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Keywords: *Lepiceridae*, *Spheriusidae*, *Torridincolidae*, *Triamixinae*, *Leehermaniinae*, evolutionary history, new subfamily, new genus, new species, new synonymy.

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New Representative of the Family Hydroscaphidae from Tunguska Basin, the Boundary of the Permian and Triassic (Coleoptera, Myxophaga) with Review on Myxophagan Fossil Records

Alexander G. Kirejtshuk ^α, Alexander A. Prokin ^σ & Alexander G. Ponomarenko ^ρ

Abstract- *Palaescapha tunguskaensis* gen. et sp. nov., the oldest representative of the family Hydroscaphidae, is described from the Tunguska Basin in Siberia, dated from the boundary of the Permian and Triassic. It is assigned to the subfamily Triamyxinae, stat. nov. New diagnoses of the Hydroscaphidae and Triamyxinae are proposed. The new subfamily Leehermaniinae subfam. nov. (type genus *Leehermania*) is erected. The fossil record of the suborder Myxophaga is reviewed and revised with some taxonomic notes and synonymy of some generic and species names in the family Lepiceridae, known from Burmese amber. Different aspects of the evolutionary history of this suborder are discussed. A synonymy of *Haplochelus* and *Lepiceratus* is proposed.

Keywords: *Lepiceridae*, *Spheriusidae*, *Torridincolidae*, *Triamyxinae*, *Leehermaniinae*, *evolutionary history*, *new subfamily*, *new genus*, *new species*, *new synonymy*.

I. INTRODUCTION

Like other myxophagan families, the Hydroscaphidae is a relatively small group in the Recent fauna, and it seems to be yet poorly known in fossils. The extant hydroscaphids were reviewed thanks to the efforts of many colleagues [4, 7, 9, 10, 23, 24, 25, 27, 28, 29, 35, 36, 37, 38, 39, 42, 45, 46, 47, etc.]. It currently comprises four genera and nearly 40 species [47], while the modern myxophagans include about 120 species in four families with apparently ancient origins. Recently one hydroscaphid specimen was found in materials in sediments from Tunguska Basin, Krasnoyarsky Krai (tentatively dated around the boundary between the Permian and Triassic). The suborder Myxophaga *sensu stricto* has only a few fossil

records [3, 4, 8, 9, 12, 13, 15, 16, 18, 19, 26, 34], which need to be reviewed and discussed to clarify the composition of this group in the past. The paper is aimed to describe the oldest fossil myxophagan representative (*Palaescapha tunguskaensis* gen. et sp. nov.), summarize the available data on the current fossil record of the myxophagans, and provide them with some essential comments, including the proposal of a new subfamily Leehermaniinae subfam. nov. (type genus *Leehermania* Chatzimanolis, Grimaldi, Engel et Fraser, 2012) [3], and a subfamily state for Triamyxidae Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg et Niedźwiedzki, 2021 (Triamyxinae stat. nov.) [26].

The suborder Myxophaga *sensu stricto* was proposed by Crowson [4] only for the groups from the Recent fauna with some characters similar to those in the suborder Archostemata (mostly apparently plesiomorphic), in contrast to others which are shared by both myxophagans and polyphagans and seem to be more derivative but probably homoplastic. The recent comprehensive studies of fossil beetles revealed close relations between the recent myxophagan families and extinct archostematan groups of the infraorder Schizophoriformia Kirejtshuk, 1991 [14] (=Schizophorimorpha, Ponomarenko, 2001 [30]) [32]. In some recent publications both these groups are sometimes regarded together in the suborder Myxophaga *sensu lato* (e.g., [1, 47]; etc.). The authors of this paper consider that such a joining remains still not reasonable and prefer to interpret them in the traditional way, viz. separating an archostematan infraorder Schizophoriformia from a suborder Myxophaga *sensu stricto*.

II. MATERIAL AND METHODS

The specimen examined was buried in volcanic rock and partially replaced by silica. As a result, the beetle remains maintains a three-dimensional appearance. This circumstance explains its comparatively good preservation. This fossil remains is one of two insects, beetle and leaf-hopper [44] found in

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Untuun River outcrop. There is no findings of similar beetles among the oryctocenoses of other volcanogenic localities of the Siberian (including Tunguska) traps. The many kilometer thickness of traps could have been accumulated over a short time and consist of a sequence of explosive thermal tuffs and a sequence of erupted basaltic lavas. All crustaceans, insects, fishes, and tetrapods from these localities belong to the first sequence of the traps. The thermal effect of lavas on coals and carbonates of the Tunguska syncline probably led to the accumulation of atmospheric methane and carbon oxides, which led to the thermal maximum in the middle of the Induan time [50]. If these assumptions are correct, the temperature maximum has fallen at the end of the Induan. Therefore, the Permian-Triassic boundary on the Tunguska should be placed on the outpouring of basalts. In this case, all locations of fossil organisms on the Tunguska traps should be considered as early Triassic and Induan, as was usually treated before with reference to the character of their fauna and flora, and not Permian as suggested by Sadovnikov [40, 41].

The specimen under description was examined by A.G. Ponomarenko and A.A. Prokin using a Leica M16 light stereomicroscope with a Leica DFC420 digital camera and an attached Tescan Vega XMU scanning electron microscope. The line drawing was prepared using Adobe Photoshop CS3. Some additional fossil and recent specimens from the collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow), and Muséum national d'Histoire naturelle (Paris) were studied for comparison of the specimen under description. Photographs of different focal depths were combined using Helicon Focus 5.1.28. Line drawing was prepared with the Autodesk AutoCAD 2015 software.

III. SYSTEMATIC PALEONTOLOGY

Order Coleoptera Linnaeus, 1758

Suborder Myxophaga Crowson, 1955 [4]

Family Hydroscaphidae Le Conte, 1874 [22]

Remarks: This family was under the attention of many researches (see above); however, the current review of available myxophagan fossils forces us to recompile an emended diagnosis for this family.

Diagnosis (adults): Body small and fusiform, more or less gently narrowing to abdominal apex; usually dark and pubescent. Head large, wide and short, prognathous to hypognathous; eyes usually large, not protruding; antennae 5-11-segmented, usually clubbed; labrum separated from frons (clypeus); ultimate maxillary palpomere small, subulate; ultimate labial palpomere small and narrowing apically; mentum very

small to relatively large. Prothorax rather short to moderately long; propleura reaching anterior edge of prothorax; prosternum relatively short and with short and pointed process; procoxal cavities transversely oval to transverse; procoxae with exposed trochantin. Mesothorax short or moderately long, with depressions for receipt base of prolegs; mesocoxal cavities widely to narrowly separated, externally opened; mesocoxae oval. Metathorax usually moderately long; metepisterna moderately widened anteriorly and well exposed; metaventrite without trace of sutures or with expressed premetacoxal sutures; metacoxae widely separated to sub (contiguous), usually short and with more or less raised plates or without them. Abdomen usually with six ventrites either rarely with five (probably in females) or seven ventrites, ventrite 1 longest (when all following segments of similar structure); 1-2 terminal segments subconical and very long. Elytra shortened and transversely truncate at apex or slightly shortened and subacute at apices; hind wing without *oblongum*, with reduced anal field and fringed along edge. Legs moderately long; trochanters elongate; femora of usual shape; tibiae relatively narrow to moderately wide or rarely strongly dilate; three simple tarsomeres.

Subfamily Triamixinae Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg et Niedźwiedzki, 2021 [26], stat nov.

Type genus. *Triamixa* Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg et Niedźwiedzki, 2021 [26].

Remarks: The taxon 'Triamixidae' was proposed as a separate family among the suborder Myxophaga [26], based on characters from the list compiled by Lawrence et al. [20] and thanks to computer software for producing cladograms interpreted as follows: 'Bayesian analyses of Coleoptera and Myxophaga datasets with constrained molecular topology suggest a sister group relationship with the entire modern Myxophaga. Maximum parsimony analyses place it either in an unresolved basal polytomy (analyses with constrained molecular topology...) or as sister to Hydroscaphidae (unconstrained analyses)'. The character matrix adopted by Qvarnström et al. [26] for analyses and determination of the placement of the studied type specimens of the fossil species contain 77 characters extracted from the set of 359 characters elaborated and defined for modern species [21]. Qvarnström et al. [26] could not obtain adequate definitions of characters to compare fossil representatives with extant myxophagans. Besides, the latter researchers did not provide their description with a proper family diagnosis, and they published only some comparison ('differentiated diagnosis') after the formalization of character definition by Lawrence et al. [21] and 'table S1' with 'family' diagnosis and comparison with other groups of the suborder Myxophaga *sensu stricto*. The new

comparison of myxophagan fossils allows us to join two fossil genera (*Triamyxa* and *Palaeoscapha* gen. nov.). The newly defined diagnostic group characters here revised gives a possibility to generate a new emended diagnosis for this suprageneric taxon with a new rank (subfamily).

Because many characters of this subfamily are poorly visible in the fossil compressions examined, the diagnostic group features of this taxon should be regarded as preliminary. They require further revision after future studies of new additional specimens. The large mentum is previously included in the triamyxid diagnosis, as it was observed in both *Triamyxa* and *Palaeoscapha* gen. nov. The precoxal part of prosternum is rather long in *Triamyxa*, but moderately long in *Palaeoscapha* gen. nov. *Triamyxa* has probably nine antennomeres with a three-segmented club, while the antennae in the holotype of *Palaeoscapha tunguskaensis* sp. nov. are missing. Therefore, the antennal characters in the subfamily diagnosis proposed below should be considered as putative for the new genus. The holotype of *Palaeoscapha tunguskaensis* sp. nov. has six exposed abdominal ventrites, while the specimens of the type series of *Triamyxa coprolithica* Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg et Niedźwiedzki, 2021 [26] have five or six exposed ventrites ([26]: 'females with 5 ventrites and males with 6 ventrites'). The reconstruction of the prothoracic structure made by Qvarnström et al. (2021) [26] needs some essential corrections. It was performed by forming a prothorax from separate pronotum and prosternum and then supposing that intervals between them could be interpreted as a space for propleura (Qvarnström et al., 2021 [26]: Fig. 3, R-T). However, it is visible that the left mesal outline of the pronotum in Fig. 3T is different from the right mesal outline of the same pronotum. Furthermore, if all three pronota (Fig. 3 R-T) are compared, it can be supposed that a narrow interval between the anterior mesal angle of the pronotum and the anterior lateral angle of the prosternum is quite acceptable. If so, the diagnostic character of Hydroscaphidae concerning the propleura reaching the anterior edge of the prothorax can certainly be defined as in the below diagnosis.

Diagnosis: Head apparently prognathous, with eyes located at base moderately arcuately protruding and rather short temples not projecting laterally. Antenna clubbed with apparently nine antennomeres. Mentum very large. Mesothorax comparable in length with prothorax. Metepisterna moderately and almost rectilinearly anteriorly widened, their mesal anterior angle very narrowly separated from outer edge of mesocoxal cavity. Metacoxae very narrowly separated to conjoining and without raised coxal plates. Elytra full to slightly shortened and narrowly transversely truncate or

subacute at apex; epipleura extending behind level of metacoxae. Abdomen with 5-6 ventrites.

Composition: The type genus (*Triamyxa*) and *Palaeoscapha* gen. nov.

Genus *Palaeoscapha* Kirejtshuk, Prokin et Ponomarenko, gen. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:05BBDE9D-F07C-4659-BF0F-B4F83BDBF5DE>

Type species: *Palaeoscapha tunguskaensis* sp. nov.

Etymology: The name of this new genus is formed from the Greek 'παλαιός' = 'palaeo' (ancient, older) plus generic root 'scapha' (*Scapha*, *Hydroscapha*, *Scaphander*, *Scaphydra*). Gender feminine.

Remarks: The new genus is represented only by one species and, therefore, the diagnoses of both somehow coincide and can be used for both species and genus in accordance of the traditional principle '*descriptio generica specifica*'.

Diagnosis: Body somewhat elongate, rather convex ventrally. Head subtriangular, apparently prognathous and truncate at anterior edge of frons (clypeus); gular sutures arcuately divergent; eyes located at base and medium-sized, moderately protruding, from below looking like equally biconvex lens; mandibles apparently slightly raised and apparently arcuate along outer edge; mentum large, widest at base and arcuately narrowing anteriorly; antennal grooves distinct, arcuate and reaching level of posterior edge of mentum; temples arcuately narrowing posteriorly. Prothorax transverse, widest at widely rounded posterior angles, gently narrowing to apparently slightly projecting anterior angles; prosternum very short and subtriangular, prosternal process very narrow, short and nearly sharply acuminate at apex, reaching midlength of procoxae; propleura reaching anterior edge of prothorax, apparently with mesal process extending along anterior edge of procoxae; procoxal cavity large, transverse and seemingly open posteriorly. Procoxae narrowly separated rather than contiguous, subacutely angular laterally and with largely exposed trochantin. Mesepisternum and mesepimeron comparable in size; mesoventrite subequal in length with prothorax; mesocoxal cavity open externally. Mesocoxae large, suboval, comparatively narrowly separated. Metathorax somewhat longer than each of pro- or mesothoraces; metaventrite transverse and with paramedian nearly rectilinear lines from inner edge of mesocoxae to outer edge of metacoxae; premetacoxal sutures slightly expressed and subparallel to anterior edge of metacoxal cavities. Metacoxae relatively short, (sub)contiguous and rectilinearly located along entire posterior edge of metaventrite. Elytra covering abdomen, about 1.5 times as long as wide together and subangular at apex;

epipleura reaching at least level of ventrite 1. Abdomen with six ventrites and comparatively short, only slightly longer than wide; ventrite 1 longest and about twice as long as each of ventrites 2-6; hypopygidium (ventrite 6) short, transverse and widely rounded at apex. Right anterior leg with elongate trochanter, femur of very usual shape and moderately wide; protibia dilated along inner side and relatively wide.

Note: Posterior edges of abdominal ventrites looking like even (without notches).

Comparison: The new genus differs from all hydroscaphids in the dilated protibiae and relatively short abdomen with all ventrites strongly transverse; and also from *Triamyxa* in the larger mentum, smaller eyes, distinct and curved antennal grooves, transverse procoxae, widely rounded posterior angles of the pronotum and subacute elytral apices.

Palaeoscapha tunguskaensis Kirejtshuk, Prokin et Ponomarenko, sp. nov.
Figs 1–3

<http://zoobank.org/urn:lsid:zoobank.org:act:37EAED97-A725-4CCA-8625-AE1F2303B33F>

Type material: Holotype, sex unknown; specimen represented by three-dimensional remains mostly visible from underside, PIN no. 2757/1, demonstrating the most part of its body, although the right part of the pro- and pterothoraces, abdominal apex, and appendages are missing (except for the observable right anterior trochanter, femur and tibia). The pictures of the holotype were published by Kirejtshuk & Ponomarenko[20] and Ponomarenko & Prokin[34].

Type locality and horizon: Russia, Krasnoyarsky Kray, Evenkiysky National Okrug, Tunguska Basin, Untuun River; intertrappean deposits; probably early Triassic or terminal Permian, Induan or ?Tatarian.

Etymology: The epithet of the new species is formed from the name of its type locality (Tunguska).

Description (holotype): Body length 1.5, body width 0.6 mm. Integument mostly smoothed, moderately finely and sparsely punctured (puncture diameter about as great as that of eye facets); prosternum transversely striate, propleura rugose, ventrites partly shagreened. Head subtriangular, apparently prognathous; distance between gular sutures subequal with maximum width of mentum and smaller than that between eyes; mentum slightly transverse, trapezoid, subtruncate at base and slightly arcuately narrowing anteriorly. Precoxal part of prosternum noticeably shorter than mesal length of procoxae. Mesocoxae about twice as widely separately as procoxae. Metaventrite slightly transverse; metepisterna subtriangular; premetacoxal sutures slightly expressed closely subparallel to anterior edge of

metacoxal cavities. Elytral integument seemingly smoothed.

IV. DISCUSSION

The subfamily Hydroscaphinae of the family Hydroscaphidae of the superfamily Sphaeriusoidea was known only after the one compression fossil from the Cretaceous of the Yxian Formation (Huangbanjigou, Liaoning, China) [2]. However, most outlines of the sclerites of this fossil are rather unclear. Therefore, the suborder and family attributions of this taxon should be regarded as rather probable. The distinctness of separated meso- and metacoxae, and also three-segmented tarsi, which are used by the co-authors of this publication as the most essential arguments, can be only traced with some probability. This fossil has not enough characters to be compared with modern genera and to justify its attribution to *Hydroscapha* rather than to any other genus in Hydroscaphidae. Thus, the species name '*jeholensis*' should be attributed rather to a *genus incertus* or cf. *Hydroscapha* than strictly to the latter genus. Nevertheless, the assignment of this species to the subfamily Hydroscaphinae *sensu stricto* is clear enough after the key to the hydroscaphid subfamilies proposed below.

The second hydroscaphid subfamily Triamyxinae stat. nov. is extinct and known only after two findings from the Permian-Triassic boundary (*Palaeoscapha* gen. nov.) and late Triassic (*Triamyxa*). It is characterized in detail in the above diagnosis and remarks, and can be easily identified after the below key to hydroscaphid subfamilies.

The late Triassic *Leehermania prorova* Chatzimanolis, Grimaldi, Engel et Fraser, 2012 [3] from Cascade (near Martinsville, Virginia, USA; Cow Branch Formation, late Carnian – early Norian), originally described as the oldest Staphylinidae [3], was recently re-examined and re-interpreted as a probable 'ancestral' Hydroscaphidae [8]. The type species of this genus seems to have enough characters to put the genus *Leehermania* near the subfamily Triamyxinae stat. nov., but this genus, in contrast to *Triamyxa* and *Palaeoscapha* gen. nov. (see the above remarks to the subfamily Triamyxinae stat. nov.), has a markedly hypognathous head, pronotum widest at the midlength, relatively short meso- and metathoraces, very short elytra with truncate apices and seven abdominal ventrites with comparatively shorter ventrite 1. These mentioned differences make it possible to propose for this genus a new subfamily. Both descriptors [3] and re-examinators [8] of *Leehermania* indicated the presence of about six ventrites (derivatives of sternites III-VIII), while the pictures of lateral view in both publications clearly show seven segments on the underside of the abdomen, although Chatzimanolis et al. [3] pointed out that the 'lateral tergal sclerites of IX becoming tapered to

narrow apex'. It is a rather important point that the specimens of *Leehermania prorova* have two basal ventrites vs. only one as indicated by Fikáček et al. [8] in the drawing-reconstruction of the Fig. 2H of their publication. This misinterpretation can be evident even comparing this reconstruction with the picture of the specimen used for this drawing-reconstruction (Fig. 2G). It is also clearly visible in Chatzimanolis et al. ([3]: Fig. 8). Besides, the abdominal ventrite 1 of *Leehermania prorova* has its length only slightly more significant than the length of the ventrites 2-6 (the proportion of the ventrite 1 is significantly greater in all other known hydroscaphids). The same also concerns the hypognathous head of *Leehermania prorova*, although some modern hydroscaphids could have their heads in hypognathous positions. The abovementioned arguments show a considerable distinctness of the considered species, which is treated as enough ground to propose a new extinct subfamily Leehermaniinae subfam. nov.

The second sphaeriusoid family is Sphaeriusidae Erichson, 1845 [6], also known in the fossil record as a single species from Burmese amber (*Burmasporum rossi*) described by Kirejtshuk [15] with 'generalized' structural features compared to the modern representatives of the family (members of the genus *Sphaerius* Erichson, 1845 [6]). It seems to have many possible plesiomorphic differences from the modern species, namely: the comparatively larger, longer and more projecting head with longer anterior part of frons and longer mouthparts, and distinctly elongate eyes; elongate scape and antennomere 2, small antennomere 3, loose antennal club with four antennomeres; movable and larger pronotum with shorter lateral parts and widely rounded anterior and posterior angles and comparatively long legs with simple and subparallel-sided femora and tibiae.

The super family Lepicerioidea is represented by the single family Lepiceridae in the Recent fauna. Some fossil representatives of this family are known from the Cretaceous Burmese amber. At first, this family had only three fossil specimens from the same source (Burmese amber), and all these specimens are rather poorly preserved for studies, so that some interpretations and conclusions appear rather ambiguous and partly inadequate because of the not quite clearly visible structures examined. On the other hand, the studies of these specimens were rather essential in understanding the myxophagan phylogeny. Therefore, the conclusions obtained after studies of the first two specimens by Kirejtshuk and Poinar [18, 19], and the conclusions obtained after comparison of the third specimen with previous information by Jałoszyński et al. [12] are different. The latter co-authors tried to find a compromise based on the available prior knowledge using the particular matrix of the characters for a cladogram or on an assumption that the facts of fossil

representatives are essentially wrong [12]. As a result, the co-authors of the last publication regarded that all Mesozoic species belong to the same genus, which is also present in the modern fauna (*Lepicerus*). They treated the description of *Haplochelus* as obscure and unworthy. They decided that the diagnostic characters of both fossil genera *Haplochelus* Kirejtshuk et Poinar, 2006 [18] and *Lepichelus* Kirejtshuk et Poinar in Kirejtshuk, 2017 [16] (= *Lepiceroides* Kirejtshuk et Poinar, 2013 [19], non Schedl, 1957 [43]), and also modern *Lepicerus* could be treated as only specific. However, most characters of *Lepichelus pretiosus* (Kirejtshuk et Poinar 2013) [19], comb. nov. and *Lepichelus mumia* (Jałoszyński et Yamamoto in Jałoszyński et al., 2017) [12], comb. nov. are correspondent to each other. Differences between them could be depended upon preservation condition of examined specimens. The situation became more confusing because these co-authors some times declared that '*Lepicerus*' *mumia* has four antennomeres, as, in their opinion, should be in the modern members of *Lepicerus*, but the drawing in their paper (Fig. 2D) clearly shows five antennomeres as should be in *Lepichelus* (indeed according to Fikáček et al. [8] modern members of *Lepicerus* have four antennomeres in one species and five in others). Thus, the contradictions between the opinions of researchers can be proved or disproved only after the examination of additional specimens and further examination of the holotypes. The description of the poorly preserved material of *Lepichelus mumia* comb. nov. does not allow to clearly discriminate it from *L. pretiosus* comb. nov. [16]. The 'curved protarsomere 1' mentioned by Fikáček et al. [8] for *Lepichelus mumia* comb. nov. could be indeed a result of an optic aberration. These co-describers also indicated the following characters of *Lepichelus mumia* comb. nov. diagnostic from '*L. pretiosus*', in the epipleural concavity located behind the middle of the elytra (at the middle in *L. pretiosus*), and in the prosternal process narrowing, and not broadening posteriorly'. Perhaps, the problem of the conspecificity of specimens and synonymy of these species names has to be finally solved after a further re-examination of both type specimens and additional specimens. The extinct Cretaceous species differ from extant ones in the structure of elytral sides and less widely separated metacoxae (almost about comparably separated with mesocoxae). Anyway, it seems to be more correct to consider that the palaeoendemic genus *Lepichelus* comprising two species from Burmese amber are enough separated from the taxon with modern representatives, and it is not reasonable to join the modern and Cretaceous species in one generic taxon or tentatively consider them as two subgenera of the same genus.

The recent publication by Jałoszyński et al. [13], unfortunately, also contains some new wrong

interpretations, but the good illustrations make it possible to solve some central problems in the contradictions and interpretations. In the last paper, the co-authors described the new genus *Lepiceratus* Jałoszyński, Luo, Yamamoto et Beutel, 2020 [13], which indeed completely fits with *Haplochelus* even in the number of antennomeres, the structure of elytra, comparatively narrowly separated all pairs of coxae of the type specimen of the genus type species (*L. ankylosaurus* Jałoszyński, Luo, Yamamoto et Beutel, 2020 [13]). The type species of both genera (*Haplochelus* and *Lepiceratus*) have some differences in the general body outline, different shapes of head and pronotum, eye sizes, presence of the visible discrimen only in *H. georysoides* vs. absence in *L. ankylosaurus*, and some other features, which are better to consider as species differences than generic ones. Even the elytra of the latter species (*L. ankylosaurus*) are distinctly separated only in the artist's reconstruction of *L. ankylosaurus* ([13]; Fig. 1C) but not so distinctly in the photograph (Fig. 1A) and tomography reconstruction (Fig. 2A and 3A). It is thought that the sutural elytral edges can be relatively sharply elevated and firmly closed together to make an impression of the united fused ridge (as in the holotype of *Haplochelus georysoides*). A median depression of the mentum with the sharp outline of this holotype could make an illusion of gular sutures [18], and also a more or less weak median depression is quite characteristic of other lepicerids. Thus, it is reasonable to consider the name *Lepiceratus* as a junior synonym of *Haplochelus*.

Taking into consideration the small body size of all known extant and fossil myxophagans and a small probability of their coming into deposits (tanatocenoses), it can be supposed that the available fossil record of this group is rather scarce among coleopterans in general. Nevertheless, the suborder Myxophaga is rather ancient and originated not later in the Palaeozoic (as suborders Archostemata and Adephaga). D.E. Shcherbakov found one unique tiny disc-like beetle larva in the extensive collection from the Middle Permian (~265 Ma) of Kargala near Orenburg, European Russia (Borissiak Paleontological Institute, Russian Academy of Sciences), whose print demonstrates a considerable similarity to larvae of some modern members of Torridincolidae Steffan, 1964 [49] (superfamily Sphaeriuoidea). The current data on this suborder is not sufficient enough for grounded phylogenetic conclusions. The rather ancient origin of Myxophaga and the scarcity of its fossil record make it impossible to use the current methods to reconstruct its phylogeny. It is thought that the groups of four myxophagan families in the Recent fauna represent only rather separate splinters of the significant diversity of this suborder in the past, although hydroscaphids (and probably something like torridincolid-like larvae) could be present in the Palaeozoic faunas. Other two

myxophagan families (Sphaeriusidae and Lepiceridae) and also true torridincolids with more specialized structural appearance could have the later (Mesozoic) origin (as traced in the current fossil record of the suborder). Nevertheless, many phylogenetic hypotheses after formal analyses of structural and molecular comparisons give a basal placement for the Hydroscaphidae ([8, 26]; etc.), i.e., showing some correspondence with the current fossil record. It is necessary to take into consideration that the result of structural analysis is somehow connected with the more generalized appearance of hydroscaphids (a greater proportion of plesiomorphies in general). At the moment, strict phylogenetic reconstructions are somewhat premature. However, it can be supposed that the phylogeny of this suborder could have a complexity analogous to that of cupedids from the suborder Archostemata. A grounded phylogenetic model will be more probable after getting more data on fossils of various ages and applying the principle of multiple parallelisms [17].

The very conspicuous peculiarity of this suborder was pointed out by Crowson [5] that the myxophagan families have structural and partly bionomically analogous groups among various small polyphagans. In particular, adults of modern Hydroscaphidae, according to the opinion of R.A. Crowson, have many similarities with 'staphylinoids', 'hydrophiloids', and basalmost eucinetids [5]. The lepicerids, in general appearance, resemble elmids [5] or georissids [18]. The species of Sphaeriusidae somehow are reminiscent of polyphagan clambids (Scirtoidea) and cybocephalines (Nitidulidae, Cucujoidea) (see notes on 'Calypotmeridae' in Crowson, 1967 [5]). Thus, in the phylogenetic reconstruction of myxophagans, it would be desirable to take into consideration many aspects of structural convergence, including adaptive and morphogenetic processes.

It can be supposed some kind of association between Palaeozoic and Mesozoic myxophagans and algae, which is somewhat similar to that between the modern representatives of this suborder and their food resource. As another Permian suborder Archostemata with little structural transformations reached nowadays mostly because of the maintenance of ancient lifestyle and habits, modern myxophagans could also have a considerable conservatism in their habitats and diet from the Palaeozoic together with their general appearance, keeping small body-size and simplification of some structures. Modern myxophagans with known bionomy, including hydroscaphids, usually inhabit aquatic to moist environments associated with algal growth [47]. Probably a certain similarity in trophic connections should also be expected in the case of the fossil *Palaeoscapha tunguskaensis* gen. et sp. nov. As to *Triamya coprolithica*, described from coprolite of

dinosaur form *Silesaurus opolensis* from the lacustrine Krasiejów deposits [26], it is thought that this beetle inhabited aquatic and moist environments associated with algal mats (most likely growing at shores of water bodies or floating). Floating mats or their aggregates are known from different Mesozoic localities and proposed as probable habitats for many aquatic insects, including beetles, as well as food resources for vertebrates such as dinosaurs [31, 33, 34].

V. TAXONOMIC CONCLUSIONS

The available data of fossil records on Myxophaga, taking into consideration the above discussion, can be summarized as follows:

Superfamily *Sphaeriuoidea* Erichson, 1845 [6]

Family *Hydroscaphidae* LeConte, 1874 [22]

Subfamily *Hydroscaphinae* LeConte, 1874[22]

- (?) '*Hydroscapha*' *jeholensis* Cai, Short et Huang, 2012 [2] – China, Liaoning Province (Huangbanjigou), Yixian Formation; Lower Cretaceous, Lower Aptian

Subfamily *Triamyxinae* Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg et Niedźwiedzki, 2021 [26], stat. nov.

- *Triamyxa coprolithica* Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg et Niedźwiedzki, 2021 [26] – Krasiejów clay pit (near Ozimek), Upper Silesia, Poland, Upper Triassic
- *Palaeoscapha tunguskaensis* gen. et sp. nov. – Siberia, Tunguska Basin, Untuun; probably early Triassic or terminal Permian, Induan or ?Tatarian

Subfamily *Leehermaniinae* Kirejtshuk, Prokin et Ponomarenko, subfam. nov.

urn:lsid:zoobank.org:act:3B6B5BDD-1CD8-40AC-BFDB-461C76B23842

Type genus *Leehermania prorova* Chatzimanolis, Grimaldi, Engel et Fraser, 2012 [3]

Diagnosis. Head seemingly hypognathous with eyes located at base moderately arcuately protruding and very short temples. Antennae 11-segmented and clubbed. Mesothorax extremely short. Metathorax comparatively short. Metepisterna strongly and almost rectilinearly widened anteriorly, their mesal anterior angle very narrowly separated from outer edge of mesocoxal cavity. Metacoxae seemingly very narrowly separated to conjoining and apparently without raised coxal plates. Elytra somewhat shortened and widely transversely truncate at apex; epipleura seemingly not extending behind level of metacoxae. Abdomen with seven ventrites.

- *Leehermania prorova* Chatzimanolis, Grimaldi, Engel et Fraser, 2012[3] – USA, Virginia, Cascade (near

Martinsville), Cow Branch Formation, Upper Triassic, Upper Carnian/Lower Norian

Family *Sphaeriusidae* Erichson, 1845 [6]

- *Burmasporum rossi* Kirejtshuk 2009 [15] – Myanmar, Burmese amber; Myanmar, Kachin, Hukawng Valley; 'mid'-Cretaceous, Albian/Ceno-manian

Superfamily *Lepicerioidea* Hinton, 1936[11]

Family *Lepiceridae* Hinton, 1936 [11]

- *Lepichelus pretiosus* (Kirejtshuk et Poinar, 2006), comb. nov. [19] [*Lepiceroides*] – Burmese amber; Myanmar, Kachin, Hukawng Valley; 'mid'-Cretaceous, Albian/Cenomanian
- Probable synonym *Lepichelus mumia* (Jaloszynski and Yamamoto, 2017), comb. nov. [12] [*Lepicerus*] – Burmese amber; Myanmar, Kachin, Hukawng Valley; 'mid'-Cretaceous, Albian/Cenomanian
- *Haplochelus georssoides* Kirejtshuk et Poinar, 2006 [18] – Burmese amber; Myanmar, Kachin, Hukawng Valley; 'mid'-Cretaceous, Albian/Cenomanian
- *Haplochelus ankylosaurus* (Jałoszyński, Luo, Yamamoto et Beutel, 2020), comb. nov. [13] [*Lepiceratus* Jałoszyński, Luo, Yamamoto et Beutel, 2020, syn. nov. [13]] – Burmese amber; Myanmar, Kachin, Hukawng Valley; 'mid'-Cretaceous, Albian/Cenomanian.

VI. KEY TO HYDROSCAPHID SUBFAMILIES

1. Elytra long, covering completely or most part of abdomen and subacute at apices; abdomen with five or six ventrites; –metacoxae (sub) contiguous; mentum large; antennae with three-segmented clubTriamyxinae stat. nov.
 - Elytra very short and truncate at apices, leaving 3-4 abdominal segments uncovered; abdomen with six or seven ventrites; – other characters different 2
2. Abdomen with six ventrites; antennae with five or nine antennomeres with ultimate sclub-shaped; metacoxae with coxal plate and clearly separated. Hydroscaphinae *sensu stricto*
 - Abdomen with seven ventrites; antennae with three-segmented club; metacoxae without coxal plate and narrowly separated or (sub) contiguous Leehermaniinae subfam. nov.

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seeking of specimens in the collection, picturing of fossil specimens, information on the larva from Kargala, valuable comments and help in providing the authors of this paper with literature. A. Nel (Muséum national d'Histoire naturelle, Paris) check the manuscript of this paper and made many very valuable comments and recommendations. The authors thank also anonymous reviewers and the editor for criticism of this manuscript during preparation and editing.

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APPENDIX A

After acceptance of this paper (November 23, 2022) two new papers on the fossil members of Sphaeriusidae appeared (December 7, 2022 and January 11, 2023):

1. Fikáček M., Yamamoto S., Matsumoto S., Beutel R.G., and Maddison D.R. (2022). Phylogeny and systematics of Sphaeriusidae (Coleoptera: Myxophaga): minute living fossils with underestimated past and present-day diversity. *Systematic Entomology* 2022,1–17. <https://doi.org/10.1111/syen.12571>
2. Li Y.D., Ślipiński A., Huang D.Y., Cai C.-Y. (2023) New fossils of Sphaeriusidae from mid-Cretaceous Burmese amber revealed by confocal microscopy (Coleoptera: Myxophaga). *Frontier of Earth Science*, 11 January 2023. <https://doi.org/10.3389/feart.2022.901573>

The first paper has a description of the sphaeriusid genus *Bezesporum* Fikáček, Yamamoto, Matsumoto, Beutel et Maddison, 2022 (type species: *Sphaerius minutus* Liang et Jia, 2018 – modern, China, Jiangxi Province, Xiping County) including as two modern species as one fossil *Bezesporum burmiticum*

Fikáček, Yamamoto, Matsumoto, Beutel et Maddison, 2022 from Burmese amber; Myanmar, Kachin, Hukawng Valley; 'mid'-Cretaceous, Albian/Cenomanian. This fossil species is rather different from *Burmasporum rossi* after the diagnosis proposed by Fikáček et al. (2022), however it is quite problematic to compare modern and fossil species because of bad preservation of the latter. The modern and fossil species seem to differ at least by shape of main body sclerites, antennal club, maxillary palpi, and protibiae. Nevertheless, the taxonomic relation between them needs further consideration. In order to avoid confusion analogous with that in lepicerids (see above Discussion) it would be better to indicate fossil species as cf. '*Bezesporum*' *burmiticum*.

The second paper is devoted to descriptions of two sphaeriusid species from Cretaceous Burmese amber. One of them is very similar to modern species of the genus *Sphaerius* Waltl, 1838 and named as *S. martini* Li et Cai, 2023, while another species is different from all other congeners of the sphaeriusid genera and, therefore, it described with proposal a new genus *Crowsonaerius* Li & Cai, 2023 (*C. minutus* Li et Cai, 2023, designated as type species of the latter genus).

These new data increase the number of the known sphaeriusid genera in fossils till four ones originated from the same resource (Burmese amber). These materials and particularly finding of a species assigned by Li et. al. (2023) to the genus of *Sphaerius* known in the Recent fauna support the opinion on probable considerable diversity of this family in the Mesozoic and conservatism of the suborder Myxophaga in general (see the above discussion).

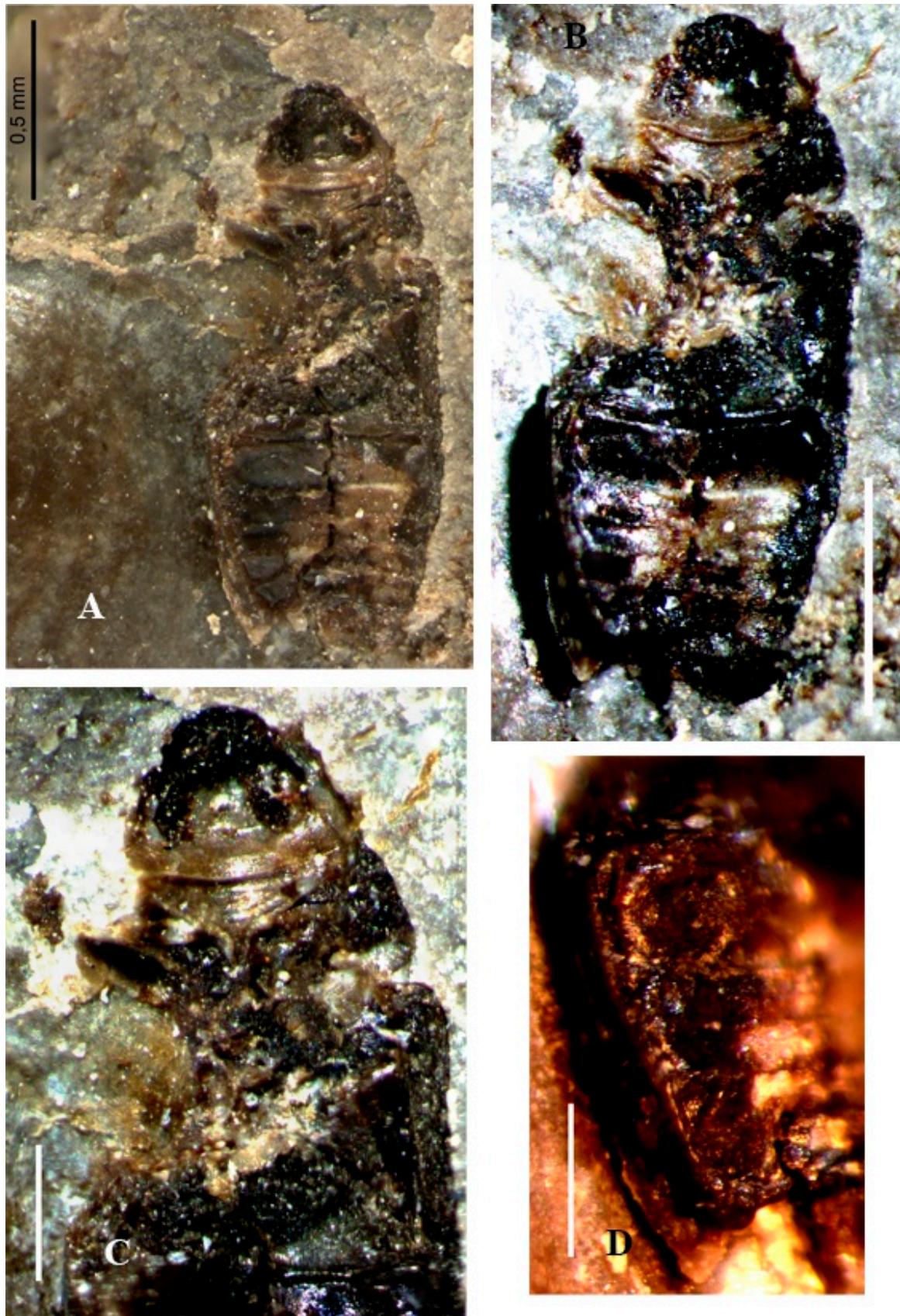


Figure 1: *Palaeoscapha tunguskaensis* gen. et sp. nov., holotype, photographs: A, B – habitus, C – head and thorax, D – abdomen. Scale bar 0.5 mm (A, B), 0.2 mm (C,D).



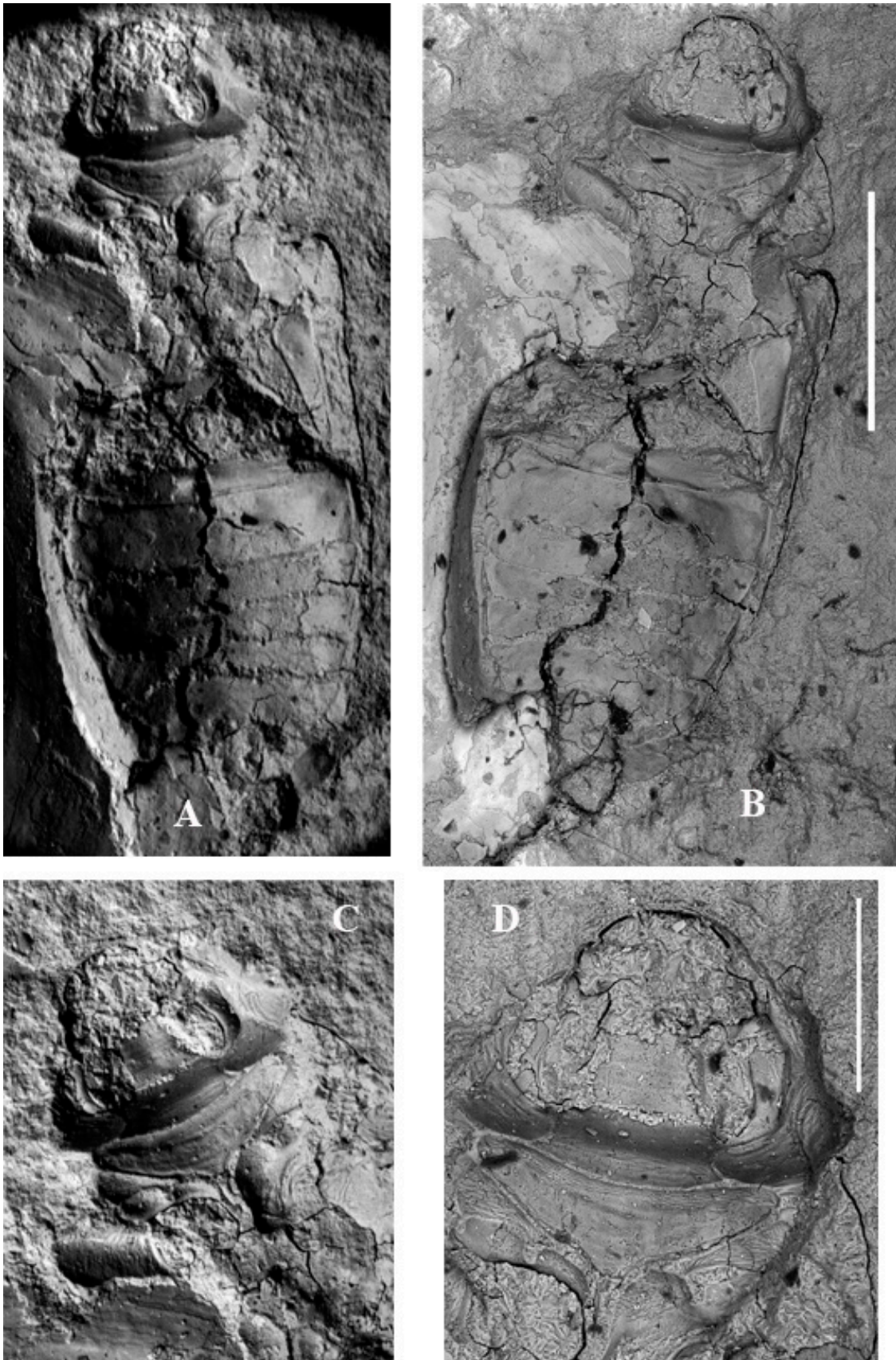


Figure 2: *Palaeoscapha tunguskaensis* gen. et sp. nov., holotype, SEM: A, B – habitus, C, D – head and prosternum. Scale bar 0.5 mm (B), 0.2 mm (D), not for scale (A,C).

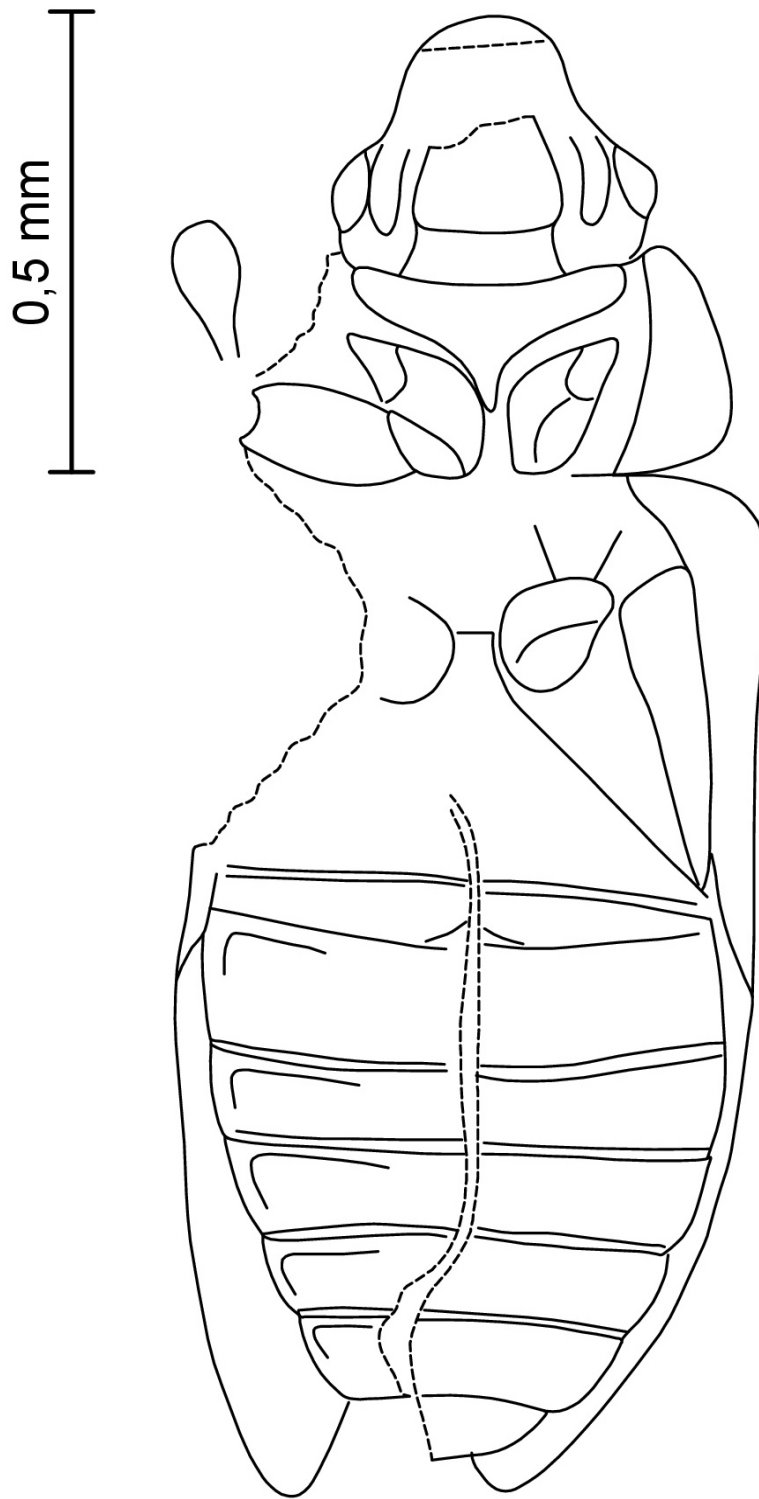


Figure 3: *Palaeoscapha tunguskaensis* gen. et sp. nov.: holotype, habitus, line drawing. Scale bar 0.5 mm.