

A Re-evaluation of the Eucnemidae larval characters (Coleoptera)

Jyrki Muona^{1,2} & Marianna Teräväinen^{1,3}

¹ Finnish Museum of Natural History, Zoological Museum, Helsinki, Finland.

² ORCID: <http://orcid.org/0000-0003-2771-1171>. E-mail: jyrki.muona@helsinki.fi (corresponding author)

³ ORCID: <https://orcid.org/0000-0002-4624-011X>. E-mail: marianna.teravainen@helsinki.fi

Abstract. The larval characters of Eucnemidae are re-evaluated. Tribe Schizophilini Muona, 1993 is considered to merit subfamily rank as Schizophilinae Muona *new status*. Larval characters congruent with previously used adult morphological characters support the earlier published sister-group hypotheses for lignicolous eucnemids with one exception, Pseudomeninae, which is here split resulting in the following evolutionary hypothesis: (Pseudomeninae (Schizophilinae (Paleoxeninae (Melasinae, Eucneminae, Macraulacinae))). The position of three remaining clades, Anischiinae, Perothopinae and Phyllocerinae remain ambiguous.

Key-Words. Evolution; Phylogenetics; Coleoptera; Eucnemidae.

INTRODUCTION

Muona (1993) presented an evolutionary hypothesis for the family Eucnemidae on the basis of 80 binary adult morphological characters; both external and internal features were included. Lawrence *et al.* (2007) added COI data and 60 binary larval morphological characters to their adult character set in an analysis of Eucnemidae relationships. Both these analyses recovered the same hypothesis for Eucnemidae, the latter study clarifying the position of *Perothops* Laporte and including *Anischia* Fleutiaux in Eucnemidae.

Lawrence *et al.* (2011) used 366 taxa and more than 600 binary adult and larval morphological characters in their “all beetle” analysis, recovering the previously found clade (Anischiinae (Melasinae + Macraulacinae)). Kundrata *et al.* (2014) analyzed the Elateroidea relationships with sequence data. Depending on the alignment used, they had 4848 to 5302 homologous positions as characters, recovering the previously suggested eucnemid clade (Anischiinae (Melasinae + Macraulacinae + Eucneminae)).

All four studies found support for the same within family relationships of Eucnemidae. Lawrence *et al.* (2011) and Kundrata *et al.* (2014) appeared to differ strongly on the position of Elateridae, however. We suggest that this disagreement may be less dramatic than one might think by looking at the trees they presented. In Lawrence *et al.* (2011, cladogram 3) all nodes are poorly supported. Only Elateridae and Eucnemidae have a

more than 50% support, the support for their relationship to each other as well as to *Brachypsectra* LeConte, *Aulonothroscus* Horn and *Cerophytum* Latreille is below 50%. In Kundrata *et al.* (2014) the bootstrap values indicate many well supported groups, but the relationships between the groups are again either poorly supported or not supported at all (Fig. 1). The lack of resampling support in the latter study is in fact an important result that should have been discussed in detail. Contrary to the view presented in the article, the support for multiple origins of the clicking apparatus in Elateroidea is not established. Actually, the result suggests another, in our view much more interesting scenario. Neither this molecular data nor previous morphological data lend support for a monophyletic Elateridae. The fact is that no study this far has recovered stable synapomorphies for this family.

Kundrata & Bocak (2011) have shown that driliids appear to be derived elaterids. Kusy *et al.* (2018) give further evidence of “modified” elaterids. Indeed, the next step is to find further sister-groups for other monophyletic groups of “non-elaterids” within the “Elateridae”. If so, the whole idea of click-beetles as a clade has to be abandoned – unless we are prepared to accept all Elateroidea *s.l.* as one family – rather than refusing to accept that Elateridae is not a natural group but just things we used to see as similar.

It is our view that the problem of unclear elateroid relationships may extend to Eucnemidae *sensu* Muona (1993) as well. It is possible that this

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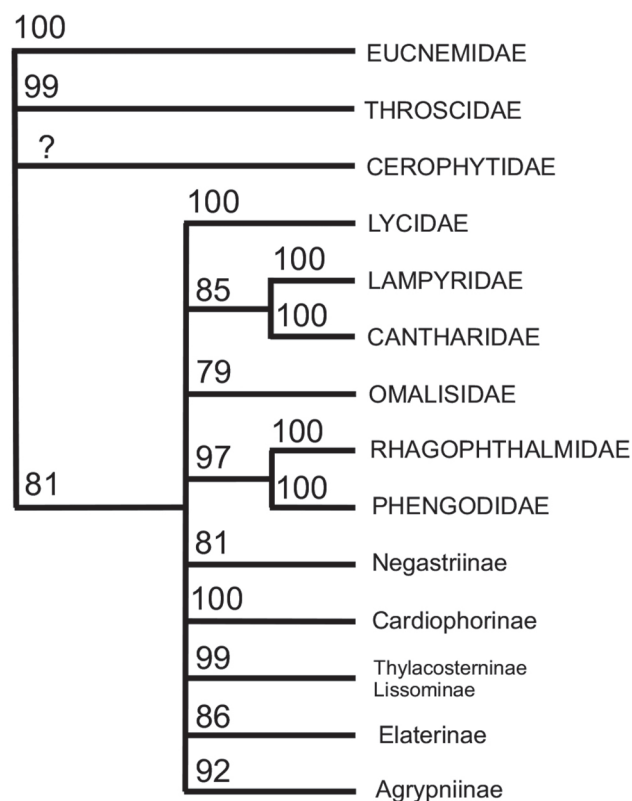


Figure 1. Kundera *et al.* (2014) elateroid relationships hypothesis with unsupported bootstrap nodes removed.

family should be split and the relationships of the basal eucnemid lineages with Cerophytidae, Throscidae and Elateridae reconsidered. Neither Lawrence *et al.* (2011) nor Kundera *et al.* (2014) included any of the basal eucnemid groups (*sensu* Muona, 1993; Perothopinae, Phyllocerinae, Pseudomeninae and Palaeoxeninae) in their analysis. Thus it is unknown whether these taxa would contribute something new to the result. The characters we point out certainly suggest this to be the case.

In the present paper we discuss the Eucnemidae larval types and the putative synapomorphies they possess. Böving & Craighead (1931), van Emden (1932) and Crowson (1955) keyed out Eucnemidae using larval features, but the diversity of existing forms was not known to them. Much new information has come to light since. The champions of early eucnemid larval descriptions were J.C.M. Gardner in India, B. Burakowski in Poland, T-E. Leiler, S. Lundberg and T. Palm in Sweden and B. Mamaev in Russia, today we owe much to the diligent efforts of R. Otto in the US.

It is our great pleasure to offer this paper in celebration of Professor Cleide Costa on her 80th birthday. Her contributions to larval coleopterology are many and of course include the Eucnemidae as well!

MATERIAL AND METHODS

We use as the backbone for our discussion the evolutionary hypotheses presented in Muona (1993) and Lawrence *et al.* (2007), as they are the only analytical

studies including a full set of Eucnemidae higher categories. A list of descriptions available and material seen is presented separately (Table 1). Our approach focuses on the structures of the head and prothorax, but other features are included when relevant. Finally we compare the larval features to the result of the existing morphological hypothesis.

Eucnemidae taxa are listed in the same order as in Muona (1993) (Anischiinae added, Lawrence *et al.*, 2007). This order is based on phyletic sequencing (Nelson, 1974). Thus every named taxon is the sister-group of all the remaining taxa of the same rank. Thus Perothopinae is the sister-group of all the other Eucnemids, and Melasinae is the sister-group of Eucneminae + Macraulacinae. Within subfamilies, tribes are listed in the same fashion. The Melasinae tribes Melasini and Hylocharini as well as the Macraulacinae tribe Nematodini are discussed separately.

The only detailed larval data set with good coverage of Eucnemidae taxa is in Lawrence *et al.* (2007). We will refer to some of the characters in that publication with the number used in it (ranging from c77 to c118).

MT took all the photographs except for 2E, 3D, 4A-C, 5A, 6A (JM) and 2F (after Lawrence *et al.*, 2017).

Eucnemidae: Perothopinae

Head (Lawrence *et al.*, 2007, figs. 26-31): Head capsule smooth (c84), undivided (c83), antennae located on surface as in all Elateridae, Cerophytidae, and Throscidae, in contrast to all other Eucnemidae (c85). Labrum fused to head as in all other discussed taxa except Phyllocerinae and Pseudomenini: Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae and in contrast to Elateridae, Cerophytidae and Throscidae (c86). Mandibles with retinaculum as in Elateridae in contrast to other Eucnemidae and Cerophytidae and Throscidae (c97), free, elongate and inwardly curved biting as in Pseudomenini, Phyllocerinae, Anischiinae and most Elateridae, different from those of Throscidae and Cerophytidae as well as other Eucnemidae. Maxillolabial complex contiguous with epicranium on each side but incapable of movement, as in Cerophytidae, Throscidae, Pseudomeninae and Anischiinae, contrary to other Eucnemidae (completely fused) and Elateridae (freely movable). Presternum subtriangular, lightly pigmented, with paired oblique endocarinae, similar to that of Phyllocerinae, Pseudomeninae, Anischiinae and Palaeoxeninae. Legs five-segmented as in Phyllocerinae, Pseudomeninae and Elateridae, Cerophytidae and Throscidae, but in contrast to those of other Eucnemidae, which are tiny and either one segment (Anischiinae) or with seta in place of leg. Abdominal segments without microtrichial patches and areoles as in Elateridae, Cerophytidae, Throscidae, contrary to other Eucnemidae except Phyllocerinae. Segment IX with small, simple urogomphi. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Table 1. List of taxa. Species marked with an “*” were available for personal inspection.

EUCNEMIDAE	
Perothopinae	<i>Perothops</i> sp. [Lawrence <i>et al.</i> , 2007]
Phyllocerinae	<i>Phyllocerus</i> sp. [Gilyarov, 1979; Klausnitzer, 1997]
Pseudomeninae	<i>Pseudomenes bakewelli</i> (Bonvouloir)*, Australia, ACT
Schizophiliinae	<i>Schizophilus subrufus</i> (Randall)* [Otto & Young, 1998]
Palaeoxeninae	<i>Palaeoxenus dohrni</i> (Horn)* [Böving & Craighead, 1931; Chang <i>et al.</i> , 2016]
Anischiinae	<i>Anischia kuscheli</i> Lawrence* [Lawrence <i>et al.</i> , 2007]
Melasinae	
Melasini	<i>Isorhipis melasoides</i> (Castelnau)* [Mamaev, 1976]; <i>I. obliqua</i> (Say)* [Van Horn, 1909]; <i>Melasis buprestoides</i> (Fabricius)* [Leiler, 1976]; <i>Melasis pectinicornis</i> Melsheimer*
Hylocharini	<i>Hylocharis cruentatus</i> (Gyllenhal)* [Brüstle & Muona, 2009]; <i>H. harmandi</i> Fleutiaux [Mamaev, 1976]; <i>H. nigricornis</i> (Say)* [Peterson, 1960]; <i>H. populi</i> Brüstle & Muona* [Brüstle & Muona, 2009]
Calyptocerini	<i>Otho sphondyloides</i> Germar* [Leiler, 1976]
Xylobiini	<i>Agalba</i> sp.*, Australia, Queensland; <i>Proxylobius gardneri</i> (Fleutiaux) [Gardner, 1935]; <i>Xylophilus corticalis</i> (Paykull)* [Leiler, 1976]; <i>X. ussuriensis</i> Mamaev [Mamaev, 1976]
Epiphanini	<i>Hyllis cariniceps</i> (Mannerheim)* [Leiler, 1976]; <i>H. foveicollis</i> (Mannerheim) [Leiler, 1976]; <i>H. procerulus</i> (Mannerheim)* [Leiler, 1976]; <i>H. olexai</i> (Mannerheim) [Lucht, 1981]
Dirhagini	<i>Adelothyreus bengalensis</i> Fleutiaux [Gardner, 1935]; <i>Arrhipis ?orientalis</i> Fleutiaux [Gardner, 1935]; <i>A. balwanti</i> Fleutiaux [Gardner, 1935]; <i>Dirrhagofarsus attenuatus</i> (Mäklin)* [Burakowski, 1989]; <i>D. lewisi</i> (Fleutiaux)* [Ford & Spilman, 1979]; <i>D. emae</i> Otto, Muona & McClarin* [Otto <i>et al.</i> , 2014]; <i>Entomophthalmus rufiolus</i> (LeConte) [Otto, 2012b] <i>Farsus dubius</i> (Piller & Mitterpacher) [Nemeth & Otto, 2016]; <i>Microrhagus audax</i> Horn [Otto, 2015]; <i>M. breviangularis</i> Otto [Otto, 2015]; <i>M. brunneus</i> Otto [Otto, 2015]; <i>M. carinicornis</i> Otto [Otto, 2015]; <i>M. emyi</i> Rouget*, Sweden; <i>M. lecontei</i> Otto [Otto, 2015]; <i>Microrhagus lepidus</i> (Rosenhauer)* [Leiler, 1976]; <i>M. pectinatus</i> LeConte* [Otto, 2015]; <i>M. pygmaeus</i> (Fabricius)* [Leiler, 1976]; <i>M. subsinuatus</i> LeConte* [Otto, 2015]; <i>M. triangularis</i> (Say)* [Otto, 2015]; <i>?Prodirrhagus cairnesensis</i> (Lea)*, Australia, Queensland; <i>Rhacopus sahlbergi</i> (Mannerheim)* [Leiler, 1976]; <i>Rhagomicrus bonvouloiri</i> (Say)* [Otto, 2012a]
Eucneminae	
Mesogenini	<i>Stethon pectorosus</i> LeConte [Otto & Gruber, 2016]
Eucnemini	<i>Eucnemis capucinus</i> Ahrens* [Palm, 1955; Lundberg, 1962; Leiler, 1976]; <i>E. zaitzevi</i> Mamaev* [Mamaev, 1976]; <i>Poecilochrus bengalensis</i> Fleutiaux [Gardner, 1935]
Galbitini	<i>Arisus bituberculatus</i> Fleutiaux [Gardner, 1935]; <i>Galbimorpha agastoceroideis</i> Fleutiaux [Gardner, 1935]; <i>Galbites fulvus</i> Fleutiaux [Gardner, 1935]
Macraulacinae	
Euryptychini	<i>Euryptychus lewisi</i> Fleutiaux [Mamaev, 1976]; <i>?Euryptychus</i> sp.*, Panama
Macraulacini	<i>Asiocnemis ?mclayi</i> Muona*, USA, California; <i>A. morawitzi</i> (Semenov) [Mamaev, 1976]; <i>Deltometopus amoenicornis</i> (Say) [[Otto, 2012b]; <i>Dromaeoloides parvulus</i> (Bonvouloir)*, Australia, NSW, reared; <i>Dromaeoloides</i> spp.*, New Caledonia, Fiji, both reared; <i>D. ?badius</i> (Melsheimer)*, USA, Idaho; <i>D. barnabita</i> (Villa)* [Leiler, 1976]; <i>?Dromaeolus lugubris</i> Lea*, Australia, NSW; <i>?Dromaeolus punctatus</i> (LeConte)*, USA, Georgia; <i>Fornax distinguendus</i> Bonvouloir [Gardner, 1935]; <i>F. hisamatsui</i> Mamaev [Mamaev, 1976]; <i>F. gardneri</i> Fleutiaux [Gardner, 1926]; <i>F. holmi</i> Leiler [Leiler, 1990]; <i>F. raja</i> Leiler* [Leiler, 1990]; <i>F. silvestris</i> Fleutiaux [Gardner, 1935]; <i>F. vestitus</i> Fleutiaux [Gardner, 1935]; <i>Fornax</i> sp. [Costa <i>et al.</i> , 2003]; <i>Isarthrus rufipes</i> (Melsheimer) [Mosher, 1919]; <i>Onichodon canadensis</i> (Brown)* [Otto, 2013]; <i>O. orchides</i> Newman [Otto, 2013]; <i>O. rugicollis</i> (Fall) [Otto, 2013]; <i>Pseudoscython parvulus</i> Fleutiaux [Gardner, 1935]
Nematodini	<i>Nematodes filum</i> (Fabricius) [Leiler, 1976]; <i>Nematodes penetrans</i> (LeConte) [Otto, 2017]; <i>Nematodes</i> sp.*, Fiji, Viti Levu, reared; <i>Trigonopleurus rugulosus</i> Bonvouloir*, Australia, NSW, reared
CEROPHYTIDAE	<i>Cerophytum elateroides</i> (Latreille) [Costa <i>et al.</i> , 2003]
THROSCIDAE	<i>Triaxagus dermestoides</i> (Linnaeus) [Burakowski, 1975]

Eucnemidae: Phyllocerinae

Gilyarov (1979, figs. 1-3); Klausnitzer (1997, figs. 1-10)

Head capsule undivided (c83), disk-shaped, solid, antennae located in deep pits as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa. Labrum free as in Pseudomenini, in contrast to all other discussed taxa (c88), wide, short, with long posterior arms attaching it to head capsule, a unique feature. Antennae with four antennomeres as in Pseudomeninae, Elateridae, Cerophytidae and Throscidae, in contrast to other Eucnemidae (c86). Mandibles without retinaculum as in other Eucnemidae except Perothopinae as well as Cerophytidae and Throscidae (c97), free, elongated and inwardly curved as in Pseudomenini, Perothopinae, Anischiinae and most Elateridae, different from those of Throscidae and Cerophytidae as well as other Eucnemidae. Maxillolabial complex completely fused to epicranium as in Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae (c100). Presternum subtriangular, large, strongly sclerotized, darkly pig-

mented, forming a single large plate. Legs five-segmented as in Elateridae, Cerophytidae and Throscidae, but contrary to them tiny, all other Eucnemidae with at most one-segmented legs. Abdominal segments without microtrichial patches contrary to other Eucnemidae except Perothopinae, segment IX without urogomphi. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Eucnemidae: Pseudomeninae, Pseudomenini (Figs. 2A, B, 7B)

Head capsule undivided (c83), wide, flattened and with anteriorly directed large tooth-like projections on both sides, longitudinally grooved, as in Schizophilini (c82), antennae located in deep pits as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa (Fig. 2A). Labrum free as in Phyllocerinae, in contrast to all other discussed taxa except Anischiinae (c88), plate-like, without posterior arms, a unique feature (Fig. 2B). Antennae with four antennomeres as in Phyllocerinae,

Schizophilini and Elateridae, Cerophytidae and Throscidae, in contrast to other Eucnemidae (c86). Mandibles without retinaculum as in other Eucnemidae except Perothopinae as well as Cerophytidae and Throscidae (c97), free, elongate and inwardly curved as in Perothopinae, Anischiinae and most Elateridae, different from those of Throscidae and Cerophytidae as well as other Eucnemidae. Maxillolabial complex contiguous with epicranium on each side and incapable of movement, as in Cerophytidae, Throscidae, Perothopinae and Anischiinae, contrary to other Eucnemidae (completely fused) and Elateridae (freely movable) (c100). Presternum subtriangular, pigmented, with paired oblique strong endocarinae, similar to those of Schizophilini and Palaeoxeninae. Legs five-segmented as in Elateridae, Cerophytidae and Throscidae, but contrary to them tiny, all other Eucnemidae with at most one-segmented legs. Abdominal segments with microtrichial patches as in other Eucnemidae except Perothopinae and Phyllocerinae, without areoles, segment 9 with large bifid urogomphi as in Schizophilini. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

sides, longitudinally grooved, as in Pseudomenini (c82), antennae located in deep pits as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa (Fig. 2C). Labrum fused to head as in all other discussed taxa except Pseudomenini, Phyllocerinae and Anischiinae, in contrast to all other discussed taxa (c88), forming an apically excavated nasale-like structure, a unique feature (Fig. 2D). Antennae with four antennomeres as in Phyllocerinae, Schizophilini and Elateridae, Cerophytidae and Throscidae, in contrast to other Eucnemidae (86). Mandibles without retinaculum as in other Eucnemidae except Perothopinae as well as Cerophytidae and Throscidae (c97), free, inward curved but not meeting medially, different from those of all other discussed taxa, laterally with large, sharp tooth-like projections as in most Eucnemidae except Perothopinae, Phyllocerinae, Pseudomenini and Anischiinae. Maxillolabial complex contiguous with epicranium on each side and incapable of movement as in Cerophytidae, Throscidae, Perothopinae, and Anischiinae, contrary to other Eucnemidae (completely fused) and Elateridae (freely movable) (c100). Legs five-segmented as in Elateridae, Cerophytidae and Throscidae, but contrary to them tiny, all other Eucnemidae with at most one-segmented legs. Abdominal segments with microtrichial patches as in other Eucnemidae except Perothopinae and Phyllocerinae, without areoles, segment IX with large bifid urogomphi as in Pseudomenini. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Eucnemidae: Pseudomeninae, Schizophilini (Figs. 2C, D, 7C)

Head capsule undivided (c83), wide, flattened and with anteriorly directed large tooth-like projections on both

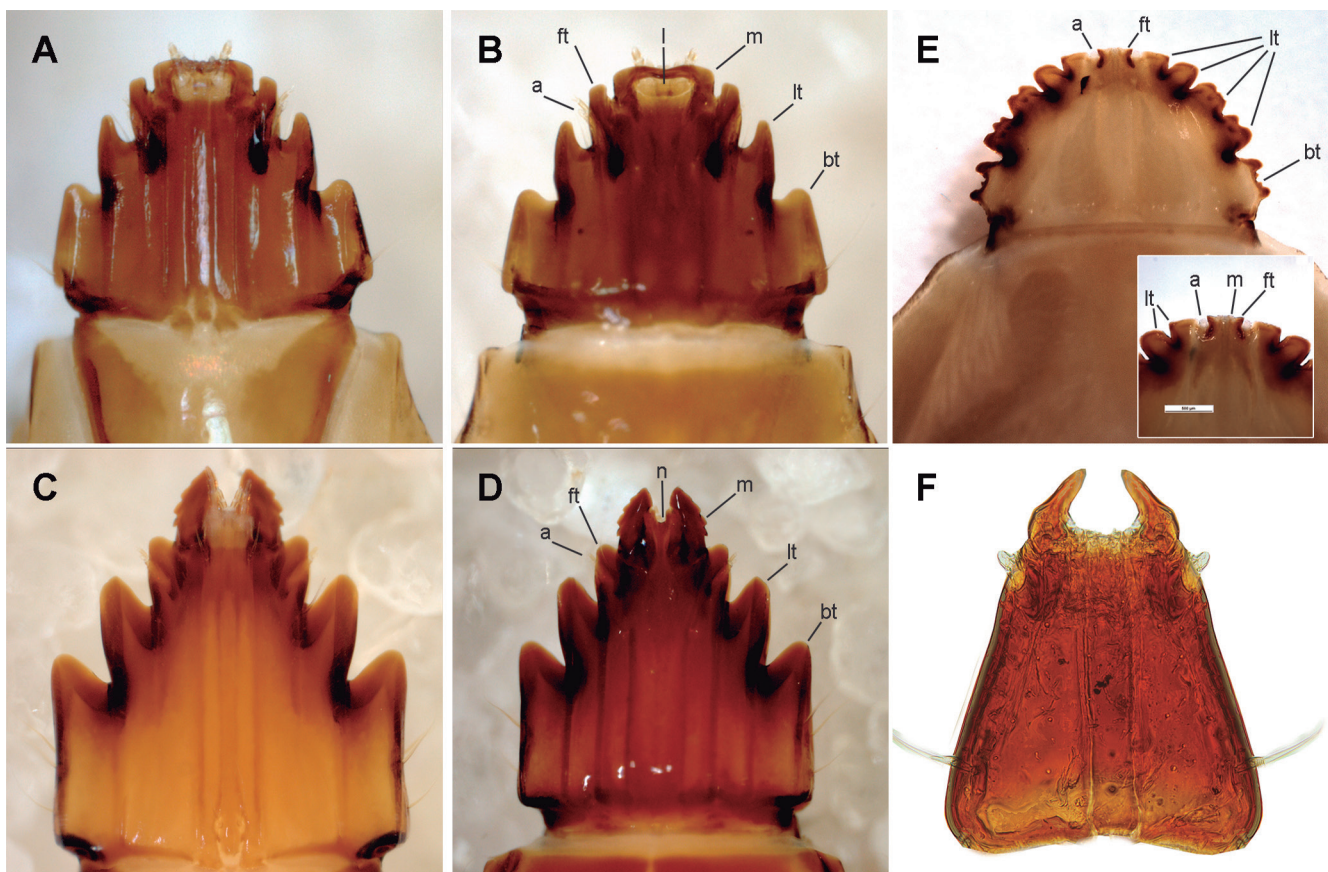


Figure 2. Eucnemidae, larval heads. (A, B) *Pseudomenes bakewelli* (Bonvouloir), ventral, dorsal; (C, D) *Schizophilus subrufus* (Randall), ventral, dorsal; (E) *Palaeoxenus dohmii* (Horn) dorsal, detail ventral; (F) *Anischia kuscheli* Lawrence, ventral. a = antenna, bt = basal tooth, ft = front tooth, l = labrum, lt = lateral tooth, m = mandible, n = nasale.

Eucnemidae: Palaeoxeninae (Figs. 2E, 7A)

Head capsule wide, flattened, smooth (c84), undivided (c83), forming a semi-circular disk with lateral tooth-like projections, antennae located in deep pits between front tooth and first lateral tooth (Fig. 2E) as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa. Labrum fused to head without trace of clypeolabral suture as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (86). Mandibles fused to front teeth without trace of sutures, a unique feature (Fig. 2F). Maxillolabial complex completely fused with epicranium as in other Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae, contrary to Cerophytidae and Throscidae (separate, but incapable of movement) and Elateridae (freely movable) (c100). Presternum subtriangular, pigmented, with paired oblique endocarinae, similar to that of Pseudomeninae. Legs present as single setae only as in most Eucnemidae, contrary to Perothopinae, Phyllocerinae, Pseudomeninae, Anischiinae and all non-eucnemids discussed. Abdominal segments with microtrichial patches, without areoles, segment IX with small urogomphi. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Eucnemidae: Anischiinae (Fig. 2F)

Head capsule elongate, flattened, smooth (c84), undivided (c83), antennae located in deep pits as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa (Fig. 2G). Labrum fused to head without trace of suture as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (c86). Mandibles without retinaculum as in other Eucnemidae except Perothopinae as well as Cerophytidae and Throscidae (c97), free, elongate and inwardly curved as in Schizopholini, Perothopinae and most Elateridae, different from those of Throscidae and Cerophytidae as well as other Eucnemidae. Maxillolabial complex contiguous with epicranium on each side and incapable of movement, as in Cerophytidae, Throscidae, Pseudomeninae and Perothopinae, contrary to other Eucnemidae (completely fused) and Elateridae (freely movable) (c100). Presternum subtriangular, lightly pigmented, weakly delimited, with paired oblique endocarinae. Legs with one segment, a unique feature. Abdominal segments with microtrichial patches, without areoles. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Eucnemidae: Phlegoninae

Larva unknown.

Eucnemidae: Melasinae, excluding Melasini, Hylocharini (Figs. 3A-D)

Head capsule wide, flattened (c84), divided into ventral and dorsal plates (c83), forming a semi-circular disk with lateral tooth-like projections, antennae located in deep pits between front tooth and first lateral tooth (Figs. 3A-D) as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa. Labrum fused to head without trace as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (86). Mandibles very small, either feebly movable or fused to head between mouth and front tooth (Fig. 3). Maxillolabial complex completely fused with epicranium as in other Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae, contrary to Cerophytidae and Throscidae (separate, but incapable of movement) and Elateridae (freely movable) (c100). Presternum mostly undefined, but proventrum usually with two pairs of sclerotizations, one longitudinal medially and one square close to front corners, similar to those of most Melasinae, Eucneminae and Macraulacinae. Legs present as single setae, often visible as dark spot only as in all Eucnemidae except Perothopinae, Phyllocerinae, Pseudomeninae, Anischiinae and all non-eucnemids discussed. Abdominal segments with microtrichial patches and areoles (Muona & Teräväinen, 2008), segment IX rarely with

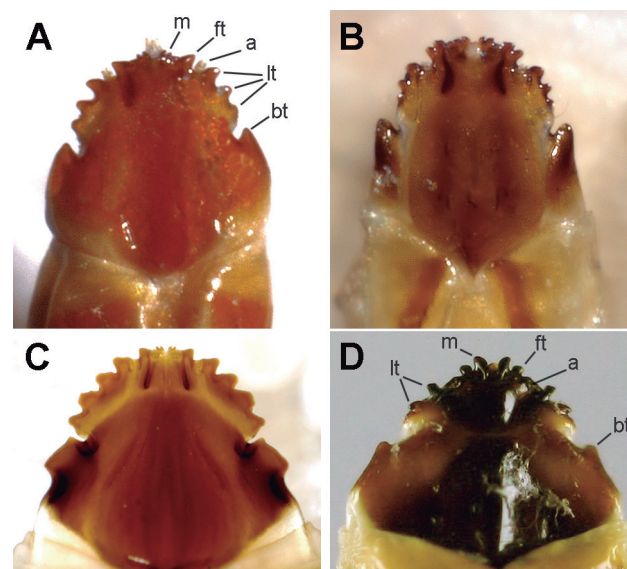


Figure 3. Eucnemidae, Melasinae, larval heads, ventral. (A) *Xylophilus corticalis* (Paykull); (B) *Hylis cariniceps* (Reitter); (C) *Prodirrhagus*; (D) *Dirrhagofarsus ernae* Otto, Muona & MvčClarín. a = antenna, bt = basal tooth, ft = front tooth, lt = lateral tooth, m = mandible.

minute urogomphi. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Several Dirhagini exhibit extreme hypermetamorphosis from small triangulin-type larvae (*Dirrhagofarsus* Fleutiaux) to ones with large exodont mandibles and finally a more “normal” looking larva (*Microrhagus* Fabricius). Others appear to have a less active, perhaps nearly sessile, development and resemble dipteran larvae (*Farsus* du Val, *Arrhipis* Fleutiaux). These unusual developmental types are found also in Nematodini (*Nematodes* Dejean, *Trigonopleurus* Bonvouloir) and Eucneminae (*Eucnemis* Ahrens) and the tendency towards different developmental solutions seems to be a feature uniting the three most speciose subfamilies, Eucneminae, Macraulacinae and Melasinae.

Eucnemidae: Melasinae, Melasini (Fig. 6B)

Head capsule small, cap-like, divided in ventral and dorsal plates but these fused (c83), antennae located in deep pits, basal, lateral and front teeth absent in contrast to all other Eucnemidae except Anischiinae, Nematodini, Hylocharini and all hypermetamorphic Eucneminae. Labrum fused to head without trace as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (c86). Mandibles freely movable, powerful and exodont, large in size as in Hylocharini and Nematodini, contrary to those in other Macraulacinae and Melasinae. Maxillolabial complex completely fused with epicranium as in other Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae, contrary to Cerophytidae and Throscidae (separate, but incapable of movement) and Elateridae (freely movable) (c100). Prothorax substantially wider than mesothorax, ventrally and dorsally with conspicuous T-formed sclerotizations as in Nematodini (3F), mesothorax with sclerotized median rod, presternum unde-

fined. Legs visible as dark spots only as in all Eucnemidae except Perothopidae, Phylloceridae, Pseudomeninae, Anischiinae and the non-eucnemids discussed. Abdominal segments without microtrichial patches and areoles contrary to Nematodini (both present) and Hylocharini (areoles present). Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Eucnemidae: Melasinae, Hylocharini (Fig. 6A)

Head capsule small, cap-like, divided into ventral and dorsal plates but these fused (c83), antennae located in deep pits, hard to see, basal, lateral and front teeth absent in contrast to all other Eucnemidae except Anischiinae, Nematodini, Hylocharini and all hypermetamorphic Eucneminae. Labrum fused to head without trace of suture as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (c86). Mandibles large, freely movable and powerful, exodont as in Melasini and Nematodini, differing from those of all other discussed taxa (6A). Maxillolabial complex completely fused with epicranium as in other Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae, contrary to Cerophytidae and Throscidae (separate, but incapable of movement) and Elateridae (freely movable) (c100). Prothorax substantially wider than mesothorax, ventrally and dorsally with conspicuous plates consisting of rows of wave-like sharp sclerotizations, a unique feature, mesothorax without sclerotizations, presternum undefined. Legs visible as dark spot only as in all Eucnemidae except Perothopidae, Phylloceridae, Pseudomeninae, Anischiinae and the non-eucnemids discussed. Abdominal segments without microtrichial patches contrary to Nematodini, with large areoles contrary to Melasini. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

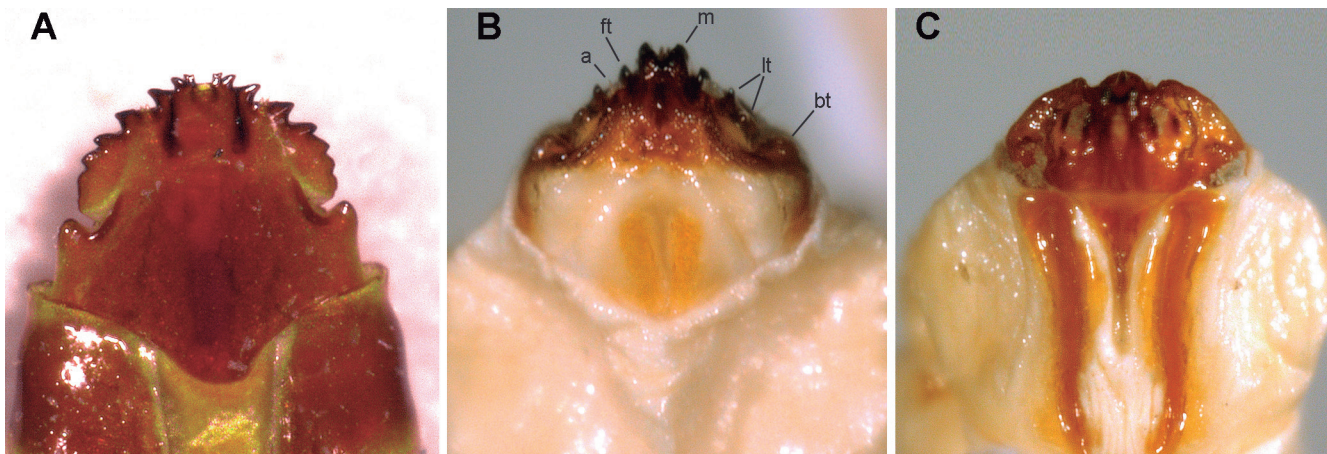


Figure 4. *Eucnemis capucinus* Ahrens, larval head. (A) Main larval form; (B) prepupal larval form, dorsal; (C) prepupal form, ventral. a = antenna, bt = basal tooth, ft = front tooth, lt = lateral tooth, m = mandible.

Eucnemidae: Eucneminae (Figs. 4C)

The complete developmental sequence of only one genus, *Eucnemis* Ahrens, is known. During most of the life-history the larva is similar to those of species belonging to Macraulacinae (*Fornax*, *Dromaeolus* (s. str.) Kiesenwetter, *Dromaeoloides* Cobos, *Onichodon* Newman) and Melasinae (*Agalba* Broun, *Hylis* des Gozis, *Microrhagus* Dejean, *Prodirrhagus* Fleutiaux, *Xylophilus* Mannerheim) (Fig. 4A). The main larval form of *Eucnemis* is, however, conspicuously strongly sclerotized and with large microtrichial patches. The totally different prepupal type has small spike-like structures on head capsule instead of teeth and mandibles and a prominent pair of strong sclerotized rods ventrally on prothorax (Figs. 4B-C). Apparently the developmental strategies are wide in the subfamily, as *Stethon* LeConte has a similar prepupal form, but the larval stage before that differs radically from the corresponding larval stage of *Eucnemis* (see Otto & Gruber, 2016). This variation may reflect the fact that the two genera belong to different tribes, Eucnemini and Mesogenini. The descriptions available for species belonging to a third Eucneminae tribe, Galbitini, suggest that the larvae of *Arisus* Bonvouloir, *Galbimorpha* Fleutiaux and *Galbites* Fleutiaux may offer still further developmental variation, partly similar to that of *Farsus* du Val in subfamily Melasinae. Unfortunately the descriptions refer only to single stages of these types.

Eucnemidae: Macraulacinae, excluding Nematodini (Figs. 5A-E)

Head capsule wide, flattened (c84), divided in ventral and dorsal plates (c83), forming a semi-circular disk with lateral tooth-like projections, antennae located in deep pits between front tooth and first lateral tooth (Figs. 2B, 3A, 5A-E) as in all Eucnemidae except Perothopinae (c85), in contrast to all other discussed taxa. Labrum fused to head without trace as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88), Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (c86). Mandibles very small, either feebly movable or fused to head between mouth and front teeth. Maxillolabial complex completely fused with epicranium as in other Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae, contrary to Cerophytidae and Throscidae (separate, but incapable of movement) and Elateridae (freely movable). Presternum mostly undefined, but proventer usually with two pairs of sclerotizations, one longitudinal medially and one square close to front corners, similar to those of most Melasinae, Eucneminae and Macraulacinae. Legs present as single setae, often visible as dark spot only as in all Eucnemidae except Perothopinae, Phyllocerinae, Pseudomeninae, Anischiinae and all non-eucnemids discussed. Abdominal segments with microtrichial patch-

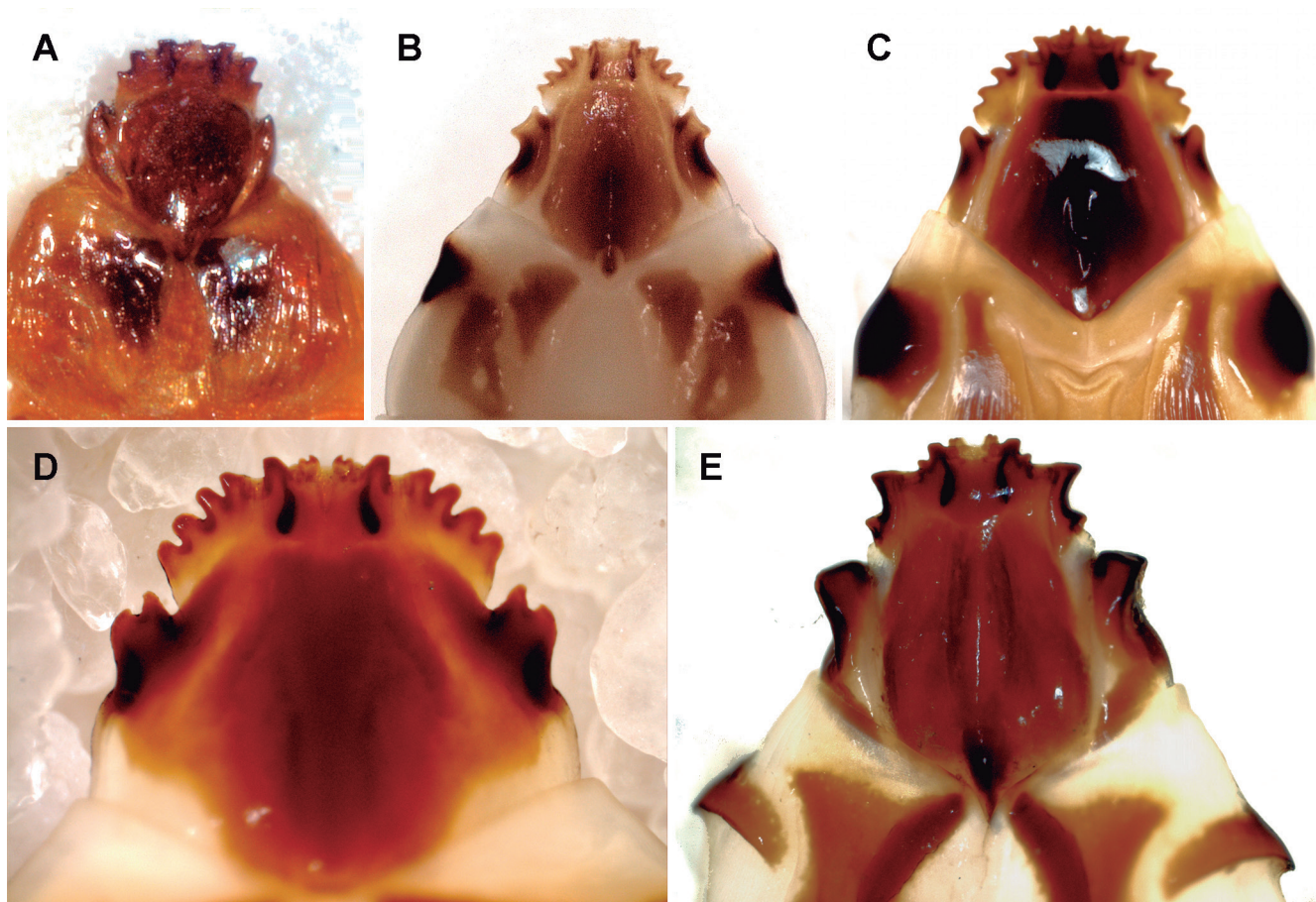


Figure 5. Eucnemidae, Macraulacinae, larval heads, ventral. (A) *Dromaeolus barnabita* (Villa); (B) *Dromaeolus* sp.; (C) *Dromaeolus ?badius* (Melsheimer); (D) *Onichodon canadensis* (Brown); (E) *Asiocnemis mcclayi* Muona.

es and areoles (Muona & Teräväinen, 2008), segment IX rarely with minute urogomphi. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Eucnemidae: Macraulacinae, Nematodini (Fig. 6C)

Head capsule small, cap-like, divided in ventral and dorsal plates but these fused (c83), antennae located in deep pits, basal, lateral and front teeth rudimentary in contrast to all other Eucnemidae except Anischiinae, Melasini, Hylocharini and all extreme hypermetamorphic Eucneminae. Labrum fused to head without trace as in all Eucnemidae except Phyllocerinae and Pseudomenini (c88). Number of antennomeres reduced as in all Eucnemidae except Phyllocerinae and Pseudomeninae, in contrast to Elateridae, Cerophytidae and Throscidae (c86). Mandibles large, freely movable and powerful, exodont as in Hylocharini and Melasini and different from those of all other discussed taxa. Maxillolabial complex completely fused with epicranium as in other Eucnemidae except Perothopinae, Pseudomeninae and Anischiinae, contrary to Cerophytidae and Throscidae (separate, but incapable of movement) and Elateridae (freely movable) (c100). Prothorax substantially wider than mesothorax, ventrally and dorsally with conspicuous T-formed sclerotizations as in Melasini, presternum undefined, mesothorax without sclerotized structures contrary to Melasini. Legs visible as dark spots only as in all Eucnemidae except Perothopinae, Phyllocerinae, Pseudomeninae, Anischiinae and the non-eucnemids discussed. Abdominal segments with both microtrichial patches and areoles contrary to Melasini and Hylocharini. Spiracles with closing apparatus as in other Eucnemidae, all Cerophytidae and Throscidae, in contrast to Elateridae.

Throscidae Burakowski (1975)

Head capsule smooth (c84), undivided (c83), antennae located on surface as in all Elateridae and

Cerophytidae, in contrast to all Eucnemidae except Perothopinae (c85). Labrum fused to head as in all other discussed taxa except Phyllocerinae and Pseudomenini (c88). Number of antennomeres not reduced as in all Elateridae and Cerophytidae, in contrast to Eucnemidae except Phyllocerinae and Pseudomeninae (c86). Mandibles without retinaculum as in most Eucnemidae and all Cerophytidae and in contrast to *Perothops* and Elateridae (c97), fused solidly to head, with single lateral blunt tooth, a unique feature. Maxillolabial complex contiguous with epicranium on each side but incapable of movement, as in Cerophytidae, Pseudomeninae and Anischiinae, contrary to most Eucnemidae (completely fused) and Elateridae (freely movable). Presternum undefined, proventer with two pairs of longitudinal and two pairs of transverse sclerotized rods, a unique feature. Legs five-segmented, medium-sized, as in Elateridae and Cerophytidae, much larger than in any Eucnemidae. Abdominal segments without microtrichial patches and areoles as in Elateridae and Cerophytidae, segment IX with very small, simple urogomphi. Spiracles with closing apparatus as in Eucnemidae and Cerophytidae, in contrast to Elateridae.

Cerophytidae Costa et al. (2003)

Head capsule smooth (c84), undivided (c83), antennae located on surface as in Elateridae and Throscidae, in contrast to all Eucnemidae except Perothopinae (c85). Labrum fused to head as in all other discussed taxa except Phyllocerinae and Pseudomenini (c88). Number of antennomeres not reduced as in all Elateridae, Throscidae, in contrast to Eucnemidae except Phyllocerinae and Pseudomeninae (c86). Mandibles without retinaculum as in most Eucnemidae and all Throscidae, in contrast to *Perothops* and Elateridae (c97), free, forward directed, non-opposable. Maxillolabial complex contiguous with epicranium on each side, but incapable of movement, as in Throscidae, Pseudomeninae and Anischiinae, contrary to most Eucnemidae (completely fused) and Elateridae (freely movable), short and wide. Presternum undefined, proventer with pair of longitudinal sclerites.

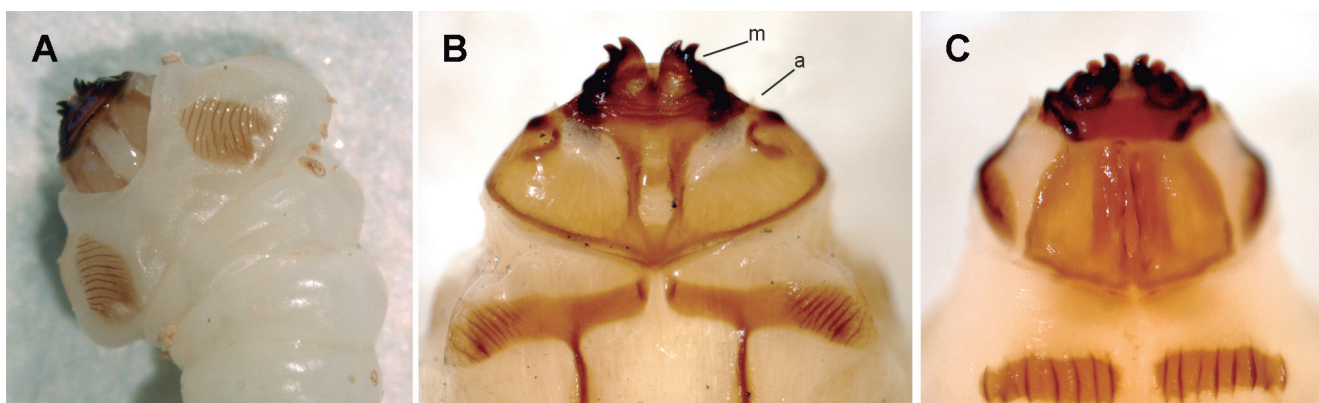


Figure 6. Eucnemidae, larval heads, solid wood boring types. (A) *Hylochaeres cruentatus* (Gyllenhal), dorsal; (B) *Melasis pectinicornis* Melsheimer, dorsal; (C) *Trigonopleurus rugulosus* Bonvouloir, dorsal. a = antenna, m = mandible.

Legs five-segmented, medium-sized, as in Elateridae and Throscidae, much larger than in any Eucnemidae. Abdominal segments without microtrichial patches and areoles as in Elateridae and Cerophytidae, segment IX with very small, simple urogomphi. Spiracles with closing apparatus as in Eucnemidae and Throscidae, in contrast to Elateridae.

“REAL” Eucnemidae?

Although not a requirement for our views to hold, we point out that we consider the clicking mechanism a synapomorphy of four elateroid families, Cerophytidae, Throscidae, Eucnemidae and Elateridae. Lawrence *et al.* (2007) recovered this result with by far the most extensive morphological data set ever analyzed. Based on a large molecular data set, Kundrata *et al.* (2014) indicated that the clicking mechanism in Elateridae had an independent origin. As we have pointed out earlier, their result was ambiguous. The critical nodes had no resampling support at all and thus the result shown was not reliably based on the data.

The greatly reduced larval legs appear to separate Eucnemidae from all other Elateroidea, including Throscidae, Cerophytidae and Elateridae. This reduction occurs in three stages. *Perothops*, *Phyllocerus* Le Peletier & Serville and *Pseudomeninae* have five segmented rudimentary legs, *Anischia* Fleutiaux one segmented legs and the remaining Eucnemidae (*Palaeoxeninae*, *Melasinae*, *Eucneminae*, *Macraulacinae*) have single setae instead of legs. The reduction of larval legs could thus be a synapomorphy for Eucnemidae *sensu* Muona (1993). Another larval character, structure of mandibles, is congruent with the larval leg reduction. Species with segmented legs have well-developed inward curving mandibles, the legless ones having exodont mandibles, nearly invariably very small ones as well. The simple larval mandibles are obviously a plesiomorphic feature found in all potential outgroups, but the exodont larval mandibles as well as the total loss of segmented larval legs are synapomorphies of the derived subfamilies: *Palaeoxeninae*, *Melasinae*, *Eucneminae*, *Macraulacinae*, a group called DE from this on. DE is further characterized by the unique semicircular chisel-shaped head with basal and frontal serrations and one to four further tooth-shaped ones in between them (Figs. 2E, 3, 4A, 5, 7A). However, the early form of this peculiar head appears to be the type found in *Pseudomeninae* (Figs. 2A-D). *Pseudomenes* Fleutiaux has unmodified mandibles and a free labrum (both plesiomorphies) and *Schizophilus* Bonvouloir mandibles with serrations on lateral surfaces and a fused labrum (both apomorphies shared with DE). These differences are significant in an evolutionary sense, uniting *Schizophilus* with the DE and separating *Pseudomenes* as the sister-group of them all. In such a scheme, using phyletic sequencing, *Schizophilinae* would become the sister-group of the (unnamed) DE clade and *Pseudomeninae* the sister-group of the combined (unnamed) clade with *Schizophilinae* and DE.

The clade (*Melasinae* (*Eucneminae*, *Macraulacinae*)) within DE shares further previously ignored synapomorphies: head divided in dorsal and ventral plates and an undefined prothoracic presternum. Its sister-group *Palaeoxenus* Horn has a plesiomorphic entire head capsule and a well-developed presternum.

Perothopinae, Phyllocerinae, Anischinae?

The larvae of the remaining three basal Eucnemidae subfamilies (*Perothopinae*, *Phyllocerinae*, *Anischinae*) are very different from each other.

Anischia has microtrichial patches and antennae placed in deep cavities, both features of eucnemids. Its position between *Palaeoxenus* and (*Melasinae* (*Eucneminae*, *Macraulacinae*)) (Lawrence *et al.*, 2007) appears problematic, as *Anischia* possesses several plesiomorphic features hard to see as apomorphic reversals needed for such a placement: unmodified head capsule, elongate, normal mandibles and legs with one real segment. We find this result untenable. To place *Anischia* basally as the sister group of (*Pseudomeninae* (*Schizophilinae* (DE))) is a reasonable possibility. It would mean that the larval labrum was fused to head at least twice in the Eucnemidae lineage, once in *Anischia* and again in *Schizophilus*. On the other hand, *Perothops* with many plesiomorphic features, *e.g.*, antennae attached to surface of head, has a fused larval labrum as well. Thus it is clear that this character state cannot be optimized without multiple changes anyway, irrespective of the cladogram. The free larval labrum in *Phyllocerinae* and *Pseudomenes* point to the basal position of eucnemids in the elateroid phylogeny, as the only other taxon to show this plesiomorphic feature is *Brachypsectra*.

The maxillolabial complex is contiguous with epicranium on each side and incapable of movement in *Perothops*, *Anischia*, *Pseudomenes* and *Schizophilus* as well as in Cerophytidae and Throscidae, whereas it is solidly fused to epicranium in *Phyllocerus* as well as in the DE. These fusions are not similar, however. In *Phyllocerus*, all ventral structures form one single hard plate without details. In *Palaeoxenus* the separate structures of ventral head as well as prothorax are still discernable (Fig. 7A), whereas in *Melasinae*, *Eucneminae* and *Macraulacinae* the fusion is nearly complete and only mentum and/or submentum can be seen (Figs. 7D-F).

Elateridae as well as all potential out-groups have a free maxillolabial complex, the contiguous state being present in cerophytids, throscids and *Perothops*, *Anischia*, *Pseudomenes* and *Schizophilus*. This could be a synapomorphy connecting the three clades together. *Phyllocerus* larva is strongly sclerotized and highly specialized for living in the black earth soil. The apparent similarity in larval maxillolabial complex to lignicolous derived eucnemids is not due to identical structures, but superficial similarity. *Phyllocerus* larva has deep antennal cavities, however. This might be seen as further support for closer relationship with eucnemids, excluding *Perothops*.

The fused maxillolabial complex appears to be another previously ignored synapomorphy for the (Pseudomenini (Schizophilini (DE))) clade. The sclerotized dark plates and rods found in most Melasinae, Eucneminae and Macraulacinae larvae may be homologs of larval features still visible in *Pseudomenes*, *Schizophilus* and *Palaeoxenus*. The longitudinal rods/fields could be the remnants of the powerful presternal oblique carinae and the paired sclerotization on front corners of proventer homologs of the sclerotized ventral suture edges (Figs. 7D-F).

Do the larval characters support existing hypothesis for Eucnemidae relationships?

Do our undoubtedly speculative ideas (based on actual character states, however) fit the adult structures and the hypothesis based on those? Traditionally eucnemids were separated from elaterids by the completely connate abdominal ventrites and concealed labrum. Neither of these characters suffices today. *Anischia* fails on both counts with three connate ventrites and a visible labrum. *Phyllocerus* has only four connate ventrites

as do Cerophytidae and Elateridae, whereas *Perothops*, Pseudomeninae, and all derived Eucnemidae have five connate ventrites, but so does Throscidae. A further character, the attachment of pedicel to scape is subapical in all Eucnemidae, but the same holds for Cerophytidae and a few Elateridae (Thylacosterninae, Lissominae). Numerous other characters prove this state in elaterids to be homoplastic, but the cerophytids might well be the sister-group to some or all eucnemids based on the antennal structure.

The female reproductive tract seems to provide illuminating evidence. First, potential out-groups Dascillidae and Artematopidae as well as Throscidae, Cerophytidae and Elateridae all have special sclerites or asperities in bursa copulatrix, Eucnemidae and Brachyspectridae do not (c73). Secondly, Elateridae have colleterial glands, while Eucnemidae, Cerophytidae and Throscidae do not (c70). Third, *Perothops*, Phyllocerinae, Pseudomeninae, *Palaeoxenus* and *Phlegon* Laporte as well as basal Melasinae (e.g., *Hylochaeres* Latreille), Eucneminae (e.g., *Phaenocerus* Bonvouloir, *Pinaroo* Muona) and Macraulacinae (e.g., *Langurioscython* Heller, *Dictyeucnemis* Lea, *Ceratogonyx* Perty) have a bifurcate

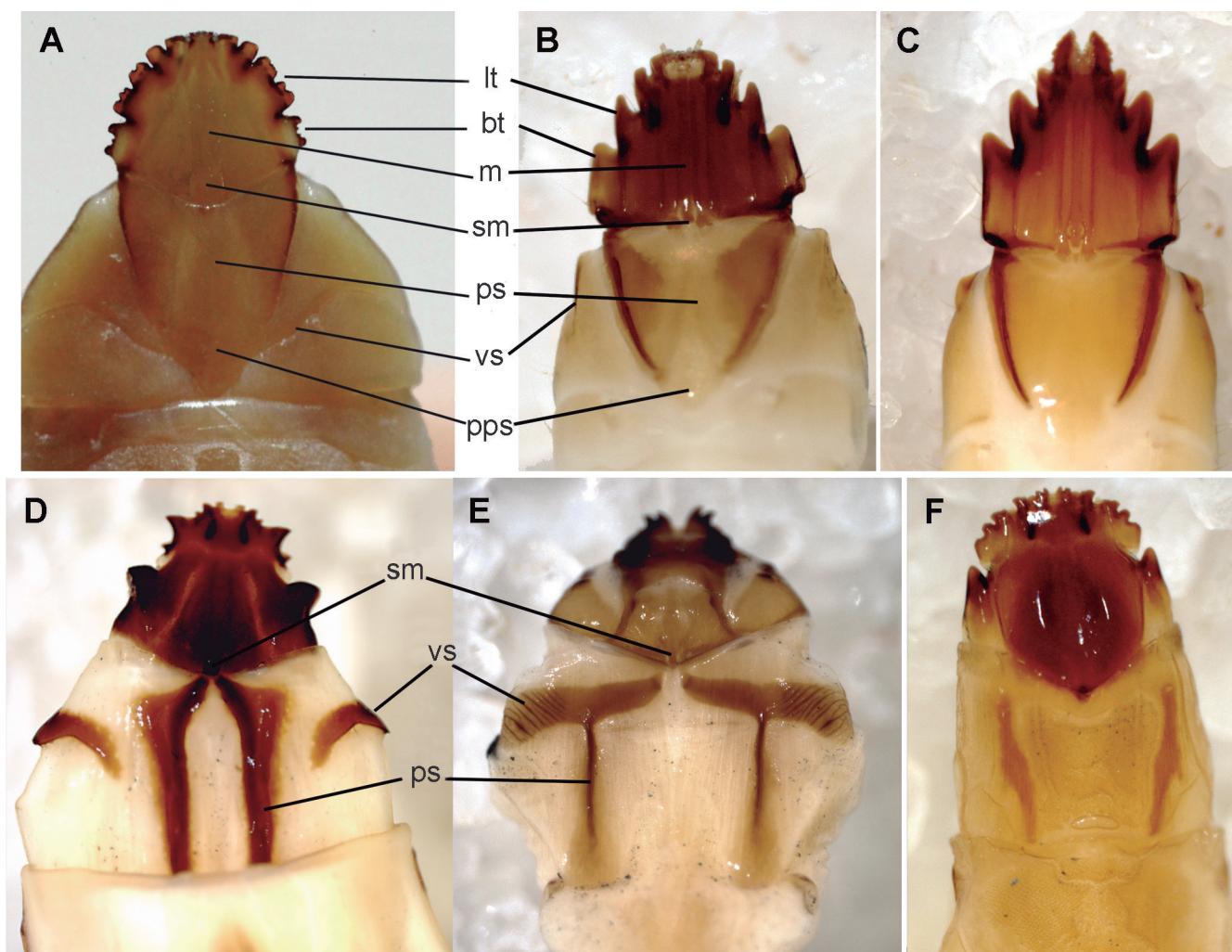


Figure 7. Eucnemidae, larval heads, ventral. (A) *Palaeoxenus dohrnii* (Horn); (B) *Pseudomenes bakewelli* (Bonvouloir); (C) *Schizophilus subrufus* (Randall); (D) *Asiocnemis mcclayi* Muona; (E) *Melasis pectinicornis* Melsheimer; (F) *Rhagomicrus bonvouloiri* (Say). bt = basal tooth, lt = lateral tooth, m = mentum, pps = posterior presternal sclerite, ps = presternum, sm = submentum, vs = ventral suture.

bursa, a synapomorphy not known in other Elateroidea (c72; Muona, 1993).

The unarmed bursa is clearly a synapomorphy for Eucnemidae *s.l.* as it is not present in any putative out-group (c72). The bifurcate bursa is a synapomorphy for eucnemids as well, but it has reversed in all derive members of Macraulacinae, Eucneminae and Melasinae, quite clearly independently in all three clades.

The colleterial glands appear to be the only elaterid synapomorphy found this far, all other related taxa lacking these. It is a strong character not known to have reversed.

Otto & Gruber (2016) drew attention to the peculiar grooves and large punctures in the elytral apices of the eucnemid *Stethon*. These specialized pores, not previously noticed, had not caught the attention they deserved. A search has shown that these structures (excretory organs?) are found in all Eucnemidae except *Perothops*, *Phyllocerus* and a few highly derived Macraulacinae. This splendid discovery appears to be a synapomorphy for all true lignicolous eucnemids.

The hypermetamorphic taxa, *i.e.*, many if not all Eucneminae, many Dirhagini and all Nematodini, are not identical either in structure or in development. There appears to be a pattern present in many Melasinae, Eucneminae and Macraulacinae of early triungulin type larvae followed by chisel-shaped head type stage and finally variable reduction of hard structures in the last stage. Either of the two final stages may dominate the full development.

The extreme larval forms, type Galbitini, resembling Diptera larvae may spend their whole life in one chamber. The extraoral digestion in wood infested with fungus makes this approach feasible.

One of the authors (JM) has followed the development of an undescribed *Nematodes* Berthold species in Viti Levu, Fiji. The first instar larva had powerful exodont mandibles, similar to the macraulacine *Fornax gardneri* Fleutiaux first instar larva (Gardner, 1926). These larvae were found in seemingly hard wood of an unidentified rattan. They developed into a typical chisel-shaped head type in a few weeks and during the same period the substrate had become soft and penetrable. After several such stages the larvae assumed the *Nematodes* appearance described by Leiler (1976) and Otto (2017). Finally, the further reduced prepupal form emerged. The key here, as with Melasini and *Hylochaes*, seems to be the consistency of the substrate. All these species start their development in hard wood infested by fungus. Early on the larvae need to be able to penetrate the substrate with strong mandibles, but later in their development, if the wood becomes soft enough, a standard derived eucnemid larval type is the solution.

Lignicolous larvae are constantly in danger of being parasitized or eaten by predators. The hydraulic method of penetrating the wood used by eucnemid larvae leaves no real galleries and the absence of working mandibles reduce the noise produced substantially. It is definitely the most advanced approach for moving around within wood in secrecy. The extraoral feeding leaves open the

further possibility of not moving at all, if fungal growth is constantly available for extraoral feeding. This may well be the reason behind the extreme larval forms, which appear to spend the whole life in one chamber. It is easy to understand, that such a solution would also benefit from highly mobile early stages capable of finding the right one location, a triungulin type larva.

The few derived eucnemids with larvae penetrating hard wood need strong mandibles and a large prothorax with strong muscles and gripping surface structures to provide the mouthparts leverage. Other beetle larvae with the same kind of approach to wood-boring have developed similar looking solutions, *e.g.*, Buprestidae and Cerambycidae. Details differ substantially; however, those taxa have a free labrum and normally biting mandibles instead of fused labrum and exodont mandibles.

In our view the external similarity of Hylocharini, Melasini and Nematodini is due to repeated invasions into hard wood. In Melasini and Hylocharini the whole development takes place in hard wood. In Nematodini, the larvae use different phases of rot during their development. This may well be the strategy for *Eucnemis* as well. We have observed minute larvae in moist, very soft inner wall of hollow trees, with larger larvae in more solid and drier wood, deeper in the substrate.

We acknowledge the fact that evolutionary hypotheses must be based on global analytical results. Evolutionary novelties, synapomorphies, exist only in connection with an analysis of a specific data set. On the other hand, we believe it is useful to examine the characters supporting the groups previously analytically established. We have here looked at larval features not used in the evolutionary hypothesis previously produced. The larval features discussed appeared to help to clarify the relationships within Eucnemidae and Elateroidea to some extent. They were especially useful in pointing out serious problems as well as strong evolutionary signals within Eucnemidae.

CONCLUSIONS

First, the true lignicolous eucnemids include Pseudomeninae, Schizophiliinae, Palaeoxeninae, Eucneminae, Melasinae and Macraulacinae. Phlegoninae with unknown larvae fits amongst the eucnemid taxa because of the unmodified, bifurcate bursa. This is in agreement with the earlier analytical hypothesis but refines the situation with respect to Pseudomeninae *sensu* Muona (1993). All sister-group relationships found new support from larval features and larval features helped to discover further adult synapomorphies. In the scheme here accepted the tribe Schizophilini Muona, 1993 is shown to be the sister-group of the subfamilies Palaeoxeninae, Phlegoninae, Melasinae, Eucneminae and Macraulacinae. To reflect this in a scheme of phyletic sequencing it is regarded a subfamily, Schizophiliinae Muona, 1993 *new status*.

Second, further evidence for the placement of Phyllocerinae and Anischiinae are needed. They may

well be true eucnemids, but the sister-group relationships need further study. *Phyllocerus* larva has many special features related to its subterranean mode of life in a special, compact environment, but the unmodified, bifurcate bursa indicates it belongs to the eucnemid lineage. *Anischia* appears to be a complex of real eucnemid synapomorphies united with reductive features.

Third, *Perothops* appears to be among basal taxa of the eucnemid lineage, but it may share sister-group relationships with non-eucnemid taxa as well. If this turns out to be the case, the families have to be redefined.

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