

4. Elateroidea

Introduction, Phylogeny

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The constitution of Elateriformia has varied over time, as discussed in detail by Beutel & Leschen (2005) (see 1–14). The series was first proposed by Crowson (1960) for his Dascilliformia (Crowson 1955) minus the family Dascillidae (which was combined with Scarabaeoidea to form the series Scarabaeiformia) and the families Eucinetidae, Clambidae and Scirtidae, which were placed in a superfamily Eucinetoidae. This classification was also used in Crowson (1981) except that a series Eucinetiformia was recognized and Rhipiceridae was added to Scarabaeiformia-Dascilloidea, based on Crowson (1971). In all of Crowson's classifications, the superfamily Elateroidea included Perothopidae, Eucnemidae, Throscidae, Cebrionidae, Elateridae, and Cerophytidae, although the last was omitted in error from the 1981 work.

Lawrence & Newton (1982) followed Crowson's classification in most respects. They did not define series as such, but considered all Eucinetiformia, Scarabaeiformia and Elateriformia as belonging to an "Elateriform lineage". Although Scarabaeoidea was tentatively included in this "lineage", some doubt was expressed about the relationship of the group to Dascilloidea. The families normally included in Elateroidea and Cantharoidea, plus the Artematopodidae and Brachypsectridae were considered to form a monophyletic group. In the first cladistic analysis of Elateriformia, Lawrence (1988) excluded Scarabaeoidea altogether, while Eucinetoidae were included as an outgroup in some analyses. The monophyly of Elateroidea + Cantharoidea + Artematopodidae + Brachypsectridae was confirmed in analyses based on both adult and larval characters, with the family Rhinorhipidae (known from adult characters only) at the base of this clade.

Elateroidea was restricted by Crowson (1955) to those taxa the adults of which have more or less rounded procoxae with concealed trochantins, no transverse metakatepisternal suture, contiguous metacoxae, hind wing with an apically truncate wedge cell, acutely projecting hind pronotal angles, head without a distinct frontoclypeal suture, trilobate aedeagus with freely articulated parameres, and 4 free Malpighian tubules, while larvae lack a free labrum or epicranial stem and have simple, non-channeled mandibles. Artematopodidae (then in Dryopoidea) were considered to be separable from elateroids on little more than exposed trochantins in the adult and a free

labrum in the larva, and Brachypsectridae were considered to be even more difficult to separate on adult features. The superfamily Cantharoidea was considered to be the most likely group to be merged with Elateroidea.

Lawrence & Newton (1982) followed Crowson in considering Artematopodidae, Brachypsectridae, Elateroidea and Cantharoidea to form a monophylum, and Lawrence (1988) formally recognized an expanded Elateroidea to include all of these groups. The position of *Rhinorhipus* Lawrence at the base of the elateroid clade was considered to be tentative because of lack of information on the larva, combined with the fact that there are six free Malpighian tubules (instead of four as in all other members of the group). Furthermore, in cladograms produced by Lawrence *et al.* (1995), *Rhinorhipus* usually formed a clade with *Dascillus* Latreille (Dascillidae), *Sandalus* Knoch (Rhipiceridae) and *Dystaxia* LeConte (Buprestidae or Schizopodidae) and was never placed within the elateroid-cantharoid group.

In cladograms produced by Beutel (1995) and based on larval characters, Elateroidea (*sensu lato*) was always monophyletic, but this was true of neither Elateroidea (*sensu stricto*) nor Cantharoidea. Most cantharoid families plus Brachypsectridae formed a clade sister to Cerophytidae + Throscidae + Eucnemidae, while Cantharidae formed a clade with Artematopodidae and Elateridae. The non-monophyly of the Cantharoidea was also supported by Bocakova *et al.* (2007) in cladograms based on nuclear and mitochondrial gene sequences. While Elateroidea (*sensu lato*) was strongly supported in all cladograms, the soft-bodied groups usually placed in Cantharoidea never formed a monophyletic group. The major clusters were formed by 1) Lampyridae (including Ototretinae) + Cantharidae, 2) Elateridae (including Drilidae and usually Omalisidae) + Phengodidae (including Rhagophthalmidae), 3) Lycidae and 4) Eucnemidae. The positions of the genera *Drilonius*, *Telegeusis*, *Trixagus* and sometimes *Omalisus* varied with type of alignment and analysis: 1) *Drilonius*, *Telegeusis* and *Trixagus* formed a clade with Chelonariidae and outside Elateroidea; 2) *Drilonius* and *Telegeusis* formed a clade sister to Elateroidea and *Trixagus* was sister to Elateroidea minus *Drilonius* and *Telegeusis*; 3) *Drilonius* was in Eucnemidae, *Telegeusis* sister to Elateroidea minus Eucnemidae, and *Trixagus* sister to Lycidae; or 4) *Drilonius* and *Telegeusis* formed a clade sister to remaining elateroids, and *Trixagus* and *Omalisus* formed a clade within Eucnemidae. Similar results were published by Sagegami-Oba *et al.* (2007) and Bocak *et al.* (2008).

The Elateroidea, as here delimited, exhibit several major evolutionary trends which deserve

further mention: 1) development of a type of defensive behavior known as “clicking” in adults of the families Cerophytidae, Eucnemidae, Throscidae and Elateridae, 2) reduction in sclerotization of the cuticle, often accompanied by chemical defense mechanisms and aposematic color patterns in adults of various families formerly included in Cantharoidea, and 3) retention of larval features (neoteny) in adults of at least some of these families; 4) the evolution of bioluminescence in both adults and larvae; 5) the occurrence of an elateroid type of ecdysis associated with biforous spiracles and the loss of the spiracular closing apparatus in larvae; and 6) consolidation of the larval maxillae and labium to form a maxillolabial complex.

The cuticular and muscular modifications which make the clicking maneuver possible have been discussed by Evans (1972, 1973) for Elateridae, but precursors of these conditions are exhibited by members of various families of Dascilloidea, Buprestoidea and Byrrhoidea. The evolution of a pro-mesothoracic interlocking device involving projections and concavities or crenulate edges at the posterior end of the prothorax, anterior ends of the elytra, scutellum and/or mesanepisterna, combined with a mesoventral cavity for reception of the prosternal process, allow these beetles to combine mobility with structural integrity, by the unlocking or locking of this device. The transformation of this condition to form the clicking mechanism involves the enlargement of the prothorax, increase in the mass of the M4 muscle (Larsén 1966), reduction of the size of the exposed portion of the procoxa, enclosure of the trochantin and (except in Cerophytidae) its fusion to the notum, enlargement and deepening of the mesoventral cavity combined with the formation of a prosternal rest and an oblique slide at the anterior end of the cavity. Based on the topology given by Bocakova *et al.* (2007), this condition could have arisen independently from three to five times in the Elateroidea. Vahtera *et al.* (2009), however, suggested that, given the complexity of the clicking mechanism, it could have evolved at the base of the elateroid clade and been subsequently lost on numerous occasions, usually in association with the development of soft-bodiedness (see below).

Cantharoidea were defined mainly on the shared morphological traits resulting from soft-bodiedness (generally reduced body sclerotisation and a soft, flexible abdomen with extensive intersegmental membranes reminiscent of those in the larvae). The molecular phylogenies mentioned above (Bocakova *et al.* 2007; Sagegami-Oba *et al.* 2007; Bocak *et al.* 2008) rejected monophyly of Cantharoidea and proposed multiple origin of both soft-bodiedness and probably closely related female neoteny of some groups within broadly defined Elateroidea. The hypothesis of frequent shifts to neotenic development opens a possibility that the morphological disparity suggesting establishment of families like Drilidae or some subfamilies like

Leptolycinae (Lycidae) is not a result of the long evolutionary history, but a consequence of relatively recent modified function of the endocrine system. These events potentially led to homoplasious modifications of morphology. The resulting similarity of soft-bodied or neotenic lineages is therefore difficult to interpret in morphology based analyses.

Crowson (1972) postulated that some neotenic groups, specifically the Southeast Asian lycid genera *Duliticola* and *Lyropaeus*, are members of primitively neotenic lineages and that fully metamorphosed winged forms re-developed from neotenic ancestors. Similar scenarios of evolutionary ‘re-imaginalisation’ were proposed for Lycidae by Kazantsev (2005), and equally for the closely related Lampyridae by Cicero (1988). Bocak *et al.* (2008) hypothesized that soft-bodiedness represents a first level of incomplete metamorphosis. Soft-bodied adults of both sexes are known in Telegeusidae, Omethidae, Cantharidae, Lycidae, Lampyridae, Phengodidae, Rhagophthalmidae, Drilidae, and Omalisidae. Some adult females within these families are neotenic, i. e., they maintain apparently juvenile features resulting in incomplete metamorphosis and, in extreme cases, the lack of adult stages. The neotenic development of females is obligatory in all Omalisidae, Drilidae, Phengodidae and Rhagophthalmidae, and in many lineages of Lampyridae and Lycidae. The modifications include females with vestigial wings, but adult-like thorax (Omalisidae, Lampyridae part), wingless females (Lampyridae part) or females with only mouthparts and head adult-like (Drilidae, Lampyridae part). Lineages affected by neoteny to the highest degree are found in Lycidae where females lack both pupal and adult stages and retain a larvae-like morphology after the last ecdysis (Wong 1996). Some neotenic lycids reach body sizes of five centimeters and more and are frequently referred to as ‘trilobite larvae’ due to their appearance (Gravely 1915; Mjöberg 1925). The corresponding males are regularly fully metamorphosed and only seldom brachelytrous (*Alyculus* in Lycidae and *Phosphaenus* in Lampyridae).

Several elateroid groups (Lampyridae, Phengodidae, Rhagophthalmidae and two independent groups of Elateridae (Agrypninae: Pyrophorini and Thylacosterninae: *Balgus*) are known for their bioluminescence. Previous morphological studies (Crowson 1972, Beutel 1995) often suggested close relationships of cantharoid luminescent lineages (Lampyridae, Phengodidae). Latest molecular analyses (Bocakova *et al.* 2007; Sagegami-Oba *et al.* 2007) showed that bioluminescent groups have arisen at least four times in Elateroidea. Likewise, recent morphological analysis (Branham and Wenzel 2001, 2003) supported several independent originations of bioluminescence in Elateroidea. Although superficially similar, molecular conclusions differ substantially. While morphological study separates Rhagophthalmidae from Phengodidae, and *Drilaster* and *Stenocladus* from Lampyridae, neither

of these conclusions were confirmed in the molecular studies, hence upholding the traditional view of the constitution of Phengodidae and Lampyridae (Crowson 1972; Lawrence *et al.* 1995). Conversely, latest molecular analyses found cantharoid luminescent groups Lampyridae and Phengodidae deeply separated which is also supported by the structural and biochemical differences of the luciferases in either group (Viviani 2002).

Vahtera *et al.* (2009) presented an hypothesis connecting the clicking mechanism with the evolution of bioluminescence. If the clicking mechanism evolved in ancestors of the entire elateroid complex, the bifunctional role of the pre-luciferase enzyme in combination with the high-energy demand of the pronotal muscle were the preadaptive features for the luminescence to evolve in the prothorax. Lineages evolving away from the compact elaterid-type body structure retained the predisposition for luminescence, once a suitable luciferin was available. The sources of luciferin type compounds in beetles, whether of symbiotic origin or not, facilitated the pronotal light spots at the muscular attachment points as well as the fat body region. This scenario predicts that the source for luciferin is most likely external and after becoming available for any elateroid clade could be picked up repeatedly. It also explains why this feature is restricted to this one group beetles – the clicking mechanism being unique within beetles.

Larval head structures of Elateroidea are quite characteristic, even though, as pointed out in Beutel (1995), several derived features are also found in larvae of all or most groups presently assigned to Byrrhoidea (see 1–2). A tendency to concentrate or reduce the stemmata is found in both lineages. Well separated stemmata occur in some groups of Byrrhoidea (e. g., Byrrhidae, Dryopidae, Heteroceridae) but in others (e. g., Psephenidae, Ptilodactylidae) they form tight clusters and in Eulichadidae there is a single large lens beneath which are two to five pigment spots. In Elateroidea there is never more than a single stemma on each side. As in all Byrrhoidea, elateroid larvae lack a basal mandibular mola, and as in Byrrhoidea excl. Byrrhidae the head is distinctly prognathous. Both conditions have evolved independently in different lineages of Coleoptera, notably in groups with predacious larvae (e. g., Adephaga, Hydrophiloidea, Cleroidea [see 1–7, 1–10, 2–9]). A characteristic feature found in larvae of Elateroidea (and Byrrhoidea excluding Byrrhidae, some Ptilodactylidae and Eulichadidae) is a maxillolabial complex, with closely connected labium and maxillae (Beutel 1995). The ventral mouthparts are moved only as a structural unit vertically. The extrinsic tentoriomaxillary muscles are vertically arranged. Similar conditions have evolved independently in Cleroidea and in some supposedly related groups of Cucujoidea (Beutel & Ślipiński 2001). As in most byrrhoid groups (excluding Byrrhidae, Ptilodactylidae, Eulichadidae and Callirhipidae) the tentorium of elateroid

larvae is strongly modified, with posterior arms very strongly developed, cranially directed and completely detached from the tentorial bridge. The dorsal and anterior parts of the tentorium are reduced. Interestingly, again a similar condition is found in cleroid larvae and in some groups of Cucujoidea (Beutel & Ślipiński 2001). Apparently this condition is linked with the formation of a maxillolabial complex. A set of features distinctly separating Elateroidea from Byrrhoidea is the presence of a strongly developed lateral tentoriohypopharyngeal muscle, a dense, preoral filter formed by long microtrichia, the immobilisation of the labrum, and the loss of the labral muscles. A labrum separated from the clypeal region is preserved only in Artematopodidae and Brachypsectridae. The preoral filter is apparently an adaptation to liquid feeding. A similar condition has evolved in Carabidae and Histeroidea (Beutel 1993, 1999). Unusual modifications of the mandibular apparatus are characteristic for larvae of most Eucnemidae and Throscidae, where mandibles may be fixed or exodont. Another specific modification is the presence of mandibular sucking channels occurring in Brachypsectridae, Lampyridae, and a few other groups. An unusual feature apparently linked with highly specialised liquid feeding habits is the origin of very strongly developed extrinsic maxillary muscles of the sclerotised ventral wall of the hypopharynx. A somewhat similar condition has evolved in Cleroidea and some cucujoid groups, where an anterior bundle of *M. tentoriostipitalis* originates from the ventral prepharyngeal wall or from the posteriormost hypopharynx (Beutel & Ślipiński 2001).

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4.1. Rhinorhipidae Lawrence, 1988

John F. Lawrence

Distribution. *Rhinorhipus tamborinensis* Lawrence has been collected in a few localities in southern Queensland, Australia, all at higher elevations in the vicinity of closed forest. It is likely that the species also occurs in montane regions in northern New South Wales.

Biology and Ecology. The largest series of adults were collected during the day on leaf surfaces of an introduced weed, *Ageratina adenophora* (Asteraceae), at the edge between rainforest and cleared areas. Unfortunately, this site has now become a suburb and recent collecting expeditions have failed to produce more specimens. At another locality, a few beetles were found in an open area on low vegetation bordering a creek. When disturbed, the beetles exhibited a death-feigning reaction, dropping to the ground. Males greatly outnumbered females in this habitat. It is likely that these clearings were the sites of mating aggregations and that the beetles flew to them from within the rainforest. Red mud was present on a number of the specimens, which suggests that they either emerged from the soil after eclosion or sheltered there. The structure of the metacoxae and hind legs also suggests fossorial habits. The ovipositor is relatively unspecialized, so it is unlikely that the eggs are embedded in plant tissue or placed deep in soil. One female laid several eggs in the laboratory, but none of them hatched.

Morphology, Adults (Figs. 4.1.1–3). Length 5–8.5 mm. Body about 3 times as long as wide; slightly flattened above but moderately convex below. Heavily sclerotized and clothed with relatively stout and somewhat flattened, decumbent hairs.

Head longer than wide, strongly declined, abruptly constricted immediately behind eyes, so that no temples are present. With very short, median occipital endocarina but no transverse line. Eyes moderately large, protuberant, more or less circular, finely faceted, without interfacetal setae; ommatidium of exocone type with thick