

Editorial

# The Evolutionary History of the Coleoptera

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**Abstract:** In this Editorial, different aspects of palaeocoleopterological studies and contributions of the issue “The Evolutionary History of the Coleoptera” are discussed.

**Keywords:** classification; problems of taxonomic interpretation of fossils; contributions for studies of palaeoenvironment and faunogenesis

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“Beetles, like other insects, spread quickly and practically simultaneously (in the geological sense), appearing in different parts of the Earth. The differences in dispersal result not from the difficulty to reach a particular location of the Earth, but because of the difficulty to enter an ecosystem already formed. Thus, the evolutionary potential of beetles is quite high, and the study of their ancient representatives is interesting from many points of view; however, it requires much effort and expertise. Unfortunately, a study of the palaeontology of beetles is a much more complicated task than that of Hymenoptera or Diptera. By the structure of the wing of the latter it is nearly always possible to determine to what large taxon it belongs. For the majority of discoveries of isolated elytra of beetles at the present state of knowledge it is impossible to identify the group to which the beetle with these elytra belongs. However there was a period—the Permian except its very end—when the evolution of elytra was the main evolutionary process in beetles.”

Ponomarenko, A.G. Paleontological discoveries of beetles. Available online: [https://www.zin.ru/animalia/coleoptera/rus/paleos\\_0.htm](https://www.zin.ru/animalia/coleoptera/rus/paleos_0.htm) (accessed on March 2003) and [https://www.zin.ru/animalia/coleoptera/eng/paleos\\_0.htm](https://www.zin.ru/animalia/coleoptera/eng/paleos_0.htm) (accessed on March 2003)

The appearance of a great deal of interest and the rapid increase of in data on fossils during recent decades has created a situation in which the addition of new facts has surpassed their conceptualization in terms of general theoretical aspects. On the other hand, many papers appear every year which use fossils to support new evolutionary hypotheses. Thus, the reconstruction and correct interpretation of the fossil record including the taxonomic interpretation of considered fossils have a major significance not only for the classification of these fossils but also for many evolutionary applications. Calibrations with fossils in cladistics and molecular phylogenetic analyses are a good example of the great significance of the correct taxonomic interpretation of fossils. Two recently published phylogenetic hypotheses for beetles were based on the same set of molecular data with slightly different approaches but with different extinct taxa taken for calibrations [1,2]. Both models produced quite different results. Regardless of the discussion on these differences by the relevant researchers it can be imagined what can be expected in the case of a third set of fossils being taken for the next attempt at such modeling. This demonstrates the importance of adequate results in palaeontological research, which can only be ideal reconstructions admitting many gaps. It can be said that the evolutionary history (historical

development) considerably increases the diversity of species and groups available for a consideration replacing the modeling of relationships, based mostly upon the properties of recent insects with knowledge of their potential ancestors.

A correct understanding of the taxonomic and phylogenetic position of fossils for evolutionary interpretation is critical. Frequently, misinterpretations of fossils result in incorrect conclusions of generalizations or phylogenetic models. In particular, it is important to clarify the systematic positions of many fossil taxa described during the 19th and 20th centuries without necessary details being missing in the original descriptions of the considered taxa. For example, some of Martynov's types of fossil beetles available in scientific collections have been redescribed and got a proper interpretation in the series of publications started by Kirejtshuk in this issue. Among other things, some taxa (for example, Martynov's genera *Lithostoma*, *Mesodascila*, *Nitidulina*) remained without re-examinations because of the absence of the type specimens of their type species. Nevertheless, they were widely used by many coleopterists for theoretical applications despite their original problematic identification. Some specimens very similar to the mentioned fossil taxa were found among additional specimens from the Karatau outcrops, and some of them were selected as the potential neotypes which were planned to be redescribed under the framework of this project. Unfortunately, it is impossible to be sure of choosing anything exactly suitable for *Eumolpites jurassicus* Martynov because of the lack of any peculiar character in its structure as indicated in the original description of the latter species. It is necessary to take into consideration that the types of these Martynov's taxa may not be completely lost and deposited in boxes with stones in the A.P.Karpinsky Russian Geological Research Institute (formerly Geological Committee) where they could be occasionally moved as a result of dividing the collection of the mentioned Committee into the collections of the recent Russian Geological Research Institute, the Palaeontological Institute of the Russian Academy of Sciences and Geological Institute of Russian Academy of Sciences. The risk of a necessity of cancelling the neotypes, if the true types are be found, prevents the creation of such neotypes for years.

It is extremely urgent to re-examine most types of the species proposed by P.B. Brodie, A. Bode, T.D.A. Cockerell, C.G.A. Giebel, A. Handlirsch, H. Haupt, O. Heer, C.H.G. Heyden, L.F.J.D. Heyden, F. Meunier, S.H. Scudder, E. Voss, E. Wasmann, H.F. Wickham, F.E. Zeuner, and by many other palaeocoleopterists of the 19th and first half of 20th centuries and also types of species described by some Chinese colleagues of the second half of the last century (first of all, Y.-C. Hong, Q.-B. Lin, D. Ren and J. Zhang) to obtain precise re-descriptions of most of these types. To date, in many cases referring to the classic fossil researchers mentioned these taxa with a more or less hypothetical consideration (because, not infrequently, no reliable opinion could be obtained from the original descriptions at all) is only possible. Both the disuse and unfounded use of many fossil taxa proposed by the classical researchers are not desirable and it would be better to recognize their contributions and clarify the systematic position of the species described by them. The correct understanding of these described fossils is as important as the finding and description of new ones. Frequently the imprints of beetles on stones or their inclusions in amber are accompanied with the remains of other organisms and other things which make it possible to reconstruct some ecological circumstances of the life of the examined specimens. Many interesting and important data on the probable ecological interrelations of these specimens and peculiarities of the palaeoecosystems (palaeoenvironment) where they lived were published by S.G. Larsson [3], G. Poinar [4,5], etc., A.G. Ponomarenko [6] and some his publications after the latter monograph, as well as many others, particularly during these recent decades. In some cases the additional ecological information was also very substantial for decisions on systematic attribution of the fossils examined. Good examples of this kind of publications are the contributions of G. Poinar [7] and M. Perreau [8] in this issue. The first contribution [7] represents the first generalization of the current data on syninclusions found with fossil beetles that have been preserved in amber pieces of different ages from Mexico, the Dominican Republic and Myanmar. The associates include mites, pseudoscorpions, spiders, insect parasites and predators, fungi, angiosperm parts, vertebrates and nematodes. Examples of present-day associations similar to those of the fossils

show that particular modern behavioral patterns are often much more ancient than could be previously thought. The second of the abovementioned contributions [8] is devoted to the description of the new leiodid beetle from the Albian amber of the Nograro Formation (Alava, Spain), which has very peculiar structural features which suggest the adaptation of the described species to subterranean or at least to soil litter environments.

The importance of reconstructions and reviews of the fossil record for different coleopterous groups (for archostematan: see [9–11]—see also the references in the contribution by A.G. Kirejtshuk [12] in this issue) scarcely can be overestimated as opposed to the essentially incomplete of these versions of the fossil record. The suborder Archostemata seems to be the oldest and most basal one and knowledge of it therefore has a particular importance for modeling phylogenetic relationships. It could also be very valuable to prepare reviews of the fossil record for other large groups (as many as possible), which will make it feasible to propose such models with a better foundation. Some preliminary attempts to summarize the very extensive data and analyze the fossil record have been published for aquatic beetles by A.G. Ponomarenko and A.A. Prokin, also for Curculionoidea by A.A. Legalov, and so on. Other coleopterists published several very important contributions in general reviews (E.A. Jarzembowski, R.G. Martins-Neto, J.V. Matthews, D. Peris, L.E. Piton, N. Théobald, G. Tröster). The fossil Adephaga became known thanks to efforts mainly of A.G. Ponomarenko, and also of A. Arillo, A. Bode, V.M. Ortuno, A.A. Prokin, X. Zhao and others. Myxophagan fossils have been studied mostly by A.G. Kirejtshuk and G. Poinar. Extermely numerous polyphagan groups with large taxa have been investigated by many coleopterists; in particular, Staphyliniformia by S. Chatzimanolis, M. Fikáček, A.Yu. Solodovnikov, Z.-W. Yin, J. Zhang, Y.-L. Zhou and others; Scarabaeiformia by M. Bai, F.T. Krell, G.V. Nikolajev and others; Elateriformia by A.V. Alexeev, H. Chang, F. Fanti, T. Hörnschemeyer, S.M. Iablokoff-Khnzorian, B. Klausnitzer, A.V. Kovalev, G. Tröster, H. Wu, E.V. Yan and others; Cucujiformia by V.I. Alekseev, J. Batelka, A. Bukejs, S. R. Davis, V.G. Gratshev, J. Hava, D.-Y. Huang, S.V. Kazantsev, J. Kolibáč, Q. Lin, M. Liu, G. Yu. Lyubarsky, A.G. Moseyko, M.V. Nabozhenko, K.S. Nadein, A.V. Petrov, G. Poinar, D. Telnov, F. Vitali, E. Voss, V.V. Zherikhin complement many others. This issue contains the contributions by A.G. Kirejtshuk with an annotated list of archostematan of the superfamilies Coleopseoidea and Cupedoidea [12], M.V. Nabozhenko devoted to his work on the fossil record of tenebrionids providing a foundation for phylogenetic modeling and other theoretical applications [13], and A.A. Legalov [14] produced a complete revised list of all curculionoids found in the Eocene amber in Europe.

The contribution to archostematan included in this issue [12], is the first of a series of reviews of the suprageneric taxa of fossil beetles in the current century and their generic and species composition. The necessity of such reviews exists because different researchers have different experiences in the study of fossils, and the absence of such generalizations can create situations when misunderstanding appear between specialists and lead to confusions in interpretations. On the other hand, reviewing the entire range of diversity makes it possible to estimate hiati between known groups for a better partition of the taxa and to give a foundation for balanced diagnoses for them. The review of the diversity of the subfamily Ommatinae allows to propose an emended diagnosis for each genus, which is comparable to that for every of other ommatine genera known in fossils. Finally, this contribution contains description of ten new genera and 12 new species, and their generic distribution in time and space, and also new synonyms and new taxonomic combinations.

This issue also includes the contribution to tenebrionids [13], which is devoted to the reviewing all taxa of the family Tenebrionidae known in fossils. It aims to show correlations for the fossil record on this family with the knowledge of the modern fauna of this family and define at least the main phyletic links between its extinct and extant members and groups. The fossil record of Tenebrionidae has a particular importance for current evolutionary reconstructions and phylogenetic models proposed for this family. The oldest Jurassic and Jurassic–Cretaceous darkling beetles of the tenebrionine lineage belong to humidity-adapted groups from the extant tribes Alleculini, Ctenopodiini (Alleculinae) and Alphitobiini (Tenebrioninae). Although different ecological groups had differences in their possibilities

of coming into deposition and fossilization, the palaeontological evidences support the idea, that the differentiation of the family started at least in the Middle Jurassic and the main phyletic lineages at this level of exploration can be traced up to the Recent epoch.

Another essential subject in palaeocoleopterological studies is palaeofaunistic generalizations. During the second half of the last century many books devoted to this subject were published and represent particularly important sources of knowledge not only for the systematic and phylogenetic placements of the fossils included in them but also for many aspects of palaeontology, faunogenesis, stratigraphy, (palaeo) biogeography and other fields of knowledge (particularly including many palaeofaunistic generalizations of data from outcrops of the former Soviet Union, Mongolia and China). The last such resource devoted to the Jurassic palaeofauna of Shar-Teg (Mongolia) appeared in 2014 [15], and now we present the monograph on the Palaeogene beetles of the Isle of Wight (England) [16]. Even preliminary faunistic lists for materials from large outcrops are rather valuable (such as those devoted to beetles from the Lower Cretaceous (Barremian) outcrops of Las Hoyas and El Montsec (Spain): [17], beetles from Mid-Jurassic Daohugou and Lower Cretaceous Liaoning (China): [18] and so on). Of course, complete data on small fossil resources are also very important and frequently informative.

In addition to significance for systematics and phylogenetic reconstructions, beetle inclusions in amber give extremely rich information for palaeoecology, palaeogeography and other fields of knowledge. Amber resources of primary deposition also have a rather great significance because of the potential possibility to estimate their more or less precise age. This concerns the Lower Cretaceous Lebanese and Spanish insectiferous amber [19,20], etc. On the other hand, specimens included in redeposited amber have great significance for systematics, although generalizations as to their origin, age, etc. can be proposed only with great caution taking into consideration that each of these resources could come from one primary outcrop of a very different age or even from some primary outcrops of different ages. This especially concerns Baltic amber which is extremely rich in bioinclusions, including many beetles. Nevertheless, the generalized data on these resources are very important in many other kinds of research [21,22]. The contribution on curculionoids from the European Eocene amber is published in this issue [14] and reviews all 142 known and documented species of Curculionoidea in the Eocene amber, including one species of Nemonychidae, 16 species of Anthribidae, six species of Belidae, ten species of Rhynchitidae, 13 species of Brentidae, 70 species of Curculionidae, two species of Platypodidae and 24 species of Scolytidae. Besides, this review on curculionoids has descriptions of nine new genera and 18 new species, and also some new generic and species synonyms. Currently only eight species are known from Oise amber, but 118 species from Baltic amber and 16 ones from Rovno amber are known. The new review on curculionoids is provided with keys to all taxa of this superfamily (of the family, tribe, generic and species ranks) recovered in the three considered amber resources, with repositories of holotypes of every species, and also with preliminary analyses of taxonomic and faunistic composition in each resource (Oise, Baltic and Rovno amber).

The studies devoted to fossils from amber of different ages are of particular significance for palaeocoleopterology, and palaeontology in general because of their usually better preservation and more informative other content (syninclusions). These fossils give the possibility to obtain a more complete information on extinct organisms (even possibilities to study inner body structures in three-dimensional view thanks to X-ray, laser, or fluorescent scannings). This issue includes a contribution by M. Perreau [8] with the description of the new cholevine genus and species, the external and internal structure of which was investigated by propagation phase contrast X-ray microtomography. The combined results of studies using optic microscopy and X-Ray tomography made it possible to obtain more or less complete information on the specimens examined, including tomographic pictures and three-dimensional anaglyphs.

The significance of the reviews published in this issue has been preliminarily estimated by M.E. Clapham in FOSSILWORKS ([fossilworks.org](http://fossilworks.org)) who calculated that the Nabozhenko's contribution contains 228 taxonomic opinions, and Legalov's one 375 taxonomic opinions and Kirejtshuk's one 490 taxonomic opinions. It was difficult to prepare a first large review on large inconsistent and disunited

data without enough experience and, therefore, to avoid some defects. There was published a junior objective synonym *Lobanovia* Kirejtshuk, 2020 (syn. nov.) to *Proterocupes* Ponomarenko, 2015 [23] with the same type species *Simmondsia permiana* Ponomarenko, 2013 [24] proposed as “Cupedidoidea incertae familiae” (also as members of this genus *Proterocupes major* Ponomarenko, 2015 [23] and *Proterocupes nedubrovensis* Ponomarenko, 2015 [23] were additionally described from Russia, Vologda Region, Nedubrovo; Permian, Lopingian, Wuchiapingian/Changhsingian (Tatarian, Vyatkian),—254.0–252.3 Ma). Consideration of groups of Cupedoidae *incertae sedis* is planned for the next review of this series. *Mallecupes* (*Mallecupoides*) *clevelyi* Jarzembowski, Wang et Zheng, 2017 [25] from the Lower/Upper Cretaceous Burmese amber is missed in this review. Besides, the species name *Barbaticupes combertiae* Jarzembowski, Wang et Zheng, 2017 is misspelt as “cobertae”, and also names *Jarzembowskiops* and *Polykius* in few cases are printed as “*Jarzembowskops*” and “*Polykius*”.

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