Vol. 84 No. 4 pp. 783–792 ACTA GEOLOGICA SINICA (English Edition) Aug. 2010

Current Knowledge of Mesozoic Coleoptera from Daohugou and Liaoning (Northeast China)

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Abstract: The present paper is devoted to an overview on fossil Coleoptera studied from Inner Mongolia, Daohugou (Middle Jurassic, Jiulongshan Formation) and Liaoning (Upper Jurassic-Lower Cretaceous, Yixian Formation) deposited in Chinese collections. As a result, species of the tribe Sperchopsini and Hydrophilini from Hydrophilidae, families and subfamilies Silphidae, Syndesinae from Lucanidae, Pleocomidae, Trogidae, Trogissitidae, Pyrochroidae, Diaperinae from Tenebrionidae, and Cerambycidae were first registered in the Mesozoic and some families were defined as new. It was shown that many superfamilies represented in the Recent Fauna were formed within the Middle Jurassic and Lower Cretaceous. The materials examined confirm the hypothesis that Cucujiformian beetles are a younger group than other infraordera of Polyphaga (Staphyliniformia and Elateriformia) and, therefore, they appeared in the fossil record only in the late Mesozoic. It was shown and confirmed that most superfamilies appeared in the fossil records before Cucujoidea. The synonymy of *Notocupes* Ponomarenko, 1964; *Sinocupes* Lin, 1976, syn. nov.; *Amblomma* Tan, Ren et Liu 2005, syn. nov.; *Euryomma* Tan, Ren et Shih, 2006, syn. nov., non Stein, 1899 and *Ovatocupes* Tan et Ren, 2006, syn. nov.; synonymy of *Tetraphalerus* Waterhouse, 1901 and *Odontomma* Tan, Ren et Ge 2006, syn. nov.; and synonymy of *Priacmopsis* Ponomarenko, 1966 and *Latocupes* Tan et Ren, 2006, syn. nov. are proposed. *Sinorhombocoleus papposus* Tan et Ren, 2009 is transferred from the family Rhombocoleidae to Schizophoridae. *Cervicatinius complanus* Tan, Ren et Shih, 2007 and *Forticatinius elegans* Tan, Ren et Shih, 2007 are transferred from the family Catiniidae (suborder Archostemata) to superfamily Cleroidea (suborder Polyphaga: first among the family Peltidae and second as a closely related group to the latter family). The family Parandrexidae is transferred from the superfamily Cucujoidea to Cleroidea. The ecological circumstances of the past ecosystems and hypotheses of historical development of the order Coleoptera are discussed. The age of faunas examined is considered. The list of the taxa described from Daohugou and Liaoning is compiled.

Key words: fossils, Jurassic, Cretaceous, Coleoptera, Archostemata, Adephaga, Polyphaga, Daohugou, Liaoning, new synonymy

1 Introduction

Recent development of paleontological collections in China has become comparable with the development of such collections in other countries. Their growth is connected with excavation in extraordinary large lagerstättes Daohugou (Jiulongshan Formation) and Liaoning (Chaomidian and Huangbanjigou: Yixian Formation). From there, numerous perfectly preserved fossil objects have been already obtained at the end of the last and current centuries. In some cases, such as Cambrian fossils and Mesozoic vertebrates, description and analysis of new discoveries are not far behind the pace of their accumulation. However, the description of many other groups collected in these places is going at a much slower pace than the collection of materials. This concerns insects, including numerous remains of Coleoptera deposited in Daohugou and Liaoning. Nevertheless, preservation of many structures in some of these specimens is maintained so perfectly that they can be better compared with recent ones than those from most other lagerstättes. Studies of these Chinese materials are very important for systematics and phylogenetics. In particular, some beetles from there give a possibility to study inner structures, gut contents, genitalia, venation and folding of posterior wings etc. There are also some collected larvae with perfect preservation. These Chinese lagerstättes are located to the south from known Cretaceous sites of South Siberia and Mongolia. It is not surprising that they contain somewhat different

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composition from the northern sources. Study and comparison of them make it possible to commence investigation of fossil Coleoptera of large areas. The studies recently performed were made possible thanks to the visit of A.G. Kirejtshuk, G.V. Nikolajev, A.G. Ponomarenko and A.A. Prokin to China in 2008 and 2009. Chang Huali made rather important assistance to the present study and seriously contributed to it. Ren Dong provided these studies with some necessary management of fossil specimens and visit of the mentioned scientists.

Some important publications on Coleoptera from both sites have been recently issued (Liaoning: Lin, 1976; Hong, 1986; Huang and Zhang, 1997; Dolin and Nel, 2002; Tan et al., 2005, 2006, 2007a; Tan and Ren, 2006a, 2009; Liu and Ren, 2006; Liu et al., 2006, 2007; Chang and Ren 2008; Chang et al., 2010 etc.; and Daohugou: Hong, 1983; Tan and Ren, 2006b, 2009; Tan et al., 2006, 2007b; Chang et al., 2009; Kirejtshuk et al., 2010 etc.). The complete information on references to the publications devoted to considered materials can be obtained from the catalogue on the web-portal <www.zin.ru> (Ponomarenko and Kirejtshuk 2010). However these papers cover only a small portion of beetles discovered from the sites under consideration. Unfortunately a considerable part of the species described before the recent studies should be re-studied and many cases completely re-described in order to provide the scientific community with adequate conception and correct interpretation of them, as many descriptions and drawings are not correspondent to the characters of the described specimens (although sometimes such correspondence can be clarified thanks to the pictures in the original descriptions). This paper aims to make only a preliminary overview on materials accessible mostly in Beijing collection and propose some corrections for some data published before. The most genera and species formerly proposed for the materials from Daohugou and Liaoning are here preliminarily regarded as valid, however a serious revision of them is still strongly required, and will be done in the course of further study. The placement of some generic taxa is changed in accordance with the proper diagnostic characters available in the specimens described and in many cases re-examined by the authors of this publication.

2 Materials

Specimens from the sites under consideration available for study are deposited in many collections around the world. Nevertheless most prints have been concentrated in the Chinese scientific organizations. The authors studied mainly specimens in the collections of the Capital Normal University, Beijing and Institute of Geology and Paleontology of the Chinese Academy of Sciences, Nanjing. Most prints with beetles available for study in these collections demonstrate comparatively larger specimens, while smaller ones are thought to be omitted during initial collecting in the outcrops.

The lagerstätte Daohugou belongs to the Jiulongshan Formation and locates near Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, (Middle Jurassic, Jiulongshan Formation [=Nei Monggol Autonomus Region]), China. The age of this deposition is estimated to be c. 165 Myr (Gao and Ren, 2006) as Oxford-Callovian, although it could be put in Bathonian-Bajocian. Many thousands of specimens are found in the locality and beetles dominate in oryctocoenosis. From Daohugou there are a strange water mammal, salamanders, pterosaurs, dinosaurs, conchostracas, mayflies (Ephemeroptera), dragonflies (Odonata), earwigs (Dermaptera), cockroaches (Blattaria), Orthoptera, Homoptera (Auchenorrhynha and Heteroptera), Megaloptera, snakeflies (Raphidioptera), scorpionflies (Mecoptera), Neuroptera, beetles (Coleoptera), Hymenoptera, Diptera and butterflies (Lepidoptera). The plants include ferns, Bennettitales, Ginkgoales and Pinales. Among fresh water insects larvae of mayflies and bugs are dominant. The mayflies inhabited lakes rather than reophilous and they seemed to live in small and shallow lakes.

The lagerstätte Liaoning belongs to the Yixian Formation, located near Chaomidian Village, Huangbanjigou: Liaoning Province, China and consists of mainly lacustrine sediments intercalated with volcanoclastics. The precise age of this formation is still uncertain, as different opinions about the age have been proposed based on biostratigraphic and radiometric geochronology (Wang et al., 2005) and some students regard it as the Upper Jurassic, others as Jurassic-Cretaceous or Cretaceous. Various sediments of this formation are uneven-aged and differ in their taphonomy, because the sediments of Liaoning and Hebei are characterized by different complexes of fossil insects. The age of the strata of remains here considered is regarded as the Late Jurassic-Early Cretaceous. There are represent numerous mayflies with a Jurassic appearance (like those from the terminal Jurassic sites of Transbaikalia and Mongolia), while from Hebei the clear Lower Cretaceous fauna with domination of *Epicharmeropsis* Huang, Ren et Shih 2007 (Huang et al., 2007, 2008) (Ephemeroptera) and *Coptoclava* Ping, 1928 (Coleoptera) is known. Liaoning presents the most important localities in both quantity and, especially, preservation of fossils among numerous sites of fossil insects in China. Many thousands of specimens are found in the locality and beetles dominate in taphocoenosis. From Liaoning biota there are described mammals, dinosaurs, birds conchostracas, dragonflies, Orthoptera, earwigs, cockroaches, leafhoppers, bugs, Neuroptera, snakeflies, scorpionflies, Hymenoptera, Megaloptera, Diptera and beetles. The plants are represented by ferns, Bennettitales, Ginkgoales and Pinales, although finding of the proangiosperms and plants formerly described as angiosperms is of particular interest. Paleobotanical data from fossil spores, pollen and plants indicate a rather warm and humid climate at that time (Ding et al., 2001). Among insects, the beetles present as the dominant group here.

3 Coleoptera of Daohugou (Jiulongshan Formation)

The order Coleoptera in these beds seems to include specimens that can be put in more than 20 families of three subordera. The suborder Archostemata is represented by the families Cupedidae Laporte, 1836; Schizophoridae Ponomarenko 1968; Tricoleidae Ponomarenko 1969 and Jurodidae Ponomarenko 1985, whose members were predominantly associated with forests as inhabitants of subcortical interspaces and wood. Their food

seemed to be fungal substrates or substances produced as a result of vital functions of fungi and bacteria. Cupedidae were very common in the Mesozoic, but they are not found in the Lower and Middle Jurassic sites of the Siberian Region. This family is rare in Daohugou and includes only four genera and not a great number of specimens with more common representation of *Mesocupes* Martynov, 1926 and *Gracilicupes* Tan, Ren et Shih, 2006 (Cupedinae). The genus *Notocupes* Ponomarenko, 1964, the most common and diverse genus among Mesozoic cupedids, is represented by only a few specimens. The species of *Notocupes* were dominating in taphocenoses of the neighboring localities by both geographic location (Liaoning in north-east China) and age (Bakhar and Shar-Teg in Mongolia). Schizophoridae have been here recorded by two described genera, although their real diversity seemed to be markedly greater. The finding of Tricoleidae, known formerly only from the Triassic, was rather rare. This family has some specimens located here, among which some remains have a rather good preservation, while the specimens studied before are represented by isolated elytra. Beetles described as archostematan Ademosynidae Ponomarenko, 1968 (*Lasiosyne* Tan, Ren et Shih, 2007; *Brachisyne* Tan et Ren, 2009 and *Pappisyne* Tan et Ren, 2009) and Catiniidae Bocquet et Stock, 1957 (*Cervicatinius* Tan et Ren, 2007) indeed belong to the suborder Polyphaga (see below).

The suborder Adephaga includes numerous prints of terrestrial and water predators, with a predominance of comparatively small Trachypachidae C. G. Thomson, 1857 from the subfamily Eodromeinae Ponomarenko, 1977. Specimens of the superfamily Carabidoidea here are more numerous than rove beetles (Staphylinidae Latreille, 1802). Among fresh water beetles Coptoclavidae Ponomarenko, 1961 are dominant. Larvae and adults *Daohugounectes* Wang, Ponomarenko et Zhang, 2009 (Coptoclavidae) with some peculiar structural features, which are important for understanding of systematics and phylogeny of both mentioned family and water Adephaga in general, have been described. *Daohugounectes* seemed to be the actively swimming predator and this genus could in many respects define a structure of trophic net in fresh water communities of Daohugou.

The fresh water Polyphaga includes some peculiar groups of Hydrophilidae Latreille, 1802 with the generic taxonomic rank. The most common group of water scavenger beetles is similar to that of the genus *Prospercheus* Prokin, 2009 described from Shar-Teg (Mongolia). Among them, there is no actively swimming form and, therefore, they seemed to inhabit water basins with shallow water and with tight thickets of water plants. The family Staphylinidae is very poorly represented in these materials. Only about 20 prints were identified as attributable to members of this family. Other Staphyliniformia belong to some families of Scarabaeoidea, in particular to Lucanidae Latreille, 1804 (including subfamilies Syndesinae MacLeay, 1819; probable Aesalinae MacLeay, 1819); Trogidae MacLeay, 1819; Hybosoridae Erichson, 1847 (subfamily Hybosorinae) and Ochodaeidae Mulsant and Rey, 1871, which seemed to be mycetophagous in a wide sense and occur mostly in wood, although some of them (Trogidae) could have larvae living in soil. Furthermore, some members of a new family have been found, with 11-segmented antennae bearing a nearly symmetric club, which seems to be related to the superfamily Scarabaeoidea or represent one of the most archaic group of this superfamily.

The highest proportion of members of the suborder Polyphaga belongs to the infraorder Elateriformia. Perhaps, the majority of them were xylomycetophagous forms, although some Byrrhoidea could have some association with water basins and some Elateridae Leach, 1815 could be predaceous at larval stages of their ontogenesis. Among the members of this infraorder, the families Cerophytidae Latreille, 1834; Elateridae and Lasiosynidae Kirejtshuk, Chang, Ren et Shih, 2010 (Mesozoic paleoendemic family) were most represented. All these families were rather numerous in specimens; however, the first two families look much more uniform, while the Lasiosynidae were rather diverse and in the collections examined include some very distinct genera in the hundreds of remains available. The latter family is better represented in the Middle Jurassic Daohugou and Upper Jurassic Karatau (Kazakhstan) than in other late Mesozoic outcrops. It has somewhat isolated position among the superfamilies of the infraorder Elateriformia, sharing some particular features with each of its superfamilies. Except the Middle Jurassic members of Lasiosynidae (*Tarsomegamerus* Zhang, 2005; *Lasiosyne* and *Bupredactyla* Kirejtshuk, Chang, Ren et Shih, 2010) described from Daohugou and also still undescribed forms related to them, there have been found some specimens with nearly clubbed antennae and metacoxae without femoral plates, which in the other features are very similar to characteristic members of Lasiosynidae. The Elateridae from Daohugou are represented mainly, as in many other Jurassic taphocenoses, by species of the subfamily Protagrypninae Dolin, 1973 (genera *Paradesmatus* Chang, Kirejtshuk et Ren, 2009; *Paraprotagrypnus* Chang, Zhao et Ren, 2009 and *Protagrypnus* Dolin, 1973). The tribe Desmatini from the above-mentioned paleoendemic Elaterid subfamily is characterized by very peculiar large metacoxal femoral plates that are strongly reminiscent of those in Eucnemidae Eschscholtz, 1829 and Throscidae Laporte, 1840. In contrast to the recent species, all members of Cerophytidae that originated from Daohugou are characterized by the raised metacoxal femoral plates and not very long trochanters as in recent members of the family. The Buprestidae and some groups with appearance similar to those in Byrrhidae Latreille, 1804 have been found in few specimens (some of them could be true Byrrhidae).

A very peculiar character of studied materials from Daohugou is the very small number of specimens and species attributed to the infraorder Cucujiformia (including Curculioniformia), which are most numerous by both families and species in the Coenozoic and Recent faunas. The cucujiformian families with comparatively great numbers of specimens in this outcrop are Peltidae Kirby, 1837 and allied groups (Parandrexidae Kirejtshuk, 1984 and few related undescribed families). Most prints examined have been determined as Peltidae (some of them belong to the subfamily Meligethiellinae Kirejtshuk et Ponomarenko, 1990), which could be mostly xylomycetophagous. The probable "anthophagous" Parandrexidae are represented by single specimens. Few specimens could be put nearby the superfamily

Tenebrionoidea (near Melandryidae Leach, 1815) and a species, which is slightly similar in body outline to some Endomychidae Leach, 1815, but with filiform antennae is certainly not related to them. Nevertheless, among Cucujiformia from Daohugou there are no Chrysomeloidea or Curculionoidea, and only true Cleroidea are represented here. This corresponds with other data from studies of other Early and Middle Jurassic outcrops.

4 Coleoptera of Liaoning (Yixian Formation)

The order Coleoptera in these beds is rather abundant and seems to include specimens that can be put in more than 40 families of three subordera. Archostemata consists of numerous Cupedidae and sparse Schizophoridae. The Cupedidae from Liaoning are about 10 times as numerous as those in Daohugou. There have been found only four genera of each of the subfamily Cupedinae represented by dozens of specimens and of the subfamily Ommatinae Sharp et Muir, 1912 with many specimens, among species of which the members of the genus *Notocupes* Ponomarenko, 1964 are more numerous than the remaining seven genera combined. The study of more than a hundred conspecific beetles related to the specimens of some species already described as *Amblomma* (Tan et al., 2005 etc.) make it possible to find in some specimens a prosternal intercoxal process exciding over the procoxae, but did not locate between them. On the other hand, it is impossible to discriminate the genera by any character in antennae (as it was admitted in the paper where such feature was proposed for the diagnoses of these taxa). Besides, few specimens belong to the genus *Sinorhombocoleus* Tan et Ren, 2009, which is a member of the family Schizophoridae, but not Rhombocoleidae Rohdendorf, 1961 (not known later than the Permian), as was indicated in the publication where it was proposed, because the elytra of the specimens of this genus have comparatively dense columellae not arranged in longitudinal rows. Finally, beetles described as Catiniidae (*Forticatinius* Tan, Ren et Shih, 2007) should be transferred into the suborder Polyphaga (see below).

The suborder Adephaga is represented by numerous Caraboidea, mostly by Trachypachidae-Eodromeinae (over than 15 specimens of at least five to six species). Among the members of the latter group some species have an appearance extremely similar to that in recent Cicindelidae Latreille, 1802 (like species of *Cicindela* Linnaeus, 1758; *Collyris* Fabricius, 1801 and *Mantichora* Gistl, 1837). Something like Cicindelid-form beetle (*Oxycheilopsis cretacicus* Cassolo et Werner, 2004) and Carabid-form (*Alexcarabus megagnathus* Martins Neto, 2002) were also described from Brazil Santana. Among fresh water beetles adults of few species of Coptoclavidae are evidently more numerous, although certain dominant species have been registered as those in some other Mesozoic outcrops. Some of them should be clearly regarded in composition of a separate genus. However, among both neustonic and nektonic forms there are no active swimmers. The predaceous diving beetles (Dytiscidae) are more frequent in materials from Yixian (some species of four genera) than from those of any other Mesozoic sources. They should be considered in composition of two or three subfamilies, one of which includes the forms very similar to recent species of Aspidytidae Ribera, Beutel, Balke et Vogler, 2002 and fossil representatives of Liadytidae Ponomarenko, 1977, while another subfamily could link the families Dytiscidae and Noteridae Latreille, 1802. It is necessary to note a rather high ecological diversity of predaceous diving beetles from Yixian rather different in body size and coloration. Among them there were nektonic predators apparently diving at a considerable depth as well as inhabitants of temporal and shallow water or inhabitants of tight thickets of water plants.

There are 10 species of three genera of the family Hydrophilidae: two of them share some similarity with the recent tribes (Sperchopsini Hansen, 1991; and Hydrophilini), although it would be more reasonable to link them with different Mesozoic groups from Asia and Australia, the third genus is close to mesozoic Hydrophilopsia Ponomarenko, 1987. All species originated from Yixian seemed to be associated with shallow water and have no evident adaptation for active swimming (in structure of legs and development of long hairs). Some of them are thought to live within thickets of water plants (most probably of Charophyta), because the beetles are characterized by a striate patterned body coloration and long thin legs.

On the other hand, some water scavenger beetles with robust body and enough thick (probably digging) tibiae could be inhabitants at the water's edge. Finally, the remaining hydrophylids from this staff with streamlined shaped and a large body and also with heavily sclerotized integument could be rather eurybiontic in their ecology, mainly living in shallow water with tight thickets of water plants. Thus, it can be admitted that water basins of Yixian were maintaining rich and diverse ecosystems, making the existence of so many predators possible. In addition a higher predator was not among beetles because the latter does not show any superdominating species to define a kind of taphocenoses (like *Coptoclava longipoda* or *Daohugounectes primitivus* in other deposits).

The terrestrial Polyphaga are represented mostly by groups from the infraordera Staphyliniformia and Elateriformia, and only some groups of the superfamily Tenebrionoidea got a rather significant representation in Yixian. The remaining superfamilies are comparatively rare. There are several hundreds of specimens of many subfamilies of rove beetles (Staphylinidae) and nearly half of them are attributed to the subfamily Oxytelinae Fleming, 1821. The second by representation in this source is the subfamily Tachyporinae MacLeay, 1825 and among the remainder few specimens of each of the subfamilies Staphylininae, Olisthaerinae C.G. Thomson, 1858 and Oxyporinae Fleming, 1821 can be surely recognized, although many prints remain without a subfamily determination.

Other Staphyliniformia include a unique specimen of the family Silphidae Latreille, 1807 (subfamily Silphinae) and rather rich Scarabaeoidea, unexpectedly numerous in specimens and number of groups with different taxonomic rank. The family Lucanidae is rather abundant with representatives of the subfamilies Aesalinae and Syndesinae. Particularly, many stag beetles belong to the tribe Ceruchini LeConte, 1862 with general appearance very similar to species of the recent genus *Ceruchus* Macleay, 1819 with forked subapical teeth on protibia (as that in recent Platycerini Mulsant, 1842). Some lucanid-like specimens

need to be studied in more detail to clarify whether they should be regarded as two to three new separate families close to Lucanidae or subfamilies in composition of the Lucanidae. Besides, the following scarabaeoid families have been recorded: Lithoscarabaeidae Nikolajev, 1992; Pleocomidae LeConte, 1861; Trogidae (subfamily Troginae); Ochodaeidae Mulsant et Rey, 1871; Hybosoridae (subfamilies Hybosorinae and Ceratocanthinae Martinez, 1968); Glaphyridae MacLeay 1819 (many specimens of some genera); Glaresidae Kolbe, 1905; Trogidae (probably genus *Cretomorgus* Nikolajev, 2007); Geotrupidae (*Trypocopris sp.*); Scarabaeidae (subfamilies; Cretoscarabaeinae Nikolajev, 1995; Melolonthinae Leach, 1819 etc.). The enormous number of prints of Scarabaeoidea in this locality presents a unique feature of it. The overwhelming majority of them seemed to have larvae inhabiting more or less decomposed wood after a long period of decay, while larvae dwelling in soil, perhaps, were comparatively rare.

The superfamily Scirtoidea was represented in Yixian mostly by specimens similar to those of the genus *Mesocinetes* Ponomarenko, 1986, also by some very Scirtid-like forms with more or less large metafemora.

The Elateriformian superfamilies Elateroroidea, Buprestoidea and Byrrhoidea are more numerous in Yixian than any other infraordera of Polyphaga. Most specimens should be regarded as members of Elateridae, Lasiosynidae and Cerophytidae, each of which shares a comparable proportion among other fossils. All these families include few species that join most prints from each of them. Such dominant species in the family Elateridae are *Cryptocoelus major* Dolin et Nel, 2002. The most abundant species of Cerophytidae (Chang et al., 2010) is more similar to representatives from the Lower and Middle Jurassic than those from Cainozoic and Recent faunas. The Buprestidae are smaller in number and, nevertheless, among prints of this family there is a series of conspecific specimens consisting of the majority of them. The superfamily Byrhoidea is not very large in number of specimens collected in Liaoning, although it seems somewhat more diverse in number of families than the remaining superfamilies of Elateriformia. For now, true Byrrhidae and Ptilodactylidae Laporte, 1836 and also those somewhat similar to Chelonariidae Blanchard, 1845 have already been defined. Many Jurassic members of this superfamily, like other Elateriformia, seem to be associated with wood rather than water basins. However, one species from Yixian, which can be put in the formal genus (morphogenus) *Heterocerites* Ponomarenko, 1986 (proposed for the species of Heteroceridae MacLeay, 1825 from Myangad from the Lower Cretaceous, Western Mongolia), has a peculiar body shape and digging anterior legs. These features should be interpreted as adaptations for life in soppy and rich soil at the water's edge.

The superfamily Cleroidea is rather numerous, but most representatives are closely related to the family Peltidae, although at least one species of the family Cleridae Latreille, 1802 and also only few species similar to recent groups of Trogossitidae and Parandrexidae were also recorded. The Peltid-like species, which are more or less similar to *Nitidulina eclavata* Martynov, 1926 from the Uppermost Jurassic Karatau (Kazakhstan), are comparatively common and diverse. Most of them could be in their trophics to a certain degree xylomycetophagous. One print found looked like a member of Melyridae Leach, 1815. Another Cleroid print has the dentate tibiae somewhat reminiscent of tibiae of recent members of Dasytidae Laporte de Castelnau, 1840.

The superfamily Tenebrionoidea is rather numerously represented mostly by Tenebrionidae Latreille, 1802 (particularly many members of the subfamilies Alleculinae Laporte, 1840 and Diaperinae Latreille, 1802). As most of the forest darkling beetles had more chances to come in deposited sediments, it could be expected that they are registered in the fossil records in a first turn, while darkling beetles that were associated with soil mostly remain unregistered in our data. Besides, many Mordellid-shaped representatives should be considered as members of the family Scraptiidae Mulsant, 1856 and Melandryidae Leach, 1815, although some Mordellidae seemed to be present in Yixian (Jehol) biota as well (some of them already described as Premordellinae: Liu et al., 2007). At the same time, some of these prints look like Rhipiphoridae Gemminger et Harold, 1870 rather than Mordellidae not only because of the not clearly acuminate abdominal apex, but also because of a very movable head with very serrate to pectinate or nearly flabellate antennae. Most specimens of Tenebrionoidea remain unnamed and even without a family attribution. Nevertheless, some species of the family Pyrochroidae Latreille, 1807 found are rather different and demonstrating a rather great variability of this group at the end of the Jurassic.

The phytophagous beetles recorded in Yixian have some peculiar features. One such very important feature is the presence of the Chrysomeloidea. This superfamily includes the families Cerambycidae Latreille, 1802 and Chrysomelidae Latreille, 1802. The first family is represented by only members of the subfamily Prioninae Latreille, 1802, one of which could not be put in any tribe proposed for the recent groups of it. The most specimens of leaf beetles recorded in Yixian belong to the same new genus, which is very different from all representatives of Protoscelinae Medvedev, 1968 and also from the subfamilies used for the recent species (which could be related to Aulacoscelinae Chapuis, 1874). One species of Yixian leaf beetles looks like an aberrant form of the subfamily Hispinae Gyllenhal, 1813. The next important character is the composition of the superfamily Curculionoidea, which consists only of long-rostrate species of the more archaic families Nemonychidae Bedel, 1881; Belidae Schönherr, 1826 and Ithyceridae Schönherr, 1823 (formerly regarded as the separate paleoendemic Mesozoic family Eccoptarthridae Arnoldi in Arnoldi, Zherikhin, Nikritin et Ponomarenko, 1977 and later synonymized with Ithyceridae: see Legalov, 2009).

5 Taxonomic Notes

5.1 On position of the genus *Sinorhombocoleus* Tan et Ren, 2009

Tan and Ren (2009) "modified" the diagnosis for Paleozoic family Rhombocoleidae Rohdendorf, 1961 and included the genus *Sinorhombocoleus* in this family without explanation as to the kind of modifications that were made by them and what reason

was taken by them to put this Jurassic genus into the Palaeozoic family. Indeed the family Rhombocoleidae with rather peculiar shape of elytra and their characteristic sparse puncturation was recorded exclusively from the Permian, although some Triassic forms from Australia demonstrate some similarity to them (Rohdendorf, 1961; Ponomarenko, 1969; Ponomarenko and Mostovski, 2005; Ponomarenko and Kirejtshuk, 2008 etc.). All characters of the genus under consideration are quite correspondent with those of Schizophoridae, particularly in the structure elytra of the specimens with comparatively dense columellae not arranged in longitudinal rows. The Rhombocoleidae can be considered as Protocoleoptera (including Archecoleoptera: Crowson, 1975, 1981; Kirejtshuk, 1992, Kirejtshuk, 2010 etc.) or Archostemata (above mentioned publications by Rohdendorf and Ponomarenko).

5.2 On synonymy of *Notocupes* Ponomarenko, 1964; *Sinocupes* Lin, 1976, syn. nov.; *Amblomma* Tan, Ren et Liu 2005, syn. nov.; *Euryomma* Tan, Ren et Shih 2006, syn. nov., non Stein, 1899 (Diptera) and *Ovatocupes* Tan et Ren, 2006, syn. nov.

The name *Euryomma* was first proposed for flies of the family Fanniidae (*Euryomma* Stein, 1899 (type species: *Anthomyia peregrina* Meigen, 1826 (=*Euryomma hispaniense* Stein, 1899) by monotypy). The proposal by Jingjing Tan and Dong Ren created a new homonymy. At the same time all species considered by these authors in composition of *Sinocupes, Amblomma* (not *Amblyomma* Koch, 1844 from the family Ixodidae (Arachnida)), *Euryomma*, and *Ovatocupes* are members of the same genus, which seems to be called *Notocupes* Ponomarenko, 1964 or *Zygadenia* Handlirsch, 1909 (Ponomarenko, 2006); however, the first was described after study of more or less complete bodies of beetles, while the second was proposed only for elytra and should be regarded as a formal morphogenus (because it is still unsolved if the elytra of the second belongs to the species congeneric with those initially considered in the composition of the first). The development of prosternal intercoxal process in the species of the "genera" is not a reliable character, because in some cases this process covering conjoined procoxae can be present in prints, but in other cases can be broken and missing. The group, for which the names *Notocupes*, *Sinocupes, Amblomma*, *Euryomma*, and *Ovatocupes* were treated, is rather abundant in many Mesozoic taphocenoses and characterized by a peculiar venation of their elytra with doubled rows of cells between veins; however, proportions between proximal antennomeres used to erect "new" genera are rather variable and also insufficient, although this character was used as a diagnostic character to discriminate *Notocupes* and *Rhabdocupes* Ponomarenko, 1966 in addition to the shape of pronotum and structure of the underside of head.

5.3 On synonymy of *Tetraphalerus* Waterhouse, 1901 and *Odontomma* Tan, Ren et Ge, 2006, syn. nov.

The species described as the member of *Odontomma* was erroneously interpreted, when it was first proposed by the descriptors, and does not show any group hiatus from *Tetraphalerus* in order to consider it separately. This group has a rather great variability in shape of head and other structures.

5.4 On synonymy of *Priacmopsis* Ponomarenko, 1966 and *Latocupes* Tan et Ren, 2006, syn. nov.

The species described as members of *Latocupes* and *Priacmopsis* were erroneously interpreted, when *Latocupes* was first proposed by the descriptors, and as a result *Priacmopsis* was applied in a wrong meaning to the species with unclear generic attribution, while for true members of it was proposed the new taxon.

5.5 On position of the genus *Cervicatinius* Tan, Ren et Shih, 2007

This genus was proposed by Tan Jingjing and Ren Dong with Chung Kun Shih (2007) in composition of the family Catiniidae (Archostemata); however, it does not have any archostematan character mentioned by the descriptors (see pictures, but not incorrect drawings and description in Jingjing Tan et al. 2007) and should be certainly put into the family Peltidae from Cleroidea (suborder Polyphaga) because of its general appearance, slightly clubbed antennae, pronotosternal sutures, strongly transverse procoxae with exposed trochantin, mesocoxal cavities not joined with the medioanterior angle of metepisterna, metacoxae somewhat oblique.

5.6 On position of the genus *Forticatinius* Tan, Ren et Shih, 2007

This genus was also proposed by Jingjng Tan and Dong Ren with Chung Kun Shih (2007) in composition of the family Catiniidae (Archostemata); however, it, as *Cervicatinius*, does not have any archostematan character mentioned by the descriptors (see pictures, but not incorrect drawings and description in Tan et al. 2007) and should be considered as a member of the superfamily Cleroidea (suborder Polyphaga) because of its general appearance, pronotosternal sutures, strongly transverse procoxae, mesocoxal cavities not joined with the medioanterior angle of metepisterna, metacoxae somewhat oblique. *Forticatinius elegans* Tan, Ren et Shih, 2007 (type species of the genus) is very similar to species of *Nitidulina eclavata.* Therefore, *Forticatinius* seems to represent a junior generic synonym of *Nitidulina* Martynov, 1926.

5.7 On position of the genera *Lasiosyne* Tan, Ren et Shih, 2007; *Brachysyne* Tan et Ren, 2009 and *Papisyne* Tan et Ren, 2009

All these taxa were first proposed in the composition of the archostematan family Ademosynidae, perhaps, because of the completely wrong descriptions and incorrect drawings in the original publication. After the recent re-study of the type specimens these taxa were transferred from the suborder Archostemata to Polyphaga and the family Lasiosynidae in the infraorder Elateriformia was described (Kirejtshuk et al., 2010).

5.8 On position of the family Parandrexidae Kirejtshuk, 1994

This paleoendemic Mesozoic family was initially regarded as closely related to Cucujoidea (Kirejtshuk, 1994b) mostly because

of their not prominent and strictly transverse pro- and metacoxae as well as of some more or less clear adaptations to "anthophilous" mode of life, partly similar to those in recent sap beetles (Nitidulidae Latreille, 1802). However, new materials on this family from Siberian, Mongolian and Chinese late Mesozoic sites, which will be described in further publications of the authors, demonstrate some "transitional" conditions in both thoracic structures and expression of slow growth of "anthophilous" adaptations in transformational rows of characters in some groups of archaic Cleroidea which should be partly regarded in the composition of the family Peltidae and maintenance of some "Peltoid" features in the forms, which are reasonable to consider as Parandrexidae rather than Peltidae because of the characteristic structure of head with appendages and prothoracic segment.

5.9 On position *Montsecanomalus* Soriano, Gratshev et Delclos, 2006 and *Abrocar* Liu et Ren, 2006

The family name Eccoptarthridae Arnoldi in Arnoldi, Zherikhin, Nikritin et Ponomarenko, 1977 was synonymized with Nemonychidae by Legalov (2009), although the genera *Montsecanomalus* and *Abrocar* should be regarded as members in the family Ithyceridae (see also: Ponomarenko and Kirejtshuk, 2010).

6 Discussions and Conclusions

As a result of the studies in collections of the Capital Normal University (Beijing) and Institute of Geology and Paleontology of the Chinese Academy of Sciences (Nanjing) some families, subfamilies and tribes were first registered in the Mesozoic Sperchopsini and Hydrophilini from Hydrophilidae, Silphidae, Syndesinae from Lucanidae, Pleocomidae, Trogidae, Trogissitidae, Pyrochroidae, Diaperinae from Tenebrionidae, Cerambycidae and also some families were defined as new. Among others, the family Lasyosynidae (one of the most common families of the Late Mesozoic of the suborder Polyphaga) has been recently described. Besides, the Aesaliinae from Lucanidae, Hybosoridae, Ochodaidae, Ptilodactylidae, Heteroceridae, Chelonariidae, Scraptiidae, Melandryidae have already been found in different sites with Cretaceous age, including Lebanese amber of the Barremian-Lower Aptian and Baissa of the Middle Neocomian (Zaza Formation) (Ponomarenko and Kirejtshuk, 2010), although findings of the mentioned groups in Yixian seem to be the oldest records of them.

The considerable part of the composition of Coleoptera in both Daohugou and Liaoning belong to the characteristic Mesozoic groups with the family taxonomic rank, particularly many groups of the suborder Archostemata (Cupedidae, Tricoleidae and Schizophoridae), some groups of Adephaga (Coptoclavidae and subfamily Eodromeinae from Trachypachidae) and Polyphaga (Lithoscarabaeidae, Lasiosynidae and Parandrexidae). Many groups of the suborder Adephaga (Dytiscidae) and infraordera Staphyliniformia (many subfamilies from Staphylinidae, Silphidae, Lucanidae, Pleocomidae, Trogidae, Geotripidae, Ochodaidae, Hybosoridae, Glaphyridae, Glaresidae, Scarabaeidae) and Elateriformia (some groups of Scirtoidea, Buprestidae, Cerophytidae, Heteroceridae, Ptilodactylidae, Trogossitidae, Cleridae) represented in the recent fauna were appearing within the Middle Jurassic and Early Cretaceous, while only a few groups of the Cucujiformia (Trogossitidae, Tenebrionidae, Scraptiidae, Mordellidae, Melandryidae, Pyrochroidae, Chrysomelidae and Cerambycidae) and Curculioniformia (Nemonychidae, Belidae and Ithyceridae=Eccoptarthridae) were found in the materials from Yixian. The materials examined confirm the hypothesis that Cucujiformian beetles are a younger group among other infraordera of Polyphaga and, therefore, they appeared in the fossil record only in the late Mesozoic. This interpretation is in accordance with other comparisons of morphological and paleontological data (Kirejtshuk, 1992 etc.) and only partly with some molecular comparisons (Hunt et al. 2007 etc.). Besides, the materials examined support also the hypothesis that the superfamily Cucujoidea, in contrast to the traditional viewpoint, should be regarded as the group much younger than Tenebrionoidea, Chrysomeloidea and Curculionoidea (Kirejtshuk, 1994a, 1996 etc.). The first was registered only beginning from the Cretaceous, but the last mentioned are regularly recorded in the end of the Jurassic.

Ecological circumstances of the Mesozoic communities, which could be traced after the last studies of Coleoptera in the taphocenoses of Daohugou and Yixian, show clear links of terrestrial beetles mainly with forest habits and those of water beetles with shallow water and tight thickets of water plants. Perhaps, all Archostemata and most terrestrial Polyphaga (Scarabaeoidea, Lasiosynidae, Elateroidea, Buprestoidea, Byrrhoidea and Cleroidea) are associated with subcortical interspaces and probably dead timber. A more or less open more of life on surface of substrate seemed to be characteristic of adults of many terrestrial Adephaga, some Staphylinidae and also some Tenebrionoidea, Chrysomeloidea and Curculionoidea, although larvae of them could have developed inside substrate. "Anthophilous" beetles represented by Parandrexidae seemed to be not common, although some Scarabaeoidea could have xylomycetophagous larvae and adults able to visit generative organs of plants (gymnosperms and proangiosperms). Some phyllophagous forms from Chrysomelidae appeared at the boundary of the Jurassic and Cretaceous.

The composition of Coleoptera in the taphocenoses can be evident in the Upper Jurassic rather than Lower Cretaceous age of these deposits in accordance with the data on mayflies from the terminal Jurassic sites of Transbaikalia and Mongolia. The absence of most groups of the infraorder Cucujifoma and in particular of any group of the superfamily Cucujoidea (see above) supports this conclusion.

Acknowledgements

The authors are greatly thankful to V.K. Odnosum (Institute of Zoology of Ukrainian Academy of Sciences, Kiev, Ukraine), A. Yu. Moseyko (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia) and Yanli Yue (Capital Normal

University, Beijing, China) for their assistance in determination of the specimens used for preparation of this paper (Staphylinidae, Scarabaeoidea, Mordellidae, Scraptiidae and Melandryidae). The senior author greatly appreciates Andre Nel (Museum National d'Histoire Naturelle, Paris) for the possibility to conduct research in the Paris Museum, and also to him and Antoine Mantilleri (Paris Museum) for their assistance in comparison of the fossils here described with other fossils and recent representatives of the Elateriformia. He is also greatly thankful to Maxwell Barclay (Natural History Museum in London) for the opportunity to make important comparisons in the London Museum. This work was supported by the National Natural Science Foundation of China (No. 40872022), Nature Science Foundation of Beijing (No. 5082002), the PHR (IHLB) Project of Beijing Municipal Commission of Education and the Programme of the Presidium of the Russian Academy of Sciences "Origin and Evolution of Biosphere" and Russian Foundation of Basic Research (grants 07-04-92105-GFEN_a and 09-04-00789-a).

Manuscript received Jan. 4, 2010
accepted April 12, 2010
edited by Jiang Shaoqing

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Appendix. List of described taxa from the materials considered

1 Daohugou (Jiulongshan Formation)

Family Cupedidae Laporte, 1836

Brochocoleus Hong, 1982 (=*Diluticupes* Ren, Lu, Guo et Ji, 1995): *magnus* Tan et Ren, 2009; *validus* Tan et Ren, 2009; *applanatus* Tan et Ren, 2009.

Gracilicupes Tan, Ren et Shuh, 2006: *crassicruralis* Tan, Ren et Shuh, 2006; *tenuicruralis* Tan, Ren et Shuh, 2006.

Mesocupes Martynov, 1926: *angustilabialis* Tan, Huang et Ren, 2007; *latilabialis* Tan, Huang et Ren, 2007; *collaris* Tan, Huang et Ren, 2007.

Family Tricoleidae Ponomarenko, 1969

Loculitricoleus Tan et Ren, 2009: *tenuatus* Tan et Ren, 2009; *flatus* Tan et Ren, 2009.

Family Schizophoridae Ponomarenko, 1968

Homocatabrycus Tan, Ren et Shih, 2007: *liui* Tan, Ren et Shih, 2007.

Menopraesagus Tan, Ren et Shih, 2007: *oxycerus* Tan, Ren et Shih, 2007; *explanatus* Tan, Ren et Shih, 2007; *grammicus* Tan, Ren et Shih, 2007.

Family Coptoclavidae Ponomarenko, 1961

Daohugounectes Wang, Ponomarenko et Zhang, 2009: *primitivus* Wang, Ponomarenko et Zhang, 2009.

Family Elateridae Leach, 1815

Paradesmatus Chang, Kirejtshuk et Ren, 2009: *baie* Chang, Kirejtshuk et Ren, 2009; *ponomarenkoi* Chang, Kirejtshuk et Ren, 2009.

Paraprotagrypnus Chang, Zhao & Ren, 2009: *superbus* Chang, Zhao et Ren, 2009.

Protagrypnus Dolin, 1973: *robustus* Chang, Kirejtshuk et Ren, 2009.

Family Lasiosynidae Kirejtshuk, Chang, Ren et Shih, 2010

Anacapitis Yan, 2009 (*Brachysyne* Tan et Ren, 2009): *plata* (Tan et Ren, 2009) (*Brachysyne*).

Bupredactyla Kirejtshuk, Chang, Ren et Shih, 2010: *magna* Kirejtshuk, Chang, Ren et Shih, 2010.

Lasiosyne Tan, Ren et Shih, 2007 (Ademosynidae) [=*Pappisyne* Tan et Ren, 2007) ((Ademosynidae)]: *euglyphea* Tan, Ren et Shih, 2007 [=*eucallus* Tan et Ren, 2009 (*Pappisyne*); *lasiospatha* Tan et Ren, 2009 (*Pappisyne*)]; *daohugouensis* Kirejtshuk, Chang, Ren et Shih, 2010; *fedorenkoi* Kirejtshuk, Chang, Ren et Shih, 2010; *gratiosa* Kirejtshuk, Chang, Ren et Shih, 2010; *quadricollis* Kirejtshuk, Chang, Ren et Shih, 2010.

Tarsomegamerus Zhang, 2005 (Chrysomelidae): *mesozoicus* (Zhang, 2005).

Family Peltidae Kirby, 1837

Cervicatinius Tan, Ren et Shih, 2007: *complanus* Tan, Ren et Shih, 2007(Catiniidae).

2 Liaoning (Yixian Formation)

Family Cupedidae Laporte, 1836

Subfamily Ommatinae Sharp et Muir, 1912

Brochocoleus Hong, 1982 (=*Diluticupes* Ren, Lu, Guo et Ji, 1995): *angustus* Tan, Ren et Shih, 2007; cervicalis Tan, Ren et Shih, 2006; *planusculus* Tan, Ren et Shih, 2006; *sulcatus* Tan, Ren et Shih, 2007.

Notocupes Ponomarenko, 1964 (=*Chengdecupes* Hong, 1983; *Conexicoxa* Lin, 1986; *Forticupes* Hong, 1990; *Picticupes*

Hong, 1990; *Lupicupes* Ren, Lu, Guo et Ji, 1995; *Sinocupes* Lin, 1976, **syn. nov.**; *Amblomma* Tan, Ren et Liu, 2005, **syn. nov.**; *Euryomma* Tan, Ren et Shih, 2006, **syn. nov.,** non Stein, 1899; *Ovatocupes* Tan et Ren, 2006, **syn. nov.**): *alienus* (*Ovatocupes*) (Ren, 2005); *cyclodontus* Tan, Ren et Shih, 2006, **comb. nov.** (*Amblomma*); *epicharis* (Tan, Ren et Liu 2005), **comb. nov.** (*Amblomma*); *eumeurus* Tan, Ren et Shih, 2006, **comb. nov.** (*Amblomma*); *lentus* (Ren, Lu, Guo et Ji, 1995), **comb. nov.** (*Tetraphalerus*); *minisculus* Tan, Ren et Shih, 2006, **comb. nov.** (*Amblomma*); *porrectus* Tan, Ren, Shih, 2006, **comb. nov.** (*Amblomma*); *protensus* (Tan, Ren et Shih, 2006), **comb. nov.** (*Amblomma*); *psilatus* (Tan, Ren et Liu, 2005), **comb. nov.** (*Amblomma*); *rudis* (Tan, Ren et Liu, 2005), **comb. nov.** (*Amblomma*); *stabilis* (Tan, Ren et Liu, 2005), **comb. nov.** (*Amblomma*); *tylodes* (Tan, Ren et Shih, 2006), **comb. nov.** (*Euryomma*); *validus* Lin, 1976 (*Sinocupes*); sp. (*Ovatocupes*) (Tan et Ren, 2006).

Tetraphalerus Waterhouse, 1901 (=*Odontomma* Tan, Ren et Ge, 2006, **syn. nov.**): *curvinervis* Tan, Ren et Shih, 2007; T. *laetus* Lin, 1976; *latus* Tan, Ren et Shih, 2007; *trachylaenus* (Tan, Ren et Ge, 2006), **comb. nov.** (*Odontomma*).

Cionocoleus Ren, 1995: *cervicalis* Tan, Ren et Shih, 2007; *planusculus* Tan, Ren et Shih, 2007.

Subfamily Cupedinae Laporte,1836

Priacma Leconte, 1874: *clavata* Tan, Ren et Shih, 2006; *latidentata* Tan, Ren et Shih, 2006; *renaria* Tan, Ren et Shih, 2006; *tuberculosa* Tan, Ren et Shih, 2006.

Priacmopsis Ponomarenko, 1966 (Latocupes Tan et Ren, 2006, **syn. nov.**): *bella* (Tan et Ren, 2006), **comb. nov.** (Latocupes); *fortis* (Tan et Ren, 2006), **comb. nov.** (*Latocupes*).

Furcicupes Tan et Ren, 2006: *raucus* Tan et Ren, 2006.

Subfamily uncertain (subfamilia incerta)

"***Priacmopsis***" (**gen. incertus**): *subtilis* Tan et Ren, 2006.

Family Schizophoridae Ponomarenko, 1968

Sinorhombocoleus Tan et Ren, 2009: *papposus* Tan et Ren, 2009 (Rhombocoleidae).

Family Staphylinidae

Glabrimycetoporus Yue, Zhao et Ren 2009: *amoenus* Yue, Zhao et Ren 2009.

Sinoxytelus Yu, Zhao et Ren, 2009: *breviventer* Yu, Zhao et Ren, 2009; *euglypheus* Yu, Zhao et Ren, 2009; *longisetus* Yu, Zhao et Ren, 2009

Family Geotrupidae Latreille, 1802

Trypocopris Motschulsky, 1859: sp. (Nikolajev, 2008).

Familia incerta: Scarabaeoidea

Geotrupoides Handlirsch, 1906: *songyingziensis* Hong, 1984 (Geotrupidae).

Family Elateridae Leach, 1815

Subfamily Protagrypninae Dolin, 1975

Bilinearisela**ter** Chang et Ren, 2008: *foveatus* Chang et Ren, 2008 .

Curtelater Chang et Ren, 2008: *wui* Chang et Ren, 2008.

Lithomerus Dolin, 1980: *buyssoni* Dolin et Nel, 2002.

Paralithomerus Chang, Zhang et Ren, 2008: *exquisitus* Chang, Zhang et Ren, 2008: *parallelus* Chang, Zhang et Ren, 2008.

Subfamily Agrypninae Candeze, 1857

Cryptocoelus Dolin et Nel, 2002: *buffoni* Dolin et Nel, 2002; *giganteus* Chang, Ren et Shin, 2008; *major* Dolin et Nel, 2002.

Family uncertain (familia incerta): Cleroidea: near Peltidae

Forticatinius Tan, Ren et Shih 2007: *elegans* Tan, Ren et Shih 2007 (Catiniidae).

Family Mordellidae (=Liaoximordellidae Wang, 1993)

Bellimordella Liu, Zhao et Ren, 2007: *capitulifera* Liu, Zhao et Ren, 2007; *longispina* Liu, Zhao et Ren, 2007; *robusta* Liu, Zhao, Ren, 2007.

Liaoximordella Wang, 1993: *hongi* Wang, 1993.

Mirimordella Liu, Lu et Ren, 2007: *gracilicruralis* Liu, Lu et Ren, 2007.

Family Nemonychidae Bedel, 1881 (=Eccoptarthridae Arnoldi in Arnoldi, Zherikhin, Nikritin et Ponomarenko, 1977)

Chinocimberis Legalov, 2009: *angustipectoris* (Liu, Ren et Tan, 2006) (*Brenthorrhinoides*); *magnoculi* (Liu, Ren et Tan, 2006) (*Brenthorrhinoides*).

Renicemberis Legalov, 2009: *latipecteris* (Liu, Ren et Tan, 2006) (*Brenthorrhinoides*).

Family Belidae Schoenherr, 1826

Microprobelus Liu, Ren et Shih, 2006: *liuae* Liu, Ren et Shih, 2006 (*liuai*).

Family Ithyceridae Schoenherr, 1823

Montsecanomalus Soriano, Gratshev et Delclos, 2006: *polychaetus* (Liu et Ren, 2007) (*Leptocar*); *punctatus* Liu et Ren, 2006 (*Cretonanophyes*); zherichini (Liu et Ren, 2006) (*Cretonanophyes*) (Eccoptarthridae).

Abrocar Liu et Ren, 2006: brachyorhinos Liu et Ren, 2006; macilentus Liu et Ren, 2007 (Eccoptarthridae).