



New fossil taxa and notes on the Mesozoic evolution of Liadytidae and Dytiscidae (Coleoptera)

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Abstract

The diagnoses of Liadytidae Ponomarenko, 1977, Liadytiscinae Prokin & Ren, 2010, *Liadytiscus* Prokin & Ren, 2010 and *Mesoderus* Prokin & Ren, 2010 (Dytiscidae) are modified, and the following new taxa are described from Mesozoic fossils: *Liadytes aspidytoides* **sp. n.** (Liadytidae); Mesoderini trib. n., *Liadyxianus kirejtshuki* **gen. n. et sp. n.**, *Mesoderus punctatus* **sp. n.**, *Mesoderus ovatus* **sp. n.**, *Mesodytes rhantoides* **gen. n. et sp. n.**, *Palaeodytes baissiensis* **sp. n.** and *Cretodytes incertus* **sp. n.** (Dytiscidae). A summarized checklist of all Mesozoic Liadytidae and Dytiscidae known from adults is given, and an identification key to the genera of Mesozoic Dytiscidae known from adults is provided for the first time. *Palaeodytes incompletus* Ponomarenko, Coram & Jarzembowski, 2005 (the suffix of the specific epithet is emended from the original *incompleta*) is found to belong not to this genus, but to another one, which remains to be described. The fossil larva *Angaragabus jurassicus* Ponomarenko, 1963 from the Lower Jurassic of Irkutsk Oblast, Russia, probably belonging to Liadytidae, is re-examined. If this larva actually belongs to Liadytidae, then its morphological characters provide additional confirmation of the conclusion, based on the characters of adult liadytids, that the family is quite separate from the recent family Aspidytidae, and the similarity between the adults of both families results from parallel processes in the evolution of the superfamily Dytiscoidea. We show that the principal trends of morphological changes of Liadytidae and Dytiscidae during the Upper Jurassic and Lower Cretaceous included a consistent increase in the area of the metacoxal plates at the expense of decreasing area of the lateral lobes of the metaventrite ("wings"), flattening and loss of the lateral border of the elevated median area of the metaventrite, and shortening and dilation of the metafemur and metatibia. These changes were probably associated with an increased load of swimming taken by the hindlegs, which required, among other things, the development of swimming muscles attached to the metacoxal plates. The development of the hindlegs allowed diving deeper, thus being an adaptation to the nektonic instead of benthic lifestyle. This is confirmed by the adaptive coloration of the Liadytidae and Dytiscidae found in Shar Teg (*Liadytes aspidytoides* **sp. n.**), Yixian (*Mesoderus magnus* Prokin & Ren, 2010) and Baisa (*Palaeodytes baissiensis* **sp. n.**), in which the dorsum was darker than underside, providing camouflage in the depths of the water.

Key words: Liadytidae, Dytiscidae, Mesozoic, new taxa, evolution, swimming.

Introduction

Relatively little is known about the earlier stages in the evolution of the superfamily Dytiscoidea (Coleoptera: Adepaga), which includes several recent and several extant families of water beetles.¹ There is no consensus among specialists about the chronological order in which the major clades of Adepaga diverged. Possible

interpretations of paleontological data are in some cases ambiguous, and the results of molecular studies remain preliminary and in some instances contradictory.

Recently, beginning with the second half of the 20th century, a number of new taxa of Mesozoic Dytiscoidea have been described, including the fossil family Liadytidae Ponomarenko, 1977, the dytiscoid larvae *Angaragabus* Ponomarenko, 1963, the recent families Aspidytidae and Meruidae, and the following fossil taxa within the family Dytiscidae: *Cretodytes* Ponomarenko, 1977 (*C. latipes* Ponomarenko, 1977), *Palaeodytes* Ponomarenko, 1987 (*P. gutta* Ponomarenko, 1987, *P. sibiricus* Ponomarenko, 1987 and *P. incompletus* Ponomarenko, Coram & Jarzembowski, 2005²) (Ponomarenko 1987; Ponomarenko *et al.* 2005), and the subfamily Liadytiscinae Prokin & Ren, 2010, including the genera *Liadytiscus* Prokin & Ren, 2010 (*L. cretaceous* Prokin & Ren, 2010, *L. longitibialis* Prokin & Ren, 2010 and *L. latus* Prokin & Ren, 2010), *Liadroporus* Prokin & Ren, 2010 (*L. elegans* Prokin & Ren, 2010), *Mesoderus* Prokin & Ren, 2010 (*M. magnus* Prokin & Ren, 2010 and *M. ventralis* Prokin & Ren, 2010) and *Sinoporus* Prokin & Ren, 2010 (*S. lineatus* Prokin & Ren, 2010) (Prokin & Ren 2010).

We examined a number of new materials identified as Mesozoic members of the families Liadytidae and Dytiscidae and re-examined some specimens described earlier. This allowed us to improve the diagnoses of some taxa, describe a number of new ones, compile a checklist of all Mesozoic Dytiscidae and Liadytidae known from adults and provide for the first time a key to the genera of Mesozoic Dytiscidae known from adults. Another aim of this study was to elucidate the principal trends of morphological changes in the evolution of the Mesozoic Liadytidae and Dytiscidae, probably related to the increasing role of their hindlegs in locomotion, which accompanied the transition from crawling underwater to active swimming in the depths of the water. To place the taxa described here into appropriate context, we provide at the beginning of the Results section a brief overview of the current state of knowledge on the earlier evolution of aquatic Adephaga.

Material and methods

The fossils studied are from the following sites: **China:** Inner Mongolia, Liutiaogou village, ca. 41°30' N 118°55' E; Liaoning Province, Huanbanjigou, ca. 41°35' N 120°55' E, environs of Chaomidian village, Shangyuan, Beipiao city (both Early Cretaceous, Yixian Formation, ca. 124–122 mya: Chang *et al.* 2009). **Mongolia:** Gobi-Altai Province, Shar Teg, ca. 44°05' N 95°50' E (Late Jurassic, precise dating unclear: Gubin & Sinitza 1996). **Russia:** Republic of Buryatia, Baisa (alternatively transliterated as Baissa), ca. 53°17' N 112°02' E (Early Cretaceous, approximately Hauterivian, ca. 135 mya: Zherikhin *et al.* 1999); Transbaikalia, Chernovskiye Kopi (alternatively transliterated as Chernovskie Kopi), left bank of the Ingoda River, 51°59'16" N 113°16'30" E (Late Malm to Early Neocomian, Late Jurassic—Early Cretaceous, Doronino Formation: Sukatsheva & Vassilenko 2011).

The fossils studied are deposited in the collections of the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia (PIN); Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (NIGP); and Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Photographs of the fossils were taken with a Leica M165c stereomicroscope and a Leica DFC420 camera. The photograph of *Lancetes lanceolatus* (Clark, 1863) was taken with a Canon D-550 digital camera with an attached Canon MP-E65 mm f/2.8 1–5× macrolens and processed in Helicon Focus software. Scanning electron micrographs were taken with a Tescan Vega XMU scanning electron microscope.

We provide authors and dates of all species and genera when cited first; of tribes, families and superfamilies only if deemed necessary.

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1. The superfamily Dytiscoidea is understood here as comprising the following recent and extinct families (the latter are marked with †), listed in alphabetic order: Amphizoidae, Aspidytidae, †Colymbotethidae, †Coptoclavidae, Dytiscidae, †Liadytidae, Meruidae, Noteridae, Paelobiidae and †Parahygrobiidae.
 2. This species was originally described as *P. incompleta*, but the suffix of the specific epithet is emended here in accordance with the masculine gender of the generic name; however, this species actually belongs to another genus, which remains to be described. See under "*Palaeodytes*" *incompletus* at the end of the *Palaeodytes* section below.

Results

Overview of early evolution of aquatic Adephaga

For a long time early aquatic Coleoptera possibly lived underwater, but did not swim, and then gradually switched from benthic to nektonic lifestyle. The earliest water beetles of the suborder Adephaga (often called Hydradephaga, but we refrain from using this name, because it is likely that it denotes a paraphyletic group; see below) were probably also benthic. Some ecological forms of Mesozoic adephagan water beetles are extinct and have no recent analogues. For instance, in *Coptoclava longipoda* Ping, 1928 (Coptoclavidae Ponomarenko, 1961) both adults and larvae swam with their paddle-like mid- and hindlegs and caught their prey with the forelegs (the adults probably behaved like those of Gyrinidae, but the larvae of Gyrinidae are entirely different), and *Megacoptoclava longiurogompha* Ponomarenko & Martinez-Declos, 2000 (Coptoclavidae) had larvae with long crawling legs, like those plecopteran and ephemeropteran larvae that live on stones in fast-flowing rivers. The ecological diversity of beetles, including the aquatic Adephaga, became close to its recent state only after the end of the Paleogene (Ponomarenko 2003).

According to Ponomarenko (1977, 1992, 2002), the earliest branch of the clade comprising the suborder Adephaga would be the Haliploidea, as suggested by the structure of their abdominal base, wing folding and venation. This and other reconstructions of the phylogeny of Adephaga were reviewed by Beutel & Ribera (2005), with an addendum by Beutel *et al.* (2010).

It was proposed recently, on the basis of morphological comparison of extant taxa, that Gyrinidae constitute the basal sister group of the other Adephaga, Haliplidae being the sister clade of Geadephaga + Dytiscoidea, Noteridae the sister group of the rest of Dytiscoidea, Amphizoidae and Aspidytidae sister groups to each other, and Paelobiidae Erichson, 1837 (syn. Hygrobiidae Régimbart, 1879) forming one clade with Dytiscidae (Beutel *et al.* 2008). The basal position of Gyrinidae within Adephaga is also tentatively supported by the old age of this group, if an Upper Permian (currently considered Middle Permian) larva described as a member of Megaloptera (Sharov 1953) in fact belongs to Gyrinidae, as suggested by Beutel & Roughley (1988). The genus *Permosialis* Martynov, 1928, in which this larva was placed by Sharov (1953), was initially considered a member of Megaloptera, but it was later transferred to Miomoptera by Riek (1976), and thus could not have aquatic larvae; therefore, the name *Permosialis* should not be used for that larva, and it is referred to hereinafter as "*Permosialis*". The placement of the "*Permosialis*" larva in Gyrinidae could be supported by only a few characters: its narrow, elongate head and its narrow pronotum, distinctly smaller than meso- and metanotum (Beutel & Roughley 1988). The most important of these characters, pronotum distinctly smaller than meso- and metanotum, cannot be critical for identification of Oligoneoptera at the order level, because it is quite variable and could change in the course of larval development. But even if the "*Permosialis*" larva was coleopteran, it could well belong to a schizophoroid beetle (see below), and cannot be reliably placed in Gyrinidae.

In spite of the supposedly old age of Gyrinidae, they are known from no reliably identified fossils earlier than the extreme Early Jurassic. The earliest haliploids, Triaplidae Ponomarenko, 1977, are known from deposits close to the boundary between the Permian and Triassic (Volkov 2013). The earliest known beetle fossil very similar to the earliest dytiscoids was found in the Middle Permian (Lin *et al.* 2010) deposits of China (Yinping fossil site, Anhui Province: Di-Ying Huang & A.G. Ponomarenko, unpublished data). The earliest known caraboid is *Ademosynoides asiaticus* Martynov, 1937 (Trachypachidae), described (in the family Hydrophilidae) from the terminal Permian or basal Triassic deposits of the Kuznetsk Basin (Babiy Kamen' fossil site, alternatively transliterated as Babii Kamen'); their position was recently clarified by Volkov (2012). As for the "*Permosialis*" larva, it is too large for all known Permian and Triassic Adephaga, as well as for all known Permian Megaloptera. However, also at the Kargala fossil site, a very large schizophoroid beetle was found and described as *Rhombocoleites adumbratus* Ponomarenko, 1969 (Rhombocoleidae Rohdendorf, 1961). Aquatic larvae similar to "*Permosialis*" are rather common in the Middle Triassic Voltzia Sandstone of northeastern France (our unpublished observation based on photographs made by D.E. Shcherbakov, PIN), where adult schizophoroids are also abundant. Schizophoroids, in our opinion, probably gave rise to Myxophaga, some recent larvae of which have filamentous gills, and therefore it is possible that the "*Permosialis*" larva could actually belong to schizophoroid beetles. Therefore, it can be concluded that no palaeontological evidence supports the particularly early age of gyrinids.

The current data on the geological history of Adephaga suggest that Haliploidea, Gyrinoidea, Dytiscoidea and

Caraboidea (including Trachypachyidae), might have branched off the adepagan lineage more or less in this order; if this interpretation is correct, the so-called Hydradephaga are paraphyletic.

A recent large-scale study on the phylogeny of Coleoptera as inferred from three genes (Hunt *et al.* 2007) suggests that the earliest bifurcation of Adephaga was to the monophyletic Hydradephaga and (also monophyletic) Geadephaga, with the Hydradephaga subsequently divided into a clade of (Paelobiidae + Aspitytidae) + Dytiscidae (including *Amphizoa* LeConte, 1853, which emerged within Dytiscidae, being a sister group of the subfamily Hydroporinae) and another clade of Gyrinidae, Haliplidae, and Noteridae (branching off in this order). This topology, however, could be an analytical artefact. McKenna & Farrell (2009), who applied molecular clocks to the phylogeny of Coleoptera, presented the same structure of the Hydradephaga tree, based essentially on the same data, and concluded that the two clades separated in the Triassic, with the divergence of Gyrinidae and Haliplidae + Noteridae in the terminal Triassic, and the divergence of Haliplidae and Noteridae on the one hand and Dytiscidae (including *Amphizoa*) and Paelobiidae + Aspitytidae on the other hand in the Jurassic. Apparently, this tree is far from final, and its reconciliation with fossil data will require further investigations.

Descriptions of new taxa and notes on selected Mesozoic Liadytidae and Dytiscidae

Family Liadytidae Ponomarenko, 1977

Diagnosis (modified from Ponomarenko 1992, English translation of Ponomarenko 1977): Medium-sized aquatic beetles with oval, biconvex body. Head noticeably retraced into prothorax, scutellum visible. Mesocoxae located close to each other. Metepisterna reaching mesocoxal cavities. Metaventricle without anteromedial process protruding between mesocoxae, medially with elevated area sharply limited laterally. Anterior margin of metacoxae forming small median emargination bounded in front by extension of transverse metaventral suture. Legs slender and long. Metatibia not shorter than metafemur and metatarsus, very slender, linear. Tarsal segments not broad or paddle-shaped. Tibiae and tarsi with swimming setae.

Notes: A broad lateral part of the metathoracic praepisternum, a metathoracic anepisternum that reaches the mesocoxal cavities, and a transverse suture of the metaventricle characterize only two known families of Dytiscoidea: Liadytidae and Aspitytidae, the only observable difference between which listed by Balke *et al.* (2003) is the absence of swimming setae in Aspitytidae. This character is, in fact, insufficient for distinguishing between families of Dytiscoidea, because the families Noteridae, Dytiscidae and Coptoclavidae include members that vary in the state of this character. The characters most clearly distinguishing Aspitytidae from the other Dytiscoidea, configuration of the scapus and pedicellus (Ribera *et al.* 2002), are not discernible in the known species of Liadytidae.

The new species *Liadytes aspitytoides* sp. n. is placed here in Liadytidae, based on the age of the fossils and on their mesocoxae located close to each other and the absence of the anteromedial metaventral process. This character distinguishes all *Liadytes* from all *Aspitytes* Ribera, Beutel, Balke & Vogler, 2002 and is reported here for the first time. Since *Liadytes* and *Aspitytes* are the single genera in the respective families, we can use this character also for distinguishing between the Liadytidae and Aspitytidae.

The monotypic genus *Ovidytes* and species *O. gaoi* Ren, Zhu & Lu, 1995 were described in the family Liadytidae (Ren *et al.* 1995). We could not study the type material of this species, but judging by the relatively short non-swimming legs, shown in an illustration to the original description, *O. gaoi* can hardly belong to Dytiscoidea.

Genus *Liadytes* Ponomarenko, 1963

Type species: *Liadytes avus* Ponomarenko, 1963

Notes: This genus includes several known species, mainly from the Jurassic of Asia. A new species of the genus is described below.

Liadytes aspidytoides sp. n.

Etymology: From the generic name *Aspidytes*; adjective in the nominative singular.

Material: Holotype PIN 2470/942±, beetle without head, prothorax and legs; Shar Teg, Upper Jurassic, beds 441, layer 4; paratype 2470/945, less complete impression of beetle from the same locality, beds 451/3; additional specimen (cannot be identified with certainty, therefore not included in the type series) PIN 2470/938, isolated elytron from the same locality, beds 451/3.

Description (Figs. 1–5): Beetle with dark elytra, which appear black due to carbonisation of organic substance in oxygen-free environment, and pale body. Maximum body width situated at level of elytral base. Mesocoxae only slightly separated, rounded. Maximum length of metacoxal plate (measured parallel to longitudinal body axis) 1.2 times as great as maximum length of lateral lobe of metaventricle (measured in same manner)³. Anterior margin of metacoxa weakly convex (metacoxal plate dilated anteriorly). Elevated median part of metacoxae with sides more or less straight, slightly diverging posteriorly; metacoxal processes rounded posteriorly, with posterior margins meeting at an obtuse angle. Transverse suture of metaventricle present; median part of metacoxae elevated. Metepisternum 1.3 times as long as wide. Abdomen tapering from base of ventrite 4; ventrite 6 twice as long as ventrite 5. Elytron 3.4 times as long as wide. Epipleuron wide in its basal third, twice as wide as distally. Surface microsculpture of underside punctate, laterally on abdominal ventrites imbricate (according to Harris 1979).

Measurements: Body length, probably around 7 mm; body width, 3.1–3.7 mm; elytron length, 4.6–5.3 mm.

Comparison: The new species is similar to *L. crassus* Ponomarenko, 1977 in the convex anterior margins of the metacoxae (dilated anteriorly), but differs from it, as well as from the other species of *Liadytes*, in the presence of the elevated median part of the metacoxae (forming plates that partly cover the metafemora, as in *Aspidytidae* and *Noteridae*; these structures are, apparently, derived from the broader femoral plates of the metacoxae⁴, homologous to those found in *Haliplidae* and many members of *Geadephaga*).

Notes: The shape of femoral plates of the metacoxae and broad epipleuron of the new species are similar to those of *Aspidytes*, but the new species differs from it and from *Noteridae* in the mesocoxae located close to each other and in the absence of the anteromedial metaventral process (see above). The metacoxal plates dilated anteriorly are characteristic of *Aspidytidae* and *Liadytiscinae* (*Dytiscidae*) (see next section), but the new species differs from representatives of *Liadytiscinae* in the presence of the transverse suture on the metaventricle. Therefore, the new species is included here in the genus *Liadytes* (*Liadytidae*).

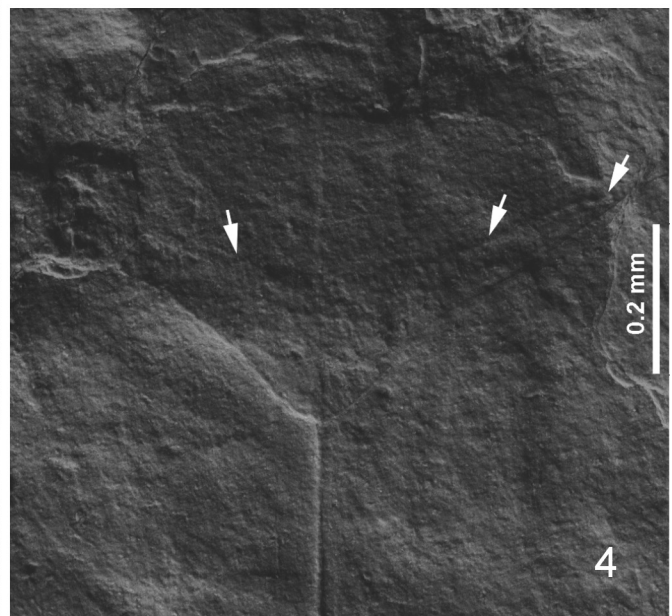
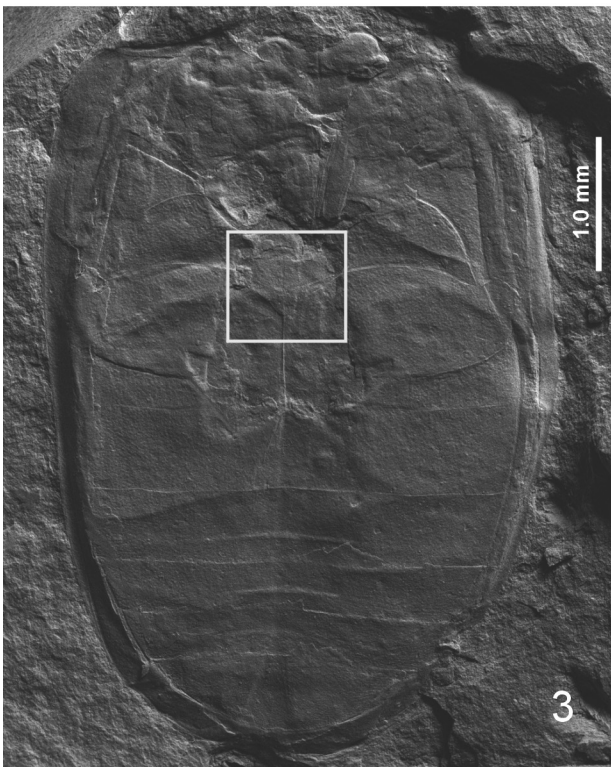
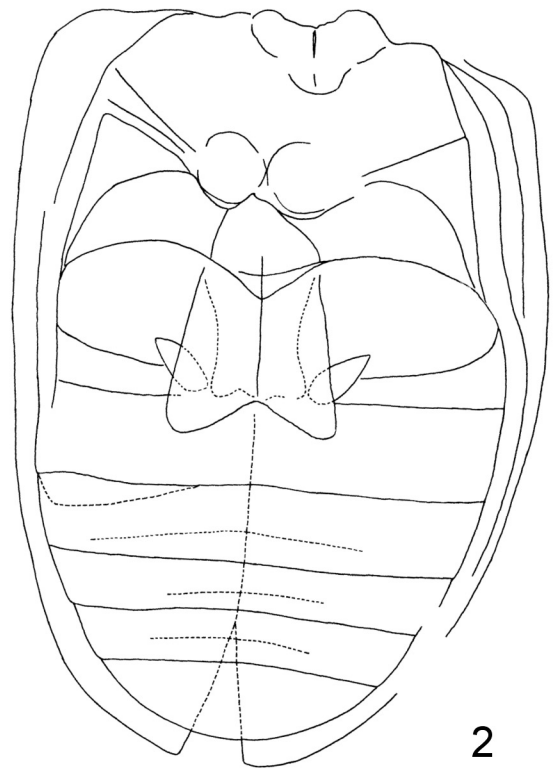
Family *Dytiscidae* Leach, 1815

Subfamily *Liadytiscinae* Prokin & Ren, 2010

Type genus: *Liadytiscus* Prokin & Ren, 2010.

Diagnosis (modified from Prokin & Ren, 2010): Medium-sized ovate beetles. Anterior margin of eye without incision. Scutellum visible. Elytron ovate, smooth, narrowed towards apex, without sulci or series of punctures,

3. Traditionally, another parameter is used to assess the relative proportions of the metacoxal plate and metaventral lobe, WC/WS, the ratio of the of the [meta]coxal plate, measured along the line perpendicular to the anterior margin of the plate at the narrowest point of the metaventral "wing", i.e., the lateral lobe of the metaventricle, and width of the "[meta]sternum" [i.e., metaventricle] (Fig. 22). We introduce here another similar parameter: ratio of the maximum lengths of the metacoxal plate and of the lateral lobe of the metaventricle (both measured longitudinally), which can be abbreviated as LC/LV. This parameter is more precise, because, according to our experience, WC/WS can vary as a result of slight deviations from the right angle between the line along which it is measured and the anterior margin of the metacoxal plate.
4. These structures are usually termed "femoral plates" in Russian literature (because they cover the metafemora), including Ponomarenko (1977) and the English translation of that work (Ponomarenko 1992). In English literature (e.g., Holmen, 1987: 67) the term "hind coxal plates" is used for *Haliplidae*. For *Dytiscidae*, however, the term "metacoxal plate", which should have the same meaning (hind coxa is the same thing as metacoxa), is used to denote the flat lateral part of the metacoxa (e.g., Nilsson & Holmen, 1995: 9). To avoid confusion, we use the term "femoral plate of metacoxa" to denote the structure that protrudes from the metacoxa laterally and partly or entirely covers the femur, and the term "metacoxal plate" as it is conventionally used in literature on *Dytiscidae*.



FIGURES 1–4. *Liadytes aspidytoides* sp. n.: (1) photo of holotype, (2) line drawing of holotype, (3) SEM photo of holotype, (4) SEM photo of details of metaventricle; arrows indicate metaventral suture.

without incision or spine apically. Pronotum not narrower than both elytra together, forming with them gently curved lateral outline. Procoxa and mesocoxa rounded. Metaventricle usually with elevated laterally limited area medially. Metacoxae transverse, slightly dilated anteriorly, with notch medially; maximum length of metacoxal plate (measured parallel to longitudinal body axis) subequal to maximum length (measured in same manner) of lateral lobe of metaventricle ($LC/LV \approx 1$). Metacoxal processes conjointly truncate or rounded posteriorly, with incision between them, not narrowing or narrowing anteriorly. Metafemur without linear series of setae, long; when stretched, reaching at least posterior margin of abdominal ventrite 3. Metatibia subequal in length to metafemur. Metatarsal claws equal.

Comparison: The morphology of the metacoxa of the subfamily Liadytiscinae is very similar to that of Liadytidae and Aspidytidae, but Liadytiscinae differ from members of these families in the absence of a transverse suture on the metaventricle.

Similar values of LC/LV , but with smaller absolute values of LV , are found in only three subfamilies of Dytiscidae: Colymbetinae, Agabinae, Dytiscinae and Lancetinae. The subfamily Liadytiscinae differs from Colymbetinae in the anterior margin of the eye without incision and equal metatarsal claws; from Agabinae, in the anterior margin of the eye without incision and absence of linear series of setae at the anteroventral angle of the metafemur; from Dytiscinae, in the smaller size and metacoxal processes not pointed apically; from Lancetinae (*Lancetes* Sharp, 1882), which have the metaventricle with a laterally limited elevated median area (Fig. 24), as in Liadytiscini Prokin & Ren, 2010 and *Mesoderus*, in the non-sinuate elytral apices and metatarsal claws equal in length. From the extinct *Palaeogyrinus* Schlechtendal, 1894 it differs in the absence of elytral sulci and in the shape of its legs, not resembling those of *Laccophilus* Leach, 1815. In addition, Liadytiscinae differ from all other subfamilies of Dytiscidae in the extremely long metafemur and metatibia.

Tribe Liadytiscini Prokin & Ren, 2010

Type genus: *Liadytiscus* Prokin & Ren, 2010.

Diagnosis (modified from Prokin & Ren, 2010): Pronotum with carina. Metacoxal lines weakly diverging anteriorly. Metacoxal processes conjointly truncate posteriorly, or rounded with incision between them, not narrowed or only slightly narrowed anteriorly. Maximum length of metacoxal plate subequal in length to maximum length of lateral lobe of metaventricle, making ratio of these two parameters $LC/LV \approx 1$. Metatibia narrow and long, longer than metafemur.

Liadyxianus gen. n.

Etymology: From the generic name *Liadytiscus* and Yixian Formation; gender masculine.

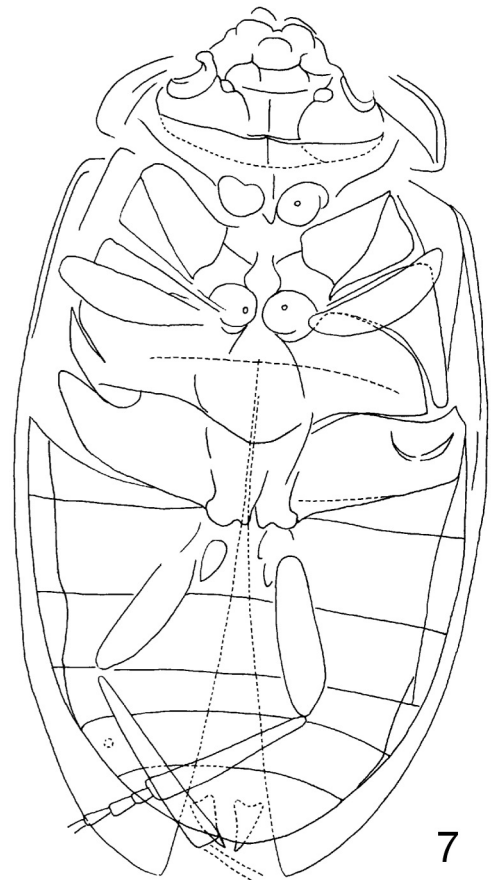
Type species: *Liadyxianus kirejtshuki* sp. n.

Diagnosis: Metacoxal plate somewhat shorter than lateral lobe of metaventricle (LC/LV slightly less than 1). Metaventricle with elevated rounded median area. Metacoxal lines weakly diverging anteriorly. Metacoxal processes more or less conjointly truncate posteriorly, with posterior margins appearing somewhat sinuate, with incision between them. Lateral lobe of metaventricle not reaching lateral margin of metepisternum and metacoxal plate. Hindleg long, equal in length to abdomen. Metafemur, when stretched, reaching posterior margin of abdominal ventrite 3; metatibia longer than metafemur. Abdominal ventrite 1 shorter medially than any other abdominal ventrite; ventrite 2 longer medially than any other abdominal ventrite.

Comparison: The new genus differs from *Liadytiscus* and *Liadroporus* in the shorter metafemur, when stretched, reaching posterior margin of ventrite 3, and metacoxa somewhat shorter than lobe of metaventricle. It differs from *Liadroporus* in the more or less conjointly truncate metacoxal processes.

Liadyxianus kirejtshuki sp. n.

Etymology: In honour of the coleopterist A.G. Kirejtshuk; noun in the genitive case.



FIGURES 5–7. (5) *Liadytes aspidytoides* sp. n., photo of specimen PIN 2470/945; *Liadyxianus kirejtszuki* sp. n.: (6) photo of holotype, (7) line drawing of holotype.

Material: Holotype MNHN A31864, counter impression of beetle; China, probably Huanbanjigou (label indicates only formation); Early Cretaceous, Yixian Formation.

Description (Figs. 6, 7): Light coloured beetle. Head triangular, 1.5 times as wide as long. Pronotum 3.6 times as wide as long, with posterolateral angles rounded. Maximum body width situated at level of abdominal ventrite 1. Mesocoxae located close to each other. Mesofemur not dilated basally. Maximum length of metacoxal plate 0.9 times as great as maximum length of lateral lobe of metaventrite ($LC/LV = 0.9$). Metacoxal processes more or less conjointly truncate, with posterior margins appearing somewhat sinuate, reaching posterior margin of abdominal ventrite 1. Metafemur with sides slightly rounded. Metatibia slightly dilated towards its apex, slightly longer than metafemur; metatarsomere 1 somewhat shorter than metatarsomeres 2 and 3. Abdominal tergite 4 with round spiracle dorsally.

Measurements: Body length, 7.4 mm; body width, 3.7 mm; elytron length, 5.9 mm.

Tribe Mesoderini trib. n.

Type genus: *Mesoderus* Prokin & Ren, 2010.

Diagnosis (modified from Prokin & Ren, 2010): Head partly sunk in pronotum. Metacoxal lines strongly diverging anteriorly. Metacoxal processes rounded posteriorly, somewhat narrowed anteriorly. Maximum length of lateral lobe of metaventrite relatively great, but maximum length of metacoxal plate more than 1.2 times as great as maximum length of lateral lobe of metaventrite ($LC/LV > 1.2$). Metatibia subequal in length to, or shorter than metafemur. Metafemur, when outstretched, reaching middle of abdominal ventrite 4.

Comparison: The new tribe is distinguished from Liadytiscini by the metacoxal lines strongly diverging anteriorly (weakly diverging in Liadytiscini), metacoxal processes slightly narrowed anteriorly (weakly narrowed or not narrowed in Liadytiscini), maximum length of the metacoxal plate more than 1.2 times as great as maximum length of the lateral lobe of the metaventrite (subequal in length, $LC/LV \approx 1$, in Liadytiscini), and metatibia subequal in length to or shorter than the metafemur (longer than the metafemur in Liadytiscini).

Mesoderus Prokin & Ren, 2010

Type species: *Mesoderus magnus* Prokin & Ren, 2010.

Diagnosis: Procoxae closely set. Mesotibia distally with swimming setae. Maximum length of lateral lobe of metaventrite relatively great, but smaller than maximum length of metacoxal plate ($LC/LV > 1$). Metacoxal lines strongly diverging anteriorly; metacoxal processes rounded posteriorly, somewhat narrowed anteriorly. Metaventrite with rounded elevated median area. Metatibia subequal in length to metafemur, flattened; metatarsomeres also flattened.

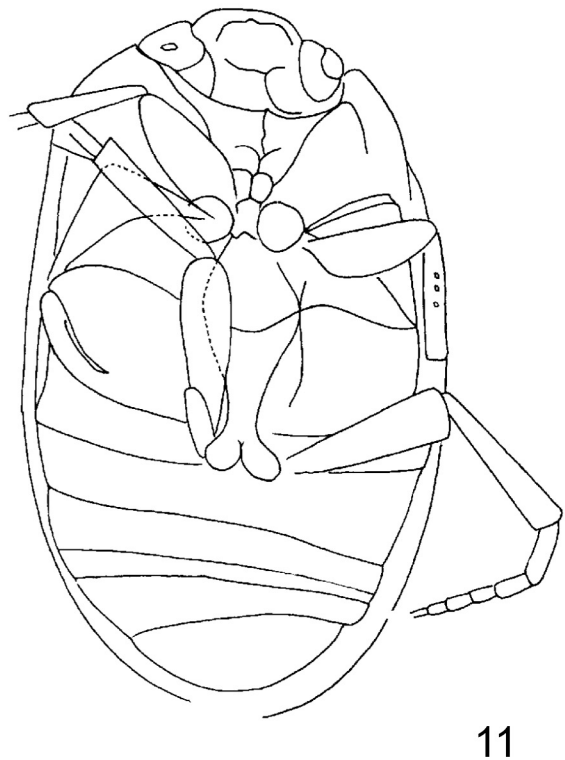
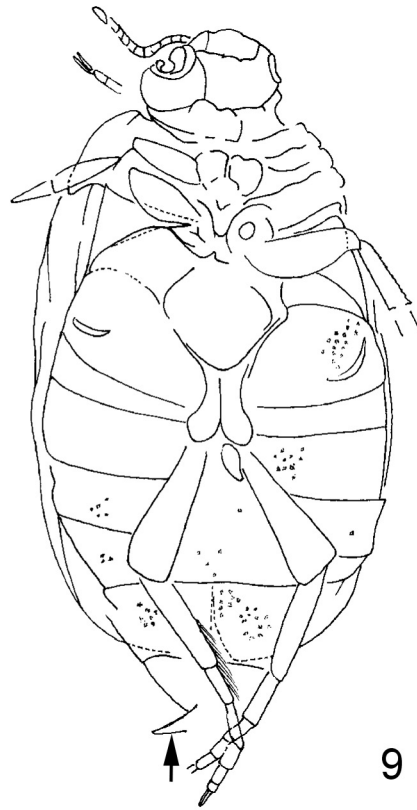
Notes: The genus was originally described in Dytiscidae incertae sedis. It is transferred here to the new tribe, Mesoderini trib. n., of the subfamily Liadytiscinae. All known species of this genus are from the Yixian Formation of China.

Mesoderus punctatus sp. n.

Etymology: The Latin *punctatus* (spotted); adjective in the nominative singular.

Material: Holotype NIGP 05622, counter impression of beetle; China, Liutiaogou; Early Cretaceous, Yixian Formation.

Description (Figs. 8, 9): Light coloured beetle. Maximum body width situated at middle of abdominal ventrite 2. Elytron light, with dark spots, distance between spots twice as great as their diameter. Head length equal to width at posterior margin of eyes. Pronotum three times as wide as long, 1.6 times as wide basally as distally. Profemur narrowed towards apex; protarsal claws equal in length. Mesocoxae slightly separated. Mesofemur with anterior margin straight and posterior margin convex, slightly protruding beyond sides of body; mesotibia straight, with



FIGURES 8–11. *Mesoderus punctatus* sp. n.: (8) photo of holotype, (9) line drawing of holotype; arrow indicates penis; *Mesoderus ovatus* sp. n.: (10) photo of holotype, (11) line drawing of holotype.

setose anterior margin. Metacoxal plate 1.2 times as long as lateral lobe of metaventrite ($LC/LV = 1.2$). Metafemur dilated towards apex. Metatibia straight, slightly shorter than metafemur, with swimming setae. Metatarsomere 1 with swimming setae, equal in length to metatarsomere 2; metatarsomere 2 equal in length to metatarsomeres 3 and 4 together; metatarsomere 5 short, only half as long as metatarsomere 4; claws of metatarsus equal in length, twice as long as metatarsomere 5. Penis pointed and curved (see arrow in Fig. 10).

Measurements: Body length, 14.6 mm; body width, 7.5 mm; elytron length, 10.5 mm.

Comparison: Similar to *M. magnus* Prokin & Ren, 2010 in size and in the pointed and curved penis, but differs from it in the dorsal coloration, LC/LV , longer metacoxal processes, shape of meso- and metafemora, and shorter metatarsomere 1.

Mesoderus ovatus sp. n.

Etymology: The Latin *ovatus* (egg-shaped); adjective in the nominative singular.

Material: Holotype NIGP 154569, counter impression of beetle; China, Liutiaogou; Early Cretaceous, Yixian Formation.

Description (Figs. 10, 11): Light coloured beetle. Maximum body width situated at middle of metacoxae. Pronotum 3.3 times as wide as long, 1.5 times as wide basally as at its anterior margin. Mesocoxae widely separated. Mesofemur with anterior margin straight and posterior margin convex, slightly protruding beyond body sides; mesotibia straight, with holes at bases of setae on ventral surface. Metacoxal plate 1.7 times as long as lateral lobe of metaventrite ($LC/LV = 1.7$). Metacoxal processes extended to level of abdominal ventrite 2. Metafemur and metatibia dilated towards their apices, metatibia slightly shorter than metafemur. First metatarsomere 1.8 times as long as metatarsomere 2 and equal in length to metatarsomeres 2 and 3 together; metatarsomeres 3 and 4 equal in length; metatarsomere 5 slightly shorter.

Measurements: Body length, 10.8 mm; body width, 6.3 mm; elytron length, 8.7 mm.

Comparison: Similar to *M. ventralis* Prokin & Ren, 2010 in size, but differs from it in the ratio of the length of the metacoxal plate and lateral lobe of the metaventrite, longer metacoxal processes, shape of meso- and metafemora and metatibia, and shorter metatarsomere 1.

Mesodytes gen. n.

Etymology: From the Mesozoic and the Greek δύτες (diver); gender masculine.

Type species: *Mesodytes rhantoides* sp. n.

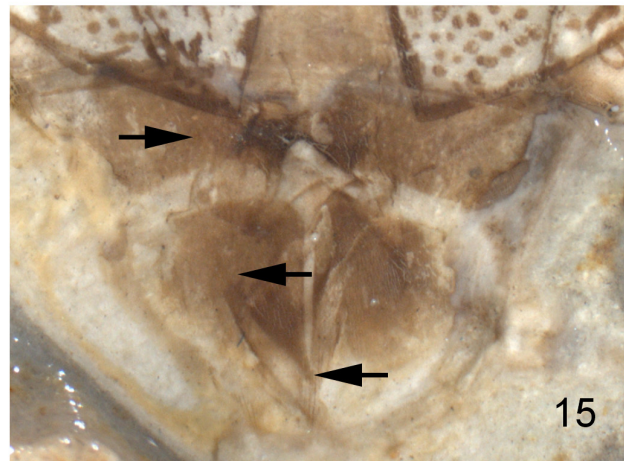
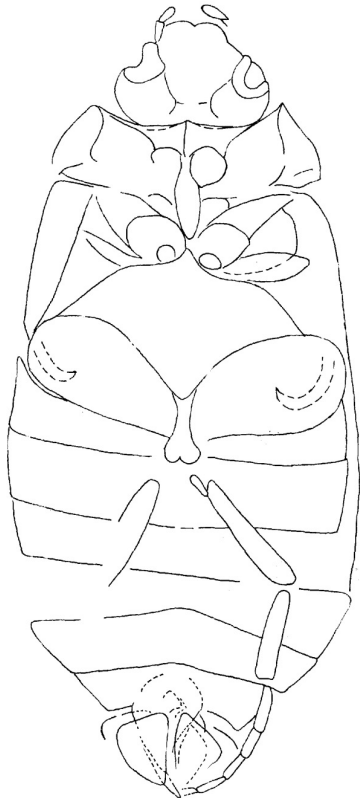
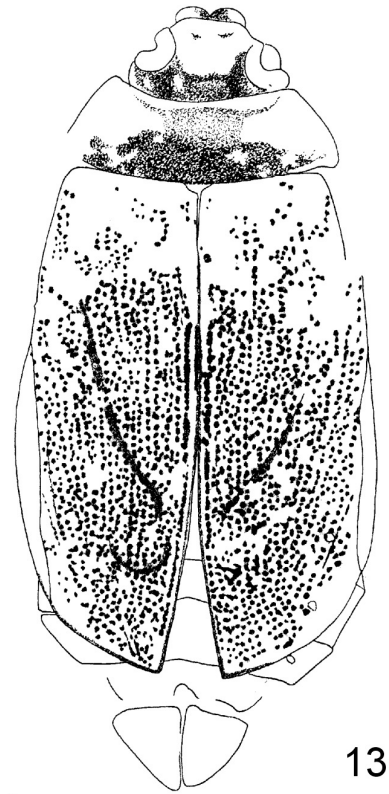
Diagnosis: Elytron smooth, translucent, covered with matted rows of dark spots, separated by a distance greater than or equal to their diameter. Lobe of prosternal process flat, elongated, reaching mesocoxae. Maximum length of lateral lobe of metaventrite relatively great, but smaller than maximum length of metacoxal plate ($LC/LV > 1$). Lateral lobe of metaventrite not reaching lateral margins of metepisternum and mesocoxal plate. Metaventrite without elevated laterally limited area medially. Metacoxal lines weakly diverging anteriorly. Metacoxal processes rounded posteriorly, slightly narrowed anteriorly. Metafemur 1.5 times as long as metatibia. Metafemur, when outstretched, reaching middle of abdominal ventrite 4. First metatarsomere 1.5 times as long as metatarsomere 2.

Comparison: The new genus differs from the genus *Mesoderus* in the absence of an elevated laterally limited area of the metaventrite, translucent and dark-spotted elytron, and shorter metatibia and metatarsomere 1.

Mesodytes rhantoides sp. n.

Etymology: From the generic name *Rhantus*; adjective in the nominative singular.

Material: Holotype NIGP 154570, counter impression of beetle; China, Liutiaogou; Early Cretaceous, Yixian Formation.



FIGURES 12–15. *Mesodytes rhandoides* sp. n.: (12) photo of holotype, (13) line drawing of holotype in dorsal view, (14) line drawing of holotype in ventral view, (15) photo of holotype (fragment, 3× enlarged): male genitalia; arrows indicate base, dorsal margin and apex of penis.

Description (Figs. 12–15): Beetle with light underside. Head length 0.7 times as great as head width at level of posterior margins of eyes; obscured behind eyes, with two small dark spots in front of clypeus. Pronotum three times as wide as long, 1.4 times as wide basally as at its anterior margin; with rounded sides and angles, with basal angles slightly protruding posteriad; with broad dark stripe basally, broadly connected medially with narrow dark stripe running along entire anterior margin, narrowing and reaching or almost reaching anterior angles. Maximum body width situated at level of abdominal ventrite 2. Procoxae and mesocoxae closely set. Metacoxal plate approximately 1.2 times as long as lateral lobe of metaventrite ($LC/LV \approx 1.2$). Metafemur not dilated towards apex. Abdominal ventrites more or less equal in length; abdominal segments 3, 4, and 5 sublaterally with large oval spiracles. Penis evenly curved, with apex rounded and base dilated (see arrows in Fig. 15). Elytron translucent, with wing venation partly visible under elytron; with dark sutural and apical margin and at least 20 rows of dark spots. Elytral epipleuron translucent, without spots, wide; its internal margin forming sharp angle with lateral margin of elytron, starting at base of abdomen and ending at posterior edge of abdominal ventrite 4; maximum width situated at level of abdominal ventrite 2. Abdominal tergites 4, 5, and 6 with round spiracles dorsally.

Measurements: Body length, 16.0 mm (17.7 mm including protruding genitalia); body width, 7.5 mm; elytron length, 10.1 mm.

Subfamily incertae sedis

Palaeodytes Ponomarenko, 1987

Type species: *Palaeodytes sibiricus* Ponomarenko, 1987.

Notes: The genus is characterized by a short band-like pronotum and short head, together about 1/3 as long as the elytra; metacoxal plates longest in their lateral third (lateral of the external margins of the mesocoxae); lateral lobe of metaventrite half as long as metacoxal plate, median platforms of mesocoxae separated from the anterior margins of mesocoxae by a line, rounded apically and notched laterally; and dilated and flattened metatibia and metatarsus, the latter longer than the former.

It differs from members of the subfamily Liadytiscinae in the shorter lateral lobe of the metaventrite, shorter and more dilated metatibia and metatarsus, and short pronotum; from *Sinoporus* it differs in the metaventrite with concave posterior margins of the lateral lobe (cf. Figs 17 and 23).

The new species described below belongs to this genus according to the combination of two characters: metacoxa nearly twice as long as the lateral lobe of the metaventrite ($LC/LV \approx 2$), and absence of an elevated laterally limited area of the metaventrite.

Palaeodytes baissiensis sp. n.

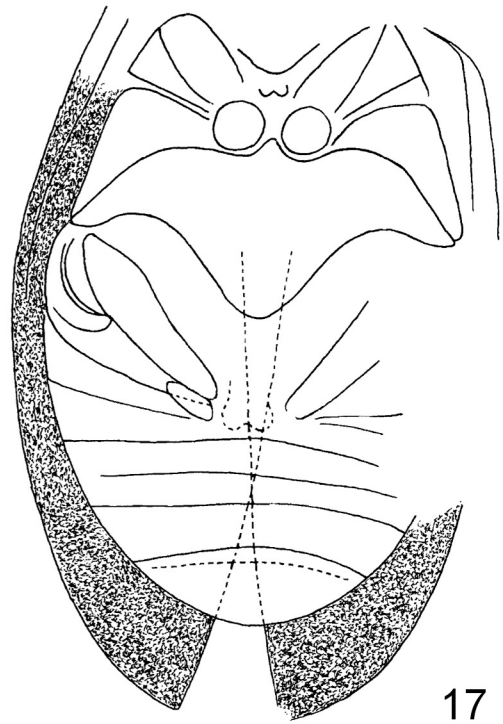
Etymology: From Baisa (also known as Baissa, an alternative transliteration) fossil site; adjective in the nominative singular.

Material: Holotype PIN 4210/380 ±, beetle without head, prothorax and larger part of legs; Baisa, Buryat Republic, Russia (Early Cretaceous, approximately Hauterivian, ca. 135 mya; Zherikhin *et al.* 1999).

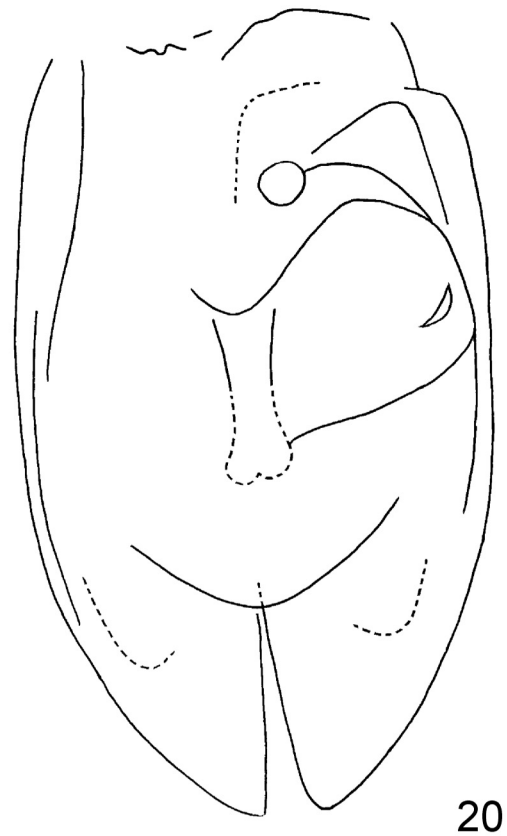
Description (Figs 16–18): Medium-sized beetle, with light underside and black elytron. Maximum body width situated at middle of metacoxae. Mesocoxae rounded, separated. Metacoxal plate 1.9 times as long as lateral lobe of metaventrite ($LC/LV = 1.9$). Metafemur dilated to 2/3 of its length, and then narrowed towards apex.

Measurements: Body length, probably around 10 mm; body width, 4.8 mm (5.6 mm with the displaced elytron); elytron length, 8.3 mm.

Comparison: The new species differs from *P. gutta* Ponomarenko, 1987 and *P. sibiricus* Ponomarenko, 1987 in its larger body size and black elytra; it also differs from *P. sibiricus*, described from the same locality, in the shape of the metafemur.



FIGURES 16–18. *Palaeodytes baissiensis* sp. n.: (16) photo of holotype, direct impression, (17) line drawing of holotype, (18) photo of holotype, counter impression.



FIGURES 19–21. *Cretodytes incertus* sp. n.: (19) photo of holotype, (20) line drawing of holotype; (21) *Angaragabus jurassicus* Ponomarenko, 1963: photo of holotype, PIN 1670/390.

"*Palaeodytes*" *incompletus* Ponomarenko, Coram & Jarzembowski, 2005

This species was recently described from the Berriasian Purbek Limestone Group, UK. Its body outline is uncharacteristic of *Palaeodytes* (cf. fig. 4 in Ponomarenko *et al.* 2005: 280) and its lateral lobe of the metaventricle has a peculiar shape (resembling, e.g., that of the recent dytiscid *Ilybius fenestratus* (Fabricius, 1781), although it may be distantly related), with the posterior and anterior margins strongly converging and then slightly diverging

again, and converging again near the epipleuron. The genus to which the species belongs is similar in morphological parameters to several recent genera of the family, and it is difficult to provide a diagnosis based on what is known about it. Having at present no opportunity to re-examine the holotype of this species in search of possible distinguishing characters of the genus, we refrain from describing the new genus here. Therefore, in this study the species is provisionally referred to hereinafter as "*Palaeodytes*" *incompletus*.

Cretodytes Ponomarenko, 1977

Type species: *Cretodytes latipes* Ponomarenko, 1977.

Notes: The genus is characterized by the short lateral lobe of the metaventrite, deep and rather wide cavity at the apex of the anterior metaventral process, and elevated median platforms of metacoxae, which are weakly diverging, but dilated and rounded apically. It differs from *Palaeodytes* in the longest point of the metacoxal plate situated at the level of the external margin of mesocoxae, and in the shorter lateral lobe of the metaventrite (which also distinguishes it from Liadytiscinae); from "*Palaeodytes*" *incompletus* it differs in the shape of the lateral lobe of the metaventrite and shape of the metacoxal processes; and from *Sinoporus*, in the concave posterior margins of the lateral lobes of the metaventrite (cf. Figs 20 and 23).

The new species belongs to this genus according to the combination of two characters: metacoxal plate three times as long as the lateral lobe of the metaventrite and absence of a laterally limited elevated median area of the metaventrite.

Cretodytes incertus sp. n.

Etymology: From the Latin *incertus* (unclear); adjective in the nominative singular.

Material: Holotype PIN 4626/628, direct impression of beetle without head, prothorax and legs; Chernovskiye Kopi (also transliterated as Chernovskie Kopi), Transbaikalia, Russia, left bank of the Ingoda River, Late Jurassic – Early Cretaceous, Doronino Formation.

Description (Figs 19, 20): Small oval light beetle. Elytron thin, wing venation visible as loop at base of oblongum. Maximum body width situated at level of middle of metacoxal plates. Mesocoxae rounded. Metacoxal plate 3.3 times as long as lateral lobe of metaventrite (LC/LV = 3.3). Metacoxal processes rounded, slightly elevated above metacoxal plates.

Measurements: Body length, probably around 7 mm; body width, 3.6 mm; elytron length, 5.3 mm.

Comparison: The new species differs from *C. latipes* Ponomarenko, 1977 in the smaller body length and width and shorter lateral lobe of the metaventrite and metacoxal processes.

Summarized checklist of the Mesozoic Liadytidae and Dytiscidae known from adults

The checklist provided below includes all Mesozoic taxa of Liadytidae and Dytiscidae known from adults. Species within each genus are listed in alphabetical order. For information on other fossil taxa of the families, see the online catalogue of Ponomarenko & Kirejtshuk (2012).

Family Liadytidae Ponomarenko, 1977

Genus *Liadytes* Ponomarenko, 1963

L. aspidytoides sp. n.

L. avus Ponomarenko, 1963

L. crassus Ponomarenko, 1977

L. dajensis Ponomarenko, 1987

L. longus Ponomarenko, 1977

L. major Ponomarenko, 1985

Family Dytiscidae Leach, 1815

Subfamily Liadytiscinae Prokin & Ren, 2010

Tribe Liadytiscini Prokin & Ren, 2010

Genus *Liadytiscus* Prokin & Ren, 2010

L. cretaceus Prokin & Ren, 2010

L. latus Prokin & Ren, 2010

L. longitibialis Prokin & Ren, 2010

Genus *Liadroporus* Prokin & Ren, 2010

L. elegans Prokin & Ren, 2010

Genus *Liadyxianus* **gen. n.**

L. kirejtshuki **sp. n.**

Tribe Mesoderini **trib. n.**

Genus *Mesoderus* Prokin & Ren, 2010

M. magnus Prokin & Ren, 2010

M. ovatus **sp. n.**

M. punctatus **sp. n.**

M. ventralis Prokin & Ren, 2010

Genus *Mesodytes* **sp. n.**

M. rhantoides **sp. n.**

Subfamily incertae sedis

Genus *Palaeodytes* Ponomarenko, 1987

P. baissensis **sp. n.**

P. gutta Ponomarenko, 1987

P. sibiricus Ponomarenko, 1987

Genus currently undescribed

"*P. incompletus* Ponomarenko, Coram & Jarzembowski, 2005

Genus *Cretodytes* Ponomarenko, 1977

C. incertus **sp. n.**

C. latipes Ponomarenko, 1977

Genus *Sinoporus* Prokin & Ren, 2010

S. lineatus Prokin & Ren, 2010

Key to the genera of Mesozoic Dytiscidae (adults)

1. Metaventricle with straight posterior margins of lateral lobes, converging posteriad at obtuse angle (Fig. 23); elytra with dark stripes (subfamily incertae sedis)..... *Sinoporus*.
- Metaventricle with concave posterior margins of lateral lobes (e.g., as in Fig. 20); elytra without dark stripes. 2.
2. LC/LV (ratio of maximum length of metacoxal plate and lateral lobe of metaventricle, both measured longitudinally, as in Fig. 22) around 1–1.7 (Liadytiscinae)..... 5
- LC/LV around 2 or greater (subfamily incertae sedis)..... 3
3. Posterior and anterior margins of lateral lobe of metaventricle strongly converging, then slightly diverging again, then converging again near epipleuron; LC/LV around 3..... "*Palaeodytes*" *incompletus*.
- Posterior and anterior margins of lateral lobe of metaventricle more or less evenly converging towards epipleuron. 4.
4. LC/LV around 3 (as in Figs 19, 20)..... *Cretodytes*.
- LC/LV around 2..... *Palaeodytes*.
5. Metacoxal lines weakly diverging anteriad; metacoxal processes with incision between them, conjointly truncate or rounded posteriorly, not narrowed anteriad (as in Figs 6, 7); LC/LV around 1; metatibia narrow and long, longer than metafemur (Liadytiscini)..... 6.
- Metacoxal lines strongly diverging anteriad; metacoxal processes slightly narrowed anteriad, with posterior margins rounded (as in Figs 8–11, 12, 14); LC/LV around 1.2–1.7; metatibia subequal in length to or shorter than metafemur (Mesoderini trib. n.)..... 8.
6. Metacoxal processes conjointly truncate posteriorly, with incision between them; metaventricle with laterally limited elevated median area triangular. *Liadytiscus*.
- Metacoxal processes conjointly truncate apically, with incision between them, or rounded with incision; metaventricle with elevated median area rounded or without such elevated area 7.

7. Metacoxal processes more or less conjointly truncate posteriorly, with posterior margins appearing somewhat sinuate, with incision between them (as in Figs 6, 7). *Liadyxianus* gen. n.
- Metacoxal processes rounded *Liadroporus*.
8. Metaventrite with rounded laterally limited elevated median area (Figs 8–11). *Mesoderus*.
- Metaventrite without laterally limited elevated median area (Figs 12, 14). *Mesodytes* gen. n.

Discussion

Comparison of Liadytidae and Aspidytidae. The recent genus *Aspidytes*, which is similar to the Mesozoic genus *Liadytes*, is known from several rocky outcrops covered with a permanent water film a few millimetres deep. Adults and larvae are usually found resting on vertical or almost vertical surfaces devoid of vegetation, but when disturbed are able to scuttle rapidly over the surface in search of cover under algae or other vegetation (Alarie & Bilton 2005). Members of *Liadytes*, in contrast to *Aspidytes*, already had swimming setae on their meso- and metatarsi and tibiae. Moreover, successful fossilization under conditions similar to those of the habitats of *Aspidytes* (in a thin film of flowing water) would have been difficult, and the habitats of *Liadytes* could have been quite different.

Therefore, members of the genus *Liadytes*, in spite of their similarity to *Aspidytes*, were probably swimming beetles with a locomotor apparatus similar to that of *Hygrobia*, and were swimming using all the three pairs of legs.

The similarity between adult Liadytidae and Aspidytidae prompted us to re-examine the larva *Angaragabus jurassicus* Ponomarenko, 1963 (Fig. 21), described from the Lower Jurassic of Ust-Baley in Irkutsk Oblast of Russia and represented, in addition to the holotype (PIN, no. 1760/390±), by several other specimens from the same locality (PIN, nos. 509/6±, 509/4, 722/9, and 1760/391±), from which *Liadytes avus* was also described. The larva and the adult were placed in the original description into the superfamily Dytiscoidea, without specifying to which family they belonged. Subsequently, describing the family Liadytidae (which includes only one known genus, *Liadytes*), Ponomarenko (1977) suggested that *Angaragabus* could be the larva of *Liadytes avus*. The absence of Dytiscidae in the fossil record from the Lower Jurassic and significant differences of *Angaragabus* from the other Mesozoic Dytiscoidea larvae of the families Colymbotethidae, Coptoclavidae and Parahygrobiidae supported the placement of *Angaragabus* in Liadytidae, although this interpretation remained (and remains) a hypothesis difficult to test.

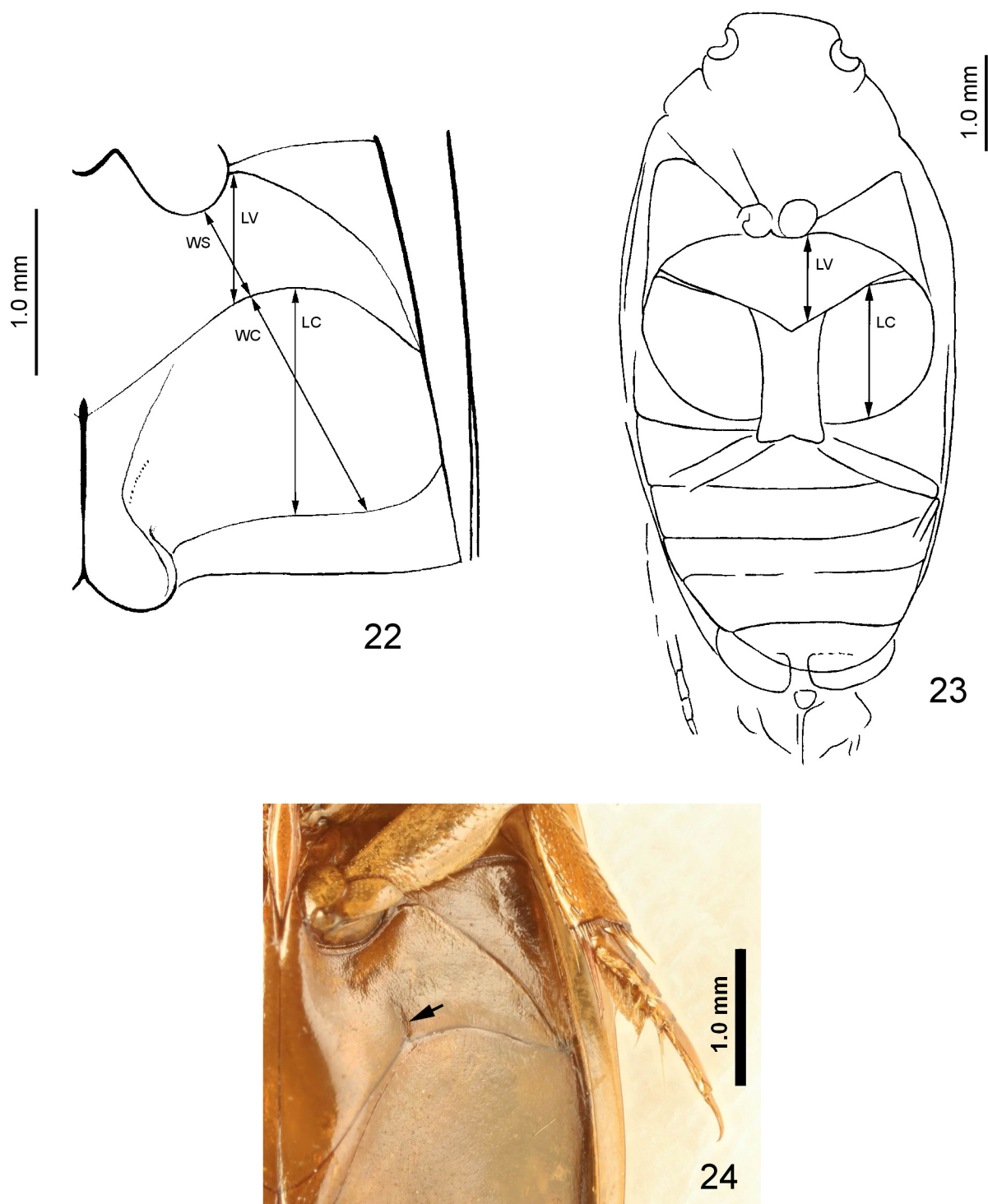
The combination of morphological characters of *Angaragabus jurassicus* is very similar to that found in representatives of recent Agabinae. The comparison of the larvae of *Angaragabus jurassicus* and *Aspidytes niobe* Ribera, Beutel, Balke & Vogler, 2002 (Wang *et al.* 2009)—according to the characters used in a recent study on the phylogeny of Dytiscoidea (Balke *et al.* 2005)—showed that *Angaragabus jurassicus* is more advanced morphologically than *Aspidytes niobe*, tentatively supporting family-level differences between Liadytidae and Aspidytidae. Our re-examination of *Angaragabus jurassicus* specimens allowed us to provide a more extensive comparison of the larvae of the two species (see Table 1 in Appendix), and the results confirm the conclusion of Wang *et al.* (2009).

This possible example of mosaic evolution, with the adult (*Liadytes avus*) being more primitive and showing less advanced adaptations to the aquatic mode of life than the supposed larva (*Angaragabus jurassicus*), displays a trend different from that found in another known example of mosaic evolution among Dytiscoidea, *Daohugounectes primitivus* Wang, Ponomarenko & Zhang, 2009 (Coptoclavidae), in which the adult is more progressive (advanced) than the larva (Wang *et al.* 2010).

The adults of Aspidytidae and Liadytidae can be reliably distinguished only by the following characters: (1) mesocoxae closely located in Liadytidae, more separated in Aspidytidae; (2) anteromedial metaventral process absent in Liadytidae, present in Aspidytidae. Apart from these characters, adult members of both families are very similar morphologically, but their similarity might be explained by parallel evolutionary processes. If *Angaragabus jurassicus* is, indeed, the larva of *Liadytes avus*, its morphological characters provide additional confirmation for the separate family status of Aspidytidae and Liadytidae.

Adaptation to swimming in early Dytiscoidea. The earliest dytiscoids were probably similar at the adult stage to *Necronectulus* Ponomarenko, 1977 (Adephaga incertae sedis; possibly belonging to the same family as the following two genera) and at the larval stage to *Colymbotethis* Ponomarenko, 1993 (family Colymbotethidae) and some specimens of *Mormolucoides* Hitchcock, 1858 (we believe that some of the larvae described as

Mormolucooides are dytiscoids close to *Colymbotethis*; see Ponomarenko & Kirejtshuk 2012). The earliest adult dytiscoids are known from the terminal Middle Permian; the earliest larvae are known from the Upper Triassic (*Colymbotethis*).



FIGURES 22–24. (22) *Ilybius adygeanus* Petrov, Shapovalov & Fery, 2010: metaventricle and metacoxa, with measurements WC, WS, LC and LV shown; modified from Petrov *et al.* (2010); (23) *Sinoporus lineatus* Prokin & Ren, 2010: holotype in ventral view, redrawn and modified from original description with LC and LV shown (in this case the longest point of the lateral lobe of the metaventricle is at the very base of the lobe; it has been measured immediately lateral of the posterior margins of the mesocoxa, i.e., at the very base of the lobe, if we define the lobe as the part of the metaventricle lateral of the mesocoxa); (24) *Lancetes lanceolatus* (Clark, 1863): metaventricle of recent specimen from Lake Cronin (Western Australia); arrow indicates impression at lateral margin of median elevated area of metaventricle.

Numerous parallel processes can be traced in the phylogeny of Dytiscoidea. The evolution of true swimming legs in this superfamily was rather parallel than divergent, and the principal events in the evolution of larvae and adults were not simultaneous, at least in Coptoclavidae (and, presumably, in Liadytidae). Adult coptoclavids had long slender legs with swimming setae on the hindlegs and sometimes also on the midlegs; larvae had the distal abdominal segments reduced, with the spiracles of the eighth segment transferred to its posterior margin, although a derivate of the ninth segment is still present in the Jurassic *Daohugounectes* Wang, Ponomarenko & Zhang, 2009, as in the recent *Aspidytes*. *Daohugounectes* is not at all the most primitive coptocladid (although the supposed larva has nine abdominal segments, the adult is rather advanced), and the adult *Aspidytes* is quite similar to some species of *Liadytes*, the supposed larva of which has no derivate of the ninth segment (see Appendix, character 49).

Ribera & Nilsson (1995) identified four functional swimming groups of recent Dytiscidae: (1) large to medium-sized species; streamlined, wide, with the maximum width in the rear part of the body and the maximum height in the front part, with short tibiae and long tarsi, considered to be adapted to high-speed swimming in open waters; (2) small to medium-sized species with spherical body and long femora, considered to be adapted to manoeuvre in stagnant waters; (3) small species with a discontinuous outline, narrow body and long and slender legs, considered to be poor swimmers in running waters; (4) small to medium-sized species, in general streamlined, relatively deep-bodied, and with short and wide legs, considered to be adapted to crawl among dense vegetation or detritus. Further analysis of these four basic types was provided in a study on the swimming behaviour of Dytiscidae and Paelobiidae by Ribera *et al.* (1997). All known Mesozoic Dytiscidae and all known members of the closely related Liadytidae are medium-sized (7–16 mm) and streamlined, but they probably represent several functional groups, hardly identical to those recognized among the recent Dytiscidae.

Especially peculiar ones among the Mesozoic dytiscids are the following two species: (1) *Sinoporus*, with its unique morphology of the underside of the metathorax (Fig. 23; the hind legs are not sufficiently well preserved, but they could have been also unusual), and the coloration pattern of the dorsum resembling that of *Coptotomus*, while the body outline resembles that of *Laccophilus*, and (2) "*Palaeodytes*" *incompletus*, which has extremely short lateral lobes of the metaventricle, quite long metacoxal plates, and maximum width of the body situated in its posterior third.

The other Mesozoic taxa of the two families clearly differ in the proportions of their legs. *Palaeodytes*, in contrast to all other Mesozoic Liadytidae and Dytiscidae, has short and wide metatibiae and metatarsi. *Liadytes*, Liadytiscinae, and *Cretodytes* have longer hindlegs, with length gradually diminishing and femora dilating in the following sequence: *Liadytes*, Liadytiscini (Figs 6–7), Mesoderini (Figs 8–11, 12, 14), *Cretodytes*. In the same sequence (which may, at least in part, coincide with the actual order of evolutionary changes), the maximum width of the metacoxal plates markedly increases, while the maximum length of the lateral lobes of the metaventricle decreases. These changes are also accompanied by the disappearance of the laterally limited elevated median area of the metaventricle.

The evolution of Dytiscoidea followed a general trend towards a decrease in the length of the metatibia relative to the total length of the hindleg (Ponomarenko 1975). This trend was probably associated with the switch to the mode of swimming by simultaneous strokes of both hindlegs. When legs with longer tibiae move forward before each stroke, their movement more strongly pushes the beetle backwards, presumably making swimming by this mode less efficient. If the metatibiae are shorter, the backward push during the forward movement of both legs is weaker, and therefore the efficiency of swimming by simultaneous strokes of both hindlegs is higher.

In the light of this trend, the Mesozoic Liadytidae and Dytiscidae form the following sequence according to the development of their hindlegs in the course of adaptation to swimming: *Liadytes*, Liadytiscini, Mesoderini trib. n., *Palaeodytes*, *Cretodytes*, "*Palaeodytes*" *incompletus*. This sequence, however, does not precisely reflect the order of morphological transformations, since the quite advanced swimmer *Palaeodytes* is known from the Jurassic deposits of Karatau, and Liadytiscinae, the branch of Dytiscidae with the highest diversity in the Mesozoic, is known only from the Yixian Formation (Early Cretaceous, ca. 124–122 mya). At the same time, we believe that the general trend of changes complied with this sequence, and interpret the early emergence of the more advanced form as a result of some of the many parallel processes in the evolution of Dytiscoidea, which can be shown for Coptoclavidae (and, tentatively, Liadytidae), as well as for the majority of the recent families (Ribera *et al.* 2002).

In addition to the shortening and dilating metafemora and metatibiae, the other principal trends of the morphological transformations of Liadytidae and Dytiscidae in the Upper Jurassic and Lower Cretaceous included a consistent increase in the area of metacoxae at the expense of the reducing area of the lateral lobes of the

metaventricle and flattening and loss of the lateral limitation of the elevated median area of the metaventricle. These processes of morphological changes probably reflected an increased swimming load on the hindlegs, which promoted the development of the corresponding muscles (increasing the area of the metacoxal plates, to which these muscles are attached) and swimming surfaces of the legs. These changes in the hindlegs allowed the beetles to dive deeper, making them more adapted to the nektonic lifestyle. This conclusion is supported by the adaptive coloration of dytiscoids found in Shar Teg (*Liadytes aspidytoides* sp. n.), Yixian (*Mesoderus magnus*), and Baisa (*Palaeodytes baissiensis* sp. n.), with the dorsum darker than the underside, which provided camouflage in the depths of the water.

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Appendix

TABLE 1. Larval character states of *Angaragabus* and *Aspidytes*. Numbers of characters and designations of character states are taken from Balke *et al.* (2005) for convenience of comparison (larval characters 32–53); only characters examined in fossil specimens are given; character 54, describing larval legs, and some character states known in extinct dytiscoids are added from Wang *et al.* (2009).

Species	Character							
	32	34	39	40	49	51	53	54
<i>Angaragabus jurassicus</i>	3	0	2	2	2	1	1	0
<i>Aspidytes niobe</i>	0	1	0	1	1	3	0	1

Explanations of characters:

- 32.** Anterior margin of clypeolabrum: (0) with nasale distinct; (1) with nasale strongly reduced, with medial indentation; (2) with nasale strongly reduced, with medial protrusion; (3) without nasale.
- 34.** Frontal suture: (0) Y-shaped with long stem; (1) Y-shaped with short stem; (2) U-shaped.
- 39.** Mandible: (0) with retinaculum distinct, (1) with retinaculum strongly reduced, (2) with retinaculum absent; (3) with three teeth.
- 40.** Mandible: (0) with groove absent; (1) with groove formed of two cutting protrusions; (2) with inner canal.
- 49.** Abdominal segment 9: (0) well developed; (1) strongly reduced; (2) absent.
- 51.** Spiracle of abdominal segment 8: (0) normally developed; (1) enlarged and terminal; (2) reduced; (3) small, shifted to dorsal side of segment 8.
- 53.** Urogomphi: (0) longer than maximum width of head capsule; (1) short.
- 54.** Legs: (0) walking, long; (1) walking, short; (2) swimming, narrow; (3) swimming, broad; (4) crawling.
- Note:** In Wang *et al.* (2009) character 54 for *Colymbotethis* is erroneously listed as (0); actually, it should be (1).