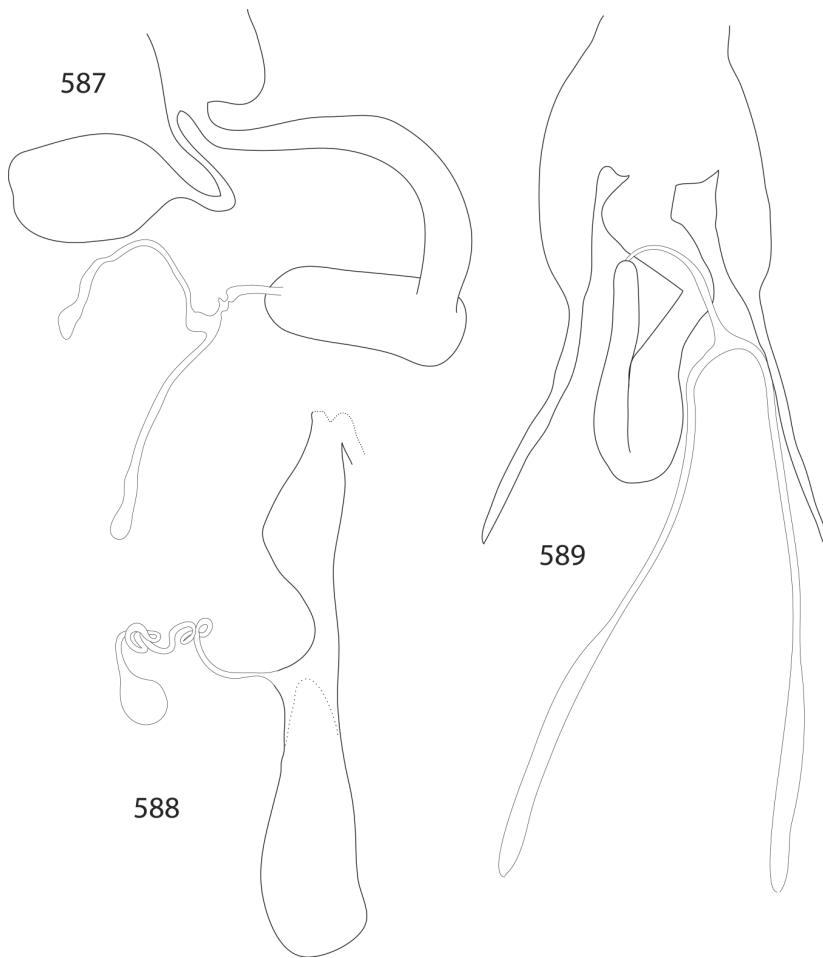


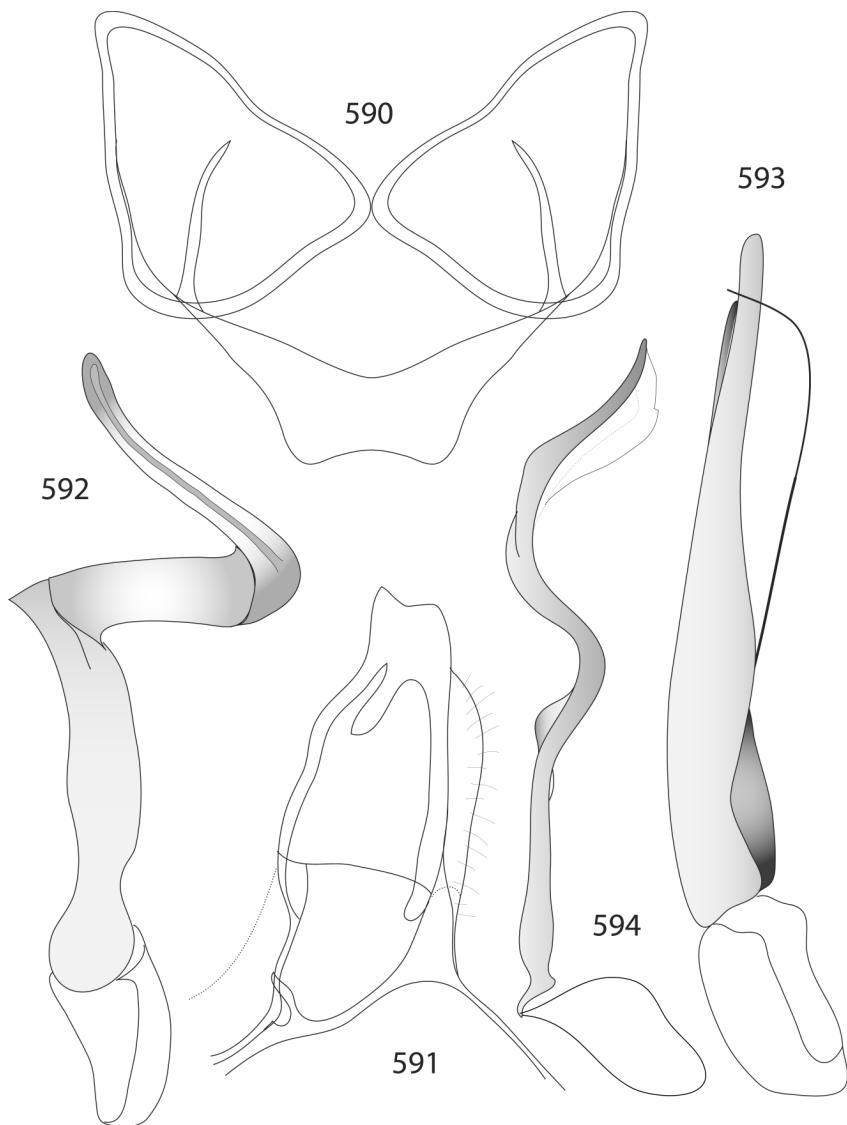
Figs 584-586: Internal female genitalia, after Bocák & Bocáková, 1990: *Dictyoptera aurora* (Herbst) (584); *Platycis minuta* (Fabricius) (585); *Pyropterus nigroruber* (Degeer) (586).



Figs 587-589: Internal female genitalia, after Bocák & Bocáková, 1990: *Conderis signicollis* (Kirsch) (587); *Plateros* sp. (588); *Metriorrhynchus helleri* Kleine (589).

and *Dilophotes* acquired a complete meral suture (Figs 449-453), the hind coxa becoming divided into the coxa proper, trochantin and meron. The tibial spurs disappeared in hypothetically advanced *Ceratoprion*, *Leptolyucus*, *Dexoris*, *Scarelus*, *Dilophotes* and *Mesolyucus* (Figs 425, 429, 430, 440, 444). The conspicuous and well-developed tarsal plantar pads characteristic of all presumably primitive lycids (e.g. Figs 422, 424, 434, 435, etc.) gradually gave way, through partial loss in certain unrelated lycid genera (e.g. *Lyroneces*, *Platerodrilus*, Figs 428, 432), to complete absence of tarsal pads in the most derived taxa, such as *Dexoris*, *Leptolyucus* or *Ceratoprion* (Figs 429, 429a, 430, 440).

In all male lycids the fused condition of tergite 9 and tergite 8 (persistent in Lampyridae, e.g. Fig. 489) gave way to complete division between them and appearance of the proctiger (tergite 10) medially attached to tergite 9. In perhaps more derived lycid taxa (e.g. in *Platerodrilus*, Fig. 478) the proctiger became



Figs 590-594: Imaginal structures: *Mesolytus shelfordi* (Bourgeois): mesoscutum (590); mesepisternum, mesepimeron and metathoracic sclerites (591); *Plateros assamensis* (Pic), aedeagus, latero-dorsal view (592); *Lyponia korotyaevi* Kazantsev, aedeagus, lateral view (593), *Plateros tryznai* Bocáková, aedeagus, lateral view (594).

separate from tergite 9. And probably the most derived lycids (e.g. *Dexoris*) acquired in all body sclerites uniform alveolate cuticle structure, similar to that of the larvae.

At least in one lycid lineage (*Platerodrilus*), but possibly in many more where neither larvae, nor females are known, the female development cycle has lost the stage of pupa, becoming completely paedomorphic and thus eliminating the beetles

from the list of insects with only complete metamorphosis. Interestingly, similar changes occurred in such distant lineages, as Phengodidae and, possibly, Micromalthidae. In *Helcophorus* the process of transition to female paedomorphic development has evidently just started, with the female metendosternite becoming a pair of widely separated transverse bars, comparable to the condition characteristic of larvae (Fig. 367).

It is clearly seen that this scenario envisages that all evolution trends are going in reverse direction in this lineage of the Coleoptera, with the most «derived» lycids acquiring both in larval and imaginal stages resemblance with what is presumed to be the generalized endopterygote insect (Lawrence & Newton, 1982).

Because of the outstanding autapomorphies, the tripartite haustellate larval mandibles, presence of the stipes of mandible and the unmatched among living organisms tendency to reverse development being perhaps the major ones, the Lycidae obviously deserve separation minimum at the suborder level; with high-level separation of taxa characterized by such apomorphies, as division of the head capsule into the preoral and gnathal segments, division of the trochanter into trochanter 1 and trochanter 2, etc.

However, as all presumed apomorphies of the Lycidae are in fact reverse developments, the evolution of this Coleopterous family seems to represent an uninterrupted series of violations of Dollo's law. On top of that, these reverse developments appear to have been occurring in the Lycidae independently in many unrelated lineages, contradicting not only to Dollo's law, but to the common sense as well. Besides, all these apomorphies must have appeared within extremely short period of time at a very high speed, as the Lycidae are considered to have emerged during the Cretaceous, presumed the most advanced among the Cantharoidea (Crowson, 1981), but should have developed into most hypothetically derived groups actually prior to that, during the Lower Jurassic, as the Gondwana continent break-up begins in the middle of Jurassic, and a variety of both derived and primitive lycid taxa are widespread in all former parts of the Gondwanaland.

All this renders the first scenario not very probable.

Scenario 2

Another option is to regard the above outlined conditions as plesiomorphies.

Due to the unchanged feeding mode the Lycidae larvae have preserved much of the type of the mouthparts their ancestors had. The primitive feeding mode was apparently confined to sucking and filtering liquids associated with decaying organic substances in the moist water-edge habitats. As they advanced to relatively drier places, such as damp tropical forest valleys, the lycids gradually developed more complicated feeding apparatus consisting of the premandible, the hypopharyngeal suspensorium and the labral lobe, together capable of effectively sucking liquids from narrow crevices in rotten wood. This type of mandibular structure which separated this lineage from the rest of the Polyphaga is presumed to be its apomorphy. In more derived groups, i.e. *Lygistopterus*, the stiletto part became fused apically to the labral lobe; in the same taxon the stipes of mandible in its posterior portion became fused to the cranial segment, thus acquiring greater similarity to the hypostomal margin (Fig. 40).

In a more derived lineage represented by Lampyridae, due to the switch to feeding on small snails, the elements of the mandibular structure acquired different

functions, as they were no longer needed to assist sucking of large volumes of liquids. The premandible, or the mandible proper, having preserved its cavity as a canal, started to function as a mandible using the canal for sucking nutritious liquids, the stiletto and labral lobe probably becoming part of the mandible, as no labrum or hypopharyngeal suspensorium are noticeable in, for example, *Pyractomena* (Figs 72, 75-76). The hypopharyngeal lobes became fused together and the stipes of mandible became clearly fused to the cranial segment becoming the hypostomal margin (Fig. 70).

The head capsule, initially divided into the preoral and gnathal segments, preserved this plesiomorphic condition in a number of taxa (e.g. *Platerodrilus*, Figs 10-11, *Lycus*, Fig. 24, *Plateros*, Fig. 60), but in some Lycidae gave way to condition where the two sclerites are fused. The Lampyridae are already uniformly characterized by the fused condition of the cranial sclerites (e.g. *Pyractomena*, Fig. 71). However, probably owing to mostly retaining their ancestral semi-aquatic habitats the Lampyridae larvae preserved the non-fused condition of their maxillary stipites, while the Lycidae larvae, having switched to the terrestrial mode of life, acquired fusion of these stipites, both lineages preserving the open ventrally head capsule (e.g. Figs 23, 70). Such fusion of maxillary stipites which also distinguishes the Lycidae from the rest of the Polyphaga is considered another apomorphy of this lineage.

Primitively, the spiracles were of the simple lip type, lacking any closing apparatus, being similar in all thoracic and abdominal segments. Such spiracles seem to have preserved in *Platerodrilus* (Fig. 20). In more derived groups a more complicated triforous spiracle developed, represented in, for example, *Lycus* (Figs 34, 36, 38), with the more advanced biforous type having developed in Lampyridae (e.g. in *Pyractomena*, Fig. 78). In some lineages the metathoracic segment started to lose some of its respiratory functions, with its spiracle becoming dissimilar to the mesothoracic one (e.g. *Lycus*, Figs 34, 37) or both dissimilar and non-functional, as in *Lygistorpterus* or *Pyractomena* (Figs 41, 44, 77, 79). The abdominal segments not considerably differing from the thoracic ones in their ancestors preserved in most of the Lycidae, but gave way to completely different structures in the Lampyridae.

The absence of distal attachment of the trochantin, characteristic of ancestors of the Hexapoda (Snodgrass, 1935), persisted in the Lycidae, while the Lampyridae acquired an apomorphic condition, with the trochantin distally attached to the coxa (Fig. 77). In some Lycidae larvae the archaic division of the trochanter into trochanters 1 and 2 was retained, as in *Platerodrilus*, *Lycus*, *Calopteron*, *Lyponia* (Figs 20, 39, 53, 64), and *Xylobanus*, while in the bulk of the family it gave way to complete fusion of these two parts.

The prementum preserving its ancestral division into a pair of annuli in certain taxa (*Calopteron*, Fig. 47, *Lycostomus*, *Lyponia*) acquired the fused condition in most of the Lycidae. The cuticle structure has become different in different parts of the body, partially clear, while the plesiomorphic condition represented by the uniform alveolate cuticle in all body sclerites persisted only in few lycids (e.g. *Platerodrilus*, *Calopteron*). In *Platerodrilus*, *Lyponia* and *Lycus* the elongate coxa making part of the limb persisted as another plesiomorphy (Figs 20, 39, 64), while in the rest of the Lycidae the coxae were shortened, attaining one of the shortest conditions in *Lygistorpterus* (Fig. 41).

The imaginal Lycidae have preserved one of the fundamental features of their ancestors, the absence of the tentorium. Some probably most archaic forms with

vestigial or undeveloped mandibles do not have any trace of this endoskeletal structure (*Dexoris*, *Lyrenececs*, Figs 110, 116), and their antennal muscles are attached to the cranium. In more derived forms ventral arms arising from the posterior tentorial pits appeared, ranging from minute (*Taphes*, *Ceratopriion*, *Lycinella*, etc., 102, 122, 126) to long and/or having anterior branches (e.g. *Macrolycus*, *Aferos*, *Plateros*, Figs 137, 144, 152). Such development of the ventral tentorial arms was hypothetically correlated with development of the imaginal mandibles. In the more advanced lineages, such as Cantharidae, the ventral arms attained the dorsal surface of the cranium (Figs 159-161), with the posterior fusion of the ventral arms occurred in yet more advanced cantharids, such as *Podabrus* or *Chauliognathus* (Brancucci, 1980). Similarly advanced, i.e. fused posteriorly, though not quite attaining the dorsal surface, became the ventral arms in *Lampyris* and *Phengodes* (Figs 153-158).

Hypothetically the most primitive forms (e.g. *Dexoris*, Fig. 113) retained uniform alveolate cuticle structure, similar to that of the larvae, in all body sclerites, while the more advanced lineages preserved such structure only in pronotal margins, being most manifest anteriorly.

The absent gula, i.e. actually open ventrally head capsule, with a narrow process connecting the cranial sclerites, persisted in a number of lycids (e.g. in *Lyrenececs*, *Aferos*, *Calopteron*, Figs 91, 114, 150), while the broad ventral closure of the head behind mouthparts developed in some hypothetically advanced lineages of the Lycidae (e.g. *Scarelus*, *Platerodrilus*, Figs 94, 117) and in all other Cantharoidea. The hypognathous head, characteristic of the hexapod ancestors (Crowson, 1935) persisted in the Lycidae (Figs 82, 84, 86), giving way to the prognathous condition in *Platerodrilus* (Fig. 83) and all non-lycid cantharoid lineages. The labrum probably evolved from the bipartite condition (e.g. *Dexoris*, *Proteros*, Figs 107, 108) first to a fused structure proximally located within the oral cavity and finally to the sclerotic segment rigidly attached to the epistoma (*Lygistorpterus*) or fused thereto (*Lucaina*). The prementum preserved its completely divided plesiomorphic condition in *Calopteron* and *Ceratopriion* (Figs 186, 189), acquiring longitudinal suture in *Macrolycus* and *Caenia* (Figs 187, 191) and becoming fused in the rest of the Lycidae as well as in other cantharoid families. In several lycid lineages the cervical sclerites preserved their ancestral condition resembling sclerites related to the thoracic spiracles, in terms of shape, position, sclerotization and pubescence (Figs 87, 142).

In certain lycid taxa (e.g. *Lyrenececs*, *Caenia*, *Plateros*, Figs 305, 308, 315) the mesoventrite also preserved its plesiomorphic condition, being divided into the mesoventrite proper and the sternopleural processes. Similarly, the prosternum in some lycids, such as *Lycostomus*, *Lyrenececs*, *Mesolyucus* (Figs 237, 238, 254), preserved its division into the prosternum proper and sternopleural processes connecting it with the hypomeron. In most of the Lycidae, however, this division gave way to fusion of the sternal sclerites into a single sclerite. The synapomorphic condition in Lampyridae, Cantharidae and Phengodidae is characterized by the further fusion of the mesoventrite, which became fused with the episternum as well (e.g. *Lampyris*, *Cantharis*, *Phengodes*, Figs 227, 322, 323, 324). Another plesiomorphic character of the Lycidae is the preservation of the non-coadapted elytron that lacks epipleuron and has unmodified ventral surface. The suture margin of a lycid elytron equally lacks the dove-tailed sclerotized flange and some hypothetically primitive groups (e.g. *Dexoris*, Fig. 330) do not have such flange altogether. The elytral structures in Lampyridae, Phengodidae and Cantharidae acquired prominent epipleures and sclerotized flanges (e.g. *Cantharis*, Fig. 334), which are hypothesized to be their synapomorphy.

The lycid metathoracic wing preserved the simplest folding pattern (Figs 387-388), with the wing folding in some of the hypothetically primitive Lycidae being so insignificant that the elytron still exceeds length even of a fully unfolded hind wing (e.g. *Lyroneces*, Figs 387, 395, 396). The wing venation in some presumably archaic taxa preserved separate running of the C, Sc and RA veins that are parallel in most of the costal area before joining the radial bar (Fig. 398). The absence of coadaptation of the abdomen with the metasternal and elytral structures evidently characteristic of the Coleoptera ancestors persisted in the Lycidae, with the coadaptation between the elytra and other thoracic segments still absent in certain primitive taxa (e.g. *Ceratopriion*, Fig. 85).

In some lycids the posterior process of the mesoscutellum preserved its plesiomorphic condition remaining vestigial (e.g. in *Caenia*, *Calopteron*, *Lyroneces*, *Ceratopriion*, Figs 270, 280, 338, 342, 344) and not having acquired yet the function of locking the elytra and protecting the elytral notch. In more derived lycids mesoscutellum became more developed and functional (e.g. in *Metriorrhynchus*, Fig. 341); attaining even greater development and functionality in other Cantharoids (e.g. in *Lampyris*, Fig. 345). The metacoxa in certain lycid lineages in addition to the trochantinal suture preserved a complete meral suture (in *Dexoris*, *Mesolycus* and *Dilophotes*, Figs 449-453), the hind coxa retaining its division into the coxa proper, trochantin and meron. Such division partially disappeared in other Lycidae. The coxal suture persists also in the imaginal pro- and mesocoxae in *Dexoris* (Fig. 429a), being absent in more derived lycid taxa. The tibial spurs are absent in hypothetically primitive *Ceratopriion*, *Leptolyucus*, *Dexoris*, *Scarelus*, *Dilophotes* and *Mesolycus* (Figs 425, 429, 430, 440, 444), having developed in other lycids. The tarsal pads, absent in presumably most primitive taxa, such as *Dexoris*, *Leptolyucus* or *Ceratopriion* (Figs 429, 429a, 430, 440) gradually developed, first into forms characterized by minute pads at the apex of tarsomere 3 and/or 4 (e.g. in *Lyroneces*, *Platerodrilus*, Figs 428, 432) and finally into conspicuous plantar pads present in all tarsomeres of the more derived genera (e.g. Figs 422, 424, 434, 435, etc.).

In all male lycids tergites retain their plesiomorphic condition, tergites 9 and 8 being completely divided and proctiger (tergite 10) present. A possible plesiomorphy is also manifest in *Platerodrilus* (Fig. 478), where the proctiger is separate from tergite 9, whereas Lampyridae acquired an apomorphic condition of tergites 9 and 8, which became fused (e.g. Fig. 489). In hypothetically derived forms, representing a probable homoplasy with other Cantharoidea and Polyphaga with reduced number of abdominal segments, the ultimate abdominal segments, one sternal and two tergal, are completely retracted in the abdomen (*Flagrax*, Fig. 468).

At least one lycid lineage (*Platerodrilus*), but possibly many others where neither larvae, nor females are known, have retained in females the primitive development cycle which lacks the stage of pupa and where the imago is inseparable from the larvae except in the presence of reproductive organs. Similar condition was also retained in certain distant lineages, such as Phengodidae and, possibly, Micromalthidae, though in the latter taxon the paedomorphism may prove to be an apomorphy. In *Helcophorus* the process of transition of the female from the paedomorphic development to complete metamorphosis probably started much later than in the male, with the female metendosternite retaining its ancestral larval condition. The latter taxon hypothetically represents a transition form from taxa with fully paedomorphic females to taxa with fully imaginal females.

Analysis of the geographical distribution of the studied lycid genera undertaken prior to their phylogenetic analysis, i.e. without any reference to possible higher

level taxa, shows that genera demonstrating greatest level of possession of hypothetically archaic features, i.e. *Dexoris*, *Lyronces*, *Ceratoprion*, *Taphes*, *Lycinella*, *Platerodrilus*, have rather limited distribution areas, confined typically to a certain zoogeographical zone each in temperate areas of the tropics, being present, on the other hand, in all primary rain forest zones. Certain presumably more derived genera, such as *Plateros* or *Lycus* (with *Lycostomus*), are distributed worldwide in all-type-of-forest zone, except in Australia and New Zealand, while the most advanced in most aspects *Calochromus* (together with the African *Adoceta* Bourgeois, from which it is hardly separable) is literally widespread in all zoogeographic zones, including the Australian region, where it forms one of the dominant lycid groups. A possible explanation of such distribution pattern may be the assumption that the most derived lycid groups, such as *Calochromus*, had been formed and widely distributed in the Gondwanaland long before its break-up. The appearance and evolution of the Lycidae probably occurred so long before the Gondwana continent started to move apart, that most its lineages had been extinct or near the extinction by the moment the break-up began in the middle of Jurassic. Transferal of the origin of the family back at least to the Carboniferous seems to perfectly correlate with this hypothesis.

The absence of some widely distributed groups in New Zealand may be accounted for, in the first instance, by its specific conditions, intolerable for Lycidae, when these islands, after shearing off from the remains of the ancient supercontinent Gondwana some 80 million years ago, went through periods of submergence, when all that showed above the waves was a string of low, swampy islets, and thousands of years in deep freeze of glaciation. The relative scantiness of the lycid fauna of Australia may be a consequence of a combination of severe dry conditions on most of its territory, which evidently (had) brought certain lycid to the extinction, on the one hand, and the relative insufficiency of entomological studies. The recent discovery of most remarkable *Omma rutherfordi* (Ommatidae) from South and Western Australia (Lawrence, 1999) and *Proteros sempiternus* (Lycidae) from New South Wales (Kazantsev, 2004b) could well be self-illustrative.

The obviously relict lycid genera characterized by maximal number of plesiomorphies and restricted to limited areas in the tropics seem to represent remnants of the taxa that had probably been already largely reduced during the Lower Jurassic. Most of these genera are known by unique or few specimens, often collected quite a time ago, and may be totally extinct nowadays.

The second scenario appeared more plausible and the defined plesiomorphies were applied to analyze the phylogeny of the group. Its immediate ancestors are presumed to have composite larval mandibular structure, open ventrally head capsule, separate maxillary stipites and paedomorphic development in at least females. This presumption effectively polarize the above-discussed characters. However, for a cladistic analysis the Phylip PARS program, version 3.6, was used, a program that assumes that the ancestral condition of characters is unknown. It is a general parsimony program, which carries out the Wagner parsimony method with multiple states.

The defined polarities did not allow to use the more derived members of the Elateriformia lineage, such as any of the elaterid genera, as the outgroup. Their alleged ancestry based on similar or more complicated metathoracic wing venation appear not to be supported by other characters. Views considering the coleopteran hind wing developing only in the direction of simplification (e.g. Kukalova-Peck & Lawrence, 1993) do not take into account possible polyphyly of the Coleoptera

and are based on the questionable hypothesis of Kukalova-Peck (1991) who assumes that the hind wing of the Endopterygota, including the Coleoptera, was evolving exclusively in the direction of oligomerization of homologous organs, in fact ignoring the opposite direction, in which the insect metathotacic wing also was and, no doubt, is developing once it had emerged.

For these reasons *Dexoris* was chosen as the outgroup as possessing the greatest number of hypothetical plesiomorphies that include several plesiomorphic characters unique for the Coleoptera. Although it is possibly close to other regarded taxa, no alternative seemed to be available. Several Cantharoidea taxa were included for verification purposes. The assumption that the ancestral condition of characters is unknown was supposed to contribute to the objectivity of the analysis.

Larval characters were taken from the same or related species of the same genera as used for the imaginal ones, with the two exceptions: for *Lycostomus* a specimen of *Lycus* and for *Lampyris* a species of *Pyractomena* were studied. The following set of characters was finally chosen, with an understanding that the number of characters separating every two taxa is indefinitely great:

- 1 Cuticle: 0, alveolate and uniform in all body sclerites; 1, at most alveolate in some body sclerites. Condition 0 was found only in *Dexoris* (Fig. 83).
- 2 Ventral tentorial arms: 0, absent; 1, minute; 2, long or having anterior processes. Condition 0 was found in *Dexoris* and *Lyroneces* (Figs 110, 116).
- 3 Corpotentorium: 0, absent; 1, present. Only *Lampyris* and *Phengodes* were found to have condition 1 (Figs 153, 157-158).
- 4 Dorsal tentorial maculae: 0, present, 1, absent.
- 5 Coronal suture: 0, complete; 1, incomplete; 2, absent.
- 6 Gula: 0, absent; 1, minute; 2, long. Condition 0 was found in *Lyroneces*, *Aferos*, *Calopteron* (Figs 91, 114, 150); condition 2 found in *Scarelus* and *Platerodrilus* (Figs 94, 117), as well as in *Lampyris*, *Cantharis* and *Phengodes* (Figs 153, 156, 159).
- 7 Head: 0, hypognathous; 1, prognathous. Condition 1 was found in *Platerodrilus*, *Lampyris*, *Phengodes*, *Cantharis* (e.g. Figs 83, 161).
- 8 Antennal prominence/fastigium: 0, conspicuous/acute; 1, inconspicuous/blunt.
- 9 Antennae: 0, 10-segmented; 1, 11-segmented. Only *Dexoris* and *Lyroneces* are characterized by condition 0.
- 10 Clypeus: 0, absent; 1, present. The only lycid taxon with condition 1 is *Calochromus* (Figs 128-131), condition 1 also present in *Cantharis*, *Phengodes*.
- 11 Labrum: 0, bilobed; 1, at most emarginate anteriorly. Condition 0 was found in *Dexoris* and *Calopteron* (Figs 92, 108).
- 12 Labrum: 0, at least proximally located within oral cavity; 1, proximally attached to epistomal margin; 2, fused to epistomal/clypeal margin. Condition 1 was found in *Lycostomus* (Fig. 88); condition 2 - in *Cantharis* and *Phengodes* (Figs 154, 160).
- 13 Mandibles: 0, vestigial; 1, minute, not exceeding length of maxillary palps; 2, relatively large, longer than maxillary palps. Condition 0 was found in *Lycostomus*, *Ceratopriion* and *Lyroneces* (Figs 88, 114, 122-123).
- 14 Ultimate maxillary palpomere: 0, pointed, 1, distally flattened and more or less dilated. Condition 0 was found in *Dexoris*, *Ceratopriion*, *Lyroneces*, *Platerodrilus*, etc. (Figs 94, 112, 114, 120).
- 15 Number of labial palpomeres: 0, one; 1, two; 2, three. 0: *Lyroneces* and *Dexoris* (Figs 188, 190), 1: *Ceratopriion* (Fig. 186).

- 16 Ultimate labial palpomere: 0, pointed, 1, distally flattened and more or less dilated. 0: *Taphes*, *Mesolycus*, *Lampyris*, Figs 201, 202, 204, 205).
- 17 Prementum: 0, divided; 1, having median suture; 2, fused. Condition 0 was found in *Calopteron* and *Ceratoprion* (Figs 186, 189) and condition 1 in *Macrolycus* and *Caenia* (Figs 187, 191).
- 18 Prosternum: 0, divided into prosternum proper and sternopleural processes; 1, fused into a single sclerite. Condition 0 was found in *Lycostomus*, *Lyroneces*, *Mesolycus* (Figs 237, 238, 254).
- 19 Mesoventrite: 0, divided into mesoventrite proper and sternopleural processes; 1, fused with sternopleural processes, but separated from episternum; 2, fused with episternum. Condition 0 was observed in *Lyroneces*, *Conderis*, *Caenia*, *Plateros* (Figs 305, 308, 311, 315); condition 2 - in *Lampyris*, *Cantharis* and *Phengodes* (Figs 227, 228, 230, 322-324).
- 20 Mesoventrite: 0, small, more than twice as short as mesepisternoepimeral suture; 1, relatively large, longer or only slightly shorter than mesepisternoepimeral suture. Condition 0 was found in *Dexoris* and *Lyroneces* (Figs 304, 307, 308).
- 21 Mesepimeron: 0, as long as mesepisternum and not extending beyond its base; 1, shorter than mesepisternum, but extending beyond its base. Condition 0 was found in *Lyroneces*, *Ceratoprion*, and *Dexoris* (Figs 295, 296, 298).
- 22 Mesepimeral fold: 0, as broad as mesepimeron; 1, narrower than mesepimeron, but broader than its half; 2, less than its half; 3, absent. Condition 0 was found in *Lyroneces* and *Dexoris* (Figs 295, 298), condition 2 found in *Plateros* (Fig. 299), condition 3 found in *Cantharis* and *Phengodes* (Figs 302-303).
- 23 Connection between mesepimeron and metaventrite: 0, by means of a separate process; 1, by a narrow projection of the marginal sulcus of the metaventrite, 2, direct. Condition 0 was found in *Dexoris* (Figs 215, 298), condition 1 found in *Lyroneces*, *Ceratoprion* and *Mesolycus* (Figs 295, 296, 591).
- 24 Posterior process of mesoscutellum: 0, vestigial, with elytroscutellar dehiscence prominent; 1, functional, locking the elytra, but with noticeable elytroscutellar dehiscence; 2, functional, both locking the elytra and covering the elytral notch. Condition 0 was observed in *Caenia*, *Calopteron*, *Lyroneces* and *Ceratoprion* (Figs 270, 280, 338, 342, 344); condition 2 found in *Calochromus*, *Lampyris* (Figs 337, 345), *Cantharis* and *Phengodes*.
- 25 Elytra: 0, not coadapted with thoracic segments; 1, coadapted with thoracic segments. Condition 0 was found in *Ceratoprion* (Fig. 85).
- 26 Elytron: 0, with longitudinal veins and regular transverse reticulation; 1, with longitudinal veins, but without regular transverse reticulation; 2, without longitudinal veins or transverse reticulation.
- 27 Elytral epipleures: 0, absent; 1, minute; 2, conspicuous.
- 28 Elytral suture margin, beyond scutellar area: 0, unmodified; 1, with membranous flange; 2, with sclerotic flange. Condition 0 was found i.e. in *Dexoris* (Fig. 330).
- 29 Metasternal posterior angles: 0, rounded; 1, pronounced. Condition 0 was found in *Lyroneces*, *Dexoris*, *Caenia*, *Ceratoprion*, *Helcophorus* (Figs 209, 212, 215, 223, 224), as well as in *Thilmanus* (Fig. 226).
- 30 Metasternal suture: 0, complete, reaching mesoventrite; 1, not reaching mesoventrite. Condition 0 was found in *Lycostomus*, *Lyroneces*, *Calopteron*, *Ceratoprion* and *Dexoris* (Figs 207, 209, 210, 215, 224).
- 31 Metendosternite: 0, small, not exceeding half length of tergite 1; 1, relatively large, considerably exceeding half length of tergite 1. Condition 0 was found in *Ceratoprion*, *Dexoris* and *Lyroneces* (Figs 351, 357, 358).

- 32 Metendosternite: transverse suture: 0, absent or vestigial; 1, present. Condition 0 was found in *Lycinella*, *Ceratoprion*, *Thilmanus*, *Lyroneces*, *Taphes* and *Scarelus* (Figs 365, 370, 372, 373, 375, 385).
- 33 Metendosternite: lateral arms: 0, absent; 1, present. Condition 0 was found in *Mesolycus* and *Dexoris* (Figs 371, 379).
- 34 Orifice of mesothoracic spiracles: 0, simple; 1, hooded dorsally. Condition 1 was found in *Macrolycus*, *Mesolycus*, *Conderis* and *Metriorrhynchus* (Figs 217, 220, 221, 222).
- 35 Metathoracic wing venation: Sc vein: 0, separate and almost parallel to C and RA veins; 1, separate, but conspicuously curved, nearly touching or joining RA vein before getting fused with C; 2, fused to RA from basal third. Condition 0 was found in *Dexoris* (Fig. 398); condition 1 in *Conderis* (Fig. 406)
- 36 Metathoracic wing venation: wedge cell: 0, present; 1, absent.
- 37 Metathoracic wing venation: Cu veins: 0, present and not fused to M; 1, present and fused to M. Condition 0 was found in *Lyroneces*, *Ceratoprion*, *Thilmanus* (Figs 395, 397, 420).
- 38 Metathoracic wing venation: number of radial cells: 0, two; 1, one. Condition 0 was found in *Dexoris* and *Lycostomus* (Figs 394, 398).
- 39 Metathoracic wing venation: anal cell: 0, closed with transverse brace; 1, closed with converging anal veins. Condition 0 was found in *Lycostomus*, *Dexoris*, *Ceratoprion*, *Scarelus*, *Conderis* (Figs 394, 397, 398, 400, 406).
- 40 Metathoracic wing venation: cu-a connection: 0, absent; 1, present. Condition 0 was found in *Ceratoprion*, *Macrolycus*, *Mesolycus*, *Lyroneces* and *Platerodrilus* (Figs 395, 397, 404, 405, 403).
- 41 Pro- and mesocoxal suture: 0, present; 1, absent. Condition 0 found in *Dexoris* (Fig. 429a).
- 42 Metacoxal meral suture: 0, complete; 1, conspicuous, but incomplete; 2, vestigial or absent. Condition 0 observed in *Dexoris*, *Mesolycus* and *Dilophotes* (Figs 449-453).
- 43 Trochanters: 0, divided into trochanter 1 and trochanter 2; 1, having conspicuous suture separating basal part; 2, not divided. Condition 0 was found in *Dexoris* (Fig. 429); condition 1 in *Caenia*, *Ceratoprion*, *Lycostomus* (Figs 422, 438-440).
- 44 Insertion of femora: 0, oblique; 1, set off. Condition 0 was found in *Dexoris*, *Lampyris*, *Cantharis* and *Phengodes* (Figs 429, 446-448).
- 45 Tibial spurs: 0, absent; 1, present. Condition 0 was observed in *Ceratoprion*, *Dexoris*, *Scarelus*, *Dilophotes* and *Mesolycus* (Figs 425, 429, 430, 440, 444).
- 46 Tarsomere 4: 0, narrow and not lobed; 1, lobed. Condition 0 was found in *Dexoris*, *Platerodrilus*, *Lyroneces*, *Taphes*, *Ceratoprion*, etc. (e.g. Figs 427, 428, 429, 432, 437, 440).
- 47 Plantar pad on tarsomere 4: 0, absent; 1, present. Condition 0 was found in *Dexoris*, *Ceratoprion*, etc. (e.g. Figs 429, 440).
- 48 Claws: 0, simple; 1, with series of minute dents on inner surface; 2, distally cleft or with basal dent. Condition 1 was found in *Dexoris* and *Lyroneces* (Figs 428, 429b); condition 2 - in *Dilophotes*, *Macrolycus*, *Mesolycus*, as well as in *Cantharis* (Figs 444, 448).
- 49 Median longitudinal suture or groove in all tergites: 0, present; 1, absent. Condition 0 was found in *Dexoris*, *Dilophotes*, *Ceratoprion* and *Lyroneces*.
- 50 Male tergites 9 and 8: 0, separate; 1, fused. Condition 1 was found in *Lampyris*.
- 51 Male proctiger (tergite 10): 0, separate from tergite 9; 1, medially attached to

- tergite 9; 2, absent. Condition 0 was found in *Platerodrilus* (Fig. 478), condition 2 in *Lampyris* (Fig. 489).
- 52 Location of abdominal spiracles: 0, ventral 1, dorsal. Condition 0 was found in *Lampyris*.
- 53 Location of abdominal spiracles: 0, on membrane; 1, at the very edge of sternite; 2, at the very edge of tergite; 3, on sternite relatively distant from edge. Condition 2 was found in *Ceratopriion* (Fig. 488).
- 54 Phallobase of aedeagus: 0, symmetric; 1, asymmetric.
- 55 Phallobase of aedeagus: 0, composite; 1, uniform.
- 56 Median lobe of aedeagus: 0, symmetric; 1, asymmetric.
- 57 Female: 0, larviform or unknown; 1, known and not larviform.
- 58 Larval cuticle: 0, uniformly alveolate; 1, partially clear. Condition 0 was found in *Platerodrilus*, *Calopteron*
- 59 Larval mandibles: 0, tripartite; 1, uniform. Condition 1 was found in *Pyractomena*, *Cantharis*, *Phengodes* (Figs 72, 75-76).
- 60 Larval mandibular stiletto part: 0, free; 1, distally fused to labral lobe; 2, completely fused to other mandibular structures. Condition 1 was established for *Lygistorpterus* (Fig. 40); condition 2 for *Pyractomena*, *Cantharis* and *Phengodes*.
- 61 Larval stipes of mandible: 0, separate, at least anteriorly; 1, fused to the cranial segment. Condition 1 was found in *Pyractomena*, *Cantharis* and *Phengodes* (e.g. Fig. 70).
- 62 Larval head capsule: 0, divided into preoral and gnathal segments; 1, undivided. Condition 0 was found in *Platerodrilus*, (Figs 10-11), *Lycus* (Fig. 24), and *Plateros* (Fig. 60).
- 63 Larval prementum: 0, divided into a pair of annuli; 1, fused. Condition 0 was found in *Calopteron*, Fig. 47, and *Lycostomus*.
- 64 Larval metathoracic spiracles: 0, functional and similar to mesothoracic spiracle; 1, functional, but dissimilar with mesothoracic ones; 2, both dissimilar and non-functional. Condition 0 was found in *Platerodrilus* (Fig. 20); condition 1 in *Lycus* (Figs 34, 36, 38); condition 2 in *Lygistorpterus* and *Pyractomena* (Figs 41, 44, 77, 79).
- 65 Larval trochantin: 0, distally not attached to coxae; 1, distally attached to coxae.
- 66 Larval coxa: 0, elongate; 1, subquadrate; 2, transverse. Condition 0 was found in *Platerodrilus* and *Lycus* (Figs 20, 39); condition 2 in i.e. *Lygistorpterus* (Fig. 41) and *Macrolycus*.
- 67 Larval coxal suture: 0, present; 1, absent. Condition 0 was found in *Pyractomena* (Fig. 77).
- 68 Larval trochanter: 0, divided into trochanters 1 and 2; 1, uniform. Condition 0 was found in *Platerodrilus*, *Lycus*, *Calopteron* (Figs 20, 39, 53).

	1									2									3																
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	
<i>Dexoris</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	1	0	0	0	0	1	1	2	0	0	0	0	0	0	0	1	0	0
<i>Aferos</i>	1	2	0	0	2	0	0	0	1	0	1	1	2	1	2	1	1	1	1	2	1	1	0	1	1	0	1	1	1	1	0	1	1	1	0
<i>Caenia</i>	1	2	0	0	1	0	0	1	1	0	1	1	2	1	1	1	0	1	1	1	2	0	1	0	0	1	0	1	1	1	1	0	1	1	1
<i>Calochromus</i>	1	1	0	0	2	0	0	1	1	1	0	2	1	2	1	2	1	1	1	1	2	2	1	1	0	1	1	1	1	0	1	1	1	0	
<i>Calopteron</i>	1	2	0	0	1	0	0	0	1	0	0	1	2	1	0	1	1	1	1	2	0	1	0	0	1	1	1	1	0	0	1	1	1	0	
<i>Ceratopriion</i>	1	1	0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0
<i>Conderis</i>	1	1	0	0	2	0	0	1	1	0	1	2	1	2	1	0	1	1	1	2	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1
<i>Dicyoptera</i>	1	2	0	0	2	0	0	1	1	0	1	2	1	2	1	2	1	1	1	1	2	1	1	0	0	1	1	1	0	1	1	0	1	0	
<i>Dilophotes</i>	1	1	0	0	0	0	0	1	1	0	1	2	1	2	1	2	1	1	1	1	2	1	1	1	0	0	1	1	1	0	1	1	1	0	
<i>Helcophorus</i>	1	1	0	1	2	0	0	1	1	0	1	1	2	1	2	1	1	1	1	2	1	1	0	0	1	0	1	1	1	0	1	1	1	0	
<i>Lycinella</i>	1	1	0	1	2	0	0	1	1	0	1	0	2	0	2	1	1	1	1	2	1	1	0	0	0	0	1	1	0	1	0	1	0		
<i>Lycostomus</i>	1	1	0	1	2	1	0	1	1	0	1	1	2	1	2	0	1	1	1	2	1	1	1	0	1	0	0	1	0	1	1	1	0		
<i>Lyroneces</i>	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	
<i>Macrolycus</i>	1	2	0	0	0	0	0	1	1	0	2	1	2	1	1	1	1	1	1	1	2	1	1	0	1	0	1	1	1	1	1	1	1	1	
<i>Mesolycus</i>	1	1	0	0	1	0	0	1	1	0	1	0	2	1	2	0	2	0	1	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1
<i>Metriorrhynchus</i>	1	1	0	1	1	0	0	1	1	0	1	0	2	1	2	1	2	1	1	1	2	1	1	0	0	1	1	1	1	1	1	1	1	1	
<i>Platerodrilus</i>	1	1	0	0	2	2	1	0	1	0	1	0	2	0	2	0	2	1	1	1	0	2	1	1	1	0	0	1	1	1	0	1	1	1	
<i>Plateros</i>	1	2	0	1	1	0	1	1	1	0	1	0	1	2	1	2	1	0	1	1	2	2	1	1	0	0	1	1	1	0	1	1	1	0	
<i>Platycis</i>	1	2	0	1	2	1	0	0	1	0	1	0	1	2	1	1	0	0	1	1	2	1	1	0	0	1	1	1	0	1	1	1	0		
<i>Scarelus</i>	1	2	0	1	2	1	0	0	1	0	1	0	2	0	2	0	2	1	1	1	2	1	1	0	0	0	1	1	0	1	0	1	0		
<i>Taphes</i>	1	1	0	0	1	0	0	0	1	0	1	0	2	0	2	1	1	1	1	2	1	1	0	0	1	0	1	0	1	0	1	0	1	0	
<i>Lampyris</i>	1	2	1	1	2	2	1	1	1	1	0	1	1	0	0	2	0	1	2	1	2	2	1	1	2	2	1	1	0	1	0	1	0	1	0
<i>Thilmanus</i>	1	2	0	0	2	1	0	0	1	0	1	0	2	0	2	0	2	1	1	0	2	2	1	0	1	0	1	0	0	1	0	1	0	1	0
<i>Phengodes</i>	1	2	1	0	2	2	1	1	1	1	2	2	0	2	0	2	1	2	1	3	2	2	1	1	0	1	0	0	0	1	1	0	0	0	0
<i>Cantharis</i>	1	2	0	1	2	2	1	1	1	1	1	2	2	1	2	1	2	1	2	1	3	2	2	1	1	2	2	1	1	1	1	1	1	1	1

	3									4									5									6								
	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	
<i>Dexoris</i>	0	1	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Aferos</i>	2	0	1	1	1	1	1	1	2	2	1	1	1	1	0	1	0	1	3	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?		
<i>Caenia</i>	2	1	1	1	1	1	1	1	2	1	1	1	1	1	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?			
<i>Calochromus</i>	2	1	1	1	1	1	1	1	2	2	1	1	1	1	0	1	0	1	1	1	1	1	0	1	0	1	2	0	2	1	1	1	1			
<i>Calopteron</i>	2	1	1	1	1	1	1	1	1	1	2	1	1	1	1	0	1	0	1	0	1	0	0	0	1	0	2	0	1	1	0	1	1	1		
<i>Ceratopriion</i>	2	1	0	1	0	0	1	1	1	1	0	1	0	0	0	0	0	1	2	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?		
<i>Conderis</i>	1	1	1	1	0	0	1	1	2	2	1	1	1	1	0	1	0	1	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?		
<i>Dicyoptera</i>	2	0	1	1	1	1	1	1	2	2	1	1	1	1	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Dilophotes</i>	2	0	1	1	1	1	1	1	1	0	2	1	0	1	1	2	0	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?		
<i>Helcophorus</i>	2	1	1	1	1	1	1	1	1	2	2	1	1	1	1	0	1	0	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?		
<i>Lycinella</i>	2	1	1	1	1	1	1	1	2	2	1	1	0	1	0	1	0	1	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?		
<i>Lycostomus</i>	2	1	1	0	0	0	1	2	1	1	1	1	0	1	0	1	1	1	0	1	1	0	1	0	0	0	1	0	1	0	1	0	1	0		
<i>Lyroneces</i>	2	1	0	1	1	0	1	2	2	1	1	0	1	0	1	0	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Macrolycus</i>	2	1	1	1	1	0	1	2	2	1	1	1	1	2	1	1	1	1	1	1	1	0	?	0	1	2	0	1	1	1	1	1	1			
<i>Mesolycus</i>	2	1	1	1	1	0	1	0	2	1	0	1	1	2	1	1	1	0	1	1	3	1	1	1	0	1	?	?	?	?	?	?	?	?	?	
<i>Metriorrhynchus</i>	2	1	1	1	1	1	1	1	1	2	2	1	1	1	1	0	1	1	1	1	1	1	0	?	0	1	2	0	1	1	1	1	1	1		
<i>Platerodrilus</i>	2	1	1	1	1	1	0	1	2	2	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	
<i>Plateros</i>	2	1	1	1	1	1	0	1	2	2	1	1	1	1	0	1	1	3	0	1	1	1	2	0	?	0	0	1	2	0	1	1	1	1		
<i>Platycis</i>	2	0	1	1	1	1	0	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	?	0	1	1	0	1	1	1	1	1		
<i>Scarelus</i>	1	1	1	1	0	0	1	2	2	1	0	1	1	0	1	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Taphes</i>	2	1	1	1	0	0	1	2	2	1	1	0	1	0	1	0	1	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Lampyris</i>	2	1	1	1	1	1	0	1	2	1	0	1	1	1	0	1	1	2	0	1	1	1	0	0	1	1	2	1	1	1	1	0	1	0		
<i>Thilmanus</i>	2	1	2	1	1	1	1	2	2	1	1	0	0	0	1	0	1																			

Dexoris, a second representing *Lyroneces* and a third *Dexoris* (Fig. 595). The «Cantharoidea» appeared to be divided into clades corresponding to Lycidae, Phengodidae, Cantharidae, Lampyridae and apparently a polyphyletic clade including *Ceratoprion*, *Scarelus*, *Thilmanus* and *Platerodrilus*. These results were deemed not quite satisfactory, because *Taphes*, a seemingly typical lycid, with fully imaginal female, was also included in the latter taxon.

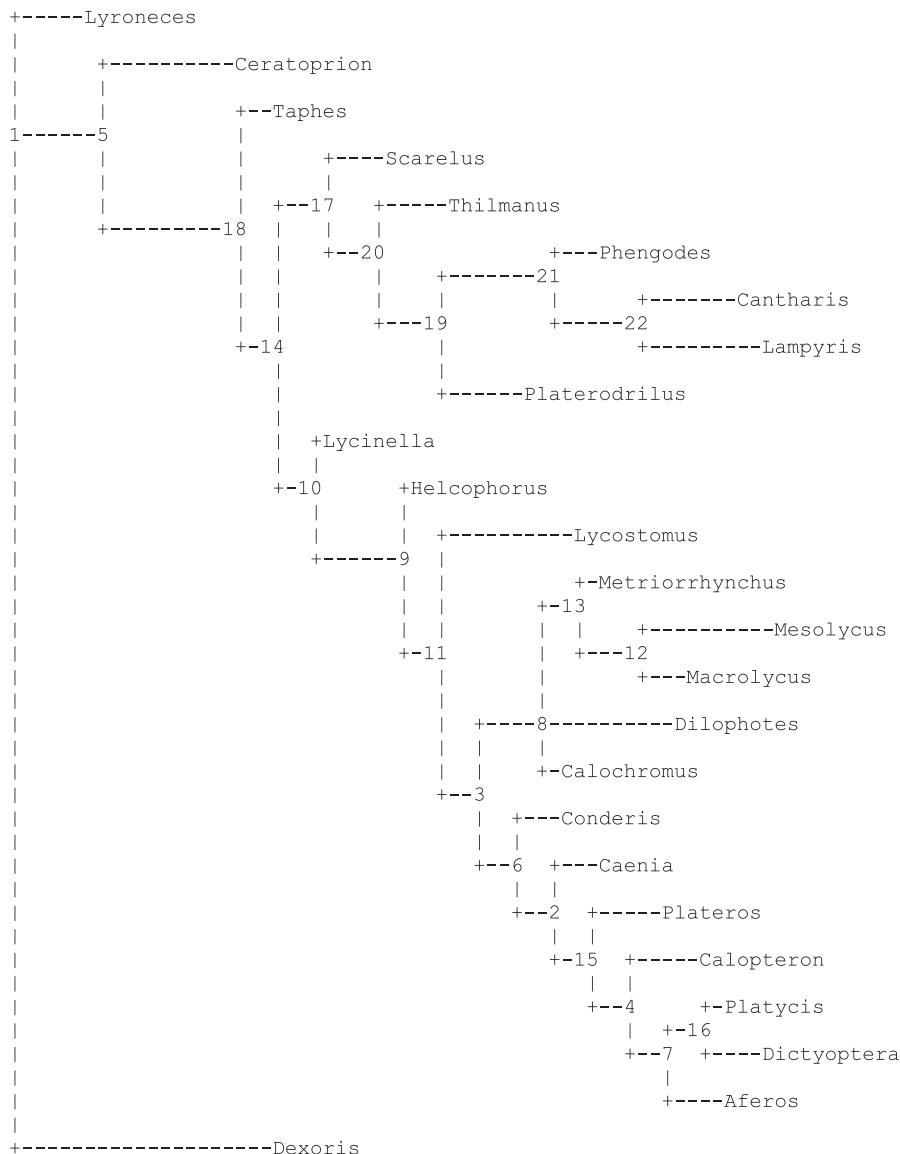


Fig. 595: Phylogenetic tree (Phylip Pars) showing relationships between various beetle families.

The analysis was repeated with weighted characters, the highest weight («9») awarded to the character that distinguish the established family level taxa (3, presence or absence of the tentorial bridge, separating Lycidae and Lampyridae + Phengodidae) and «5» to characters that are hypothesized to be least subject to modification and reverse development (6, 7, 10, 22, 28, 54, 57). The search produced three most parsimonious trees, with *Taphes*, as well as *Thilmanus* and *Scarelus* included in the Lycidae (Fig. 596).

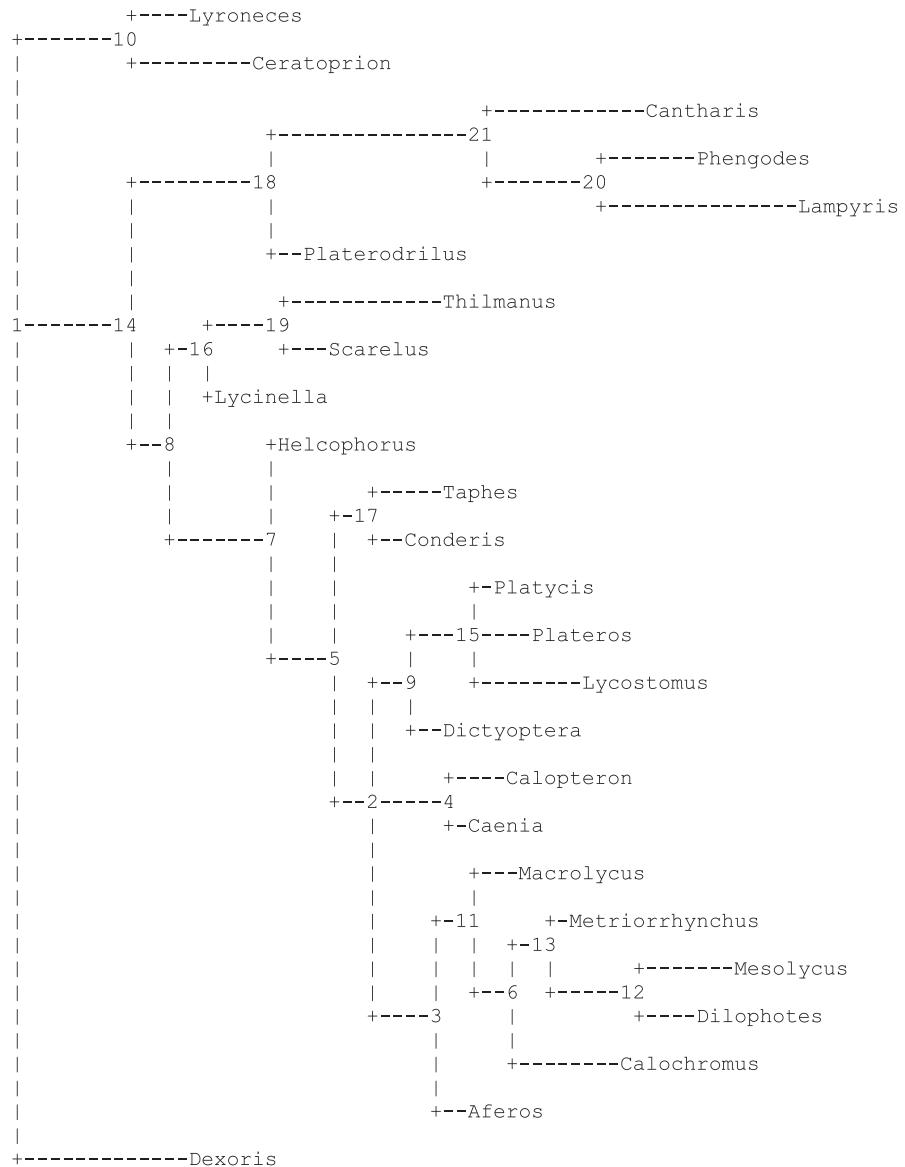


Fig. 596: Phylogenetic tree (Phylip Pars) using adult characters, characters weighted.

Then, the analysis was repeated with the larval characters taken into consideration. The analysis with unweighted characters again resulted in three most parsimonious trees, one of which is illustrated in Fig. 597. *Taphes* is again included in the polyphyletic clade with *Ceratopriion*, *Scarelus*, *Thilmanus* and *Platerodrilus*.

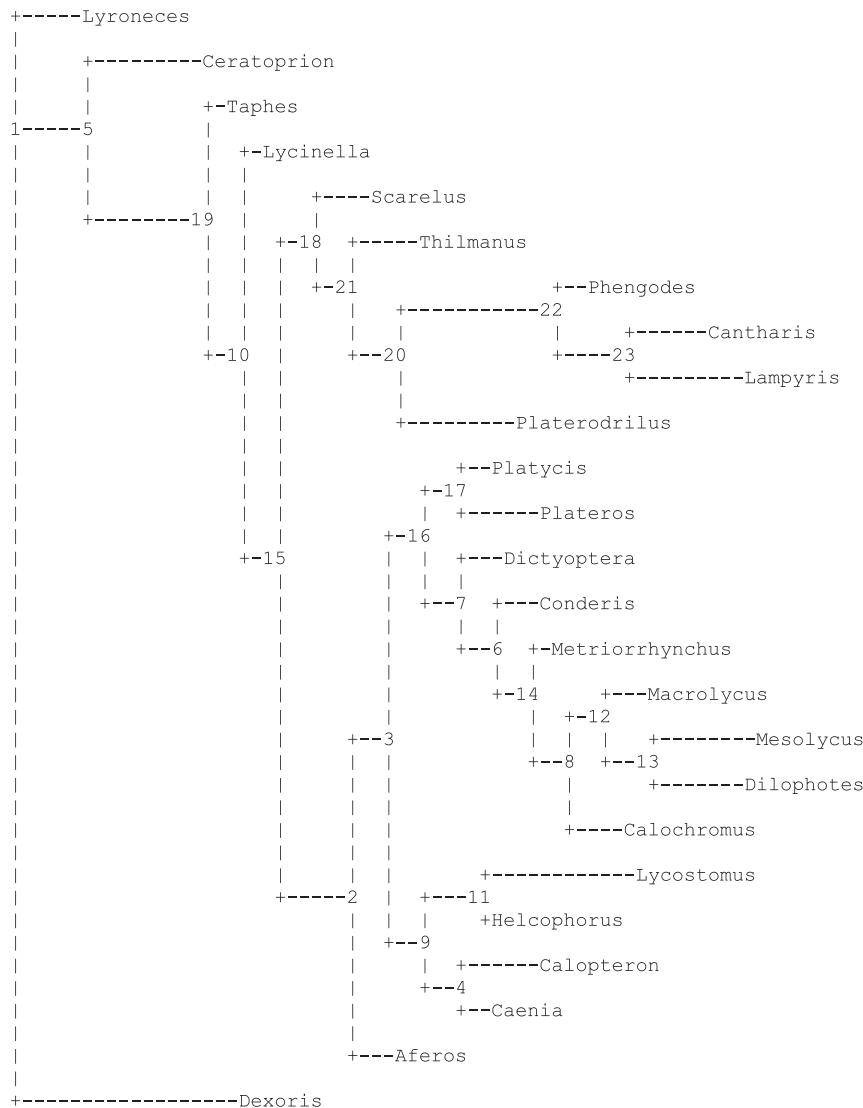


Fig. 597: Phylogenetic tree (parsimony) based on adult and larval characters, no characters weighted.

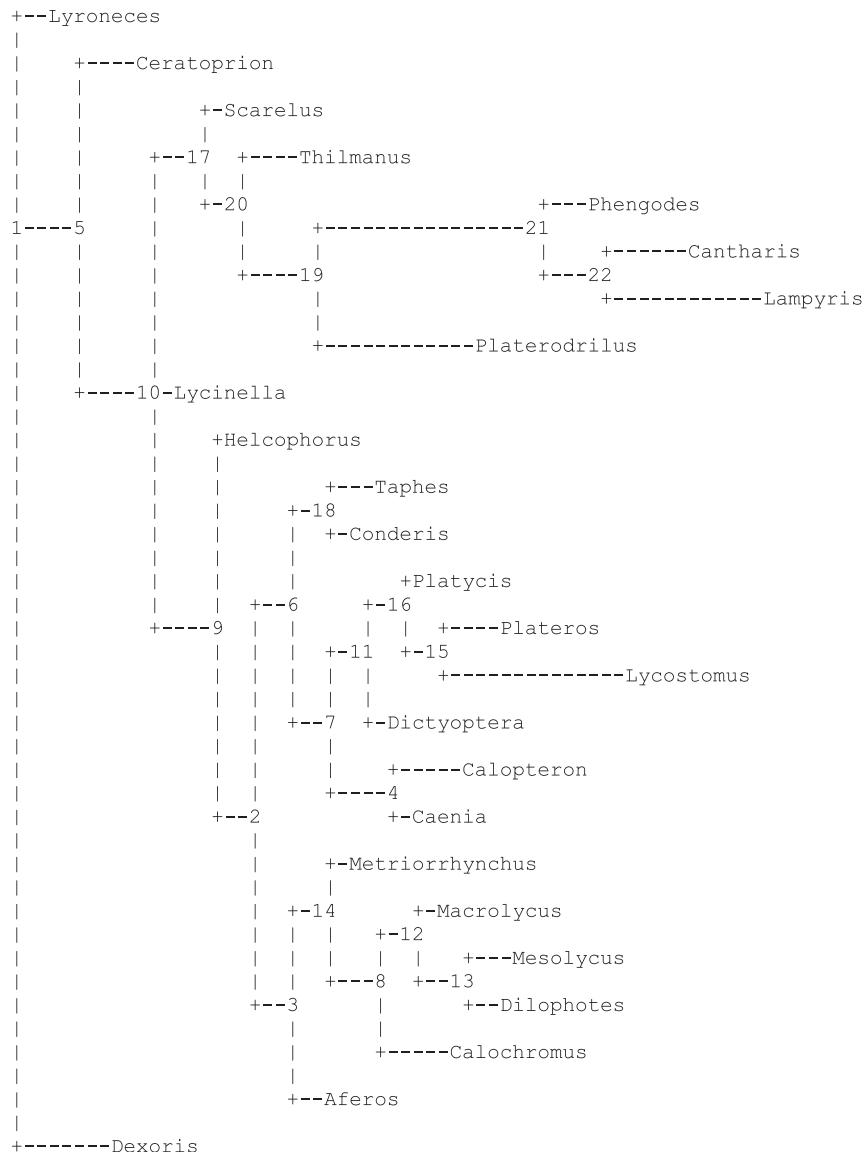


Fig. 598: Phylogenetic tree (Phylip Pars) using adult and larval characters, characters weighted.

This cladogram was taken as the basis for a phylogenetic reconstruction. The phylogeny tree of the family level taxa is hypothesized to consist of two clades (Fig. 599), Dexorididae stat. n. and Lycidae + Cantharoidea, the latter including the families Lampyridae, Phengodidae and Cantharidae. The taxa included in Lycidae, which may deserve being separated at the suborder level, are distinguished by two fundamental synapomorphies, the tripartite larval mandibles and the fused larval maxillary stipites, confirmed in three of the seven subfamilies, Miniduliticolinae,

stat. n., Lycinae and Calochrominae. The holophyly of Lycinae + Calochrominae is presumed to be the complete metamorphosis of development of both sexes. All of Lyropaeinae, stat. n., Leptolycinae, Ateliinae, Thilmaninae, subfam. n. and Miniduliticolinae, stat. n. are (hypothetically - in all taxa, except Miniduliticolinae) characterized by the paedomorphic female development, presumed to be their symplesiomorphy. Some of the apomorphies of *Platerodrilus* and *Miniduliticola* placed in Miniduliticolinae stat. n., such as present gula and prognathous head, fairly well distinguish both from the rest of the lycids. The Cantharoidea clade is separated by the one-partite larval mandibles, which are considered their synapomorphy.

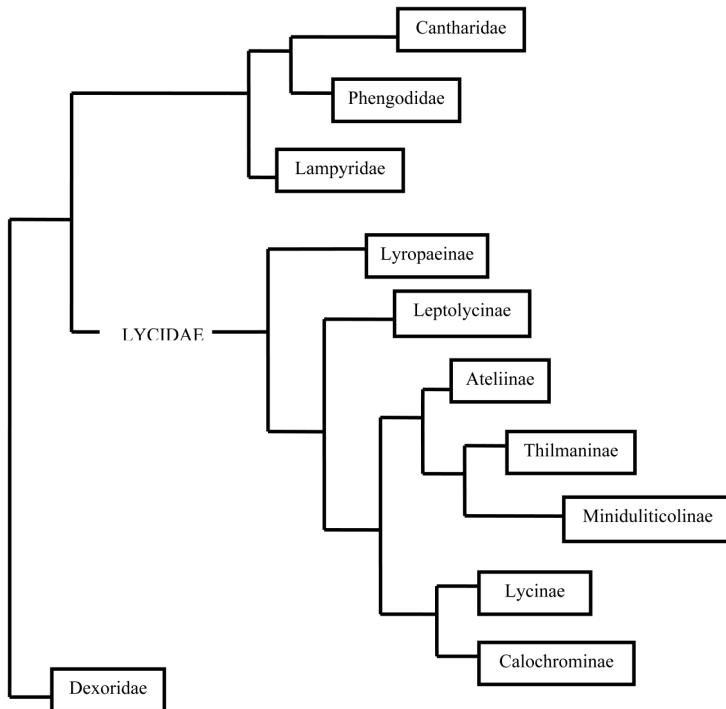


Fig. 599: Presumed phylogeny tree of Lycidae and allied taxa.

The Lycidae with complete metamorphosis are hypothesized to be divided between two subfamilies, Lycinae and Calochrominae, with the current tribes retaining their status, although in some cases placed in a different subfamily (Fig. 600). The holophyly of Calochrominae is presumed to be the asymmetric phallobase considered a synapomorphy of the subfamily, while the symmetric phallobase appears to be a plesiomorphy of Lycinae. It is of interest that *Helcophorus* having certain remarkable features related to the winglessness of the female of its type species, which suggests possible relatively recent paedomorphic past of the lineage, in most cladograms was placed at the root of the lycid tree, though none of such features were included in the character set used for the computer analysis. *Lycinella* is another genus, whose characters are generally close to the Lycinae proper, but the absence of knowledge on its females and larvae, with relative abundance of

males in collections, is suggestive of its possible current paedomorphic female development. Both *Lycinella* and *Helcophorus* are included in Lycinae incertae sedis.

The Lycinae Laporte is hypothesized to include tribes Erotini Leconte, Platerodini Green, Dictyopterini Kleine, Calopterini Kleine, Taphini Bocák & Bocáková, Lycini and Conderini Bocák & Bocáková. The Calochrominae Lacordaire is assumed to consist of Macrolycini Kleine, Dilophotini Kleine, Calochromini Lacordaire, Metriorrhynchini Kleine and Aferotini Kazantsev. The preliminary considerations on placement of the subtribes appear to be as follows. Libnetina Bocák & Bocáková is placed incertae sedis in Lycinae; Trichalina Kleine and Hemiconderina Kleine are tentatively placed in Metriorrhynchini, while Lyponiina Bocák & Bocáková, as evidently not related to Platerodini due to the asymmetric phallobase, is hereby transferred to Calochrominae incertae sedis; Flagraxina Kazantsev is placed in Dictyopterini.

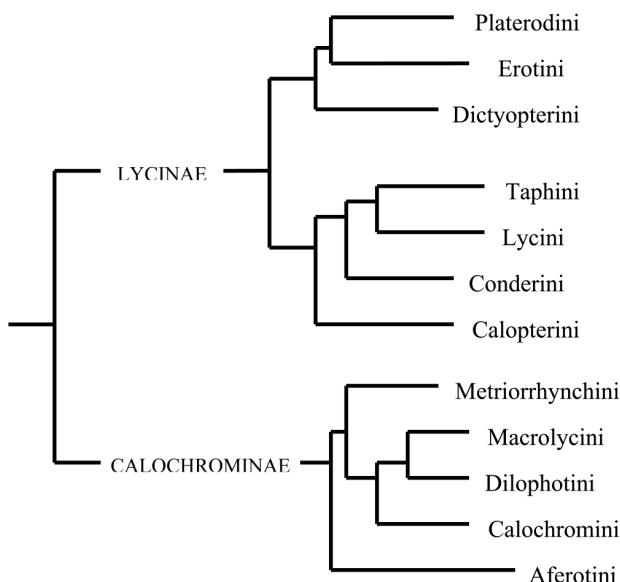


Fig. 600: Presumed phylogeny tree of Lycidae.

The taxonomic changes to be made with respect to the above mentioned considerations are as follows.

Dexorididae Kleine, 1933, stat. n.

type genus: *Dexoris* Waterhouse, 1878

Dexorididae Kleine stat. n. is raised to the family level. *Lampyrolycus* Burgeon and *Mimolibnetis* Pic are tentatively included in the family in addition to *Dexoris* Waterhouse. Dexorididae is characterized by numerous plesiomorphies, the hypothesized non-fused maxillary stipites of its larvae being one of them. Among the few synapomorphies that distinguish Dexorididae is the oblique attachment of the femora to the trochanters (Figs 231, 429).

Lyropaeinae Bocák & Bocáková, 1989, stat. n.type genus: *Lyropaeus* Waterhouse, 1878

Lyropaeinae stat. n. is raised to the subfamily level. Introduced as a tribe in the Leptolycinae, this taxon is characterized by a number of apomorphies, the most evident being perhaps 10-segmented antennae and the set off femur-trochanter articulation (Fig. 427), the latter character distinguishing it from the Dexoridae that have also 10-segmented antennae.

Thilmaninae subfam. n.type genus: *Thilmanus* Baudi, 1871

The hypothesized apomorphies of the new subfamily are the peculiarities of the hind wing structures and venation (the Cu veins fused to the A veins, present anal lobe, etc., Fig. 420), seven ventrites in the male abdomen and present tibial spurs. Thilmaninae subfam. n. belongs in the group of taxa characterized by probable plesiomorphic condition of the female development, which is presumably not metamorphic. This presumption comes from the fact that no females (and no larvae) have so far been discovered in the two European species of the type genus, *Th. obscurus* Baudi and *Th. longipennis* Pic. *Thilmanus* cannot not be classified with Omalisidae, which also have seven ventrites, due to the absent tentorium (Figs 162-164), different structure of the prosternum lacking long intercoxal process (Fig. 226), differently structured mesoventrite not meeting the prosternum (Fig. 226) and the non-coadapted abdomen. The same features plus the reticulated elytra do not allow placing *Thilmanus* in Drilidae. On the other hand, all morphological characters of *Thilmanus*, except the number of abdominal ventrites, suggest it is a lycid. The seven ventrites are assumed to be an apomorphy of the clade within the Lycidae, possibly analogous with similar reduction of the number of ventrites in certain Lampyridae and Cantharidae. Another apomorphy of Thilmaninae subfam. n. is its noticeable epipleuron, presumably a homoplasy with Aferotini and most of other «Cantharoidea».

Miniduliticolinae stat. n.type genus: *Miniduliticola* Kazantsev, 2002

Miniduliticolinae stat. n. is raised to the subfamily level, as Duliticolinae Kazantsev, 2002 is unavailable in accordance with Articles 11.7.1.1 and 64 of the ICBN, as derived from the synonymous name *Duliticola* Mjöberg. *Miniduliticolinae* includes Miniduliticolini and Platerodrilini tr. n.

Platerodrilini tr. n.type genus: *Platerodrilus* Pic, 1921

Platerodrilini tr. n. is erected to replace Duliticolini Kazantsev, 2002, unavailable in accordance with Articles 11.7.1.1 and 64 of the ICBN, as derived from the synonymous name *Duliticola* Mjöberg. The Platerodrilini tr. n. is tentatively included in *Miniduliticolinae*. The hypothesized apomorphy of the new tribe distinguishing it from *Miniduliticolini* is the reticulated elytra.

KEY TO SUBFAMILIES OF LYCIDAE

1 Females larviform or unknown	2
- Females known and not larviform	5

2	Male antennae 10-segmented	Lyropaeinae stat. n.
-	Male antennae 11-segmented	3
3	Male head prognathous, gula present	Miniduliticolinae stat. n.
-	Male head hypognathous, gula absent.....	4
4	Male tibial spurs absent; male abdomen with 8 ventrites; male metathoracic wing without anal lobe; elytron without epipleuron	Ateliinae
-	Male tibial spurs present; male abdomen with 7 ventrites; male metathoracic wing with anal lobe; elytron with noticeable epipleuron	Thilmaninae subfam. n.
5	Phallobase symmetrical (e.g. Figs 511-512, 519-526).....	Lycinae
-	Phallobase asymmetrical (Figs 513-518, 533, 534)	Calochrominae

SOME CONSIDERATIONS ON EVOLUTION OF THE COLEOPTERA

The Strepsiptera, not so long ago considered a family within the Coleoptera (Stylopidae, e.g. in Crowson, 1981) has proved to be the sister group of Diptera (Wheeler *et al.*, 2001). The Coleoptera sensu lato has thus already been demonstrated to be a polyphyletic taxon. Where the emergence of elytron was possible in not closely related groups, as an obviously useful acquisition of flying insects, it may easily have emerged twice and more times both in unrelated and related pterygote lineages.

The brief reassessment of the morphological characters of the Archostemata (which generally lies beyond the scope of the present study, with no relevant cladistic analysis carried out) demonstrates that most of them are in a derived condition and the few characters that appear plesiomorphic (i.e. reticulated elytra or scale-like pubescence) are shared by other Coleopterans (e.g. Lycidae). As a matter of fact, the only two apparent plesiomorphic characters not shared by the otherwise more hypothetically primitive Polyphaga are the additional imaginal posterior metasternal sclerites and the short scutellar elytral costa. At the same time certain fundamental features characterizing the Archostematan lineage, such as the 6-segmented larval legs with a paired claw, the fused larval hypopharyngeal, paragnathal and premental structures, the absent cervical sclerites, the propleuron incorporated in the prothoracic wall, the spiral folding pattern of the hind wing with adequately modified wing venation, the so-called «adephagan» aedeagus, which lacks a phallobase, etc., being unequivocally derived and/or foreign to the Polyphaga, seem to provide sufficient evidence of the independent origin of the group; in other words, the Polyphaga and Archostemata-Adephaga-Myxophaga appear not to have had an immediate common ancestor. Therefore, it is here hypothesized that the Coleoptera, even with the Strepsiptera excluded, is a polyphyletic taxon, not including the common ancestor of its two major lineages (Fig. 601).

The Protocoeloptera, which is usually regarded as a paraphyletic coleopteran stem assemblage (Kukalova-Peck and Lawrence, 2004), could be a possible common ancestor of the Coleoptera possessing presumably plesiomorphic morphological features both of the Polyphaga and Archostemata, i.e. the tuberculate cuticle, the additional metasternal sclerites, the irregularly reticulated elytra, not meeting each other at the suture, not coadapted with the abdomen and extending far beyond its apex, the scutellar elytral costa, the soft 10-segmented abdomen, etc. (Ponomarenko,

1969; Lawrence & Newton, 1982). However, due to such synapomorphies of the Neuroptera-Protocoleoptera-Archostemata-Adephaga-Myxophaga, as the segmented metaventrite and the closure of the procoxal cavity, these taxa appear more likely to form an independent lineage, not related to the Polyphaga. The latter lineage, along with the Protorrhynchota, is characterized by the non-segmented metaventrite and the open procoxal cavity.

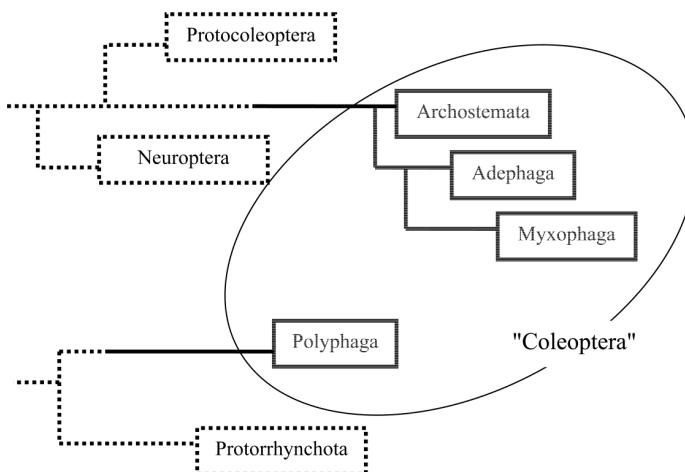


Fig. 601: Presumed phylogeny tree of «Coleoptera».

The hind wing of Protocoleoptera is known from the single specimen of *Moravocoleus permianus* Kukalova (Kukalova-Peck & Lawrence, 1993: Fig. 1), with only part of the wing preserved, the wing apparently torn off and its apical portion totally absent. Though the specimen possesses developed non-coadapted elytra, the authors assume that the wing apex could not be folded. It seems, however, improbable that the elytron could have developed into a protective cover of the wing without being correlated with the wing in length, which would leave a considerable portion of the wing unprotected. It appears more plausible that the elytron and the hind wing were being reduced more or less simultaneously, from the point when the latter acquired the folding capacity. A spread foldable hind wing not surpassing the elytron in length is characteristic of some presumably primitive Lycidae (e.g. *Lyroneces*, Figs 387, 395, 396). Examples of the folded coleopteran hind wings exceeding the elytra in length (manifest in some Tegeusidae, Phengodidae, Cantharidae, Rhipiphoridae) are obviously secondary modifications most probably occurred due to mimicry or other biological factors. On the other hand, a hind wing incapable of folding does exist in some Polyphaga, namely in Lycidae (*Alyculus*) and Tegeusidae (*Atractocerus*), but the elytron in both cases is significantly shorter than the wing and seems to be secondarily reduced. If this is not also true for *Moravocoleus permianus*, condition supposed by Kukalova-Peck and Lawrence could have been acquired if the mesothoracic wing had been initially shorter than the metathoracic one, which is not too plausible, as nothing suggests that the coleopteroid stem assemblage had this kind of wings. The wing venation

pattern presumed in *M. permianus* in this case may be an artifact of overlaying of the two wings of the protocoleopteran or inclusion of a wing from another insect. At the same time, apart from the irregular elytral and the odd hind wing venation, *Moravocoleus permianus* does not significantly differ from an extant lycid male, with its ten tergites and the long and narrowed distally apical abdominal segment, from which the aedeagus may also be protruding (as in *Platerodrilus*). The antennal and pronotal structure and the non-compact body form with non-coadapted thoracic and abdominal sclerites closely resemble those of a number of contemporary Lycidae as well.

Absence of mandibles in the ancestors of the Mandibulata and wide distribution of the non-chewing and non-mandibular mouthparts in different unrelated hexapod lineages seem to provide good evidence that primitive insects did not possess chewing mandibles, and may not have possessed mandibles altogether. It appears plausible to presume that Polychaeta gave rise to Trilobitomorpha, whose limbs became segmented in connection with inhabitancy on bottom of the sea; the segmented limbs, inherited from the trilobitomorphs, were retained in eucrustaceans, on the one lineage, and, after going terrestrial, in Myriapoda and Hexapoda, on the other, with their anterior pairs of limbs transformed in both lineages, becoming parts of mouth apparatus. The lycid larval type of mouth apparatus seems to be one of the least modified in all known living terrestrial arthropods.

The ancestors of the Polyphaga were hypothetically one of the first terrestrial hexapods. They were water-edge-dwelling consumers of organic substances including the microfauna that they sucked with the water or, later, liquids from the wet and decaying organic debris. It appears that the Lycidae, though undoubtedly very different from them in many other ways, due to the unchanged feeding mode have preserved the ancient type of the mouthparts. The wings are known to have been developed by the insects already in the Devonian some 400 million years ago. In more derived forms they acquired more complicated venation pattern. It appears unlikely that the elytron started to form in insects with the most complicated wing venation only in the Permian and emerged at once as a fully coadapted organ. On the contrary, it seems more probable that this process started earlier, when crawling in the moist substrate resulted in development of protection of the wings and that the coleopterans could well be among the first flying insects with primitive wings characterized by simple venation.

This hypothesis does not contradict to Kukalova-Peck and Lawrence's (1993; 2004) conclusions from the study on the coleopteran and endoneopteran hind wing that the ancestor of Archostemata and Adephaga-Myxophaga is the sister group of Polyphaga. Böving & Craighead's (1931) acknowledgement of the primitiveness of the «larval types to which the Polyphaga could be traced» also conforms to this opinion. A study on morphology of larviform females of some of the Cantharoidea, i.e. Lampyridae, Phengodidae and Drilidae (Cicero, 1988) demonstrates that the larviform end of the gradient is primitive, and the fully imaginal condition of some female fireflies was gained as the result of an evolutionary process, which also supports the presented hypothesis. In this respect Riley's (1887) suggestion that these larviform females are «an archetypal hexapod form, which prevailed before complete metamorphosis had originated» appears quite true, with the ultimate form of paedomorphosis (the «neoteny») appearing an obvious symplesiomorphy of several lycid lineages. More advanced forms of paedomorphism seem to be symplesiomorphic of certain lineages in a number of other Polyphaga, such as most

cantharoid families, Dermestidae (*Thylodrias*), Rhipiphoridae (Rhipidiinae), Dascillidae (Karumiinae), Elateridae (Cebrioninae), etc. The paedomorphism of Micromalthidae (Archostemata) may be plesiomorphic, too, though in this case it may equally represent an apomorphy of the other «coleopterous» branch.

The discovery of the tripartite mandibular structure in lycid larvae and the generalized sucking type of their feeding apparatus suggests considering homologies between these structures of the Polyphaga (i.e. Lycidae), on the one hand, and several distant extant or extinct taxa, such as Protorrhynchota (including Palaedictyoptera), Thysanoptera, Copeognatha (=Psocoptera) and Mallophaga, on the other, where the «mandibles» are in one way or another similar (Snodgrass, 1935; etc.). Additional interesting parallels may lie between the Polyphaga and the Copeognatha (=Psocoptera), the only other Neoptera order where both simple and complete metamorphoses occur, as well as both chewing and sucking mouth structures are encountered. Discovery of division of the trochanter into two segments in the Polyphaga also seem to necessitate a reconsideration of the Pterygota phylogeny.

On the other hand, the broadly separated condyles of the mandible proper manifest in the lycid larvae, with the anterior/lateral one positioned on the dorsal surface, seem to have compromised the holophyly of Metapterygota, characterized by approximate condylitic bases (Kluge, 2000). The same refers to the hypopharyngeal lobes and the suspensorium, which may in fact prove to be the superlinguae, the loss of which is considered an autapomorphy of the Metapterygota (Kluge, 2000). The absent gula in most of the adult Lycidae also seems to have compromised the holophyly of the clade formed by the Coleoptera sensu lato and the Neuropteroidea, supported among other characters by such a synapomorphy as the presence of a gula (Lawrence & Newton, 1982).

The paired structure of the phallobase in a number of lycids is suggestive of considering homology with paired penes of two such unrelated orders of the Pterygota as the Ephemeroptera and Dermatoptera, and the apterygote insects, except the Protura (Snodgrass, 1935).

The presented considerations may appear to be contradicting to the paleontological data that provide evidence of abundance of the Archostemata in the Permian and first appearance of the Polyphagan fossils in the Triassic, with the first fossil cantharoids dating back to the Middle Cretaceous (Crowson, 1981; Lawrence & Newton, 1982). However, the only thing that a fossil record can prove is the occurrence of a certain taxon at a certain time, whereas absence of a fossil record in no way proves that a group was nonexistent at that moment or any time earlier. Besides, small and/or soft-bodied insects, prior to appearance of the Coniferae and a possibility to be immortalized in their resins, had much less chance to be preserved than large insects with harder exoskeleton. Occurrence of Lycidae species that are actually not separable from modern ones in the Baltic amber (Kazantsev, 1995; 1997), i.e. some 50 million years back, suggests taking more seriously hypotheses contemplating possible origin of the group earlier than just 100 million ago in the Cretaceous. Presence of hard-bodied beetles in ancient deposits and absence of soft-bodied ones does not also necessarily mean that, for instance, recent soft-bodied beetles evolved from the hard-bodied stock. On top of that, it is common knowledge that generally only relatively few terrestrial insects associated with lake shore habitats became fossilized, because it is predominantly lake deposits that preserved petrified images of the ancient fauna. Similarly, the sometimes applied assumption that the earlier the deposit the more plesiomorphies its fossils have, does not seem justified and cannot be accepted.

On the other hand, the main means of determining the age of hexapod fossils often remains the comparison method, consisting of dating deposits according to their faunistic complexes and their phylogenetic relationships (Rohdendorf, 1957). In other words, if a complex of entomological fossils contains only Polyphaga it will probably never be dated earlier than Jurassic, while that containing only Archostemata will probably be dated Upper Permian and not later than Triassic, when this group was presumed to be dominant among the Coleopterous insects. This approach does not appear to be consistent with the actual situation with the hexapod, including the Coleoptera, phylogeny.

There are also certain doubts about attributing all of the Permian Coleopterous fossils to Archostemata. While the metasternal sutures seem to rather confidently separate the archostematans from the polyphagans, the only elytral feature characteristic of the suborder is the presence of a scutellar costa, as the tuberculate and reticulate structure and scaliform pubescence are not uncommon in the Lycidae as well. However, in many Permian «Archostemata» known only by their elytra (e.g. Ponomarenko, 1969), the scutellar costa is indistinguishable and evidently absent or represents what in the Lycidae is called a reduced costa 1, which makes them inseparable from the latter group. The same refers with ca. 50 % certainty to the fossil Archostemata described from pieces of reticulated elytra, not showing their scutellar area.

ACKNOWLEDGEMENTS

This study would not have been possible without support and advice from many colleagues, willingly involved in numerous fruitful discussions on hexapod morphology and phylogeny. The expert opinion of Dr. N.Y. Kluge (St. Petersburg State University), Dr. M.A. Alonso-Zarazaga (Museo Nacional de Ciencias Naturales, Madrid), Dr. J.F. Lawrence (CSIRO Entomology, Canberra), Dr. A.F.Jr. Newton (Field Museum of Natural History, Chicago), Dr. N.B. Nikitsky (Zoological Museum, Moscow University) and Dr. A.S. Konstantinov (US National Museum of Natural History, Washington, D.C.) who commented on the manuscript in the course of its preparation is gratefully acknowledged. Special thanks are due to Dr. K.V. Makarov (Pedagogical University, Moscow) and Dr. A.Y. Solodovnikov (Field Museum of Natural History, Chicago) for their valuable practical assistance.

REFERENCES

- BEUTEL, R. G. 1995. Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *J. Zool. Syst. Evol. Research*, 33: 145-171.
- BEUTEL, R. G. & HAAS, F. 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, 16: 103-141.
- BLAIR, K. G. 1930. *Brachypsectra* LeC. - the solution of an entomological enigma. *Transactions of the Entomological Society of London*, 78 (1): 45-50.
- BOCÁK, L. & BOČÁKOVÁ, M. 1990. Revision of the suprageneric classification of the family Lycidae (Coleoptera). *Polskie Pismo Entomologiczne*, 59: 623-676.
- BOCÁK, L. & MATSUDA, K. 2003. Review of the immature stages of the family Lycidae (Insecta: Coleoptera). *Journal of Natural History*, 37: 1463-1507.
- BOCÁK, L. 1998. Nomenclatural notes on taxa of the family Lycidae described by Guérin Meneville (Insecta: Coleoptera). *Annales Zoologici*, 48 (3/4): 245-251.

- BOCÁKOVÁ, M. 2001. Revision and phylogenetic analysis of the subfamily Platerodinae (Coleoptera: Lycidae). *European Journal of Entomology*, 98: 53-85.
- BOURGEOIS, J. 1882. Monographie des Lycides de l'Ancient-Monde. *L'Abeille*, 20: 1-120.
- BÖVING, A. G. & CRAIGHEAD, F. C. 1930-1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana*, 11 (1-4): 1-351.
- BRANCUCCI, M. 1980. Morphologie comparée, évolution et systématique des Cantharidae. (Insecta: Coleoptera). *Entomologica Basiliensis*, 5: 215-388.
- BRANHAM, M. A. & WENZEL, J. W. 2003. The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics*, 19: 1-22.
- BUGNION, E. 1907. Les métamorphoses du *Ditoneces pubicornis* Walk. (Lycide). *Annales de la Société entomologique de France*, 76: 118-122.
- BUGNION, E. 1929. Le ver-luisant provencal et la luciole niçoise. *Mémoires de l'Association des Naturalistes de Nice et Alpes-maritimes*: 131.
- BURAKOWSKI, B. 1988. Notes on the biology of *Xylobanellus erythropterus* (Baudi a Selve) (Coleoptera, Lycidae) with description of the immature stages. *Polskie pismo entomologiczne*, 58: 575-585.
- BURAKOWSKI, B. 1990. *Lopheros lineatus* (Gorh.) - a species new to the Central European fauna (Coleoptera, Lycidae) with a description of the immature stages. *Polskie Pismo Entomologiczne* 59: 719-729.
- CAMPAU, E. J. 1940. The morphology of *Chauliognathus pennsylvanicus* (De Geer) (Coleoptera: Cantharidae). *Microentomology*, 5 (3): 57-85.
- CARPENTER, G. D. H. & FORD, E. B. 1933. *Mimicry*. London, VIII + 133 pp.
- CASPER, A. 1913. Die Körperdecke und die Drüsen von *Dytiscus marginatus*, ein Beitrag zur feineren Bau der Insektenköpfe. *Zeitschr. wiss. Zool.*, 107: 387-508.
- CHAPMAN, R. F. 1998. *The Insects, Structure and Function*. 4th ed. University Press, Cambridge, VIII+770 pp.
- CHOLODKOWSKY, N. 1891. Die Embryonalenentwicklung von *Phyllodromia (Blatta) germanica*. *Mémoires de l'Académie des Sciences de St. Petersburg*, sér. 10 (7): 281-286.
- CICERO, J. M. 1988. Ontophylogenetics of cantharoid lariforms (Coleoptera: Cantharoidea). *The Coleopterists Bulletin*, 42 (2): 105-151.
- CICERO, J. M. 1994. Composite, Haustellate Mouthparts in Netwinged Beetles and Firefly Larvae (Coleoptera, Cantharoidea: Lycidae, Lampyridae). *Journal of Morphology*, 219: 183-192.
- COSTA, C., VANIN, S. A. & CASARI-CHEN, S. A. 1988. *Larvas de Coleoptera do Brasil*. Museu de Zoologia, Universidade de São Paulo, São Paulo, 282 pp.+165 pls.
- CROWSON, R. A. 1972. A review of classification of Cantharoidea, with the definition of two new families, Cneoglassidae and Omethidae. *Revista de la Universidad de Madrid*, 22 (82): 35-77.
- CROWSON, R. A. 1938. The metendosternite in Coleoptera: a comparative study. *Transactions of the Royal Entomological Society of London*, 87 (17): 397-416 + 13 pls.
- CROWSON, R. A. 1981. *The Biology of the Coleoptera*. Academic Press, London, 802 pp.
- FEDORENKO, D. N. 2002. The coleopteran wing: Some notes on the structure of the articular area, with reference to the nomenclature of wing venation. *Russian Entomological Journal*, 11 (1): 5-14.
- FERRIS, G. F. 1940. The myth of the thoracic sternites of insects. *Microentomology*, 5 (3): 87-90.
- FOLSOM, J. W. 1900. The development of the mouthparts of *Anurida maritima* Guer. *Bulletin of the Museum of Comparative Zoology*, 36 (5): 87-158.
- GARDNER, J. C. M. 1946|1947. Larvae of Cantharoidea (Coleoptera). *Indian Journal of Entomology*, 8: 121-129.
- GREEN, J. W. 1950. The Lycidae of the United States and Canada. II. Lygistopterini (Coleoptera). *Transactions of the American Entomological Society*, 76: 13-25.
- HAMMOND, P. M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of Adephagan phylogeny (Coleoptera). In: *Carabid beetles: their evolution, natural history, and classification. Proceedings of the First International Symposium of Carabidology*. Pp. 113-180. The Hague.
- HAYASHI, N. & TAKENAKA, H. 1960. Notes on immature stages of *Plateros coracinus* Kiesenwetter (Lycidae) (Studies on coleopterous larvae X). *Kontyu*, 28 (2): 138-141.
- HAYASHI, N. 1954. Larva and pupa of *Lyponia quadricollis* Kiesenwetter (Studies on coleopterous larvae I). *New Entomologist*, 3 (2-3): 11-15.
- HLAVAC, T. F. 1972. The prothorax of Coleoptera: origin, major features of variation. *Psyche*, 79 (3): 123-149.
- HLAVAC, T. F. 1975. The prothorax of Coleoptera: (except Bostrichiformia-Cucujiformia). *Bulletin of the Museum of Comparative Zoology*, 147 (4): 137-183.

- KAPZOV, S. 1911. Untersuchungen über den feineren Bau der Cutikula bei Insecten. *Zeitschr. wiss. Zool.*, 98: 297-337.
- KAZANTSEV, S. V. 1995. New data on the Russian fauna of Lycidae (Coleoptera). *Zoologicheskij Zhurnal*, 74 (5): 35-44 [in Russian with English summary].
- KAZANTSEV, S. V. 1997. A recent species of the fossil genus *Kolibaceum* Winkler (Coleoptera, Lycidae) from Eastern China. *Entomologica Basiliensis*, 20: 159-164.
- KAZANTSEV, S. V. 2002. A generic review of Duliticolinae, new subfamily (Coleoptera, Lycidae). *Elytron*, 16: 5-21.
- KAZANTSEV, S. V. 2004a. Contribution to the knowledge of Macrolycini with description of *Calcaeron*, new genus (Coleoptera, Lycidae). *Zootaxa*, 493: 1-32.
- KAZANTSEV, S. V. 2004b. Phylogeny of the tribe Erotini (Coleoptera, Lycidae), with descriptions of new taxa. *Zootaxa*, 496: 1-48.
- KLUGE, N. Y. 2000. *Modern systematics of insects. Part I.* Lan', St. Petersburg, 336 pp. [in Russian with English summary].
- KORSCHESKY, R. 1951. Bestimmungstabelle der bekanntesten Lyciden-, Lampyriden- und Drilidenlarven. *Beiträge zur Entomologie*, 1 (1): 60-64.
- KUKALOVA-PECK, J. 1991. Fossil history and the evolution of hexapod structures. In: *The Insects of Australia* (Naumann I.D., editor). Pp. 141-179. CSIRO, Melbourne Univ., Carlton.
- KUKALOVA-PECK, J. & LAWRENCE, J. F. 1993. Evolution of the hind wind in Coleoptera. *Canadian Entomologist*, 125: 181-258.
- KUKALOVA-PECK, J. & LAWRENCE, J. F. 2004. Relationships among coleopteran suborders and major neopteran lineages: Evidence from hind wing characters. *European Journal of Entomology*, 101 (1): 95-144.
- LAMEERE, A. 1900. Notes pour la classification des Coléoptères. *Annales de la Société Entomologique de Belgique*, 44: 155-165.
- LAWRENCE, J. F. 1991. Order Coleoptera. Lycidae (Cantharoidea). In: *Immature insects. 2.* (Stehr F.W., editor). Pp. 423-424. Kendall Hunt Publishers, Dubuque, Iowa.
- LAWRENCE, J. F. 1999. The Australian Ommatidae (Coleoptera: Archostemata): new species, larva and discussion of relationships. *Invertebrate Taxonomy*, 13 (3): 369-390.
- LAWRENCE, J. F. & NEWTON, A. F. Jr. 1982. Evolution and classification of beetles. *Annual Revue of Ecology and Systematics*, 13: 261-290.
- LAWRENCE, J. F. & NEWTON, A. F. Jr. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: *Biology, Phylogeny and Classification of Coleoptera: Papers celebrating the 80th Birthday of Roy A. Crowson* (Pakaluk J. and Slipinski S.A., editors). Pp. 779-1006. Muzeum i Institut Zoologii Pan, Warszawa.
- LINSLEY, E. G., EISNER, T. & KLOTS, A. B. 1961. Mimetic assemblages of sibling species of lycid beetles. *Evolution*, 15 (1): 15-29.
- MCCABE, T. L. & JOHNSON, L. M. 1979a. The biology of *Platycis sculptilis* (Say) (Coleoptera, Lycidae). *The Coleopterists Bulletin*, 33 (3): 297-302.
- MCCABE, T. L. & JOHNSON, L. M. 1979b. Larva of *Calopteron terminale* (Say) with additional notes on adults behavior (Coleoptera, Lycidae). *New York Entomological Society*, 87 (4): 283-288.
- MEDVEDEV, L. N. & KAZANTSEV, S. V. 1992. A new subfamily and a new genus of Lycidae from Southeast Asia. In: *Systematics and ecology of insects of Vietnam* (Medvedev L.N., editor). Pp. 55-60. Nauka, Moscow [in Russian].
- MILLER, R. S. 1988. Behavior of *Calopteron reticulatum* (F.) Larvae (Coleoptera: Lycidae). *Ohio Journal of Science*, 88 (3): 119-120.
- MILLER, R. S. 1991. *A revision of Leptolycini (Coleoptera: Lycidae) with a discussion of paedomorphosis.* PhD Dissertation. The Ohio State University, 403 pp. (unpublished).
- MILLER, R. S. 1997. Immature Stages of *Plateros floralis* (Melsheimer) and Discussion of Phylogenetic Relationships (Coleoptera: Lycidae). *The Coleopterists Bulletin*, 51 (1): 1-12.
- MJÖBERG, E. 1925. The mystery of the so-called «trilobite larvae» or «Perty's larvae» definitely solved. *Psyche*, 32 (3): 121-154.
- PONOMARENKO, A. G. 1969. *Historical development of the Coleoptera-Archostemata.* Trudy Paleontologicheskogo Instituta, V.125. Nauka, Moscow, 238 pp. [in Russian].
- PONOMARENKO, A. G. 1995. The geological history of beetles. In: *Biology, Phylogeny and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson* (Pakaluk J. and Slipinski S.A., editors). Pp. 155-171. Muzeum i Institut Zoologii PAN, Warszawa.
- POTOTSKAYA, V. A. 1981. Morphology and ecology of larvae of the genera *Aplatopterus* Rtt. and *Xylobanus* C. O. Waterh. (Coleoptera, Lycidae). *Entomologischeskoye Obozreniye*, 60: 337-347 [in Russian].

- RILEY, C. V. 1887. On the luminous larviform females of Phengodini. *Entomologist's monthly Magazine*, 24: 148-149.
- ROHDENDORF, B. B. 1957. *Paleontological research in the USSR*. AN SSSR, Moscow, 102 pp. [in Russian].
- ROSENBERG, E. C. 1943. Neue Lyciden-Larven (Beitrag zur Kenntnis der Lebensweise, Entwicklung und Systematic der Käfer. V.). *Entomologiske Meddelelser*, 24: 1-42, 8 tbs.
- SNODGRASS, R. E. 1935. *Principles of Insect Morphology*. McGraw Hill, New York, 667 pp.
- WHEELER, W. C. Whiting, M., Wheeler, Q.D. & Carpenter, J.M. 2001. The phylogeny of the extant hexapod orders. *Cladistics*, 17 (2): 113-169.
- WONG, A. T. C. 1996. A new species of neotenous beetle, *Duliticola hoiseni* (Insecta: Coleoptera: Cantharoidea: Lycidae) from Peninsular Malaysia and Singapore. *Raffles Bulletin of Zoology*, 41 (1): 173-187.