On taxonomy and distribution of fossil Cerophytidae (Coleoptera: Elateriformia) with description of a new Mesozoic species of *Necromera* Martynov 1926

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Abstract. In this paper the data on fossils of the family Cerophytidae are reviewed. New synonymy on generic names *Necromera* Martynov 1926 (proposed in composition of the family Oedemeridae); *Idiomerus* Dolin in Dolin *et al.* 1980, **n. syn.** (proposed in composition of Elateridae) and *Leptocnemus* Hong & Wang 1990, **n. syn.** (proposed without any family attribution) is established. New materials on this family from Mesozoic deposits of Asia are cited. As a result, it was established that this spreads in deposits of both Upper Jurassic and Lower Cretaceous. *Mercata festira* Lin 1986 described from Lower Jurassic as member of Silphidae and *Abrotus reconditus* Dolin in Dolin *et al.* 1980 described from Upper Jurassic as a member of Elateridae are transferred to Cerophytidae. Diagnoses of the genus *Necromera* and family Cerophytidae in compression fossils are elaborated. *Necromera admiranda* **n. sp.** is described from the Upper Jurassic-Lower Cretaceous in Liaoning, China. The historical development of the family from the Lower Jurassic is discussed.

Résumé. Sur la taxonomie et la distribution des Cerophytidae fossiles (Coeloptera : Elateriformia) avec la description d'une nouvelle espèce de *Necromera* Martynov 1926. Dans cet article, les données disponibles sur les fossiles de la famille des Cerophytidae sont revues. Une nouvelle synonymie est établie pour les genres *Necromera* Martynov 1926 (proposé comme Oedemeridae) ; *Idiomerus* Dolin in Dolin *et al.* 1980, **n. syn.** (proposé comme Elateridae) and *Leptocnemus* Hong & Wang 1990, **n. syn.** (proposé sans famille définie). Du nouveau matériel est cité du Mésozoique d'Asie pour cette famille. Comme résultat, on a pu établir la dispersion dans les dépôts du Haut Jurassique et du Crétacé Inférieur. *Mercata festira* Lin 1986, décrit du Jurassique Inférieur comme membre des Silphidae, et *Abrotus reconditus* Dolin in Dolin *et al.* 1980, décrit du Haut Jurassique comme membre des Elateridae, sont transférés dans les Cerophytidae. Les diagnoses du genre *Necromera* et de la famille Cerophytidae en compressions fossiles sont élaborées. *Necromera admiranda* **n. sp.** est décrite du Haut Jurassique-Crétacé Inférieur de Liaonig, Chine. Le développement historique de la famille au Jurassique inférieur est discuté.

Keywords: New synonymy, Oedemeridae, Elateridae, Liaoning.

Recent studies have recovered a considerable representation of the family Cerophytidae Latreille 1834 in Mesozoic outcrops of Asia. Among fossil specimens from Karatau (Kazakhstan, Upper Jurassic) and Liaoning (China, Upper Jurassic - Lower Cretaceous), this family represents 1/2–2/3 of that of Elateridae Leach 1815, and in materials from Ningcheng (Inner Mongolia, Middle Jurassic) number of cerophytid fossils is even greater than that of elaterids. Species of this family are characterized by some features reminiscent of those from specimens of other families, therefore, they were recognized as members of the Cerophytidae only recently (Zherichin 1977), who described two Upper Cretaceous species from Taimyr amber (North West Siberia). Later Hieke & Pietrzeniuk (1984) found that Larsson (1978) had published a picture of a representative of this family from the Upper Eocene Baltic amber erroneously determined as a member of the family Rhipiphoridae. Martynov described in 1926 a species (*Necromera baeckmani*) from Upper Jurassic Karatau shales in composition of the family Oedemeridae, which certainly belongs to the Cerophytidae. Dolin studied materials from this locality and published some cerophytid species as members of the family Elateridae (species of the genus *Idiomerus* Dolin in Dolin *et al.* 1980). Recent extensive examination of additional materials from Karatau made possible to clarify that the species proposed by Martynov and Dolin belong to the same cerophytid genus. Lin (1986) published *Mercata festira* from Lower Jurassic Xiwan (Guangxi Province, China) as a representative of the family Silphidae, which, in the authors opinion, seemed to be closely related to *Necromera* Martynov 1926 and other

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Cerophytidae rather than to Elateridae (*M. festira* is redescribed and reinterpreted in Ponomarenko, in litteris). Hong and Wang (1990) described *Leptocnemus longus* from Lower Cretaceous Laiyang (China) without any family attribution, which demonstrates also a significant similarity to other fossil Cerophytidae. Finally, Kirejtshuk & Azar (2008) described of a very aberrant cerophytid genus (*Lebanophytum*) from the Lower Cretaceous Lebanese amber. Recently, new and rich materials from another Upper Jurassic-Lower Cretaceous site of the Yixian Formation (Beipiao, Liaoning Province, China) allowed the authors to establish the family attribution of the latter and its synonymy with *Necromera*. More detailed information on representation of this coleopterous family in the fossil record can be got in the catalogue by Ponomarenko & Kirejtshuk (2009).

During preparation of this paper, we have looked through all available limestone specimens deposited in the collections of Capital Normal University (Beijing; further in the text – CNU) and Palaeontological Institute of the Russian Academy of Sciences (Moscow; further – PIN). The Cerophytidae (more than 300 specimens) were discovered among materials mostly from Mikhailovka (Upper Jurassic Karatau, Kazakhstan), Beipiao (Upper Jurassic-Lower Cretaceous, Liaoning Province, China), and also from Galkino (Karatau), Baisa (Lower Cretaceous, Transbaikalia, Russia), Laiyang (Lower Cretaceous, Shandong Province, China) and Ningcheng (Middle Jurassic, Inner Mongolia). The specimens examined belong to many species from some genera. One new species of the genus *Necromera* is described in this paper.

The two authors studied specimens and prepared this paper. Dong Ren was responsible only for the management of collection at CNU and supported the study and publishing of color illustrations.

Material and methods

Most fossil specimens for the type series of the new species described in this publication were collected recently near Chaomidian Village, Liaoning Province. Materials from this site stratigraphically belong to the Yixian Formation consisting mainly of lacustrine sediments intercalated with volcanoclastics (Ren *et al.* 1995). Paleobotanical data from fossil spores, pollen and plants indicate a rather warm and humid climate at that time (Ding *et al.* 2001). The exact 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 etc.). At present, the age of the strata is regarded as the Late Jurassic-Early Cretaceous.

The specimens were examined using a Leica MZ 12.5 stereomicroscope. All photographs were taken with a Nikon Digital Camera DXM1200C. Body length was measured along the midline from the anterior margin of the mandibles to apex of the elytra or abdomen (depending on which of these sclerites is the longest), and width was measured across the broadest part of body; length of pronotum was measured along the midline. The holotype and most paratypes are deposited in the CNU and few paratypes are housed in the Zoological Institute of the Russian Academy of Sciences (St. Petersburg; further – ZIN), PIN and Museum National d'Histoire Naturelle, Paris.

Systematic palaeontology

Infraorder Elateriformia Crowson 1960
Superfamily Elateroidea Leach 1815
Family Cerophytidae Latreille 1834

Specimens of compression fossils usually do not have a complete set of characters displayed in specimens collected in the recent fauna or represented in amber. Therefore the diagnosis of the family proposed by Costa *et al.* (2003) needs to be revised in accordance with the peculiarities of these fossils.

Diagnosis of compression fossils. Body elongate; head transverse and with narrowly separated antennal insertions, frons gently narrowing anteriorly (not widened before anterior edge), somewhat reduced mouthparts and comparatively large eyes; rather long (sub) filiform or/to (sub) serrate 10-11-segmented antennae; pronotum with arcuate lateral edges, subtruncate to gently convex anterior edge and posterior one consisting of lateral oblique parts and median (sub) emarginate portion, anterior angles somewhat rounded to (sub) pointed, but not projecting posteriorly posterior ones; long elytra with subacute apices and dense longitudinal rows of large punctures; posterior wing with radial cell rather distinct and longitudinal; rather convex pronotum more or less widened anteriorly, with anterior edge hung over the base of head and posterior angles distinct, but not projecting, comparatively short collar of prosternum, pronotosternal sutures more or less parallel-sided (not divergent anteriorly); small suboval procoxae separated by rather short and not narrow prosternal process; suboval and narrowly separated to (sub) contiguous mesocoxae, very narrow metepisterna, strongly oblong and contiguous metacoxae with reduced femoral plates (at most presented only at median coxal part) or without them; 5 visible abdominal ventrites, 4 of them fused; all trochanters of elongate type and comparatively long; all tibiae narrow and usually subparallel-sided; 5-5-5 tarsi usually with more or less lobed tarsomeres 1-4; aedeagus comparatively short and stout, and also usually with acute apex of its penis trunk and wide and articulate parameres; ovipositor with long gonocoxites and distinct styli.

Notes. Some specimens of Jurassic and Cretaceous Cerophytidae have the exposed labrum and mandibles anteriorly from antennae. This peculiarity means that the frons of head in these species is not so strongly turned downwards as in most other species. Or these specimens were subjected to an unusual way of fossilization. Some Mesozoic cerophytid species include exclusively specimens with the exposed labrum or labrum together with mandibles. Other groups of Elateriformia represented in the Recent fauna by the forms with strongly deflected head show sometimes in fossils the labrum and mandibles exposed anteriorly before eyes (f.i. Elateridae: Dolin *et al.* 1980 etc.). Some fossil

specimens demonstrate part of venation on the wings exposed from under elytra and the remains accessible for observation are very similar to corresponding parts of wings of the recent species. Finally, all studied fossils attributed to Cerophytidae, in contrast to recent forms show no protuberance at anterior edge of their frons.

Because of the characters defined as "synapomorphies" of the family for recent species of Cerophitidae (Costa *et al.* 2003) are mostly not presented in compression fossils, on the one hand, and Mesozoic faunas of both Elateridae and Cerophytidae include many palaeoendemic groups the researchers are obliged to seek for other features for discrimination of these families. On the other hand, extinct representatives, which could be regarded as closest relatives of the recent ones show some structural differences. The great difficulty is to formulate a dignosis for Elateridae which is very diverse family in the Recent fauna and, perhaps, was even more diverse in extinct ones. The Elateridae consists of many characteristic forms and some groups with rather aberrant condition of the "diagnostic" characters. The most expressive differences of recent and fossil Cerophytidae from Elateridae are the followings: narrowly separated antennal insertions; rather convex pronotum with anterior angles not or scarcely projecting anteriorly and posterior ones with more or less distinct apex but not projecting posteriorly or lateroposteriorly; rather short prosternal process; femoral plates of metacoxae raised at most at median part of coxae and with gently outlined along posterior edge; usually coarse and seriate puncturation on elytra. This complex of characters can be used as a reliable syndrome of this family quite constant in its Mesozoic groups. The metatrochanters of many groups of fossil and recent Elateridae are more or less similar to *Necromera* and some other Mesozoic Cerophytidae, but very different from those in recent Cerophytidae). However, if to take into consideration of variability of this organ in fossil groups (f.i. *Lebanophytum* Kirejtshuk & Azar 2008, *Aphytocerus* Zherichin 1880 and some undescribed forms), it is easily to clarify that the recent forms demonstrate an extreme of this variability. Finally, some Mesozoic Cerophytidae (*Lebanophytum* and undescribed forms from Cretaceous deposits) show no remains of femoral plates of metacoxae (as recent members of the family) sharing the rest characters with other Cerophytidae. The metacoxae in all recent Cerophytidae is rather stable in outline and becoming longer externally, while variability of this organ in extinct forms is rather great and in some cases metacoxae looks like shorter at outer edge. The metacoxae in species of *Necromera* are not so long as in the recent species, but in general comparably longer than in many Elateridae.

The most Late Mesozoic Cerophytidae demonstrate the most similarity in many characters (in particular, pronotal shape and femoral plates of metacoxae) with some recent species of *Pleonomus* Ménétriés 1848 (mostly with *P. laticornis* Reitter 1900: Pleonomini Dolin 1961 from Aplastinae Stibick 1979), but the latter have the rather widely separated antennal insertions, very short and wide frons, and also rather acute posterior pronotal angles and emarginate (to excised) outline of femoral plates of metacoxae and very different dorsal sculpture. Besides, species *Necromera* differs from *Pleonomus canaculatus* (Falderman 1835) in the characters listed above, but the posterior pronotal angles of this species are rather long and acute. But other species of the genus have also very different pronotum (narrow and more subparallel-sided), narrow prosternal process and particularly different femoral plates of metacoxae. The same concerns some similarity with species of *Hemiops* Dejean 1833 (Pleonomini), which are as different from Cerophytidae as *Pleocomus laticornis* (see above) and and in addition species of *Hemiops* have also the very long and narrow prosternal process, bilobed labrum and rather long femoral plates of metacoxae.

On the other hand, the Mesozoic Cerophytidae show also some similarity with recent species of *Tylotarsus* Germar 1840; *Meristhus* Candèze 1857: some *Lacon* Laporte 1836 and *Compsolacom* Reitter 1905 (Agripnini Candeze 1857 from Agripninae) and Pheletes Kiesenwetter 1858 (Dendrometrini Gistel 1856 from Dendrometrinae). All mentioned recent groups are characterized by the very short posterior angles of pronotum, but in contrary to Cerophytidae they have the rather widely separated antennal insertions, long and narrow prosternal process, collar far projecting anteriorly, different pronotal shape (longer and not widened anteriorly), different puncturation and sculpture of dorsum, much wider femoral plates of metacoxae reaching outer edge of coxae.

Recent representatives of the genus *Dima* Charpentier 1825 (Dimini Gandéze 1863 from Dendrometrinae Gistel 1856) have the comparatively convex pronotun with rather shortly projecting posterior angles, narrow femoral plates of metacoxae and comparatively elongate metatrochanters, but all other its features about as those in most of rest Elateridae, namely: widely separated antennal insertions, including narrow and long prosternal process, pronotum with anterior edge not strong hung over the head, rather long femoral plates with not even outline of their median part. Besides, different recent species of Cardiophorinae Gandéze 1860 have somewhat shortened posterior angles of their pronotum, but not so short as those in Cerophytidae, and also their antennae, prosternal process, femoral plates of metacoxae and rest features of Cardiophorinae in general are similar to those in most Elateridae rather than those in Cerophytidae. Although *Nyctor expallidus*

Semenov & Pjatakova 1935 (Nictorini Semenov & Pjatakova 1935 from Cardiophorinae) is characterized by the femoral plates of metacoxae somewhat similar to those in fossil Cerophytidae but the rest characters of this species (including long prosternal process and long posterior angles of pronotum) as those in most Elateridae. Some recent members of the genus *Melanotus* Schwarz 1892 (Melanotini Candèze 1859 from Melanotinae) have somewhat less separated antennal insertions than those in most Elateridae, but not so narrowly separated as those in Cerophytidae, and the rest diagnostic characters of *Melanotus* are quite correspondent with the structural syndrome of Elateridae, but not Cerophytidae. Some recent representatives of Ampedini Gistel 1856 from Elaterinae (f.i., *Brachygonus* Buysson 1912; *Haterumelater* Ohira 1968; *Ischnodes* Germar 1844 and others) show the comparatively short prosternal process and comparatively short femoral plates of metacoxae, however the first structure has the quite Elateroid outline and the latter with a very long and very narrow distal projection. Recent species of *Loboederus* Guérin-Méneville 1831 (Ampedini) have comparatively narrowly separated antennal insertions, but not so narrowly as those in Cerophytidae and the rest characters of the species of the genus lastly mentioned are similar to those in other Elateridae rather than in Cerophytidae (including posterior angles of pronotum, prosternal process femoral plates of metacoxae and so on). The posterior angles of pronotum in recent Cebrioninae Latrielle 1802 are rather short, however the members of this subfamily demonstrate many extraordinary features different from those in Cerophytidae (widely separated antennal insertions, particularly subdascilloid pronotum not narrowed posteriorly, narrow prosternal process, diffuse and sparse puncturation of elytra and very long tibial spurs).

Dolin in the original descriptions of *Idiomerus* and *Abrotus* (Dolin *et al.* 1980) mentioned that these genera are characterised by the narrow femoral plates and very abnormally short posterior angles of pronotum (although indeed the type species of the genus *Abrotus* (*Abrotus sepultus* Dolin *et al.* 1980) has rather short posterior angles of pronotum but markedly longer than in members of Cerophytidae).

Another family, members of which could be mixed in compression fossils with Cerophytidae, is Eucnemidae Eschscholtz 1829. Rather characteristic member of this family, as characteristic members of Elateridae and Throscidae Laporte 1840 were recorded in Lower Cretaceous Lebanese amber, while the member of Cerophytidae is represented in this staff only by the rather aberrant form (Kirejtshuk & Azar 2008). The Eucnemidae could distinguished from Cerophytidae by the following peculiarities: frons widened before antennal insertions, long projecting posterior angles of pronotum, frequently narrower prosternal process, much wider femoral plates of metacoxae (usually reaching outer edge of coxal cavities), metacoxae becoming shorter externally and somewhat smaller metatrochanters. Nevertheless, some Jurassic Elateroids have a mixture of characters of Elateridae and Eucnemidae, demonstrating the frons not widening anteriorly (as in Elateridae) and very large femoral plates of metacoxae (as usually in Eucnemidae). This group was named as tribe Desmatini Dolin *et al*. 1980 (its position will be discussed in detail in a further paper). Besides, Eucnemidae in contrast to Cerophytidae, have usually the head markedly larger in general proportion, prothoracic segment not narrowing posteriorly and with rather clear antennal grooves on ventral surface.

Fossil Praelateridae and Cerophytidae share some common characters, namely: nine rows of coarse punctures on the elytra and cross-shaped apex of prosternal process, but Praelateridae demonstrate the much longer and wider metacoxal femoral plates and lack of clear cavity in the middle of mesoventrite. Differences between these groups and relation between them and their relation to Desmatini should be clarified after a further detailed comparison of these groups. This further comparison make possible to find a reasonable placement of each in hierarchic system of the superfamily Elateroidea and define a respective taxonomic rank for each of these groups.

Genus *Necromera* Martynov 1926

Diagnosis. Head about half as wide as pronotum; elytra with 9 longitudinal rows of coarse transverse and quadrangular punctures; 11-segmented antennae filiform or (sub) serrate; antennomere 2 smallest; ultimate antennomere elongate; antennomeres 3–10 usually subflatened and widened apically; pronotum about 1.5 times wider than head; sides narrowly (sub) explanate; anterior edge shallowly emarginated to widely convex, lateral edges arcuately convex, posterior angles pointed but very short; scutellum arcuate at apex; elytra more than twice as long as combined width; an elongate and well outlined elevated stripe along the entire length of prosternum outlined by subparallel lines between notosternal sutures; prosternal somewhat extended behind procoxae; femoral plates of metacoxae somewhat raised only at median part of coxae.

This genus differs from:

- *Cerophytum* Latreille 1806; *Phytocerum* Costa, Vanin, Lawrence & Ide 2003 and *Brachycerophytum* Costa, Vanin, Lawrence & Ide 2003 in the subexplanate pronotal sides, shorter meso- and metatrochanters, metacoxae becoming shorter externally, femoral plate of metacoxae somewhat developed in the median part and tarsomere 4 apparently not so dilated;

- *Mercata* Lin 1986 in the apparently more narrowly separated antennal insertions (type specimen of *Mercata*

festira Lin 1986 show only few characters which can be used for comparison with species of *Necromera*);

- *Aphytocerus* Zherichin 1880 in the much larger body, head of usual size and not so strongly retracted into prothoracic segment and moderately developed eyes, 11-segmented antennae, slightly reduced mouthparts without dolabriform ultimate maxillary palpomere, prosternal process without angular apex, tarsomeres 1 and 2 not so narrow; acute apex of median lobe of aedeagus;

- *Lebanophytum* Kirejtshuk & Azar 2008 in the much larger body size, seriate puncturation of elytra, shorter and transverse head, longer palpi, more oval pronotum with emarginated to excised anterior edge, oval procoxae, prosternal process enlarged behind coxae, conjoining metacoxae with raised femoral plates.

On synonymy of genus *Necromera*

The type of *Necromera baeckmanni* is deposited in in PIN and re-tested by the authors (see below). Dolin in his study of Mesozoic Elateridae used mostly collection of PIN and the characters of the type specimens of the species included by him in the genus *Idiomerus* completely correspond those in *Necromera*. The re-testing of the type specimens of *Idiomerus* (Figs 2-4) supported their attribution to the genus *Necromera*. *Leptocnemus longus* (type species for *Leptocnemus*) remains unknown to the authors. However, taking into consideration of the generic diagnostic characters, including the femoral plates of metacoxae slightly developed in median parts, and distribution of its species at the same horizon, the synonymy of the names can be regarded as reasonable. Thus, the complete synonymy of the genus under consideration is:

Necromera Martynov 1926; type species *Necromera baeckmani* Martynov 1926 by monotypy;

Idiomerus Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980, **n. syn.**; type species *Idiomerus inflatus* Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980, by original designation;

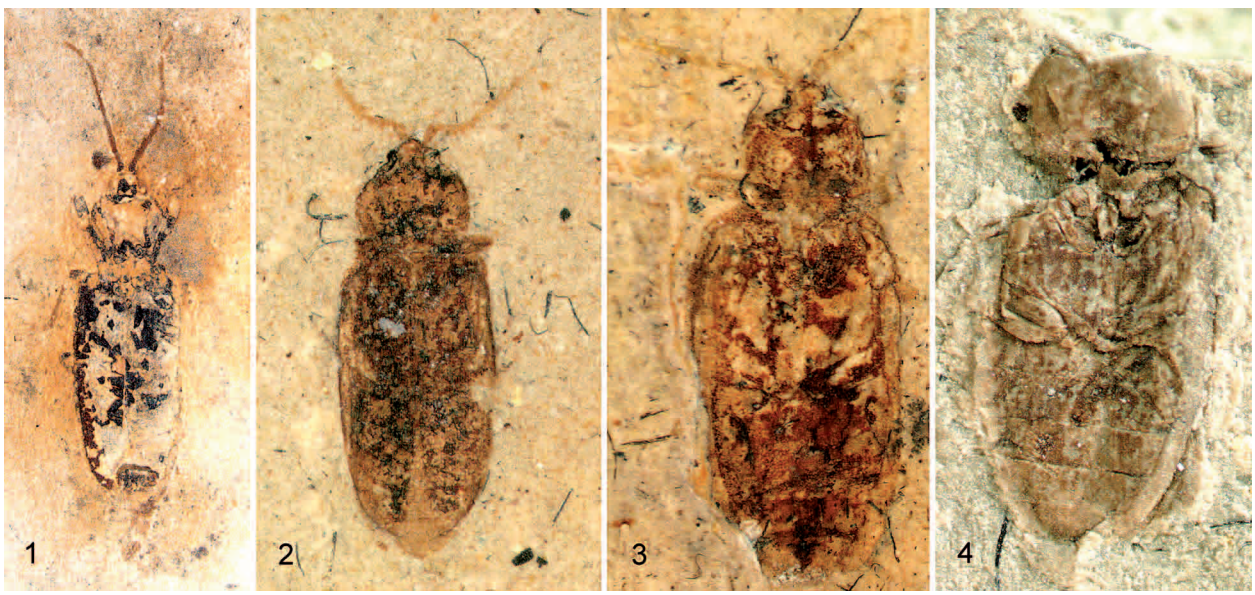
Leptocnemus Hong & Wang 1990, **n. syn.**; type species *Leptocnemus longus* Hong & Wang 1990; by monotypy.

Abrotus reconditus Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980 according to the original description has the very short posterior angles of pronotum, narrow femoral plates of metacoxae and narrowly separated antennal insertions. It is apparently Cerophitydae rather than Elateridae. However, another member of this genus, *Abrotus sepultus* Dolin in Dolin, Panfilov, Ponomarenko & Pritykina 1980 (type species of the genus) is somewhat similar to the first, however the latter has the rather projecting posterior angles of pronotum and wider femoral plates of metacoxae. It is needed to re-test the type series of the type species of the genus *Abrotus* Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980 in order to clarify the attribution of it and the generic name to either Cerophytidae or Elateridae.

Necromera baeckmanni Martynov 1926 (Fig. 1A)

Type specimens: **Holotype**: "170", "1789/46" (female); imprint of dorsum of the complete specimen with antennae, most femora and tibiae, left mesotarsus and exposed ovipositor; deposited in PIN. In comparison with the original description, at the moment of re-testing the specimen had most remains of integument already missing.

Locality and horizon. Galkino, Kara-Tau Range, Algabass



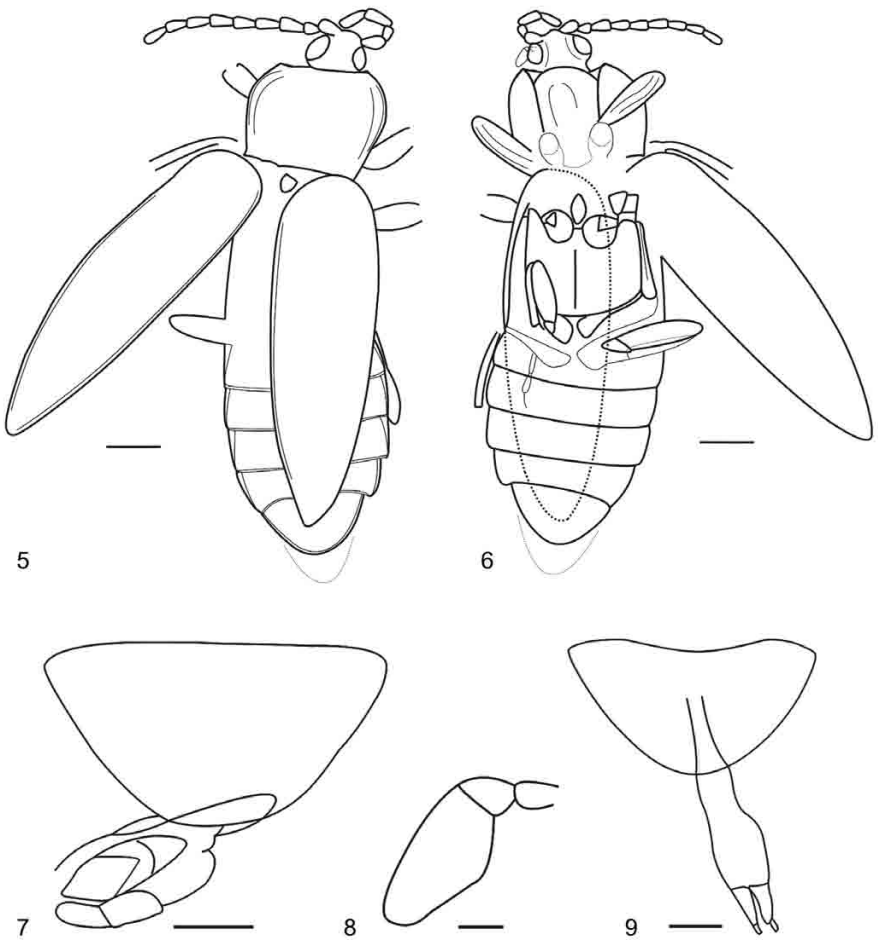
Figures 1–4
Necromera baeckmanni view and *Idiomerus* Dolin 1980 with body length. **1,** Holotype of *Necromera beckmanni* (7.75 mm); **2,** *Idiomerus brevicornis* Dolin 1980. No. 2784/1374 (5.0 mm); **3,** *Idiomerus longicornis* Dolin 1980. No. 2904/911 (6.0 mm); **4,** *Idiomerus musculus* 2997/1991 (4.5 mm).

District, Chimkent Region, Kazakhstan; Upper Jurassic, Karabastau Formation.

Diagnosis. This species differs from all already described species in the more slender body, strongly narrowing pronotal base and less arcuate elytral sides. Some specimens of *N. admiranda* **n. sp.** look somewhat like the holotype of this species, however, they have different configuration of the dorsal sclerites, namely the pronotum not so strongly widening anteriorly and their elytra leaving a considerable part of pygidium uncovered. Besides, the species under consideration shares some similarity with *N. brevicornis* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980), **n. comb.**, but it is much more slender than the latter and with the pronotum strongly widening anteriorly. Besides, *N. baeckmanni* is clearly different from *N. longa* (Hong & Wang 1980), **n. comb.** in the much longer prothoracic segment.

Addition to description. Length 7.8 mm. Body rather slender; pronotum very narrow and rather accuate at sides, distinctly long and distinctly narrow antennomeres, rather projecting anterior part of head, very narrow mesotibia, narrow and slightly arcuate at sides elytra (each about 4.5 times as long as wide) with apices not so acute as on the Martynov's drawing, elytral surface with very slightly seriate sculpture and microtuberculate (impunctured). Ovipositor moderately sclerotized.

Note. Martynov (1926) mentioned that the holotype of this species is a male and the exposed genitalia were interpreted by him as aedeagus. Indeed the exposed genitalia represent an ovipositor with clear gonocoxites and in proximal part of it a pair of very long sclerites (probably baculi) are visible. All peculiarities which can be seen in this specimen correspond those in females of the new species.



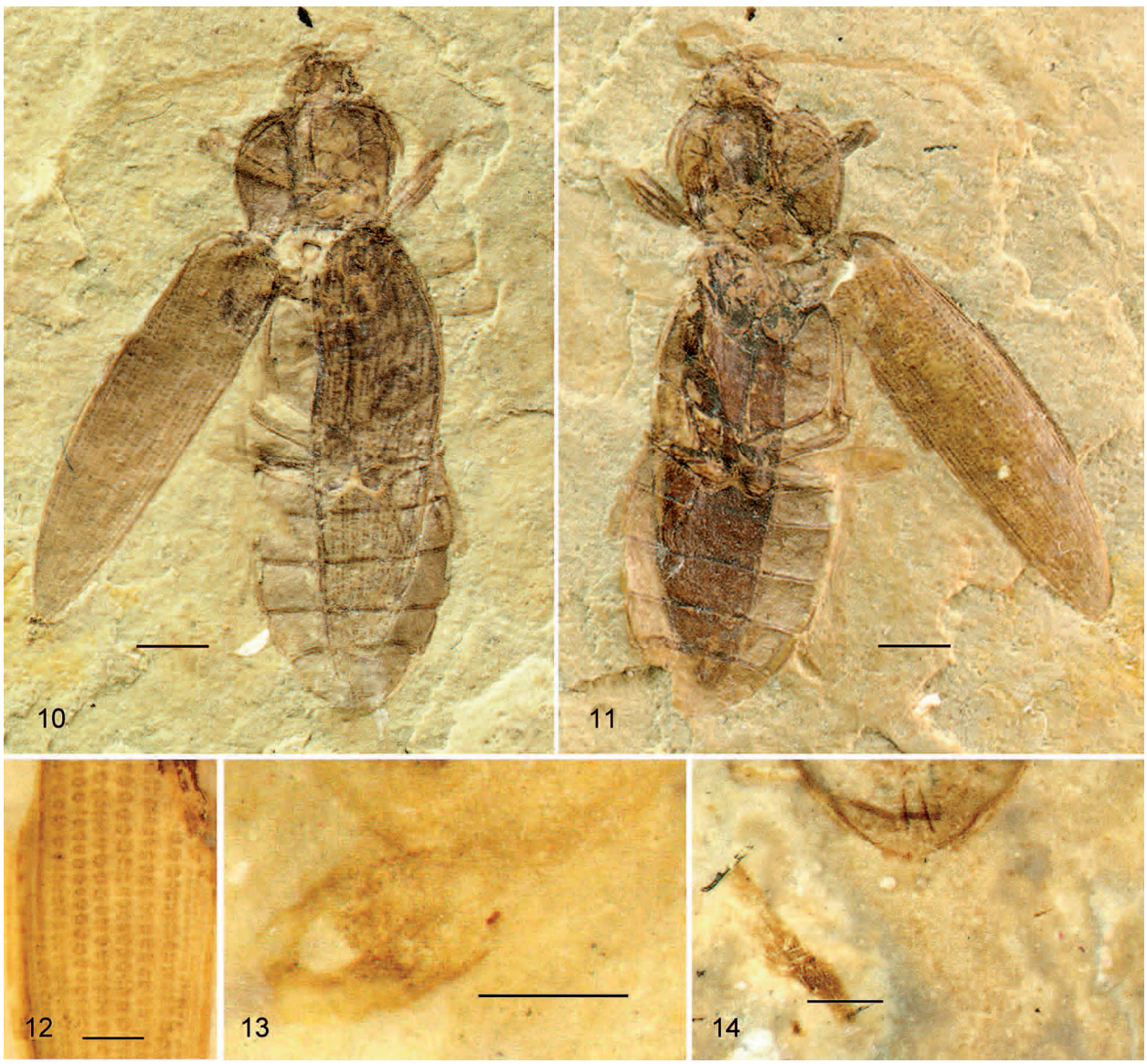
Figures 5–9
Necromera admiranda **n. sp. 5,** body of holotype, dorsal view; **6,** idem, ventral view; **7,** aedeagus of CNU-COL-LB2008987, ventral view; **8,** maxillary palpomere of the holotype; **9,** ovipositor of CNU-COL-LB2008927, ventral view. Scale bars: for figs 5, 6, 1.0 mm; for figs 7, 9, 0.5 mm; for fig. 8, 0.1 mm.

Necromera admiranda Chang & Kirejtshuk, n. sp. (Figs 5–38)

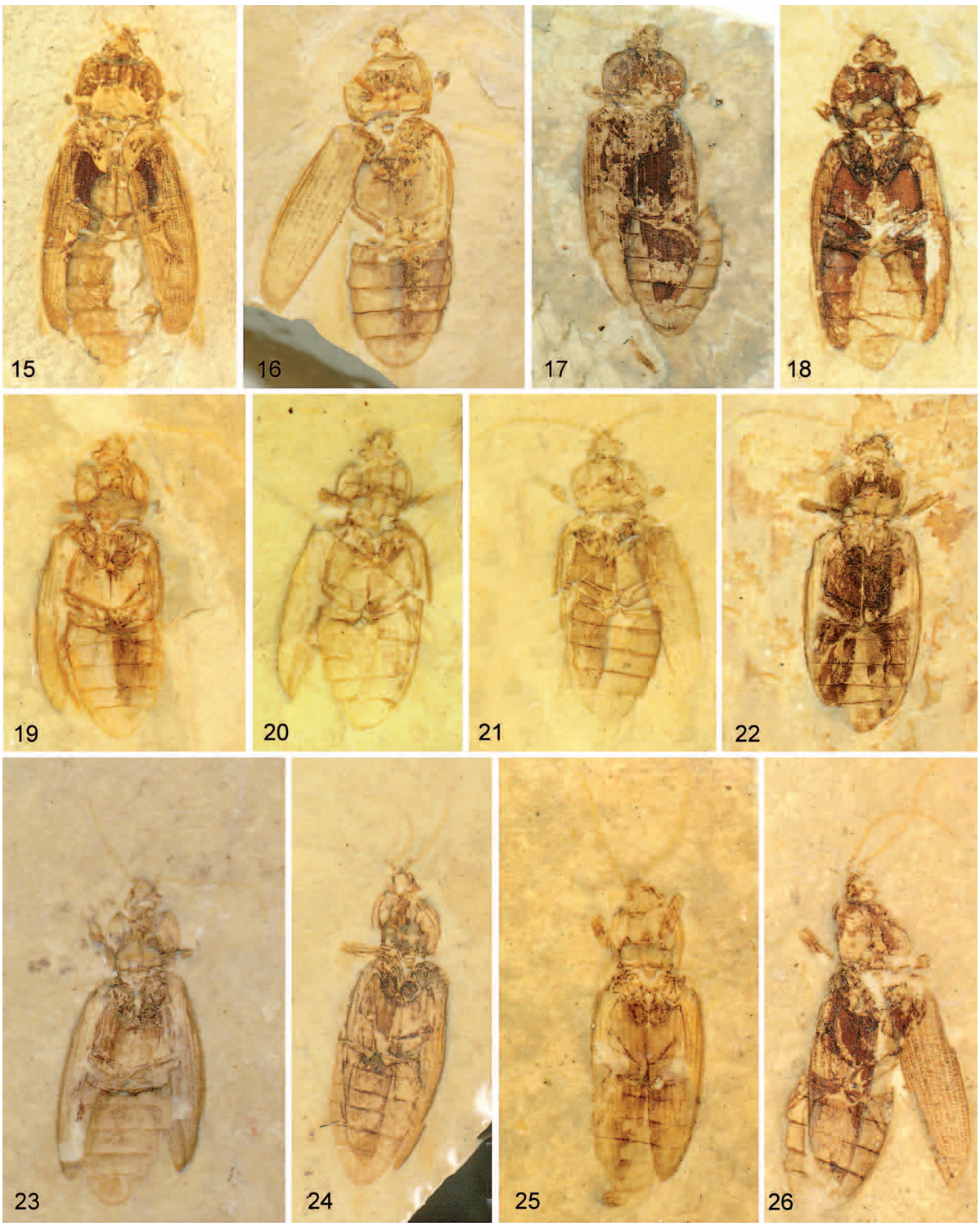
Type specimens: **Holotype**: CNU-COL-LB2008892PC, part and counterpart, probable female; impressions with almost complete body: most parts of antennae, pro- and metafemora, right mesofemur, pro- and metatibiae, left metatibia and part of right metatarsus (collection of CNU).

Paratypes: All paratypes originated from the same site as holotype: CNU-COL-LB2007801/7808 (female); /7810; /8883 (PC, female); /8884 (PC, female); /8887 (PC, female); /8893; /8904; /8907; /7808; /8926 (female); /8922; /8927 (female); /8932 (female); /8933 (female); /8938 (male); /8940 (male); /8949 (female); /8979 (PC, male); /8980 (PC, female); /8981 (female); /8983; /8984; /8986; /8987 (male); /8989 (male); /8990; /8998; /7846; /8912 (female); /8915 (PC, male); /8916; /8918 (female); /8923; /7817; /7820; /7828; /7823 (female) (most the above mentioned paratypes in collections of CNU, 3 paratypes in collection of ZIN, 1 paratype in collection of PIN); A31860, A31961, A31962, A31964, A33342 (deposited in Museum National d'Histoire Naturelle, Paris).

Additional specimens from the type locality (but their conspecificity with the holotype is doubted): CNU-COL-



Figures 10–14
Necromera admiranda **n. sp. 10,** body of holotype, dorsal view; **11,** idem, ventral view; **12,** elytron of CNU-COL-LB2008981; **13,** aedeagus of CNU-COL-LB2008987, ventral view; **14,** ovipositor of CNU-COL-LB2008927, ventral view. Scale bars: for figs 10, 11, 1.0 mm; for fig. 12, 0.4 mm; for fig 13, 14, 0.5 mm.



Figures 15–26
Necromera admiranda **n. sp.**, paratypes with body length. **15,** CNU-COL-LB2008949 (female, 10.2 mm); **16,** CNU-COL-LB2008926 (female, 9.2 mm); **17,** CNU-COL-LB2008927 (female, 10.0 mm); **18,** CNU-COL-LB2008916 (10.0 mm); **19,** CNU-COL-LB2008915-1 (male, 9.8 mm); **20,** CNU-COL-LB200898915-2 (male, 9.8 mm); **21,** CNU-COL-LB2008887-1 (female, 9.0 mm); **22,** CNU-COL-LB2008884-2 (female, 8.0 mm); **23,** CNU-COL-LB2007801 (8.5 mm); **24,** CNU-COL-LB2008918 (female, 9.1 mm); **25,** CNU-COL-LB2008987 (male, 8.7 mm); **26,** CNU-COL-LB2008980-1 (female, 8.6 mm).

LB2008934/8935; /8978; /8911 (PC); /8993 (female); /8920; /8913; /8925; /8930; /8948; /8952 (female); /8890 (PC, female); /8921; /7816; /7831; /7833; /7823;7835; /8908; /8931 (collections of CNU).

Locality and horizon. 2nd Bed of the Yixian Formation Huangbanjigou, near Chaomidian Village, Shangyuan County, Beipiao City, Liaoning Province, China; Upper Jurassic-Lower Cretaceous, Yixian Formation.

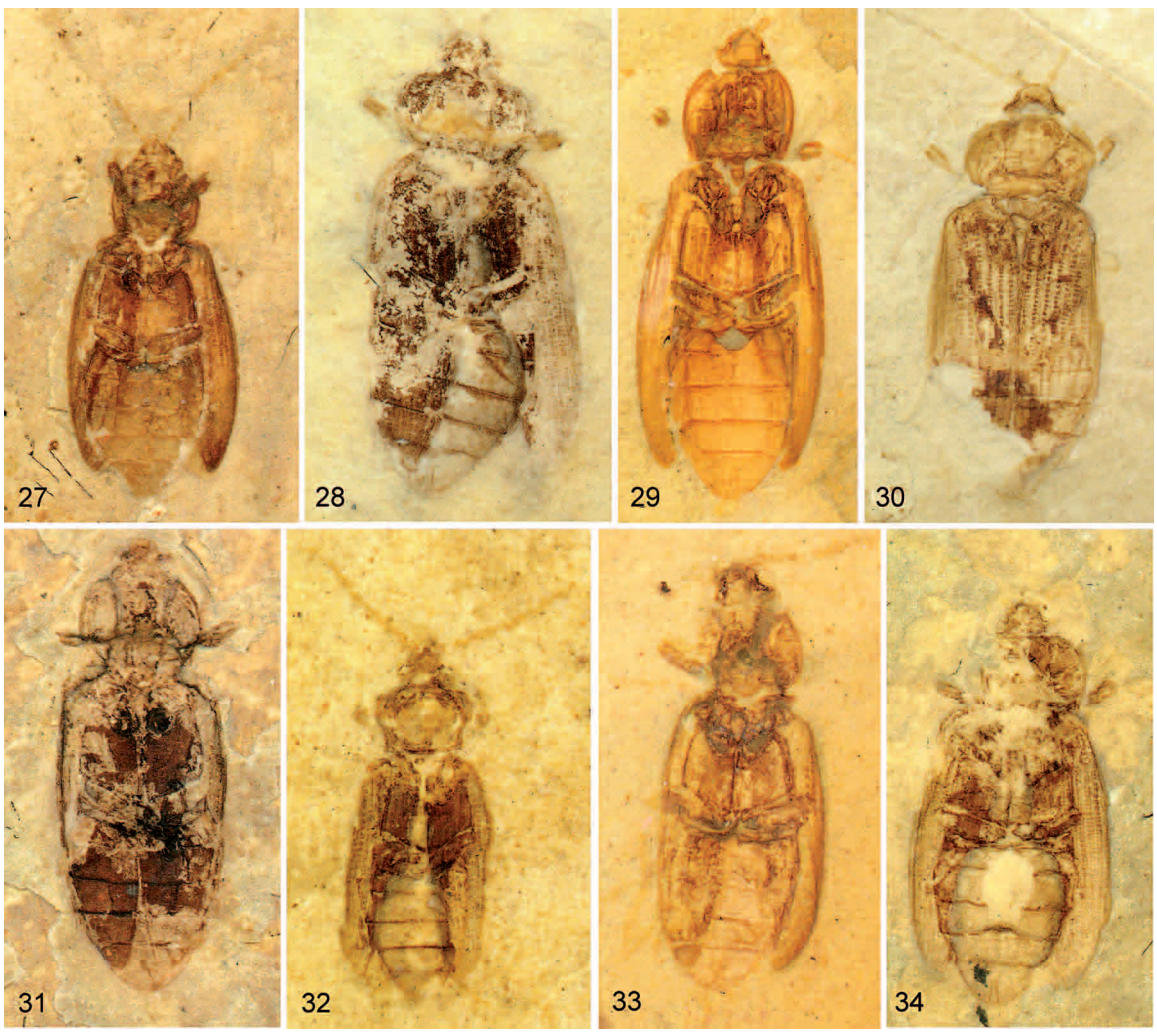
Diagnosis. This new species differs from most other species of *Necromera* in the rather wide pronotum. Only two species of this genus described have such wide pronotum and *N. admiranda* **n. sp.** can be diagnosed from both of them by the elytral apices not reaching the abdominal apex and also by the following characters:

- from *N. longa* (Hong & Wang 1990), **n. comb.** by the longer pronotum with slightly acute anterior angles, less arcuated sides, markedly shorter part of frons projecting anteriorly before antennal insertions and procoxae more narrowly separated;

- from *N. muscula* (Dolin in Dolin *et al*. 1980), **n. comb.** by the markedly larger body, less arcuate sides of pronotum, clearly separated mesocoxae, longer last abdominal ventrite.

Some unnamed specimens from Karatau (collection PIN: 2239/1325; 2239/953; 3997/371; 2554/460 etc.: Figs 35–38) from Mikhailovka (Kara-Tau Range, Algabass District, Chimkent Region, Kazakhstan; Upper Jurassic, Karabastau Formation) are somewhat similar to the specimens from the type series of *N. admiranda* **n. sp.**, although different in the outline of some body sclerites and antennae. The specimen 3997/371 from Karatau is in particular rather similar to some paratypes of *N. admiranda* **n. sp.**, but it has the subparallel-sided elytra with rather stump apices.

Description of holotype (Figs 5–14). Body length 9.4 mm, width 3.0 mm, elytra length 6.4 mm. Integument with very small and rather dense punctures, narrow interspaces between



Figures 27–34
Necromera aff. admiranda **n. sp.**, additional specimens with body length. **27,** CNU-COL-LB2008911-2 (female, 7.0 mm); **28,** CNU-COL-LB2008930 (female , 7.6 mm); **29,** CNU-COL-LB2008948 (female, 9.0 mm); **30,** CNU-COL-LB2008931 (8.3 mm); **31,** CNU-COL-LB2008993 (female, 9.1 mm); **32,** CNU-COL-LB2008913 (6.1 mm); **33,** CNU-COL-LB2007835 (4.9 mm); **34,** CNU-COL-LB2008952 (female, 9.2 mm).

them densely microreticulated; elytra with 9 longitudinal rows of transverse subquadrangular punctures, becoming less distinct to completely confluent apically. Abdomen and particularly elytra covered with very fine and extremely dense hairs.

Head transversely subtriangular, slightly convex; eyes oval and large; antennal grooves more or less distinctly outlined. Mentum small and subtrapeziform. Ultimate maxillary palpomere subsecuriform, slightly smaller than scape. Antennae filiform, incomplete: right one with 4 preserved antennomeres and left with 8 antennomeres; scape robust, subcylindrical; pedicel much shorter than scape (about 2/3 as long as scape) and antennomere 3; antennomere 3–8 subflattened and somewhat widened apically. Pronotum about 1.6 times as wide as long; anterior edge shallowly emarginate, lateral edges arcuately convex and subsinuate at posterior angles, basal edge apparently nearly straight, although slightly and widely emarginate in the middle; posterior angles sharply pointed; lateral explanations distinct. Scutellum slightly longer than wide at base. Elytra markedly wider than prothorax, 3.6 times as long as combined width; apices slightly obtuse, widest before middle.

Prosternum with collar (chin piece) arcuate anteriorly; notosternal sutures subparallel and between them there is an elongate and well outlined elevated stripe along the whole length of prosternum. Prosternal process wide and with apparently subtransverse apex. Procoxae apparently somewhat rounded. Mesepisterna subtriangular, mesepimera subrhombous. Mesocoxae oval, somewhat larger than procoxa. Metepisterna very narrow. Metacoxae moderately oblique. Abdomen with 4 first ventrites subequal in length, hypopygidium longest and rounded at apex; laterotergites rather narrow. There are two lines in the middle of the last abdominal segment divergent distally, which could be correspondent to apparently transparent baculi.

Femora comparable in thickness and rather long. Metatrochanter elongate, subtriangular and about half as long as metafemur. Tibiae moderately long and about half as thick as femora, metatibiae about as long as metafemora.

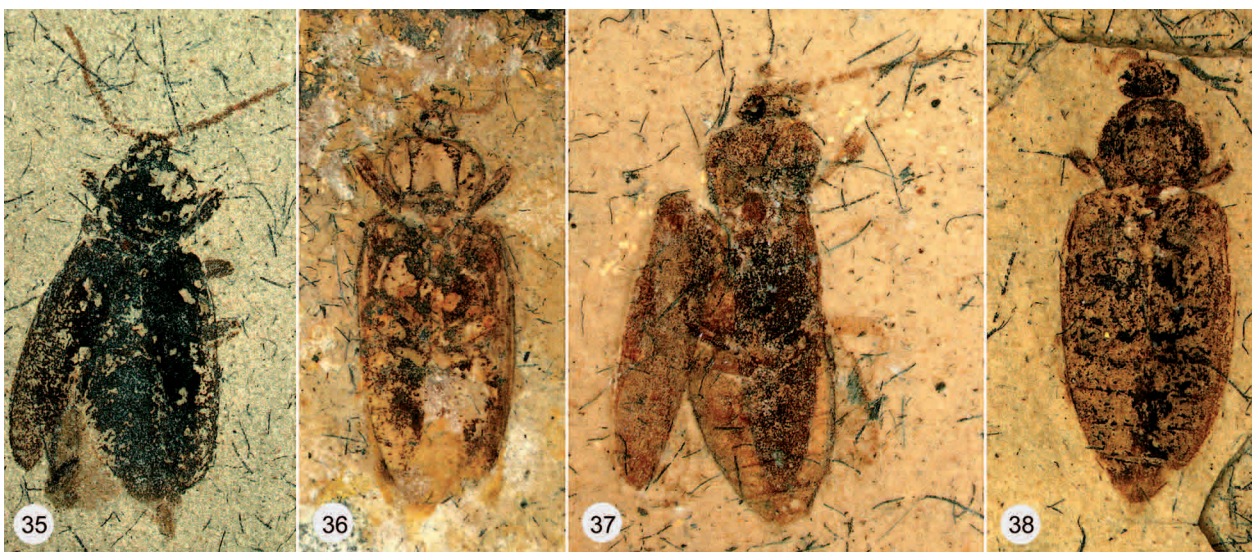
Paratypes. (Figs 15–26) Body length 6.0–10.2, width 2.0–3.7, elytra length 4.5–6.5, length of pronotum 1.2–2.0, width of pronotum 1.8–2.9 mm. Most paratypes have sclerites the same shape as those in the holotype. Sometimes lateral edges of the pronotum are with the maximum width rather at the middle than in anterior half and not subsinuate at posterior angles. Scutellum in most paratypes more or less transverse. Sometimes the last abdominal segment is retracted into the previous one (CNU-COL-LB-2008922). Some variability is observed in puncturation on elytra, expressed in density of punctures and intervals between longitudinal rows. Females have 2 lines on last abdominal segment divergent distally. Aedeagus (CNU-COL-LB-2008987) moderately to heavily sclerotized, with rather acute apex of median lobe, clearly articulated parameres and rather thick lateral part of phallobase. Ovipositor (CNU-COL-LB-2008927) with gonocoxites apparently membraneous and moderately developed styli.

Additional specimens (Figs 27–38)**.** Differs from the type specimens in the narrower body with the subsemicircular pronotum (CNU-COL-LB-2008911/8993), more transverse pronotum (CNU-COL-LB-2008952/8930), very small dimensions of body with body length 4.9 mm (CNU-COL-LB-2007835), subquadrate pronotum (CNU-COL-LB-2008935/8948/7831), or with antenomere 2 the same length as the first one and the third one (CNU-COL-LB-2008931).

Etymology. The epithet of this new species means "surprising", "remarkable", "noteworthy".

List of Fossil Cerophytidae

- *Aphytocerus communis* Zherichin 1977 – Lower Cretaceous, Yantardakh, Taimyr, North West Siberia;
- *Aphytocerus dolganicus* Zherichin 1977 – Lower Cretaceous, Nizhnyaya Agapa, Taimyr, North West Siberia;
- *Lebanophytum excellens* Kirejtshuk & Azar 2008 – Lower Cretaceous, Lebanese amber;



Figures 35–38
Necromera aff. admiranda **n. sp.**, specimens from Karatau with body length. **35,** No. 2239/1325 (9.4 mm); **36,** No. 2239/953 (11.1 mm); **37,** No. 3997/371 (9.1 mm); **38,** No. 2554/460 (7.7 mm).

- *Mercata festira* Lin 1986 – Lower Jurassic, Xiwan, Guangxi Province, China;
- *Necromera admiranda* **n. sp.** – Upper Jurassic-Lower Cretaceous, Beipiao, Liaoning Province, China;
- *Necromera baeckmani* Martynov 1926 – Upper Jurassic, Galkino, Karatau Kazakhstan;
- *Necromera brevicornis* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980) (*Idiomerus*), **n. comb.** – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- *Necromera inflata* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980) (*Idiomerus*), **n. comb.** – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- *Necromera intermedia* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980) (*Idiomerus*), **n. comb.** – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- *Necromera latissima* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980) (*Idiomerus*), **n. comb.** – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- *Necromera longicornis* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980) (*Idiomerus*), **n. comb.** – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- *Necromera longa* (Hong & Wang 1980) (*Leptocnemus*), **n. comb.** – Lower Cretaceous, Laiyang, China;
- *Necromera muscula* (Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980) (*Idiomerus*), **n. comb.** – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- Genus incertus: "*Abrotus*" *reconditus* Dolin *in* Dolin, Panfilov, Ponomarenko & Pritykina 1980 – Upper Jurassic, Mikhailovka, Karatau, Kazakhstan;
- Genus and species incerti – Upper Eocene, Baltic amber (Hieke & Pietrzeniuk 1984).

Discussion

Instead of some difference the fossil groups linked here with recent Cerophytidae can be outlined together as one family surpassed some stages reflected in structural transformations which gave a syndrome now observed in few descendants in the Recent fauna. Some characters regarded as diagnostic for recent forms of this family seemed to appear in different related groups and in different time. Nevertheless, most fossil representatives which here treated as members of this family show clear stability in prothoracic segments, including the type of thoracic interlocking mechanism, and narrowly separate antennal insertions. Besides they demonstrate more or less expressed tendency to shortening of frons and reduction of mouthparts, althougth frons of *Lebanophytum excellens* is comparatively far projecting. Other external "diagnostic characters" (shape of metacoxae with lack of femoral plate and long trochanters) formulated by Costa *et al.* 2003 are thought to be changed on time from states similar to those in other Elateroidea. Otherwise, the fossils here considered as Cerophytidae cannot be regarded in composition of other families with admission that they got structure of prothoracic segment and head independently from those in recent Cerophytidae.

The new discoveries make possible to outline a part of the Mesozoic history of the family Cerophytidae. This family is thought to have appeared no later than the Early Jurassic (finding of *Mercata festira*) and in the Middle Jurassic this groups probably became comparatively usual, as many species of this group with quite recognizable diagnostic characters have been found in materials of that age. The Cerophytidae seemed to be more diverse and much more common at least in some Asian Mesozoic faunas than in the recent fauna (only few species of this family are known from the recent Holarctic and Neotropical Regions: Costa *et al*. 2003; Sasaji 2004 etc.). However, it is very probable that this family even from its beginning did not have very wide variability in many characters in comparison with other groups of the Elateriformia. At least the general appearance, most prothoracic and head structures of the Mesozoic groups are rather similar to those in recent representatives of the group.

The largest genus of Mesozoic Cerophytidae is *Necromera* including at least more than 30 species spread through the Early Jurassic (Xiwan: Shiti Formation) and Upper Aalenian-Lower Bajocian, (Daohugou: Jiulongshang Formation, Middle Jurassic) to Lower Neocomian (Laiyang, Laiyang Formation, Lower Cretaceous). The members of this genus and some other Mesozoic genera (waiting for description) are only slightly different from those in the recent fauna. This circumstance presumes some stability in the mode of life of this lineage during the long time. Bionomy of both adults and larvae of the recent species is connected with angiosperm trees, larvae have been collected in old decomposing (brown rotten) wood. Nevertheless, some Mesozoic groups of the family have some peculiarities separating them from the main lineage of the family. One of them is the genus *Aphytocerus* described from Upper Cretaceous Taimyr amber, which is characterized by the rather small body (2.6–3.3 mm), extremely large eyes, very reduced mouthparts with dolabriform ultimate maxillary palpomere, 10-segmented antennae and very narrow tarsomeres 1 and 2. Another such group is *Lebanophytum* described from Lower Cretaceous Lebanese amber, which was also characterized by the rather small body (2.1 mm) as well as by the diffuse puncturation of elytra, comparatively projecting frons, comparatively small eyes, subquadrangular pronotum without projecting posterior angles, transverse scutellum, rather shortened elytra, rather narrowly separated procoxal and metacoxal cavities, transverse procoxae, very long abdominal ventrite 1, very narrow tarsi etc. These mentioned peculiarities of both genera are evidence of deviations from the standard mode of life of rest known representatives of the Cerophytidae. These studies supports that the formation of the Cerophytidae happened at the time when the related family Elateridae started its evolutionary history. Zherikhin (1980) regarded that the Mesozoic subfamily Protagrypninae (Elateridae), as other ancient elaterids had carnivorous

larvae inhabiting in wood. The Cerophytidae showing a considerable conservatism in structures seemed to maintain the initial mode of life scarcely during the long period of their existence and probably the larvae of early Cerophytidae as recent ones were associated with feeding on decayed wood. It is thought that later, when elaterids mastered xylomycetophagous feeding, they could in some sense dislodge cerophytids in the habitats, where the representatives of both groups could live simultaneously.

The most recognized interpretation of placement of this family links it with Throscidae and Eucnemidae (Lawrence *et al*. 1995, 2007 etc.), considering absence of femoral plate in the recent Cerophytidae as a plesiomorphyc feature. The indication on the development of these plates in the Upper Cretaceous *Aphytocerus* was usually ignored. New materials on fossil members of this group disproves this interpretation because the femoral plates are present in most extinct species of this group (only the species from Lower Cretaceous Lebanese amber has no femoral plates). If the propleurocoxal mechanism could be regarded as a structure more stable in time, it indicates a close relationship of the family under consideration with Artematopodidae Lacordaire 1857 and Brachypsectridae LeConte et Horn 1883 (Hlavac 1975). However, the comparable representation of the Cerophytidae and Elateridae and their distinctness in the Middle Jurassic are evidence of a rather ancient origin of both groups. Therefore the placement of this family at base of superfamily Elateroidea seems to be regarded as quite reasonable (Lawrence *et al*. 1995), although a further detailed study of abundant materials on the Mesozoic faunas of this superfamily is needed.

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