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On subfamily structure of the Cupedidae (Coleoptera, Archostemata): data from paleontology and an approach to solving conflicting classifications

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Abstract

This paper demonstrates some of main differences between the systematic constructions based mostly on paleontological research and constructions involving the other approaches. Some reasons for these differences are discussed, together with an approach to solve contradictions between the conflicting hypotheses. The multiple (multidimensional) parallelism gives a possibility to solve many problems of phylogenetic interrelations due to reconstructions based on coincidence of patterns of changes (series of interconnected facts) traced in different aspects of evolutionary processes. This principle originates in the ideas by Jean Agassiz and Ernst Haeckel defined as the principle of triple parallelism. Other aspects of the evolution can be added to the morphology, embryology, and paleontology, initially included in this method. The molecular method is one of such aspects. It is shown that the potential resolution of the morphological and molecular approaches in some cases could be rather restricted, particularly applying ancient groups with main evolutionary transformations passed far in the past. The infraorder Cupediformia and suborder Archostemata in general are examples of such cases. It is advisable in the current research period that has followed the previous interpretation of the systematic structure of the family Cupedidae recognizing three subfamilies with not quite distinct hiatus between them (Cupedinae, Ommatinae and Triadocupedinae). Some recent morphological and molecular approaches proposed to divide the Cupedidae into two separate families on the basis of incomplete information accessible after study of only modern representatives, as most events in the family evolution occurred during the Palaeozoic and Mesozoic, and these events are scarcely possible to trace without considering fossils. As the principle of multiple parallelism cannot be currently used for archostematans to the full extent of its power, it is necessary to choose the paleontological method of phylogenetic reconstruction as crucial. This approach is preferable for groups that are well-documented through very diverse fossils, and for which only few of its remnants of the past diversity reached the modern epoque.

Keywords: Cupedinae, Ommatinae, paleontological method, principle of triple parallelism, principle of multiple (multidimensional) parallelism

Introduction

The reason for this paper is connected mainly with the taxonomic rank of two rather common groups of archostematans, one of them usually treated as the subfamily or family Cupedidae and another as a subfamily or family Ommatidae. Every year some publications appear with descriptions of new fossil genera and species from these groups. The number of concerned taxa is quickly increasing. On the contrary, the taxonomy of the extant representatives is comparatively stable. Fossils of some of these archostematan groups are important components of many Mesozoic oryctocenoses. Therefore, they are considered as important indicators for stratigraphic and paleoecological purposes. Besides, these fossils are of great scientific importance because of the inclusive position of the Archostemata in the phylogenetic system of the order Coleoptera. Thus, a clear understanding of the affinities of these fossils has a great theoretical and practical meaning.

As in many other cases, the base to clarify the classification of these taxa has been taken from neontology. The family name Cupedidae (as "Cupesidae") was proposed by Laporte (1836) for members of the extant fauna (type genus *Cupes* Fabricius, 1801 with type species *Cupes capitatus* Fabricius, 1801) and the name Ommatinae was proposed by Sharp & Muir (1912) for members of the modern fauna (type genus *Omma* Newman, 1839 with type species *Omma stanleyi* Newman, 1839). The first fossil genera to be described as members of cupedids are *Mesocupes* (Martynov, 1926) and *Liassocupes* (Zeuner, 1962), although the latter indeed is an Ommatinae *sensu stricto*. In 19th and the beginning of 20th centuries some fossil cupedine and ommatine genera were described under other family attributions (*e.g.*, *Blapsium* Westwood, 1854, *Curculionites* Giebel, 1856, non Heer, 1847, *Procarabus* Oppenheim, 1888, *Chalepocarabus* Handlirsch, 1906, *Kakozelia* Handlirsch, 1906, *Pyrochroophana* Handlirsch, 1906, *Zygadenia* Handlirsch, 1906, etc.). If some of

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these genera and species still have unclear phylogenetic positions, those of several others were clarified (see Kirejtshuk *et al*., 2016; Kirejtshuk, 2020; internet catalogue by Kirejtshuk & Ponomarenko, 2021, etc.). Zeuner (1933) pointed out the phylogenetic importance of the elytral venation, tracheation, transformations of cells with primary membrane, in the Palaeozoic, Mesozoic, and recent Archostemata. Rohdendorf (1956) traced the transformations of the archedyction and the cells into the true elytral punctures in the Palaeozoic representatives of the Siberian archostematans. Rohdendorf (1961) included 11 species of the family 'Cupidae' in his monograph on the Palaeozoic insects of the Kuznetsk Basin. All of them were later transferred to other families of the superfamily Cupedoidea (*sensu* Kirejtshuk, 2020).

The studies of the abundant material of cupedids (and more generally archostematans) from the Triassic of Madygen and the Jurassic of Karatau (*e.g*., Rohdendorf & Ponomarenko, 1962; Ponomarenko, 1964, 1966a, b, 1968) and fossil specimens from other Asian outcrops made it possible to elaborate and ground the general system of the suborder Archostemata and the system of the family Cupedidae in accordance with new data on extinct faunas. As a result, Ponomarenko (1969) proposed in his classic monograph a classification of the Archostemata and also of the family Cupedidae with three subfamilies (Cupedinae, Ommatinae, and Triadocupedinae Ponomarenko, 1966), which seems to be still the most reasonable one, although after great increase of new data on fossil archostematans, the tribal level of this classification can be scarcely applicable for group discrimination of supraspecific taxa (see below). Some decades after publication of this monograph many researchers followed it in their own interpretations. However, in the 21st century, new paleocoleopterists preferred to apply new methods of study based not only on fossils, but also on new theoretical approaches. Most of them are obtained through detailed studies of many structures of the modern representatives of archostematans and intensive usage of molecular data in phylogenetic interpretations. This preference of the new achievements shows great progress in taxonomic and phylogenetic studies. However, it produces also some negative effects. For example, most recent researchers called archostematan cells as 'window punctures' because of a considerable similarity of these structures with the true 'window punctures' in elytra of some advanced polyphagan groups of different phyletic roots. But these structures have completely different origins (elytral cells have inherited from initial cells of winged insects and should be treated as monophyletic, while the 'window punctures' independently originated from the true elytral punctures in groups of different infraorders). Therefore these 'primitive' cells are not directly homologous with the 'window punctures'. Another example illustrating the current state of the art, is the interpretation of the 'ridges' on the archostematan elytra without their morphogenetic connection with the initial primary veins, *i.e*., without taking into consideration their primary homology and probable parallelisms in their modifications. Some other important structural features are mentioned below.

This paper aims to demonstrate some of main differences between the systematic constructions based mostly on paleontological research and constructions recently proposed and obtained involving other approaches that tend to neglect the fossil data. It is also here considered some reasons for these differences and contradictions, and proposed a way to solve contradictions between the conflicting hypotheses.

Discussion

Every year some publications appear concerning phylogeny of coleopterans in general, but also of archostematans and cupedids-ommatids. Therefore, it is impossible to make a short review of all of them. Many general and particular hypotheses were proposed for phylogenetic relationships between archostematans including the two taxa under consideration. For discussion, it is sufficient to consider only one of these phylogenetic hypotheses, which includes all the important characteristics for our scope. One of most grounded by the great number of characters in the matrix is the cladogram elaborated by Lawrence *et al*. (2011). According to it, 'neither Ommatidae nor Cupedidae is monophyletic, Ommatinae forming a clade with Cupedinae and Tetraphalerinae with Priacminae'. Nevertheless, these authors followed somehow the tradition of recognizing the Ommatidae with Tetraphalerinae, and Cupedidae with Priacminae.

However, if the extinct genera of these groups are added to the taxonomic analysis, it becomes obvious that all these groups can no longer take on a diagnostic ground because a great part of the diagnostic characters of extant taxa remain unknown (frequently not accessible) in the fossils, while others are also losing their diagnostic meaning when fossil representatives are included in the analysis. Most suprageneric cupedine-ommatine fossil taxa (*e.g*., Brochocoleinae Hong, 1982 [Brochocoleidae], Clessidrommatini Jarzembowski, Wang & Zheng, 2017, Lithocupedini Ponomarenko, 1969, Mesocupedini Ponomarenko, 1969, Notocupedini Ponomarenko, 1966, Pronotocupedini Tan, Wang, Ren & Yang, 2012 and Tetraphalerini Crowson, 1962) have no proper diagnostic characters in their original definitions. Thus, it would be better to avoid their usage that quite frequently creates confused situations in taxonomy (Kirejtshuk *et al*., 2016; Kirejtshuk, 2020). However, further revisionary examination can reveal more reliable argumentation to restore some of these names for designation of any particular group. For example, Kirejtshuk (2020) regarded that the pair Ommatini and Tetraphalerini can be restored if the subglobular and laterally incarinate prothorax of some genera similar to *Omma* is accepted as synapomorphy, and, therefore, these genera can be treated as very closely related (Ommatini *sensu stricto*). In this case, the remaining genera (*i.e*., most genera of the subfamily) should be recognized as members of Tetraphalerini (Crowson, 1962: 'laterally margined prothorax'). The tribe Priacmini was proposed without any diagnosis and the subsequent diagnoses of other researchers are inaccurate (Ponomarenko, 1969; Tan & Ren, 2009, etc.). Li *et al*. (2019) described one Cretaceous congener with very expressively similar characters to those of the modern *Priacma serrata* (LeConte, 1861) and compared it with 'other' (maybe undescribed) species. Nevertheless, this tribe is still without any proper diagnosis and scarcely can be distinguished in fossils in other cases. By the way, the modern species of the genus *Priacma* has an extremely unique structure of the male aedeagus, more similar to hymenopteran than to coleopteran aedeagi (Edwards, 1953a, b). This feature could be an extremely important character, but, unfortunately, this organ is very rarely exposed in fossil specimens. Such a structure of male genitalia is not known in any modern beetle, but something similar occurs in two Mesozoic beetles, one species in 'cupedines' (*Gracilicupes* Tan, Ren & Shin, 2006) and another in 'ommatines' (*Echinocups* Kirejtshuk & Jarzembowski in Kirejtshuk, 2020). At the moment, it seems to be impossible to explain this event in terms 'appearance' and 'disappearance' in the phylogeny of the family, except the probability of it being a plesiotypy. Thus, *Priacma* (at least its extant species) is a part of very complex taxonomic mystery, which still remains not understandable and unsolved. It probably shows enough characters for its accurate attribution to the subfamily Cupedinae, but no group character, except the male aedeagus, is currently accessible to be recognized as diagnostic for a tribal state. Traditionally, the type of junction of abdominal ventrites is regarded as a stable diagnostic group character, which can be used for determination of supraspecific and suprageneric taxa in archostematans in general. But, even if from time to time a few exceptions are found in any large group, they usually fail to gain the attention of researchers. Ponomarenko (1969) regarded that this junction is very important for tribal diagnostics of Cupedidae *sensu lato*: either abdominal ventrites co-planar (abutting) or overlapping (tegular). The revision of the 'Baltic' amber Eocene fauna of the genus *Cupes sensu lato* demonstrates a variation of this structural feature with presence of both types of junction in more or less contemporaries (Kirejtshuk, 2005), although according to Ponomarenko (1969) all 'Cupedini' should have the overlapping abdominal ventrites. As a result, identification of most tribes (or subfamilies) of the Cupedidae-Ommatidae *sensu stricto* is rather problematical and, therefore, there are so many contradictions between the opinions of researchers.

There are several serious difficulties in the discrimination of the groups treated with the family rank by neontologists (Cupedidae and Ommatidae) and formerly recognized as subfamilies of the same family by paleontologists (Cupedinae and Ommatinae). One of most 'stable' diagnostic characters to place the genera in the neontological Cupedidae (= paleontological Cupedinae) or Ommatidae (Ommatinae), is the position of the procoxae, *viz*. procoxae separated by prosternal process in the former *vs*. contiguous in the latter. Recently, Jarzembowski & Wang (2016) found that the Ommatine *Stegocoleus* described by them from the Cretaceous Burmese amber has the procoxae distinctly separated by a rather raised prosternal process. These authors put this genus in the subfamily Ommatinae with a question mark (?), despite the fact that all its other structural features are of ommatine rather than cupedine type. Li *et al*. (2020), considering this structural peculiarity, came to the conclusion that the 'elongated prosternal process and separated procoxae evolved independently in Cupedidae and *Stegocoleus*', although no one has proved that the absence of prosternal process between procoxae is a plesiomorphy for the family Cupedidae *sensu lato* or even for the superfamily Cupedoidea.

Nevertheless, this case is far from unique among ommatines. Another example can be taken among cupedines. These should 'always' have their procoxae clearly separated by the prosternal process. Some cupedine genera with the apparently rather raised prosternal process have a subglobular and laterally incarinate prothorax, as in Ommatini *sensu stricto* (see Kirejtshuk *et al*., 2016: some *Anaglyphites* Ponomarenko, 1964: *A*. *capitatus* Ponomarenko, 1966: figs 97 and 98; *A*. *clavatus* Ponomarenko, 1964: figs 101 and 102; *A*. *mongolicus* Ponomarenko, 1997: figs 99 and 100; some *Mesocupes*: *Mesocupes paulus* Ponomarenko, 1964: figs 105 and 106). It seems impossible to phyletically connect the tribe Ommatini *sensu stricto* and these cupedine genera, and, therefore, these fossils need to be re-examined with more attention to correct estimation of their subfamily attribution (Kirejtshuk, 2020). Besides, some difficulties in discrimination of Cupedinae and Ommatinae are also conditioned by many other parallelisms in transformations of many structures, like the shape of head, pronotum and elytra, sculpture of integument and elytral venation, structures of legs, etc. Thus, the question appears what rank is more reasonable to attribute to the groups with so subtle and not reliable differences: separate families *vs*.

subfamilies of the same family. Recent studies of many fossil representatives of both considered subfamilies (families) repeatedly demonstrated parallelisms during all periods of the Mesozoic, which are not clearly traced in the few genera surviving in the modern fauna. Thus, most of 'plesiomorphic' and 'apomorphic' character states in the interpretation of Lawrence *et al.* (2011) in fact seem to be homoplasies.

The third important facet of general phylogenetic reconstruction is connected with studies and comparison of nucleotide sequences, which are usually connected with great expectations for biologists. Archostemata is a rather ancient group and includes only three modern groups accessible for phylogenomic reconstructions by molecular method. It can be noted that the three relict Mesozoic groups of the archostematans in the Recent fauna are two subfamilies of Cupedidae (Cupedinae and Ommatinae) and one species of Micromalthidae. McKenna *et al.* (2015, 2019) after comparison of their nucleotides recently proposed the following relations for them: Cupedidae + (Ommatidae + Micromalthidae). This hypothesis is very different from those based on morphological characters of the modern representatives, among which one group, the family Micromalthidae, belongs to a separate infraorder Micromalthiformia (Kirejtshuk, 1991), while, the 'Cupedidae' *sensu stricto* and the 'Ommatidae' *sensu stricto*, are included within another infraorder, Cupediformia, which, in turn, is closely related to the extinct infraorder Schizophoriformia (Kirejtshuk, 1991), but not directly to the Micromalthiformia. Moreover, the two groups 'Cupedidae' and 'Ommatidae' cannot be interpreted with a higher rank than subfamily in the composition of the same family (Ponomarenko, 1969; Kirejtshuk *et al*., 2016; Kirejtshuk, 2020), which are rather weakly morphologically separated from each other, particularly after recent studies of the fossil Mesozoic diversity (see above) appeared at least not later than the Middle Triassic, while the family Micromalthidae appeared in the fossil record in the Upper Permian (Yan *et al*., 2020), and is strongly separated from all other archostematans by many structural characters of both active instars of development, ontogeny, and bionomy. Thus, the above phylogenomic reconstructions strongly contradicts the morphological and paleontological data, because the joining of Micromalthidae and Ommatinae as apposed Cupedidae has no support beyond molecular comparison. The paraphyly or polyphyly in the molecular 'phylogeny' are theoretically scarcely possible. The contradictions between diagrams (or trees) created on the basis of structural characters of modern species and those summarizing results of comparison of sequences of different genes should have some explanations with biological meaning of these contradictions in addition to difference in formal patterns. The general scheme of relations within Archostemata after Lawrence *et al.* (2011) is the following: Micromalthidae + ((*Tetraphalerus* + *Priacma*) + (*Omma* + *Cupes*)) and this pattern also cannot be recognized (see above). Nevertheless, most new paleocoleopterists usually start the 'Introduction' of their publications by indicating that they followed the most advanced scientific achievements published by the creators of cladograms and molecular taxonomists, and only few of these coleopterists mention that some other opinions based on other methodological tools, including paleontological ones, exist and have been published. It is strange to prefer an opinion without any discussion of the alternatives, based on the apparent 'regularities' with very few facts and with contradictions in the theoretical ground but not on the evident regularities documented by hundreds of reliable facts.

Returning to the contradictions between the conclusions of different approaches, it has a sense to restore the principle (method) of multiple (multidimensional) parallelism, which gives a possibility to solve many problems of phylogenetic interrelations due to reconstructions based on coincidence of patterns of changes (series of interconnected facts) traced in different aspects of evolutionary processes. This principle (method) originates in the ideas of Jean Agassiz and Ernst Haeckel, defined by the former of the two as the principle of triple parallelism. This principle can be extrapolated to the multiple (multidimensional) parallelism (including molecular and ecological aspects). In accordance with the integrity of all biological systems, other aspects of their evolution can be added to the morphology, embryology, and paleontology initially included in this method. In other words, the reconstruction of relationships can be considered as 'proven' (meaning most probable under the current knowledge) in case of finding in them independent congruences between morphological analysis, results of comparison of nucleotide sequences and in the fossil record. If the reconstructions obtained after matching the patterns of different aspects in accordance with the principle of the multiple parallelism show contradictions, the data of all considered aspects (series) or at least the data, in which these contradictions are expressed, should be re-investigated to resolve the reasons of these contradictions. Unfortunately, a comparable completeness of each of these aspects (series) is difficult to achieve, and, therefore, researchers often resort to mixing of unconnected data from different aspects (calibration of diagrams by few facts). Each aspect of the phylogenetic process has its own specific limitations for interpretation and extrapolation. However, if only some concrete facts are used for calibration of any tree based on facts and regularities of another aspect (series of facts), there is a considerable risk to make a mistakable calibration. The purpose of re-investigations is to reach a coincidence of patterns but not of separate facts, taking into consideration that in some cases the principle of multiple parallelism may not be applicable due to the impossibility of obtaining the necessary information.

The phylogenomists utilize fossil evidence, which they consider as an incomplete and unreliable record, only to confirm the models obtained by comparing "reliable" nucleotide sequences through time references, so-called calibration (Parham *et al*., 2012; Tong *et al*., 2015; Toussaint *et al*., 2017, etc.). In contrast to the evidence of the fossil record, the differences in the age estimations determined on the basis of molecular calculations show that the results of these calculations are to some extent related to the computer programs used to obtain them. For example, based on the current level of knowledge, the superorder Coleopteroidea was first noted in the fossil record about 300 million years ago (*Stephanastus polinae* Kirejtshuk & Nel in Nel *et al*., 2013 (Skleroptera, Stephanastidae) – 303.7–298.9 million) (Kirejtshuk & Nel, 2013), as well as oldest true beetles a little later (*Coleopsis* Kirejtshuk, Poschmann & Nel, 2014 (Archostemata, Coleopseoidae) and *Moravocoleus* Kukalová, 1968 (Archostemata, Tshekardocoleidae) (Kirejtshuk *et al*.,) 2014) – 298.9–295.0), and according to the molecular calculations calibrated by some fossils, the origin of this superorder determined by McKenna *et al*. (2015) 278.3 (288.3–272.0) Ma, while Toussaint *et al*. (2017) gave a clearly overestimated age of the order at 356.0 (375.0–336.8) Ma. It should be noted that McKenna *et al*. (2015) and Toussaint *et al*. (2017) used the same sequencing data, but different representatives for calibration and slightly different computer applications (and associated algorithms) for data processing. Since such discrepancies in dating are of a systemic nature, they require special consideration. It is possible to imagine which model can be obtained if we take for modeling the third set of fossils for calibration and the third set of software for data processing. This example clearly shows how important is the reliable theoretical base for usage of facts of the fossil record obtained only as a result of paleontological research. It can also be assumed that research methods will improve and reach a level when it will be possible to resolve those contradictions in the patterns of various aspects of consideration that now seem insoluble, although only the paleontological data, in contrast to data of other aspects of consideration, can give a direct support and an *a priori* argument for phylogenetic or historical hypotheses without necessity of additional reasoning.

The proportion of the available facts of the various aspects of consideration gives the impression that molecular data can be used in the situation in Cupedidae *sensu lato* to calibrate a dendrogram based on fossil data, but this calibration will be about as reliable as calibrating a molecular dendrogram from examples of fossils. Possibly, molecular calibration of paleontological data can in other cases give some positive results, but not in the case of Cupedidae because of the considered fundamental contradictions between the data on these aspects. In case of absence of a congruence in comparable data on molecular, structural and paleontological aspects, each such calibration must be substantiated with additional reasoning, taking into account that sometimes the calibration may in principle be impossible (at least at the current level of the research methodology).

Conclusion

This analysis shows that the potential resolution of the morphological and molecular approaches in some cases can be rather restricted, particularly in ancient groups with great phylogenetic changes taken place far in the past. Because the principle of multiple (multidimensional) parallelism cannot be used to the full extent of its power, it is necessary to choose the paleontological method of phylogenetic reconstruction as a main and preferable one for groups that are well-documented through very diverse fossils, and for which only few of its relict remnants reached the modern epoch. The infraorder Cupediformia and suborder Archostemata in general are good examples of such cases. Taking into consideration the abovementioned circumstances, it is advisable in the current research period to follow the interpretation by Ponomarenko (1969) of the systematic structure of the family Cupedidae including three subfamilies with not quite distinct hiatus between them (Cupedinae, Ommatinae and Triadocupedinae), and not split this family into two separate families (Cupedidae and Ommatidae) on the basis of the recent morphological and molecular approaches conducted with only very incomplete data of phylogeny, as most events of their phylogeny occurred in the Palaeozoic and Mesozoic, which are difficult to trace without paleontology. It can be expected that similar situations are quite possible as well in some other insect groups.

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