

Insect Evolution in an Amberiferous
and Stone Alphabet

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Proceedings of the 6th International Congress on Fossil
Insects, Arthropods and Amber

Edited by

Dany Azar, Michael S. Engel, Edmund Jarzembowski,
Lars Krogmann, André Nel and Jorge Santiago-Blay



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On the systematic position of the genera *Lepiceroides* gen.n. and *Haplochelus*, with notes on the taxonomy and phylogeny of the Myxophaga (Coleoptera)

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Abstract

Lepiceroides pretiosus gen. et sp. n. (Coleoptera: Lepiceridae), which is closely related to the recent species of *Lepicerus* Motschusky, 1855, is described from Lower Cretaceous Burmese amber. The two genera differ from each other in the shape of the labrum, maxillary palpi, number of antennomeres, elytral sculpture, separation of the meso- and metacoxae and shape of the tibiae. The distinctiveness of the genus *Haplochelus* within the superfamily Lepicerioidea (Myxophaga) and its unique characteristics as related to the order Coleoptera are reiterated. The long and narrow gula, completely fused elytra without the trace of a suture, faint longitudinal costae, 7-segmented antennae, narrowly separated pro-, meso- and metacoxae, long mesoventrite and very short metaventrite justify the retention of the taxon in the family group with the rank of subfamily. Explanations for the wide family diversification of this group are presented. Phylogenetic scenarios regarding the age and origin of the Myxophaga are proposed.

Keywords

Myxophaga; Lepiceridae; new genus; new species; phylogeny; fossil record; Lower Cretaceous; Burmese amber

Introduction

The Myxophaga is a small isolated group proposed comparatively recently (Crowson, 1955) and over the past decades it was a choice topic for systematic and morphological studies. The fossil members of this group were described in the last decade from the Lower Cretaceous Burmese amber (Kirejtshuk & Poinar 2006; Kirejtshuk 2009) and from Liaoning

(Cai et al. 2012). Very recently some extinct families were included in this group (Bouchard et al. 2011) and some hypotheses were proposed regarding its “phylogeny” (Beutel 1999, 2005; Ge et al. 2010, among others). Nevertheless the fossil record of this group is still too insufficient to make reliable phylogenetic reconstructions. In this paper a new genus closely related to the recent *Lepicerus* Motschusky, 1855 is described and some comments on the evolutionary and systematic significance of the Myxophaga are presented.

Materials and Methods

The Burmese amber piece was obtained from a mine first excavated in 2001, at Hukawng Valley, southwest of Maingkhwan in Kachin State (26°20' N, 96°36' E) in Burma (Myanmar). This new amber site, known as the Noiye Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian, on the basis of paleontological evidence (Cruckshank & Ko 2003), placing the age at 97 to 110 mya. Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noiye Bum 2001 Summit site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007). For study ordinary optic equipment was used, in particular the stereomicroscope Leica MZ 16.0 in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg; stereomicroscope Olympus SCX9 and inverted microscope Olympus CK 40 in the Muséum National d'Histoire Naturelle Museum; and also stereomicroscope Nikon SMZ-10 in the Oregon State University, Corvallis.

Description

Family Lepiceridae Hinton, 1936

Subfamily Lepicerinae Hinton, 1936

Genus *Lepiceroides* gen. nov.

Type species

Lepiceroides pretiosus sp. n.

Etymology

The name of the new genus is formed from the generic name “*Lepicerus*” and the Greek “*oides*” (“οιδεζ”, like resembling similar to). The gender is masculine.

Diagnosis

The new genus differs from other members of the subfamily (*Lepicerus*) in possessing a very large subquadrangular labrum, rather short maxillary palpi, 5-segmented antennae, narrower prosternal process, four rows of tubercles (not 2–3 carinas) on each elytron, elytral sides without excavations for intermediate legs (but with deep excavations for posterior legs), metacoxae more narrowly separated than mesocoxae and tibiae at least twice as wide as tarsi.

Description

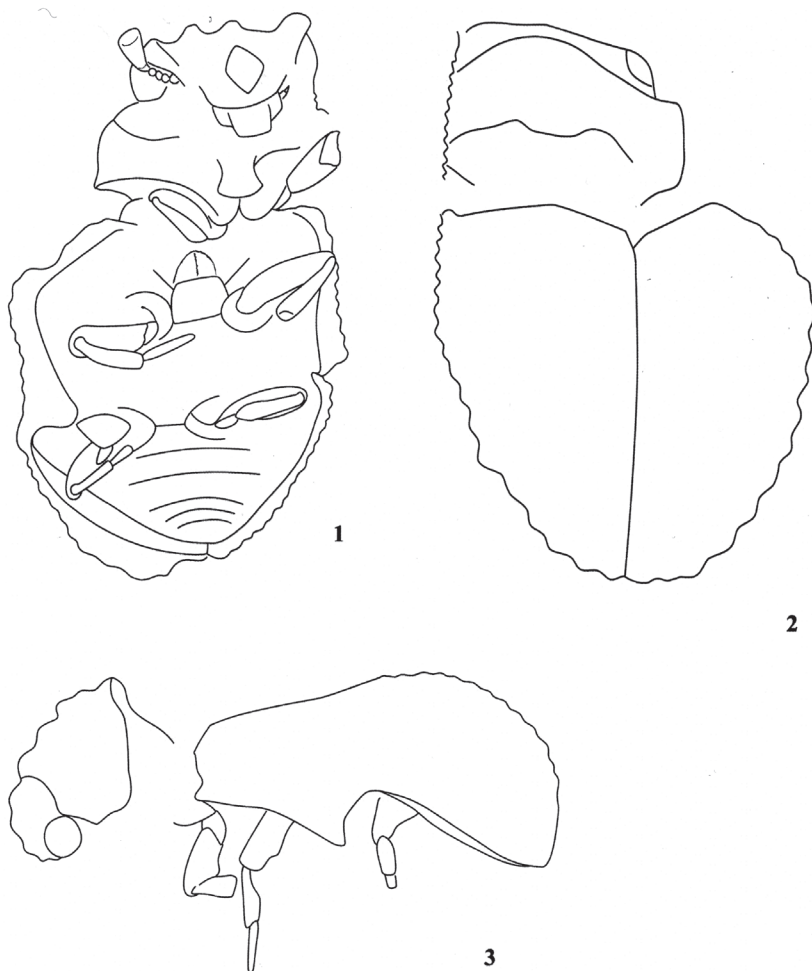
Body small, under 2 mm in length, rather convex dorsally and subflattened to concave ventrally; dorsum with very coarse and slightly irregular sculpture, represented on elytra by distinct tubercles arranged in five rows, without visible pubescence; frons ventrally oriented, rather reduced mouthparts dislocated ventrally and concealed by very large subquadrate labrum with median projection; maxillary palpi very short; antennae five-segmented, with ultimate antennomere subtriangular and widest at subtruncate apex; pronotum with coarse tubercles formed along middle four pairs of paramedian ones; thorax with rather wide prosternal process, moderately long mesoventrite and rather short metaventrite; all coxae moderately large: procoxae rather narrowly separated; mesocoxae more widely separated than metacoxae; legs moderately raised, with distinct trochanter and spinose tibiae, tarsi one-segmented, long and straight, with large terminal, scarcely curved single claw; abdomen with six apparent ventrites; elytra with four rows of coarse tubercles completely covering abdomen; epipleura with deep excisions for posterior legs.

Lepiceroides pretiosus* sp. n. (Figs 1–7)Etymology*

The epithet of the new species means “valuable”, “important”, “precious”.

Material

Holotype in Burmese amber, deposited in the Poinar amber collection (Accession No. B-C-46) maintained at Oregon State University. The specimen is in a small elongate and irregular piece of amber together with many very small gas bubbles and fragments of dark organic matter. It was

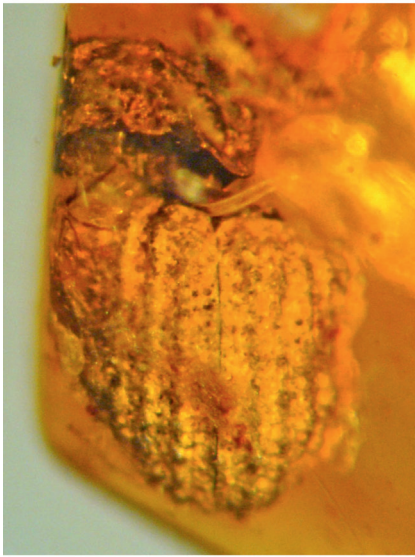


Figures 1–3. *Lepiceroides pretiosus* gen. et sp. n., holotype, body. (1) Ventral view, (2) dorsal view, (3) lateral view. Length of specimen 1.4 mm.

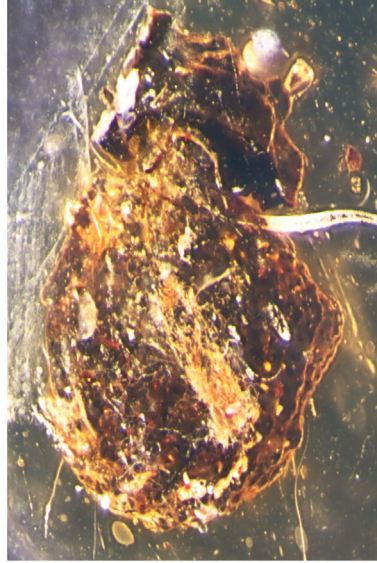
subsequently placed in Canada balsam and mounted between two square microscope slides. It is difficult to study because of its position in the amber and its dark and somewhat deformed body.

Type locality

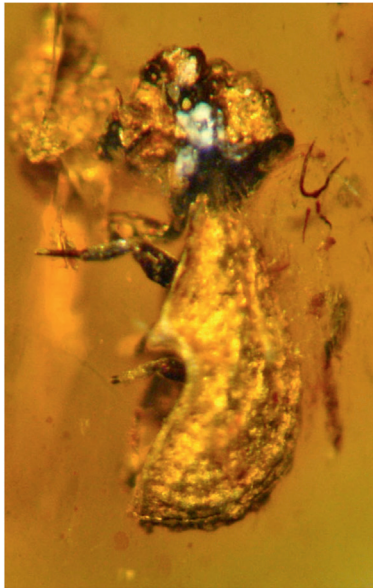
Lignitic seams in sandstone-limestone deposits in the Hukawng Valley, Myanmar (Burma).



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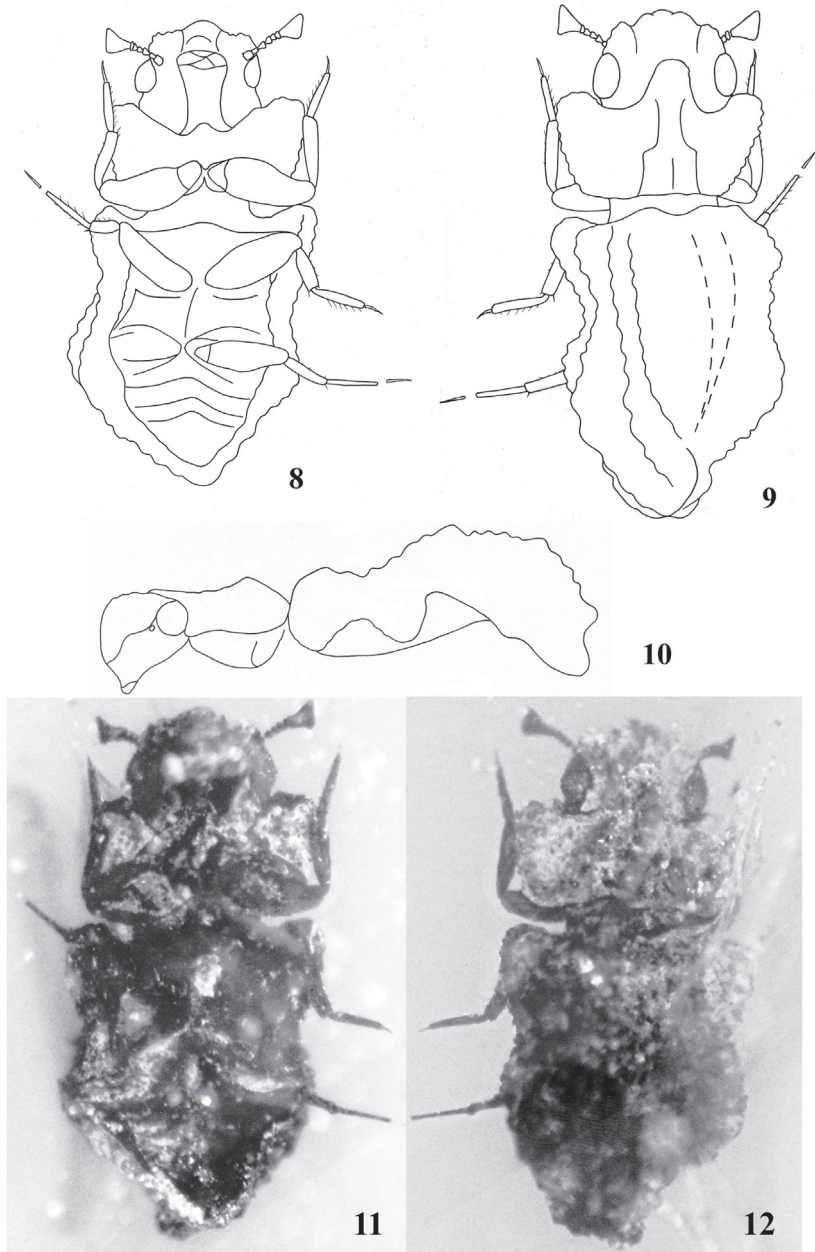


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Figures 4–7. *Lepiceroides pretiosus* gen. et sp. n., holotype, body. (4–5) Dorsal view, (6) lateral view, (7) ventral view. Figures 4 and 6 made on stereomicroscope Nikon SMZ-10; figures 5 and 7 made on stereomicroscope Leica MZ 16.o. Length of specimen 1.4 mm.



Figures 8–12. *Haplochelus georissoides*, holotype, body. (8, 11) Ventral view, (9, 12) dorsal view, (10) lateral view. Figures 11 and 12 made on stereomicroscope Nikon SMZ-10. Length of specimen 1.4 mm (Figures 8–10 modified from Kirejtshuk & Poinar 2006).

Description

Length 1.4, width 0.7, height nearly 0.3 mm (with greatest height at distal third of elytra); elongate-oval, moderately convex dorsally and subflattened to concave ventrally; subunicolourous dark brown with lighter (partly nearly yellowish) appendages; dull; integument without trace of punctations; dorsum with extremely coarse sculpture but mostly without pubescence; underside with sparse and very short, recumbent and nearly inconspicuous hairs.

Head transverse, turned ventrally with very short underside behind mouth orifice; mouthparts directed ventrad and concealed by large subquadrate labrum (about third as wide as head) with median projection; only short left penultimate and ultimate maxillary palpomeres exposed from under labrum; antennae with five antennomeres, four of them suboval and approximately of equal length, antennomere 5 (club) nearly as long as previous antennomeres combined.

Pronotum strongly transverse, apparently subparallel-sided, rather convex medially with four pairs of paramedian tubercles and very widely excavated sides; both anterior and posterior angles widely rounded; anterior edge bisinuate. Prosternum very short, with very short, wide subtruncate process at apex. Mesoventrite with a median plate in distal half and a deep concavity divided by a sharp median carina in anterior half. Procoxae not visible. Scutellum not visible. Elytra convex, each with four longitudinal rows of tubercles; not explanate at sides. Epipleura appearing as stripe with deep excavations for posterior legs. Abdomen apparently with six ventrites; ventrites 1–3 and hypopygidium comparable in length; ventrites 4 and 5 much shorter; hypopygidium widely rounded at apex.

Tibiae rather wide (somewhat narrower than femora) and slightly dorsoventrally compressed and sub-parallel sided, apparently widened at base along inner edge. Femora rather robust and apparently of usual shape (probably thickest and widest at the middle), although their apices apparently rather wide. Single tarsomere of each leg very long and subcylindrical, gradually narrowing apically, unique claw of each leg very slightly curved (approximately one third as long as tarsomere).

Discussion

Systematic placement and phylogenetic position were discussed by many coleopterists, and recently Beutel (1999) made his phylogenetic analysis for the recent representatives of the “suborder” Myxophaga.

Kirejtshuk & Poinar (2006) proposed a new family Haplochelidae for for the Cretaceous *Haplochelus*. Ge et al. (2010) attempted to “re-evaluate” the phylogenetic attempt of Beutel (loc. cit.), and concluded that *Haplochelus* should be transferred to the family Lepiceridae. However certain significant features of this genus, which separate *Haplochelus* from its closest relative (*Lepicerus* Motschusky, 1855), were not taken into consideration by Ge et al., since they were omitted from their matrix. Other characters were erroneously coded, i.e., characters 21 (“moderately broad” prosternal process for (sub) contiguous procoxae of *Haplochelus*, which are not covered or separated by a process at all), 27 (“broadly separated” for (sub) contiguous mesocoxae), or coded without evidence, i.e., 33 (metacoxal plates in *Haplochelus*). As a result, the list of characters used by Ge et al. (2010) did not include any features of *Haplochelus* that differ from other groups of Myxophaga. Therewith the characters 21 do not take into consideration that the procoxae of *Lepicerus* are covered by prosternal process as in *Lepiceroides pretiosus* gen. et sp. nov. Using this matrix, the authors concluded that the distinctness between these genera is not great enough to regard them as separate families. Their decision is not “objective” in the cladistic sense.

Both members of the Myxophaga described from Burmese amber previously, *Haplochelus georissoides* Kirejtshuk & Poinar, 2006 and *Burmasporum rossi* Kirejtshuk, 2009 (the latter not included in the matrix or considered by Ge et al. 2010), and also *Lepiceroides pretiosus* sp. et gen. n., have a characteristic small body size (0.8–1.4 mm long) and rather unique features that separate them from their probable recent relatives, although *Lepiceroides* gen. n. is less distinct from its recent close relatives. *Haplochelus* Kirejtshuk & Poinar, 2006 has completely fused elytra without the trace of a suture and *Burmasporum* Kirejtshuk, 2009, in contrast to other members of the “suborder” Myxophaga, possesses the ability for the prothoracic segment and head to move downwards. These apomorphic characters have different interpretations for taxonomic and phylogenetic analyses. Transformation of the thorax, which makes it possible to roll the prothoracic segment, occurs not infrequently in different polyphagan lineages. This feature is certainly not as significant as the complete fusion of the elytra, which causes crucial transformations of the thoracic sclerites, changing the type of movement and probably the physiology of *Haplochelus*. While *Burmasporum* was placed in a family with its closest relative (*Sphaerius* Waltl, 1838), a separate family was erected for *Haplochelus*. However, the description of *Lepiceroides* gen. n. that is close to the recent *Lepicerus* calls for a revision of the rank of the latter taxon.

Haplochelus (Figs 8–12) differs from the recent lepicerids in the following characters: long and narrow gula; completely fused elytra (strongly excavate medially in the anterior 2/3 and without the trace of a suture); faint longitudinal costae; seven-segmented antennae; narrowly separated to (sub) contiguous coxae in each pair; very long mesoventrite and very short metaventrite (metaventrite shorter than mesoventrite). Also, the fused elytra are strongly transformed dorsally in the apterous *Haplochelus* (concave in the anterior part) and along the epipleura (very deep excisions for movement of intermediate and posterior legs), while the known recent representatives of *Lepicerus* have moderately developed posterior wings and normal shaped elytra, although with shallow depressions on the epipleura for reception of the femora. The deeply excised elytral sides in *Haplochelus georissoides* indicate great restrictions in movement of the intermediate and posterior legs, the coxae of which approach each other. The rather unique character of this species is the very sharp, polished median ridge in the apical forth of the elytra. Besides, the very deeply excavate gula clearly visible in the holotype of *H. georissoides* could be a sequence retraction during fossilization causing a certain deformation of some body sclerites. However, the remaining characters are suitable for diagnostics. All these peculiarities provide sound evidence for the erection of a separate family. In addition, these features suggest that the Cretaceous *Haplochelus* is certainly much more specialized than the recent *Lepicerus*, which contains more plesiomorphic characters than the extinct genus. It would appear that *Lepicerus* is closer to the common ancestor than to the Cretaceous genus. In conclusion, differences between the *Lepicerus-Haplochelus* generic lineages are quite significant, which is why they could be treated in separate, but closely related families.

The structural peculiarities of the united *Lepicerus-Lepiceroides-Haplochelus* lineage are also significant (one-segmented tarsi with a single claw; head with vertical frons; mouthparts dislocated ventrally; ultimate antennomere much larger than preceding ones, subtriangularly enlarged and abrupt apically; pronotum widened anteriorly; dorsum coarsely sculptured and without distinct punctation, etc.). The synopsis of these three genera makes them rather distinct among the known Myxophaga. On the cladogram presented by Ge et al. (2010), the uniqueness of this lineage in the configuration of the Myxophaga is rather clear and supported by many characters. This cladogram agrees with the synopsis specified in the description of *Haplochelus* (Kirejtshuk & Poinar 2006) and supports the separation of the “suborder” into two superfamilies.

The difficulties encountered when comparing extant groups with extinct ones are well known. Many diagnostic characters that are stable in a particular group are frequently not accessible in fossils. As a result researchers need to make a predictable interpretation regarding the presence or absence of established characters in the fossil and decide if they are similar to those of its recent relatives. Not fulfilling this action can result in conclusions without rational explanations.

The time of the origin and main diversification of the Myxophaga is still very unclear. The only three fossil myxophagan species were described from the Lower Cretaceous of Liaoning (Northeastern China, Yixian Formation) and Burmese amber (see above). Some other compression fossils of different ages may belong to this group, but they remain undescribed because of difficulties in interpreting their characters. Even in the case of *Hydroscapha jeholensis* Cai, Short & Huang, 2012, many characters are not discernible enough for a clear interpretation to be made. Nevertheless the forms described from Burmese amber scarcely can give rise to doubt. If we recognize the age of Burmese amber as 100–105 Myr (Cruickshank & Ko 2003) and the lower boundary of the Cretaceous as 135 Myr, we might surmise that 30 Myr would be long enough for this group to diverge. On the other hand, the Myxophaga certainly should have some ancient ancestors. The long dialogues on whether Myxophaga aligns with Adephaga or Polyphaga based on structural similarities are well known. They began with Crowson (1955) and continue to the present based mostly on morphological but recently also on molecular comparisons. Analyses of different nucleotides (mitochondrial or ribosomal) led even to a greater antipathy; not only Adephaga (Caterino et al. 2002, among others) and Polyphaga (Hughes et al. 2005, among others), but also Archostemata (Hunt et al. 2007, among others) are mentioned as the closest clades to Myxophaga. Some thoughts on this subject were expressed by Beutel (including Beutel 1999) and also in the description of *Haplochelus* (Kirejtshuk & Poinar 2006). Ponomarenko (2001) considered that the recent groups of Myxophaga could have arisen from within the schizophoroid lineage of Archostemata sensu Ponomarenko 1969. This is a general idea which needs to be documented by fossils. Beutel (2005) concluded that the Mesozoic family Catiniidae can be linked with Myxophaga because they are “relatively small body-sized” groups (indeed the known beetles in this schizophoroid family are longer than 5.0 mm and often reaching 15.0 mm). The further supposition of Ge et al. (2010) on the Jurassic root of the family Lepiceridae and Triassic origin of the “suborder”

is not explained in the paper and is probably based on data from comparison of nucleotide sequences. It certainly requires further verification, including direct fossil evidence.

The adults of Myxophaga exhibit a tendency toward miniaturization with a simplification of some structures. This could be due to an incomplete development of basic features or from a pedomorphic transformation, such as a reduced number of antennomeres, unilobed maxilla, reduced number of tarsomeres, shortening of the elytra, etc. This tendency seemed to affect different organs in various related groups that maintain a rather similar bionomy (inhabiting moist substrates at banks of running water, spray zone of waterfalls or hydropetric habits, with an excepted likely terrestrial habitat for *Sphaerius africanus* Endrödy-Younga, 1997). This secondary simplification results in a comparatively rapid reduction of most recently acquired structures and, as a result, traces of common relatedness would manifest rather obscurely. This could explain why such a small group in number of species with a similar bionomy as the Myxophaga demonstrates a comparatively wide family diversification. The very wide transcontinental distribution of species of the genera *Sphaerius* and *Hydroscapha* Leconte, 1874 seems to indicate that these groups were maintaining their structural unity during a rather long time, which could support the above scenario.

Another possible explanation is that the "suborder" could be rather old in origin with the recent fauna representing only the remains of an earlier biodiversity after various extinction events. However, there are some problems with this supposition. First of all, no true Myxophaga are known earlier than the age of Lionic Yixian Formation and Burmese amber. If this was originally a diverse group one would expect earlier forms to occur under a wider range of ecological conditions. However all recent members of the "suborder" with known bionomy show a striking similar mode of life and habits, even though they vary rather greatly in structure. The occurrence of most myxophagans in Burmese amber could have some ecological explanation, however, they need a detailed analysis of other components of the Burmese amber biota.

A compromise hypothesis is also possible. The Myxophaga could be a rather old group which was initially highly specialized for occupying ecological zones similar to those inhabited by recent representatives. Inhabitants of such environments are not suitable for fossilization and therefore, the fossil record of Myxophaga is greatly minimized. This ecological specialization over time resulted in structural diversification

leading to a gradual miniaturization of group members. While the body size of Cretaceous Myxophaga is comparable to recent members, we propose that larger forms were more susceptible to various extinction events. Each of the above hypotheses have merit, however they all require more evidence, especially from additional fossil material.

The Myxophaga was proposed by Crowson (1955) for a few recent families. After this proposal, Forbes (1957) pointed out some serious contradictions in this interpretation, which are based mainly on the hindwing venation and folding, and which gave reasons for alternative interpretations. Ponomarenko (1973, 2002) insisted that it was impossible to separate the Myxophaga from other Archostemata, including extinct groups, except for differences in larvae of recent representatives (not available in fossils), and regarded these recent families as a superfamily Microsporoidea in the infraorder Schizophoromorpha (Ponomarenko 2002; Kirejtshuk & Ponomarenko 2012). In most current publications the Myxophaga are frequently treated sensu Crowson with four families represented in the recent fauna or also with some extinct families from Archostemata (Bouchard et al. 2011). In the latter case, the “suborder Myxophaga” seems to lose its significance in the context of phylogeny-based systematics, because at the moment, the extrapolation of the “suborder” features of “Myxophaga” in the initial sense with extinct groups similar to other Archostemata, seems premature (Kirejtshuk et al. in press). A correct interpretation of the subordinal characteristics will be possible only after a revision of the basal Palaeozoic groups of beetles.

Thus, the proposal for *Haplochelus* as a separate taxon of family group with a separate superfamily Lepiceroidea for its relatives is justified, although for equilibrium and stability, *Haplochelus* is regarded here as a separate subfamily of the Lepiceridae. Our interpretation of the “Myxophaga” is shown in the following key.

Key to families and subfamilies of “Myxophaga”

1. Tarsi one-segmented, each segment bearing one claw; mouthparts oriented ventrally, ultimate antennomere much larger than preceding ones, subtriangular and abrupt apically; pronotum widened anteriorly; dorsum coarsely sculptured and without distinct punctation.....superfamily Lepiceroidea.....(Lepiceridae Hinton, 1936)....2
- Tarsi three- or four-segmented, each terminal segment bearing two claws; mouthparts oriented apically; ultimate antennomere of

- various shapes, but never much larger than preceding ones, never subtriangular or abrupt apically; pronotum widest at base and more or less gradually narrowing anteriorly; dorsum variable in sculpture and punctation.....superfamily Sphaerioidea.....3
- 2 (1). Elytra with distinct suture and distinct longitudinal costae; scutellum clearly exposed; gular sutures widely separated; protrochanter rather transverse and moderately developed; antennae 4–5-segmented; prosternal process rather wide, separating procoxae; meso- and metacoxae moderately separated; mesoventrite moderately short and markedly shorter than metaventrite; pronotum with distinct top of anterior and posterior angles. Lepicerinae sensu str.
- Elytra completely fused, without trace of suture; without longitudinal costae (except for a rather sharp ridge dislodged elytral suture at distal third); scutellum not exposed; gular sutures rather narrowly separated; protrochanter narrow and rather long; antennae seven-segmented; procoxae not separated by prosternal process; meso- and metacoxae narrowly separated to (sub) contiguous; mesoventrite longer than metaventrite; pronotum with rounded anterior and posterior angles Haplochelinae Kirejtshuk & Poinar, 2006, stat. nov.
- 3 (1). Tarsi 4–5 segmented; metacoxae without femoral plates; abdomen with 4–5 ventrites; elytra with longitudinal furrows (recent forms in Western Hemisphere) or without (recent forms in South Africa and Eastern South Asia); legs comparatively long with rather narrow subparallel-sided tibiae; antennae 9- or 11-segmented with urn-shaped structure of antennomeres 1 and 2.....Torridincolidae Steffan, 19644
- Tarsi three-segmented; metacoxae with femoral plates; abdomen with three or 6–7 ventrites; elytra without longitudinal furrows; legs not long with somewhat dilated tibiae; antennae 5–11-segmented but never with urn-shaped structure of antennomeres 1 and 2.....5
- 4 (3). Antennae nine-segmented; body contracted between pronotum and elytra; elytra with serial punctation; dorsum and underside bare; integument with extensive sculptural elements Torridincolinae sensu str.
- Antennae 11-segmented; body regularly oval; elytra without serial punctation; dorsum and underside finely pubescent; integument without pronounced sculptural elements Deleveinae Endrödy-Younga, 1997

- 5 (3). Abdomen with three ventrites; metacoxae oblique and contiguous; elytra completely covering abdomen; antennae 11- segmented with 3–4-segmented club; posterior wings with “oblongum” Sphaeriusidae Erichson, 1845
- Abdomen with six ventrites; metacoxae transversely disposed and more or less separated; elytra not complete and leaving apex of abdomen uncovered; antennae 5–8 segmented with one-segmented club; posterior wings without “oblongum”.....Hydroscaphidae LeConte, 1874

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