin piece. A study of the female holotype (by JM) showed this to be an error.

**Anischia stupenda** Fleutiaux (Figs 2, 14–16)

*Anischia stupenda* Fleutiaux 1897: 555. Type data: NEW GUINEA: Ighibirei, vii–viii.1890 (Loria); INDONESIA: Ile Engano [off southwest coast of Sumatra], Malacconii, vi.1891 (Modigliani).


**Diagnosis.** – This species is easily distinguished by the relatively short and broad pronotum, with inner discal carinae distinctly closer together than in other described species (greatest distance between them less than 0.7 times greatest pronotal width) and the outer discal carinae more obvious and well separated from the lateral carinae. *A. stupenda* differs from both New Caledonia species in having the two postcoxal lines on each wide of ventrite 1 separated and not forming a continuous curve. From *A. monteithi*, with which it is sympatric in Australia, it differs in having a 4-segmented antennal club. The parameral tube is also unique in being laterally sinuate.

**Redescription.** – Total length 2.5–3.0 mm. Body about 2.6 times as long as wide. Color reddish-brown except for elytra and legs, which are yellowish-brown; vestiture of moderately long, dense, decumbent, yellow hairs. Antennae with weak, 4-segmented club; ratio of antennomere lengths: 2.2: 1.1: 1.5: 1.1: 1.1: 1.1: 1.3: 1.3: 3; length/width ratios of antennomeres: 2, 1.67, 2.2, 1.5, 1.36, 1.2, 1.2, 1.1, 0.86, 0.87, 0.87, 2. Pronotum about 0.7 times as long as wide; disc moderately convex, moderately coarsely and densely punctate; inner discal carinae relatively close together, the greatest distance between them about 0.63–0.695 times greatest pronotal width; inner discal carinae swell developed, moderately long, straight and well deparated from lateral carinae. Elytra about 1.9 times as long as wide and 3 times as long as pronotum. Aedeagus (Fig. 16) slightly longer than median lengths of last 2 ventrites combined; parameral tube gradually expanded and sinuate apically; apex of each paramere expanded laterally, forming a blunt tooth.

**Variation.** – Measurements in mm (n = 11): TL 2.30–3.00 (2.63 ± 0.18); PL 0.92–1.04(0.99 ± 0.06); PW 1.32–1.68 (1.44 ± 0.10); EL 2.76–3.16 (2.93 ± 0.16); EW 1.40–1.76 (1.51 ± 0.10). Ratios: BL/EW 2.50–2.66 (2.59); PL/PW 0.64–0.71 (0.69); EL/EW 1.84–2.00 (1.94); EL/PL 2.83–316 (2.97).
Genus Perothops Laporte

Perothops Laporte 1838: table. Type species, Perothops cervinus Germar, by subsequent monotypy (Germar 1839: 197) (see Hayek 1983).

Redescription of Adult. – Total length 10–18 mm. Body moderately elongate, about 3 times as long as wide, parallel-sided, moderately to strongly convex dorsally and ventrally. Colour brown to gray; vestiture consisting of very short, fine, decumbent hairs and longer suberect hairs, more or less uniformly distributed. Head about as long as wide, moderately declined, deeply inserted into prothorax; posterior edge (dorsal rim of occipital foramen) biemarginate; occipital carina fine, incomplete at middle and laterally behind each eye, continuing below eyes as weak subgenal ridges. Eyes large, vertically oval, not protruding, slightly emarginate posteriorly, finely facetted; ommatidium of acone, without clear zone; median endocarina absent. Frontoclypeal area at midline only slightly, gradually declined. Laterally raised to form weak supra-antennal ridges, which may or may not be joined at middle by sharp ridge; antennal insertions exposed, separated by about 1.5 times diameter of antennal socket. Frontoclypeal suture absent; clypeus broadly rounded apically; subantenal grooves absent. Gular sutures well developed; gula 0.6 times as long as wide. Corporotentorial bridge narrow and slightly arched; laminatentoria slightly expanded but not meeting one another. Cervical sclerites well developed, each divided into 2 parts. Antennae 11-segmented, filiform, extending posteriorly to about anterior fourth of elytra; scape 2 to almost 3 times as long as pedcel, which is attached subapically; antennomere 3 more than twice as long as wide; apical antennomere, slightly expanded, flattened and wedge-like apically. Labrum not or only barely visible, lying beneath clypeus, strongly transverse, well sclerotized, emarginate apically. Mandibles stout, strongly curved, unidentate and acute; mola and prostheca absent. Maxillary lobes subequal, narrowly elongate; galea narrowly rounded apically and generally setose; lacinia obliquely truncate with dense setae along oblique edge; terminal maxillary palpmere slightly expanded and obliquely truncate apically. Labium with bilobed ligula; terminal palpmere expanded and obliquely truncate apically. Proventriculus weakly developed, with setose pads but no saw-like teeth. Pronotum about 0.75 times as long as wide, widest at about middle, sides moderately rounded, sinuate posteriorly, with lateral carinae very fine and incomplete to almost absent, not visible for their entire lengths from above; anterior angles absent; posterior angles acute and more or less produced; posterior edge more or less bisinuate forming median truncate lobe with pair of lateral incisions; interlocking device well-developed. Disc strongly convex, with weak median groove extending from posterior edge to middle or anterior third. Hypomeran without antennal grooves or cavities; notosternal suture complete. Prosternum well developed in front of coxae, moderately convex, produced anteriorly to form short, broad, truncate chin-piece, which is slightly curved ventrally and bears a broad, concave, head rest above; prosternal process extending well behind coxae, slightly convex, about as wide as coxal cavity, parallel-sided to posterior edge of coxae, where sides abruptly converge to narrowly rounded apex. Procoxae globular with almost no internal extension; trochantinopleuron reduced, concealed and fused to wall of hypomeran. Procoxal cavities moderately broadly open; notal projections short and subacute. Scutellum well developed, abruptly elevated basally, with straight basal edge, slightly rounded lateral edges and broadly rounded apex. Elytra about 2.25 times as long as wide, subparallel, broadly, conjointly rounded apically; anterior edge of each with sharp transverse carina extending from sides of scutellum, to humerus and concealing deep cavity into which a notal process fits when prothorax and elytra interlocked; second carina begins beneath humerus and extends to elytral apex delimiting epipleura; disc with 9 fine striae, which may be interrupted in several places, and no scutellar strole; epipleura broad at base, gradually narrowing to metacoxae, then abruptly narrowing and complete to apex. Mesoventre almost as long as wide; anterior edge at middle with deep notch bordered by raised lip continued posteriorly as diagonal slide leading into large, deep cavity, extending well beyond anterior edges of mesocoxae, which are globular and separated by distance about half the longest diameter of one. Mesocoxal cavity on each side laterally open (partly closed by meseponer and not by meeting of meso- and metaventre). Mesanepisternum separated from meseponer by complete pleural suture. Meso metaventral junction distinctly sinuate, with metaventral knob fitting into cavity in mesoventre. Metaventre slightly transverse,
Spiracles on segments I–VIII, located in pleural acute. Tergites membranous or lightly sclerotized. Able; posterolateral corners of 2–4 produced and 2 distinctly connate, 3–5 at least slightly movable; ventrites 1 somewhat longer than 2, with apex strongly oblique, CuA1+2 arising near apical third of cell and only slightly curved apex. Penis long and slender, extending well beyond parameral apices, slightly flattened, anteriorly with paired ventral struts and dorsal process which is fused to parameres. Ovipositor elongate and slender; paraprocts with longitudinal baccula about 5 times as long as coxite, which is indistinctly divided into 2 parts of equal width, apical one slightly longer than basal one, styli well developed, terminal. Female genital tract with large, bilobed bursa; spermatheca elongate, attached by short duct between bases of two bursal lobes; spermathecal gland attached by long, narrow duct to base of spermatheca.

**Description of presumed larva** (Figs 26–31). – Material. One unassociated larva (late instar), of either *Perothops cervinus* or *P. witticki*. San Diego, California, U. S. A., 1-4-65, USDA 65-1485. In soil. E. D. Algert, coll. ‘Family unc., poss. Elateridae’ D. M. Anderson (L. 166) (NMNH). Although this larva was neither reared nor associated with adult *Perothops*, we feel that identification to the generic level is reasonable based on the following considerations: 1) the larva definitely belongs to the elateroid complex and has most of those features characterizing the family Euconemidae and lacking in Elateridae, such as the highly modified and immovable ventral mouthparts and highly reduced legs; 2) it lacks those character states found in the many known examples of the more derived eucnemid subfamilies Melasinae, Euconeminae and Macraulacinae, and is of a type to be expected in a more basal member of the family; 3) of those more basal Euconemidae occurring in North America, larva of *Palaeoxenus dohroni* and *Schizophilus subrufus* are known and are of a very different type; 4) larvae of *Anelastes* moderately convex, with discrimen about three-fourths as long as ventrite; postcoxal lines absent. Visible portion of metepisternum about 5 times as long as wide and more or less parallel-sided, anterior edge distant from mesocoxal cavity. Metacoxae slightly oblique, contiguous, extending laterally to meet epipleura; coxal plates well developed, complete but narrowed laterally. Metendosternite with long, narrow stalk, relatively short, oblique arms and short, bilobed anterior process with anterior tendons well separated (one on each rounded lobe). Hind wing about 2.75 times as long as wide; apical region about 0.15 times total wing length, with vague anterior and posterior linear oblique sclerites. Radial cell about 4.5 times as long as wide with posterobasal angle more or less right; cross-veins r3 very slightly oblique, almost longitudinal; cross-vein r4 arising towards apex of cell, long and slightly sinuate. Basal portion of RP long, extending to basal third of wing, slightly angulate; radio-medial loop relatively narrow; medial spur slightly curved, reaching wing margin. Medial field with 5 free veins, all reaching wing margin; MP3+4 with well developed basal cross-vein and spur, CuA1 joining it before MP3-MP4 fork; base of MP3 incomplete; wedge cell distinctly longer than medial spur, 4 times as long as wide, with apex strongly oblique, CuA1+2 arising near apical third of cell and only slightly longer than CuA1; AA3 meeting CuP near base of wedge cell. Anal notch absent; AP long, straight, reaching margin. Legs moderately short and stout; fore leg and mid leg with trochanterofemoral joint slightly oblique and femur subequal in length to tibia; protibia slightly expanded apically; protibia and mesotibia with paired spurs. Hind leg with trochanter enlarged and mesally expanded with trochanterofemoral joint strongly oblique; tibia distinctly longer than femur; metatibia with single spur. Tarsomeres simple, but 1–4 densely clothed and 2 distinctly longer than femur; metatarsomere 1 enlarged in trochanterofemoral joint strongly oblique; tibia; protibia slightly expanded apically; protibia slightly oblique and femur subequal in length to fore leg and mid leg with trochanterofemoral joint either reaching margin. Legs moderately short and stout; coxae slightly oblique, contiguous, extending laterally to meet epipleura; coxal plates well developed, complete but narrowed laterally. Metendosternite with long, narrow stalk, relatively short, oblique arms and short, bilobed anterior process with anterior tendons well separated (one on each rounded lobe). Hind wing about 2.75 times as long as wide; apical region about 0.15 times total wing length, with vague anterior and posterior linear oblique sclerites. Radial cell about 4.5 times as long as wide with posterobasal angle more or less right; cross-veins r3 very slightly oblique, almost longitudinal; cross-vein r4 arising towards apex of cell, long and slightly sinuate. Basal portion of RP long, extending to basal third of wing, slightly angulate; radio-medial loop relatively narrow; medial spur slightly curved, reaching wing margin. Medial field with 5 free veins, all reaching wing margin; MP3+4 with well developed basal cross-vein and spur, CuA1 joining it before MP3-MP4 fork; base of MP3 incomplete; wedge cell distinctly longer than medial spur, 4 times as long as wide, with apex strongly oblique, CuA1+2 arising near apical third of cell and only slightly longer than CuA1; AA3 meeting CuP near base of wedge cell. Anal notch absent; AP long, straight, reaching margin. Legs moderately short and stout; fore leg and mid leg with trochanterofemoral joint slightly oblique and femur subequal in length to tibia; protibia slightly expanded apically; protibia and mesotibia with paired spurs. Hind leg with trochanter enlarged and mesally expanded with trochanterofemoral joint strongly oblique; tibia distinctly longer than femur; metatibia with single spur. Tarsomeres simple, but 1–4 densely clothed...
species (two of which occur in California) are unknown, but adults are always less than 13 mm usually less than 10 mm in length; 5) Perothops cervinus and P. witticki both occur in southern California and may be as large as 16 and 22 mm, respectively.

Length about 40 mm. Body (Fig. 26) elongate, subcylindrical to slightly flattened, more or less parallel-sided, but widest at metathorax, then slightly narrowing posteriorly to abdominal segment VI, segments VII to IX distinctly narrower and of equal width; thoracic segments and abdominal segments I–VI more or less inflated at middle and strongly narrowed at either end; very lightly pigmented and whitish-cream in color, except for dark brown mandibles, pretarsi and urogomphi, and light yellow pigment on head, at middle of protergum, on pre sternum and on posterior portion of tergum IX; surfaces appearing simple under lower magnifications, but most of them covered with light, variable rugosity; vestiture of short fine hairs. Head (Figs 27, 29–31) about half as long as wide, prognathous, protracted and strongly raised, depressed and wedge-like anteriorly; ecdysial lines not apparent; posterior edge with moderately broad, mediiodorsal emargination flanked by two narrower emarginations; occipital foramen entirely lined with thick supporting ridge, from which arise dorsal and ventral endocarinae; dorsal endocarinae arising from median emargination, separated at base, relatively short, extending to middle of head capsule, and slightly diverging; ventral endocarina on each side arising from junction between labium and maxilla and that between maxilla and ventral portion of head capsule, the two converging and meeting at posterior edge of head, and the lateral pair extending anteriorly to meet mandibular articulations. Stemmata absent. Antennae 2-segmented, about 0.125 times as long as head width; antennomere 1 about twice as long as wide and twice as long as 2, which is much narrower; sensorium on basal antennomere shorter than apical antennomere. Frontoclypeal and clypeolabral sutures absent; clypeolabrum projecting in front of mandibular articulations forming nasale which is about a third as long as wide and broadly emarginate at apex. Mandibles about as long as head capsule, symmetrical, stout, about twice as long as wide at base, very slightly curved mesally but not or barely meeting at midline; mandibular apex forming single, narrowly rounded lobe; incisor edge with short, apically projecting retinaculum; mesal surface at base with brush of hairs; mola absent. Ventral mouthparts deeply retracted; maxilla consisting of fused cardo and stipes, which form an elongate sclerite narrowing to point posteriorly, with slender, sclerotized mala, 4-segmented palp and no articulating area. Postmentum narrowly elongate, slightly widening posteriorly, more or less connate with maxillae, and extending to posterior edge of head; pre mentum bifid apically, with 2-segmented palps; ligula absent. Hypostomal region absent (labium contiguous with thorax). Prothorax slightly shorter and narrower than meso- or metathorax; protergum lightly pigmented mesally (light yellow), sculpturing relatively simple with pair of irregularly branched, oblique lines converging posteriorly and almost meeting at midline, where there is a short median longitudinal line; lateral regions transversely rugulose; presternum subtriangular, lightly pigmented, with paired oblique endocarinae and a short, longitudinal endocarina. Legs (Fig. 28) articulated, 5-segmented, highly reduced, separated by about 7 basal coxal diameters; coxa short, broad, dome-like, trochanter and femur less than half diameter of coxa, short and broad, disk-like; tibiotarsus about as long as wide; pretarsus longer than remaining segments combined, very slender, curved, dark brown basally, depigmented apically, without apparent setae. Mesothorax, metathorax and abdominal segments I–VI usually with paired, complexly rugulose areas on dorsum separated by longitudinal rugulæ and bordered anteriorly and posteriorly by transverse rugulæ; lateral regions with longitudinal rugulæ; venter with rugulose areas more or less similar to those on dorsum; surfaces of segments VII and VIII with simpler, finely transversely rugulose. Tergum IX lightly sclerotized near posterior end; surface very lightly but complexly sculptured; urogomphi short, about 0.1 times as long as basal width of segment, approximate, strongly upturned, darkly pigmented and acute apically; sternum 9 deeply emarginate, without teeth or asperities; segment X elongate, oval, without teeth or asperities. Spiracles biforous, with closing apparatus, more or less equal in size, surrounded by spiracular ring; thoracic spiracle lying between prothorax and mesothorax, those on abdomen located laterally near anterior edge.

**Distribution.**—Three species of *Perothops* are known from North America: *P. mucida*
(Gyllenhal) from the eastern United States (Pennsylvania, North Carolina, Florida), *P. cervinus* Lacordaire from southern California, and *P. witticki* from northern California. A key to the species and illustrations of the aedeagi are given in Cobos (1964: 430–435).

**Cladistic Analyses**

We used parsimony as the optimality criterion in all our analyses. The morphological matrix was analyzed with the program PARANONA, a parallelized multiprocessor version of NONA (Goloboff, 1999) operating under the WinClada front-end (Nixon, 2002). All characters were treated unordered. The analyses were run using both the parsimony ratchet (Nixon, 1999) and a traditional heuristic approach (Goloboff, 1999). When calculating with the parsimony ratchet we used the programs default values except for the number of replicates, which was increased to 1000. In the standard analyses with PARANONA we used the command line hold*; hold/2; mult*100; max*; ss*; swap*. These commands perform a standard heuristic search, their exact meaning is explained in the NONA manual (Goloboff, 1999). If multiple trees were obtained, we used the strict consensus tree as the most reasonable representation of the result.

The “stability” of the result is often measured

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**Fig. 32. Consensus tree, morphological data.**
with resampling frequencies or clade support measures. It is useful to remember, that the earlier elateroid studies were based on well supported trees and still in conflict with each others (Muona, 1995). Support is of course only a reflection of the particular data set analyzed. Bergsten (2005) stressed the importance of sampling in order to avoid problems due to long branch attraction (LBA). Such problems may well affect morphological data sets as well as molecular ones. In the combined analysis of morphological and molecular data we used a heuristic search. The command line was:

```
po -norandomizeoutgroup -gap 1 -seed -1 -noleading -replicates 100 -buildsperreplicate 10 -stopat 10 -minstop 30 -slop 2 -checkslap 30 -maxtrees 100 -fitctrees [DATA].
```

The commands are explained in the POY manual (Janis & Wheeler, 2002).

We used the parsimony jackknifer (Farris) as implemented in POY to estimate the clade support of our combined data set result. The command line used was:

```
po -norandomizeoutgroup -gap 1 -seed -1 -noleading -jackboot -replicates 1000 -jackfre- quencies all -jackftree [DATA].
```

**Results**

*Morphological analyses.* – The parsimony ratchet option and the traditional heuristic search gave identical results as follows:

1. Including all taxa and having *Phaneus* as the outgroup resulted in five trees, length 536 steps. In the strict consensus (Fig. 32), a polytomy with three main clades is present: the thorscid clade (*Brachyspectra, Cerophyrum, Aulonothroscus*), the elaterid clade and the Eucnemidae clade. *Perothops* is the most basal eucnemid and *Anischia* is placed between the subfamilies Palaeoxeninae and Melasinae within Eucnemidae.

2. When *Dascillus* is removed from the analysis and *Phaneus* is the outgroup, 11 trees of 521 steps were obtained. Their strict consensus (Fig. 33) shows the ingroup taxa in a polytomy, with elaterids and the derived eucnemids as separate groups as well as *Cerophyrum + Aulonothroscus* and *Schizophilus + Pseudomenes*, but the other relationships are unresolved, including the placement of both *Perothops* and *Anischia*. The result is identical if *Nycteus* is used as the outgroup instead. Also, the removal
of either *Nycteus* or *Phanaeus* together with *Dascillus* will result in the disintegration of the throscid clade, separation of *Brachyspectra* from the *Cerophytm-Aulonothroscus* clade and unresolved relationships within the eucneomid clade.

(3) When both *Phanaeus* and *Nycteus* are removed from the analysis and *Dascillus* is the out-group, five trees of length 490 were obtained. The strict consensus (Fig. 34) is essentially identical with that obtained in the analysis (1), the only difference being in the ambiguity in the placement of *Austrelater* in the analysis (1).

On the basis of the morphological analyses it was clear that *Dascillus* was the proper out-group for the clicking elateroid data set. Using the *Dascillus* characters for polarizing the in-group characters provided the most detailed resolution within the in-group. All the main branches recovered had at

Fig. 34. Consensus tree, morphological data, *Nycteus* and *Phanaeus* removed. Bremer support values mapped on branches.
Fig. 35. Consensus tree, morphological data, Nycteus and Phanaeus removed. Synapomorphies mapped on branches. Open circles refer to homoplasious charac-

- Onichodon
- Eucnemis
- Galbites
- Nematodes
- Isorhipis
- Palaeoxenus
- Phyllocerus
- Perothops
- Lissomus
- Drapetes
- Austrelater
- Cussolenis
- Selatosomus
- Aulonothroscus
- Cerophytum
- Brachypsectra
- Macropogon
- Dascillus
least modest Bremer support (Fig. 34), but the morphological data available were not able to resolve the relationships of the three major clades of clicking elateroids. However, the placement of *Perothops* and *Anischia* within Eucnemidae was well supported. Consequently we proceeded using this set of data in the combined analysis.

The character changes supporting the nodes in this cladogram are given in Fig. 35.

**Combined data.** – (4) The analysis of the combined data set with *Dascillus* as the outgroup and both *Phanaeus* and *Nycteus* removed produced one tree, length 2021 steps (Fig. 36). The significant change when compared with the result of the morphological analysis (3) was the unambiguous recovery of the three ingroup clades. The *Brachyspectra-Cerophytum-Aulonothroscus* clade is placed as the sister-group to the Eucnemidae clade and this combined clade as the sister-group of the Elateridae clade.

In the combined analysis the molecular data were assessed with direct optimization. A reasonable way of showing clade support for a result based on these data is to show the resampling frequencies of the nodes in a majority rule consensus tree (Fig. 37).

**Discussion**

On the basis of the cladistic analyses we conclude that both *Perothops* and *Anischia* should be placed in the eucnemid clade. It would not serve much purpose to divide the family Eucnemidae into several families. As suggested by Muona (1993), Perothopinae can be regarded as the most basal
eucnemid subfamily. Anischia, on the other hand, is not an elaterid and should be imbedded within the clade containing the more derived Eucnemidae. It is best placed as a separate subfamily, Anischiinae Fleutiaux, 1936, between the subfamilies Phelgoninae and Melasinae. Although superficially quite distinct, many of the Anischia features are present in other eucnemids. Melasis, Compsocnemis and Pseudomene, for instance, have a partly exposed labrum, Phyllocerus has a free terminal ventrite and clubbed antennae are common among the basal eucnemids. The pronotal carinae and strongly reduced metacoxal plates are the most striking external adult features of Anischia species.

The inclusion of Dascillus in the morphological data set had a significant effect on the results, more so than the inclusion of Nycteus or Phanaeus. The most important thing was not which genus was the out-group but whether Dascillus was included or not. The inclusion of Dascillus as the outgroup provided the analysis with a character combination that polarized the ingroup characters with less conflict than in the other analyses. Surprisingly the inclusion of Dascillus in the ingroup was clearly helpful as well. This strongly suggests that both Phanaeus and Nycteus were too far removed from the ingroup to provide unambiguous character information for the analyses. As pointed out by Bergsten (2005), such situations may arise with morphological data as well as with molecular data, leading to spurious results.

It is often claimed that certain genes are useful for certain phylogenetic problems only. CO1 is frequently seen as a tool for resolving species or genus level problems only. The principle of total evidence provides a philosophical framework against such a presupposition. There being only one “true” phylogeny, the information that can be recovered from CO1 data can only increase the accuracy of the total evidence analysis. The present study showed this to be the case. The morphological data left the relationships between the three major clades open. The inclusion of the CO1 data turned the scales in support of the Throscidae/Brachypsectridae/Cerophytidae + Eucnemidae clade.

Resampling support for this resolution is low, however (Fig. 35). Four derived clades: Throscidae + Cerophytidae; Pseudomenes + Schizophilus; derived Eucnemidae; Elateridae – have clear support, whereas the lower nodes are not recovered.

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Phylogeny of the Elateroidea 229

References


Appendix 1. Morphological characters and character states

In discussions of character state distribution, Pseudomeninae includes *Pseudomenes* and *Schizophilus*, Melasinae includes *Isorhipis* and *Microrhagus*, Eucneminae includes *Eucnemis* and *Galbites*, Macraulacinae includes *Onicodon* and *Nematodes*, derived Eucnemidae includes the previous six genera, Eucnemidae includes all previous (8) genera plus *Perothops*, *Phyllocerus*, *Palaeoxenus*, Lissominae includes *Austrelater*, *Drapetes* and *Lissomus*, Thylacosterninae includes *Cussolenis* and *Pterotarsus*, and typical Elateridae includes *Danosoma*, *Ampedus* and *Selatosomus*.

1. Antennal insertion: 0. exposed from above; 1. concealed from from above by ridge. The insertions are said to be exposed if any portion of the articular cavity can be seen from directly above the head, when mouthparts are facing forward. State 1 occurs in *Phanaeus*, *Cerophytum*, Pseudomeninae and typical Elateridae.

2. Head beneath antennal insertion: 0. without mesally directed pocket; 1. with mesally directed pocket (Muona 1993, Figs 15, 65). State 1 (which does not include the presence of a pit or furrow between antennal socket and eye) occurs in derived Eucnemidae, except *Isorhipis*.


4. Antennomere 2 attached to antennomere 1: 0. apically; 1. subapically. State 1 occurs in *Anischia* and all Eucnemidae.

5. Antennomere 2: 0. not distinctly wider than 3; 1. distinctly wider than 3, 4 or 5; 2. distinctly wider than 3 but much shorter than 4 or 5. State 1 occurs in *Aulonothroscus*, and state 2 in Lissominae and Thylacosterninae.

6. Antennomeres 9 and 10: 0. similar in size and shape to 5 and 6; 1. distinctly longer and/or wider than 5 or 6, combining with 11 to form club. State 1 occurs in *Phanaeus*, *Anischia*, *Palaeoxenus* and *Aulonothroscus*.

7. Antennal rami or serrations: 0. absent; 1. beginning on antennomere 3; 2. beginning on antennomere 4 (or occasionally beyond this). State 1 occurs in *Dascillus*, *Cerophytum*, *Galbites*, *Onichodon* and *Danosoma*, and state 2 in *Macroponogon*, *Brachypsectra*, *Phyllocerus*, Pseudomeninae, Melasinae, *Eucnemis*, Lissominae, Thylacosterninae, *Selatosomus* and *Ampedus*.


9. Frontoclypeal region at midline: 0. not or slightly, gradually sloping anteriorly; 1. moderately to very steeply sloping at apex, without carina; 2. forming transverse carina. State 1 occurs in *Brachypsectra*, *Cerophytum*, *Phyllocerus*, Pseudomeninae and Lissominae, and state 2 in *Phanaeus* and *Ampedus*.


11. Mandible: 0. less than twice as long as wide; 1. more than twice as long as wide. State 1 occurs in *Dascillus*, *Perothops* and *Phyllocerus*.

12. Mandibular apex: 0. unidentate; 1. bidentate or occasionally tridentate. State 1 occurs in *Nycteus*, *Anischia*, *Microrhagus*, ONIS, Lissominae, Thylacosterninae and typical Elateridae.

13. Mandibular apex in anterior view: 0. not or slightly, gradually sloping anteriorly; 1. moderately to very steeply sloping at apex, without carina; 2. forming transverse carina. State 1 occurs in *Microrhagus*, Lissominae and Thylacosterninae.


15. Mandibular mola: 0. well developed; 1. reduced; 2. absent. State 0 occurs in *Phanaeus*, *Nycteus* and *Ampedus*, state 1 in *Anischia*, and state 2 in all remaining taxa.
16. Apical maxillary palpmere: 0. cylindrical to subulate, not apically widened; 1. slightly to strongly widened apically (securiform or triangular). State 1 occurs in *Macropogon, Cerophytum, Perothops, Pseudomeninae, Palaeoxenus, Microrhagus, Euemenis, Nematodes, Aulonothroscus, Lissominae* and typical Elateridae.

17. Lateral pronotal carinae: 0. complete; 1. incomplete anteriorly; 2. absent. State 1 occurs in *Pterotarsus, Palaeoxenus* and *Microrhagus*, and state 2 in *Cerophytum*.

18. Sublateral pronotal carinae: 0. absent; 1. present. These carinae begin at the posterior edge of the pronotum and extend anteriorly for a short distance. State 1 occurs in *Anischia* and *Perothops*.

19. Prothoracic antennal groove: 0. absent; 1. located on prosternum and hypomeron, extending posterolaterally, not connected to concealed pocket; 2. located on prosternum and hypomeron, extending posteriorly or posteromesally towards coxae, not connected to concealed pocket; 3. located mesally on hypomeron, flanked by notosternal suture and connected to deep concealed pocket; 4. located laterally on hypomeron and uniformly shallow to moderately deep; 5. located laterally on hypomeron and forming very deep pocket towards posterior end. State 1 occurs in *Aulonothroscus*, state 3 in *Microrhagus*, state 3 in *Drapetes, Lissomus*, Thylacosterninae and *Danosoma*, state 4 in *Onichodon* and state 5 in *Eucneminae*.

20. Prosternum: 0. without paired carinae; 1. with paired carinae extending from sides of prosternal process onto body of sternum. State 1 occurs in *Macropogon, Aulonothroscus* and *Drapetes*.

21. Prosternal chin piece: 0. absent; 1. short and truncate apically; 2. long and strongly rounded apically. State 1 occurs in *Brachypsectra, Cerophytum, Perothops, Palaeoxenus, Microrhagus, Onichodon, Aulonothroscus* and AUS, state 2 in *Anischia, Pseudomeninae, Drapetes, Lissomus*, and typical Elateridae.

22. Prosternal head rest: 0. absent or very narrow; 1. moderately broad and horizontal to slightly oblique; 2. moderately broad and distinctly oblique. This refers to the infolded anterior edge of the prosternum, which may form a slightly concave platform on which the head rests. State 1 occurs in *Brachypsectra, Anischia, Pseudomeninae, Palaeoxenus, Drapetes, Lissomus* and typical Elateridae, and state 2 in *Cerophytum, Perothops, Microrhagus, Euemeninae, Onichodon, Aulonothroscus, Austrelater* and Thylacosterninae.

23. Prosternal process in lateral view: 0. not or slightly curved apically; 1. moderately to strongly, evenly or sinuately curved from base to apex; 2. straight basally, strongly but gradually elevated near apex; 3. straight basally, strongly and abruptly elevated near apex, forming step or emargination; 4. moderately to strongly curved basally but abruptly notched near apex. State 0 occurs in *Phanaeus, Nycteus, Dascillus, Macropogon* and *Anischia*, state 1 in *Brachypsectra, Perothops, Phyllocerus, Isorhipis, Austrelater* and Selatosomus, state 2 in *Pseudomeninae* and *Palaeoxenus*, state 3 in most taxa, and state 4 in *Danosoma* and *Ampedus*.

24. Visible portion of procoxa: 0. distinctly transverse; 1. more or less globular. State 1 occurs in all taxa except for *Phanaeus, Nycteus, Dascillus, Macropogon* and *Brachypsectra*.

25. Propleurocoxal articular area: 0. well developed and more than half as long as exposed portion of procoxa; 1. well developed but less than half as long as exposed portion of procoxa; 2. highly reduced or absent. State 0 occurs in *Dascillus, Macropogon* and *Cerophytum*, state 1 in *Phanaeus, Nycteus, Brachypsectra* and *Aulonothroscus*, and state 2 in most taxa.

26. Propleurotrochantin: 0. at least partly exposed; 1. concealed but well developed and free; 2. highly reduced and fused to notum, apparently absent. State 0 occurs in *Nycteus, Dascillus* and *Macropogon*, state 1 in *Phanaeus, Brachypsectra, Cerophytum* and *Aulonothroscus*, and state 2 in most taxa.

27. Anterior edge of scutellum: 0. not to moderately, usually gradually, elevated, without or with weak carina and diagonal to straight anterior wall; 1. strongly and abruptly elevated forming sharp carina and concave anterior wall. State 1 occurs in *Nycteus, Dascillus, Cerophytum, Anischia, Aulonothroscus, Lissominae* and *Danosoma*.

28. Posterior edge of scutellum: 0. narrowly rounded or acute; 1. broadly rounded or truncate. State 1 occurs in all taxa except *Phanaeus, Nycteus, Macropogon, Cerophytum, Anischia, Aulonothroscus, Lissominae* and *Danosoma*. 
29. Mesoventrite: 0. completely separated from mesanepisterna; 1. at least partly fused to mesanepisterna, sutures incomplete or absent. State 1 occurs in Anischia, Microrhagus, Galbites and Macraulacinae.

30. Anterior edge of mesoventrite: 0. on same plane as or slightly higher plane than metaventrite; 1. on much higher plane than metaventrite. State 1 occurs in Phanaeus, Eucneminae and Aulonothroscus.

31. Distance between mesocoxal cavities: 0. less than half shortest diameter of coxal cavity; 1. more than half but less than diameter of coxal cavity; 2. more than shortest diameter of coxal cavity. State 0 occurs in Nycteus, Dascillus, Macropogon, Brachyspectra, Perothops, Phyllocerus, Isorhipis, Onichodon and Austrelater, state 1 in Cerophytum, Palaeoxenus, Pseudomeninae, Microrhagus, Eucneminae, Nematodes, Thlacosterninae, and typical Elateridae, and state 2 in Phanaeus, Anischia, Aulonothroscus, Drapetes and Lissomus.

32. Mesoventral cavity: 0. shallow or absent; 1. moderately to very deep. State 1 occurs in Cerophytum, Anischia, all Eucnemidae, Aulonothroscus, Lissominae, Thylacosterninae and typical Elateridae.

33. Mesanepisternum and mesepimeron: 0. separated by pleural suture and underlying pleural ridge; 1. more or less fused together, without pleural ridge. State 1 occurs in Cerophytum, Anischia, Phyllocerus, Pseudomeninae, and derived Eucnemidae.

34. Metaventral discrimen: 0. long, extending anteriorly beyond middle of ventrite; 1. shorter, not extending anteriorly beyond middle of ventrite; 2. absent. State 1 occurs in Nycteus, Anischia and Isorhipis, state 2 in Phanaeus, Cerophytum, Microrhagus and Aulonothroscus.

35. Metaventrite: 0. without postcoxal lines; 1. with one pair of postcoxal lines; 2. with two pairs of postcoxal lines. State 1 occurs in Eucnemis, Drapetes and Lissomus, state 2 in Anischia.

36. Metaventrite: 0. without grooves for reception of tarsi; 1. with grooves for reception of tarsi. State 1 occurs in Aulonothroscus.

37. Exposed portion of metaneupisternum: 0. less than 2.5 times as long as wide; 1. between 2.5 and 5 times as long as wide; 2. more than 5 times as long as wide. State 0 occurs in Phanaeus and Nycteus, state 1 in Dascillus, Macropogon, Melasinae, Drapetes and Pterotarsus.

38. Metacoxae separated by: 0. less than half the largest diameter of one of them; 1. more than half the longest diameter of one of them. State 1 occurs in Anischia.

39. Metacoxal plate: 0. well developed and of more or less equal width from midline to lateral edge; 1. well developed, widest at mesal third and distinctly narrowed towards lateral edge; 2. weakly developed or absent. State 0 occurs in Nycteus, Macropogon, Brachyspectra, Galbites, Aulonothroscus, Drapetes, Lissomus and Thylacosterninae, state 1 in Perothops, Phyllocerus, Palaeoxenus, Pseudomeninae, Melasinae, Eucnemis, Macraulacinae, and typical Elateridae, state 2 in Dascillus and Austrelater, and state 3 in Phanaeus, Cerophytum and Anischia.

40. Apical field of hind wing: 0. with one or two anterior oblique linear sclerites, one posterior oblique one and another straight central one, forming epsilon design; 1. with 2 parallel anterior oblique linear sclerites and usually another posterior one; 2. with one anterior oblique and one posterior oblique linear sclerite; 3. with one anterior oblique linear sclerite (sometimes with broader, and often vaguely indicated posterior sclerite); 4. with broad vague sclerites only or without sclerites. State 0 occurs in Brachyspectra, Pseudomeninae, Microrhagus, Eucneminae, Macraulacinae, Austrelater and Ampedus, state 1 in Phanaeus, Dascillus, Cerophytum, Isorhipis and Thylacosterninae, state 2 in Perothops, Phyllocerus, Palaeoxenus, Lissomus and Danosoma, state 3 in Selatosomus, and state 4 in Nycteus, Macropogon, Anischia, Aulonothroscus and Drapetes.

41. Base of radial cell of hind wing: 0. present; 1. absent (cell open basally, incomplete or absent). State 1 occurs in Phanaeus, Microrhagus and Aulonothroscus.

42. Cross-vein r3 of hind wing: 0. moderately to very long; 1. short; 2. absent. State 1 occurs in Brachyspectra, Phyllocerus, Eucnemis and Drapetes, state 2 in Phanaeus, Anischia, Melasinae, Macraulacinae and Aulonothroscus.

43. Cross-vein r3 of hind wing: 0. strongly oblique (almost perpendicular to long axis); 1. slightly to moderately oblique; 2. more or less horizontal (parallel to long wing axis). State 0 occurs in Nycteus, state 1 in Dascillus, Macropogon, Brachyspectra, Cerophytum, Phyllocerus, Palaeoxenus, Galbites, Drapetes and Lissomus, and state 2 in Perothops, Pseudomeninae, Eucnemis, Austrelater,
Thylacosterninae and typical Elateridae. Cross-vein r3 is absent in Phanaeus, Anischia, Melasinae, Macraulacinae and Aulonothroscus, and this character is coded as inapplicable.

44. Medial field of hind wing: 0. with five free veins; 1. with four free veins; 2. with three or fewer free veins. State 1 occurs in Nycteus and Cerophytum, state 2 in Phanaeus, Anischia and Aulonothroscus.

45. Wedge cell of hind wing: 0. well developed, apically oblique; 1. well developed, apically truncate; 2. reduced and apically acute; 3. absent. State 0 occurs in Nycteus, Dascillus, Perothops, Phyllocerus, and Isorhipis, state 1 in Macropogon, Schizophilus, Palaeoxenus, Lissomus, Austrelater, Selatosomus and Ampedus, state 2 in Phanaeus, Brachypsectra, Cerophytum, Anischia, Pseudomenes, Microrhagus, Eucneminae, Macraulacinae, Aulonothroscus, Drapetes, Thylacosterninae and Danosoma.

46. MP3+4 of hind wing: 0. with basal spur; 1. without basal spur. State 1 occurs in Phanaeus, Brachypsectra, Cerophytum, Anischia, Palaeoxenus, Microrhagus, Eucneminae, Macraulacinae and Aulonothroscus.

47. CuA2 of hind wing: 0. joining MP3+4; 1. joining MP4; 2. absent or not joining MP. State 1 occurs in Austrelater, Pterotarsus, Selatosomus and Ampedus, state 2 in Phanaeus, Nycteus and Eucneminae.


49. Protrochanter: 0. less than twice as long as wide; 1. more than twice as long as wide. State 1 occurs in Macropogon, Brachypsectra, Anischia, Drapetes and Lissomus.

50. Mesotrochanter: 0. less than twice as long as wide; 1. more than twice as long as wide. State 1 occurs in Macropogon, Cerophytum, Anischia, Drapetes and Lissomus.

51. Tibiae: 0. not strongly expanded and flattened; 1. strongly expanded and flattened. State 1 occurs in Phanaeus and Thylacosterninae.

52. Protibia: 0. with two apical spurs; 1. with one apical spur; 2. without apical spur. State 1 occurs in Isorhipis, Eucnemis and Macraulacinae, and state 2 in Brachypsectra, Microrhagus, Galbites, Aulonothroscus, Lissomus, Pterotarsus and Danosoma.

53. Outer edge of mesotibia: 0. without sharp carina; 1. with sharp carina. State 1 occurs in Eucneminae, Aulonothroscus, Drapetes, Lissomus and Thylacosterninae.

54. Mesotarsus: 0. without membranous ventral lobes; 1. with membranous ventral lobe on tarsomeres 4 only; 2. with membranous ventral lobe on tarsomeres 2 to 4; 3. with membranous ventral lobes on tarsomeres 1 to 3. State 1 occurs in Cerophytum, Pseudomeninae, Melasinae, Macraulacinae and Aulonothroscus, state 2 in Macropogon and Galbites, and state 3 in Dascillus, Lissominae and Thylacosterninae.

55. Pretarsal claws: 0. neither serrate nor pectinate; 1. serrate or pectinate. State 1 occurs in Cerophytum and Perothops.

56. Number of basal abdominal ventrites connate: 0. none or two; 1. three; 2. four; 3. five. State 0 occurs in Nycteus, Dascillus and Brachypsectra, state 1 in Anischia, state 2 in Cerophytum, Phyllocerus, Lissominae, Thylacosterninae and typical Elateridae, and state 3 in Phanaeus, Macropogon, Perothops, Pseudomeninae, Palaeoxenus, derived Eucnemidae and Aulonothroscus.

57. Posterolateral angles of ventrites 2 to 4: 0. not or only slightly produced; 1. strongly produced and acute. State 1 occurs in Perothops and Palaeoxenus.

58. Male: sternite IX: 0. open basally (with paired lateral struts not meeting at midline; 1. closed basally (struts meeting at midline and enclosing broad plate or sometimes forming single anterior strut). State 1 occurs in Anischia.

59. Male: tegrite IX: 0. apically truncate or slightly emarginate; 1. apically moderately to deeply emarginate; 2. not distinguishable from tergite X. State 0 occurs in Nycteus, Dascillus, Perothops, Phyllocerus, Schizophilus, Palaeoxenus, Isorhipis, Eucnemis, Macraulacinae, Aulonothroscus, Austrelater and Danosoma, state 1 in Macropogon, Brachypsectra, Cerophytum, Pseudomenes, Drapetes, Lissomus, Thylacosterninae, Selatosomus and Ampedus, state 2 in Phanaeus, Anischia, Microrhagus and Galbites.

60. Male: aedeagus: 0. dorsoventrally flattened; 1. laterally compressed. State 1 occurs in Phanaeus, Anischia, Pseudomeninae, Palaeoxenus and derived Eucnemidae.
61. Male: phallobase: 0. without or with slight anterior emargination; 1. with deep anterior emargination. State 1 occurs in Brachypsectra, Cerophytum and Aulonothroscus.

62. Male: phallobase: 0. symmetrical; 1. asymmetrical. State 1 occurs in Anischia.

63. Male: parameres: 0. articulated to apex of phallobase; 1. partly fused to phallobase, connected to it by incomplete, oblique sutures. State 1 occurs in Drapetes, Lissomus and Thylacosterninae.

64. Male: parameres: 0. completely free from one another or partly fused at base; 1. completely fused together for about half their lengths forming parameral tube. State 1 occurs in Anischia, Schizophilus, Melasinae, Galbites and Macraulacinae.

65. Male: ventral basal penile struts: 0. absent or barely indicated; 1. less than half as long as body of penis; 2. more than half as long as body of penis. State 0 occurs in Phanaeus, Cerophytum and Microrhagus, and state 2 in Anischia, Isorhipis, Eucneminae, Macraulacinae, Aulonothroscus, Drapetes and Thylacosterninae.

66. Male: ventral basal penile struts: 0. not articulated at base; 1. articulated at base. State 1 occurs in Anischia, Perothops, Palaeoxenus, Isorhipis, Eucneminae and Macraulacinae.

67. Female: spiculum ventrale (anterior strut on sternite VIII): 0. absent; 1. basally fixed; 2. basally articulated. State 0 occurs in Phanaeus and Nycteus, and state 2 in Palaeoxenus and derived Eucnemidae.

68. Female: gonocoxites: 0. divided into three lobes; 1. divided into proximal and distal lobes; 2. undivided. State 0 occurs in Cerophytum, Eucnemis, Nematodes, Lissominae and Thylacosterninae, state 1 in Dascillus, Brachypsectra, Anischia, Melasinae, Aulonothroscus, and typical Elateridae, and state 2 in Phanaeus, Nycteus, Macronopogon, Perothops, Phyllocerus, Pseudomeninae, Palaeoxenus, Galbites, Onichodon.

69. Female: gonostyli: 0. apical; 1. subapical; 2. absent. State 1 occurs in Anischia, Microrhagus, Eucnemis, Macraulacinae, Austrelater, Danosoma and Ampedus, and state 2 in Phanaeus, Isorhipis, Drapetes, Lissomus, Thylacosterninae and Selatosomus.

70. Female: colleterial glands: 0. absent; 1. present. State 1 occurs in Lissominae and typical Elateridae.

71. Female: bursa copulatrix: 0. beginning at or posterior to gonopore; 1. beginning anterior to gonopore. State 1 occurs in Phanaeus, Brachypsectra, Cerophytum, derived Eucnemidae, Aulonothroscus, Lissominae, Thylacosterninae and typical Elateridae.

72. Female: bursa copulatrix: 0. not bifurcate; 1. bifurcate. State 1 occurs in Perothops, Phyllocerus, Pseudomeninae and Palaeoxenus.

73. Female: bursa copulatrix: 0. without armature; 1. with one or more sclerites; 2. with one or more patches of asperities. State 1 occurs in Dascillus, Macronopogon, Cerophytum, Aulonothroscus, Lissominae and Danosoma, and state 2 in Thylacosterninae, Selatosomus and Ampedus.

74. Female: spermathecal complex: 0. not attached to bursa, entering tract posterior of bursa; 1. attached to bursa. State 1 occurs in Phanaeus, Dascillus, Cerophytum, Anischia, Perothops, Phyllocerus, Pseudomeninae, Palaeoxenus and typical Elateridae.

75. Female: spermatheca: 0. unpigmented; 1. pigmented. State 1 occurs in Phanaeus, Nycteus, Macronopogon, Pseudomenes, Microrhagus, Eucneminae, Macraulacinae, Aulonothroscus, Austrelater, Thylacosterninae and Ampedus.

76. Female: spermatheca: 0. consisting of single lobe; 1. with two or more lobes. State 1 occurs in Macronopogon, Pseudomeninae, Palaeoxenus, Microrhagus, Macraulacinae, Aulonothroscus, Lissomus, Austrelater, Thylacosterninae and Selatosomus.

77. Larva: prothorax: 0. subequal in width to metathorax; 1. distinctly wider than metathorax; 2. distinctly narrower than metathorax. State 1 occurs in Isorhipis and Nematodes, state 2 in Brachypsectra, Cerophytum, Perothops, Galbites, Aulonothroscus and Thylacosterninae.

78. Larva: ratio of head length to head width: 0. less than 0.5; 1. 0.5 to 0.8; 2. more than 0.8. State 0 occurs in Cerophytum, Perothops, Phyllocerus, Isorhipis, Galbites, Aulonothroscus, Austrelater and Thylacosterninae, and state 2 in Brachypsectra, Anischia, Schizophilus, Microrhagus, Eucnemis and Macraulacinae.

79. Larva: head capsule: 0. not wedge-like, anterior edge in lateral view only slightly narrower than posterior edge and not blade-like; 1. wedge-like, anterior edge in lateral view much narrower than pos-
terior edge and more or less blade-like. State 1 occurs in *Phyllocerus*, Pseudomeninae, *Palaeoxenus*, *Microrhagus*, *Eucnemis* and Macraulacinae.

80. Larva: base of head capsule dorsally: 0. not or only slightly emarginate; 1. distinctly emarginate. State 1 occurs in *Cerophytum*, *Anischia*, *Perothops* and Austrelater.

81. Larva: sides of head capsule posteriorly: 0. more or less curved, simple; 1. straight and subparallel, simple; 2. straight or slightly converging with distinct anteriorly or anterolaterally projecting tooth; 3. straight or slightly converging with two or more laterally projecting teeth. State 1 occurs in *Brachypsectra*, *Cerophytum*, Pseudomeninae and *Danosoma*, state 2 in *Microrhagus*, *Eucnemis* and Macraulacinae, and state 3 in *Palaeoxenus*.

82. Larva: sides of head capsule anteriorly: 0. simple and more or less converging; 1. strongly converging with two or more laterally or anterolaterally projecting teeth or lobes; 2. with three anteriorly projecting, rounded lobes separated by deep emarginations. State 1 occurs in *Palaeoxenus*, *Microrhagus*, *Eucnemis* and Macraulacinae, and state 2 in Pseudomeninae.

83. Larva: head capsule: 0. undivided; 1. divided into dorsal and ventral plates. State 1 occurs in *Microrhagus*, *Eucnemis* and Macraulacinae.

84. Larva: sides of head capsule posteriorly: 0. more or less curved, simple; 2. straight or slightly converging with distinct anteriorly or anterolaterally projecting tooth; 3. more or less straight from base to apex; 4. curved laterally or exodont. State 1 occurs in *Anischia* and *Phyllocerus*, state 2 in *Macropogon*, *Brachypsectra*, *Microrhagus* and Pseudomenes. Most taxa have a completely fused labrum.

85. Larva: number of antennomeres: 0. three or four; 1. two or one. State 1 occurs in *Cerophytum*, *Phanaeus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack a completely fused labrum.

86. Larva: basal width of mandible: 0. more than 0.2 times head width; 1. less than 0.2 times head width. State 1 occurs in *Brachypsectra*, *Anischia*, *Phyllocerus*, Pseudomeninae, *Palaeoxenus*, *Microrhagus*, Eucneminae, Macraulacinae and *Aulonothroscus*.

87. Larva: number of antennomeres: 0. more than one; 1. two or one. State 1 occurs in *Anischia*, *Perothops*, *Palaeoxenus* and derived Eucnemidae.

88. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. The majority of taxa lack antennae.

89. Larva: mandible: 0. articulated; 1. solidly fused to head capsule. State 1 occurs in Eucneminae and *Aulonothroscus*.

90. Larva: mandibular apex: 0. more or less rounded; 1. unidentate and acute; 2. bidentate or tridentate. State 0 occurs in *Schizophilus* and Eucneminae, and state 2 in *Phanaeus*, *Nycteus*, *Macropogon*, *Isorhipis*, Macraulacinae, *Aulonothroscus* and Thylacosterninae.

91. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.

92. Larva: mandible: 0. less than twice as long as wide; 1. more than twice as long as wide. State 1 occurs in Eucneminae, Macraulacinae and derived Eucnemidae.

93. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.

94. Larva: mandible: 0. less than twice as long as wide; 1. more than twice as long as wide. State 1 occurs in *Macropogon*, *Perothops*, *Schizophilus*, Lissominae, Thylacosterninae and typical Elateridae.

95. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.

96. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.

97. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.

98. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.


100. Larva: antennae: 0. located on surface; 1. located within deep cavities. State 1 occurs in *Phanaeus*, *Nycteus*, *Dascillus*, *Macropogon*, *Brachypsectra*, *Phyllocerus* and *Pseudomenes*. Most taxa lack antennae.
Lissominae.

98. Larva: mesal edge of mandible at middle: 0. concave; 1. convex. State 1 occurs in Cerophytum, derived Eucnemidae and Aulonothroscus.

99. Larva: mesal surface of mandibular base: 0. with mola; 1. with tuft of hairs; 2. simple. State 0 occurs in Phanaeus, Nycteus and Dascillus, state 1 in Perothops, Lissominae, Thylacosterninae and typical Elateridae.

100. Larva: maxillolabial complex: 0. more or less enclosed within hypostomal cavity, distinctly separated from epicranium on either side and capable of movement; 1. contiguous with epicranium on each side and incapable of movement; 2. solidly fused to epicranium on each side. State 1 occurs in Cerophytum, Anischia, Perothops, Pseudomeninae and Aulonothroscus, and state 2 in Phyllocerus, Palaeoxenus and derived Eucnemidae.

101. Larva: cardo: 0. separated by suture or membrane from stipes; 1. indistinctly separated from stipes; 2. completely fused with stipes (no suture between them). State 1 occurs in Pseudomeninae, Palaeoxenus, Aulonothroscus and Thylacosterninae, and state 2 in Phanaeus, Nycteus and Dascillus.

102. Larva: maxilla: 0. with distinct galea and lacinia; 1. with single mala; 2. without apical lobes. State 1 occurs in Cerophytum, Perothops, Phyllocerus and Aulonothroscus, and state 2 in Anischia, Pseudomeninae, Palaeoxenus and derived Eucnemidae.

103. Larva: mala or galea: 0. palpiform, 2-segmented; 1. palpiform, 1-segmented; 2. lobate, setose or spinose; 3. falciform; 4. absent. State 0 occurs in Macropogon, Lissominae and typical Elateridae, state 1 in Brachypsectra, Perothops and Thylacosterninae, state 2 in Phanaeus and Nycteus, state 3 in Dascillus, Cerophytum, Phyllocerus and Aulonothroscus, and state 4 in Anischia, Pseudomeninae, Palaeoxenus and derived Eucnemidae.

104. Larva: number of maxillary palpomeres: 0. three or four; 1. two. State 1 occurs in Anischia, Palaeoxenus, Microrhagus, Eucnemis and Macraulacinae. Galbites lacks labial palps and is coded as inapplicable.

105. Larva: labial palps separated by: 0. less than a basal width; 1. more than a basal width. State 1 occurs in Brachypsectra, Schizophilus, Palaeoxenus, derived Eucnemidae (except Galbites which lacks labial palps).

106. Larva: gular region: 0. clearly delimited, base of labium well separated from thorax; 1. apparently absent, base of labium abutting anterior edge of thorax. State 1 occurs in Phanaeus, Cerophytum, Anischia, Perothops, Phyllocerus, Palaeoxenus, Pseudomeninae and derived Eucnemidae.

107. Larva: prothoracic presternum: 0. not completely delimited; 1. completely delimited. State 1 occurs in Macropogon, Brachypsectra, Phyllocerus, Pseudomenes, Palaeoxenus, Eucneminae, Lissominae, Thylacosterninae and typical Elateridae.

108. Larva: prothoracic presternum: 0. not divided into two parts by longitudinal suture; 1. divided into two parts by longitudinal suture. State 1 occurs in Thylacosterninae, Lissominae and Selatosomus.

109. Larva: posterior prosternal sclerite: 0. absent; 1. present. State 1 occurs in Palaeoxenus, Lissominae and Selatosomus.

110. Larva: prothoracic venter: 0. without paired, sclerotized supporting rods; 1. with paired, posteriorly converging rods; 2. with paired, longitudinal, T-shaped or L-shaped rods. State 1 occurs in Cerophytum, Anischia, Palaeoxenus, Pseudomeninae, Aulonothroscus, Drapetes and Austrelater, and state 2 in Isorhipis and Nematodes.

111. Larva: leg: 0. with 4 or 5 distinct segments; 1. with a single segment; 2. absent or represented only by setal cluster. State 1 occurs in Anischia, and state 2 in derived Eucnemidae.

112. Larva: abdominal terga: 0. without patches of specialized setae; 1. with patches of specialized setae. These specialized setae are relatively short, stout, flattened and arising from modified bases allowing each seta to move either anteriorly or posteriorly without breaking off. State 1 occurs in Lissominae.

113. Larva: abdominal sterna: 0. without microtrichial patches; 1. with microtrichial patches. State 1 occurs in Pseudomeninae, Palaeoxenus, Microrhagus, Eucneminae and Macraulacinae.

114. Larva: abdominal sterna: 0. without microtrichial patches; 1. with microtrichial patches. State 1


116. Larva: tergum IX: 0. without urogomphi; 1. with simple urogomphi; 2. with bifurcate urogomphi. State 1 occurs in *Dascillus*, *Perothops*, *Palaeoxenus*, *Aulonothroscus* and Thylacosterninae, and state 2 in Pseudomeninae, Lissominae, *Danosoma* and *Selatosomus*.

117. Larva: ventral portion of tergum IX and anterior edge of sternum IX: 0. without rows or patches of teeth; 1. with rows and patches of small teeth more or less enclosing segment X. State 1 occurs in *Anischia*, *Phyllocerus*, Pseudomeninae, *Palaeoxenus*, *Microrhagus*, Macraulacinae, *Drapetes* and *Lissomus*.

TABLE 2. Distribution of morphological characters

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PHYLOGENY OF THE ELATEROIDEA

INSECT SYST. EVOL. 38:2 (2007)