

First record of fossil comb-clawed beetles of the tribe Cteniopodini (Insecta: Coleoptera: Tenebrionidae) from the Jehol Biota (Yixian formation of China), Lower Cretaceous



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ABSTRACT

A new genus and species *Platycteniopus diversoculatus* is described from the Lower Cretaceous (Yixian Formation, Laoning, China). The new genus belongs to the tribe Cteniopodini as shown by six visible abdominal ventrites (ventrite 6 is sternite VIII), in comparison with other Alleculinae which have five abdominal ventrites; epistomal canthus of eyes not emarginate; anterior margin of first abdominal ventrite not bordered. On the other hand, *Platycteniopus diversoculatus* has some characters not typical for Cteniopodini: bifid mandibles and serrate antennae. The oldest representative of the tribe has combination of characters of tribes Alleculini and Cteniopodini. Recent representatives of Cteniopodini are associated with flowers of angiosperms, while other groups of Alleculinae, especially Gonoderini and Alleculini are mainly saprophagous and lichenophagous. Age of *Platycteniopus* finding coincides with the beginning of the angiosperms heyday.

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1. Introduction

The Yixian Formation (Liaoning, China) is very well known in the field of palaeontology for yielding feathered dinosaurs, mammals, birds, angiosperm plants and a great number of insects that have contributed significantly to our understanding of the evolution of those groups (Chang, 2003) (Fig. 1).

The age of this formation is the subject of incessant disputes and is believed by many researchers to be Lower Cretaceous, – 125Ma (Swisher, Wang, Wang, Xu, & Wang, 1999). Some evidence suggests an Upper Jurassic age (Lo, Chen, Tsou, Sun, & Lee, 1999). Other opinions, based on both radiological methods (Wang et al., 2005) and biostratigraphical comparisons of beetles and other insects (Kirejtshuk et al., 2010, 2011 etc.), more probably point to the boundary between the Jurassic and the Cretaceous.

The coleopterofauna of Yixian Formation is diverse. More than sixty species of beetles from 12 families are known in this formation (Kirejtshuk et al., 2010). In the latter publication numerous

representatives of the family Tenebrionidae (subfamilies Alleculinae and Diaperinae) were mentioned. Later the oldest and currently the only known representative of the tenebrionoid branch (the subfamily Tenebrioninae) *Alphitopsis initialis* Kirejtshuk et al., 2011 was described (Kirejtshuk et al., 2011). The genus *Alphitopsis* demonstrates that at the Rubicon of the Jurassic and Cretaceous Yixian the tribe Alphitobiini was represented by forms that were rather similar to the recent ones.

Recently the second fossil representative (new genus and species) of Tenebrionidae from the subfamily Alleculinae (the tribe Gonoderini) was described from the Yixian Formation (Nabozhenko et al., in litt).

In this paper the third representative (new genus and species) of Tenebrionidae is described from Yixian Formation. The new species belongs to the subfamily Alleculinae, tribe Cteniopodini, of which fossil representatives were known only from Baltic Amber.

2. Material and methods

Material is deposited in Henan Geological Museum, Zhengzhou, China with registration number 41HII0137 PC (P: Part; C: Counterpart). The specimen was studied using a stereomicroscope MOTIC SMZ-168. Photographs were made with and without

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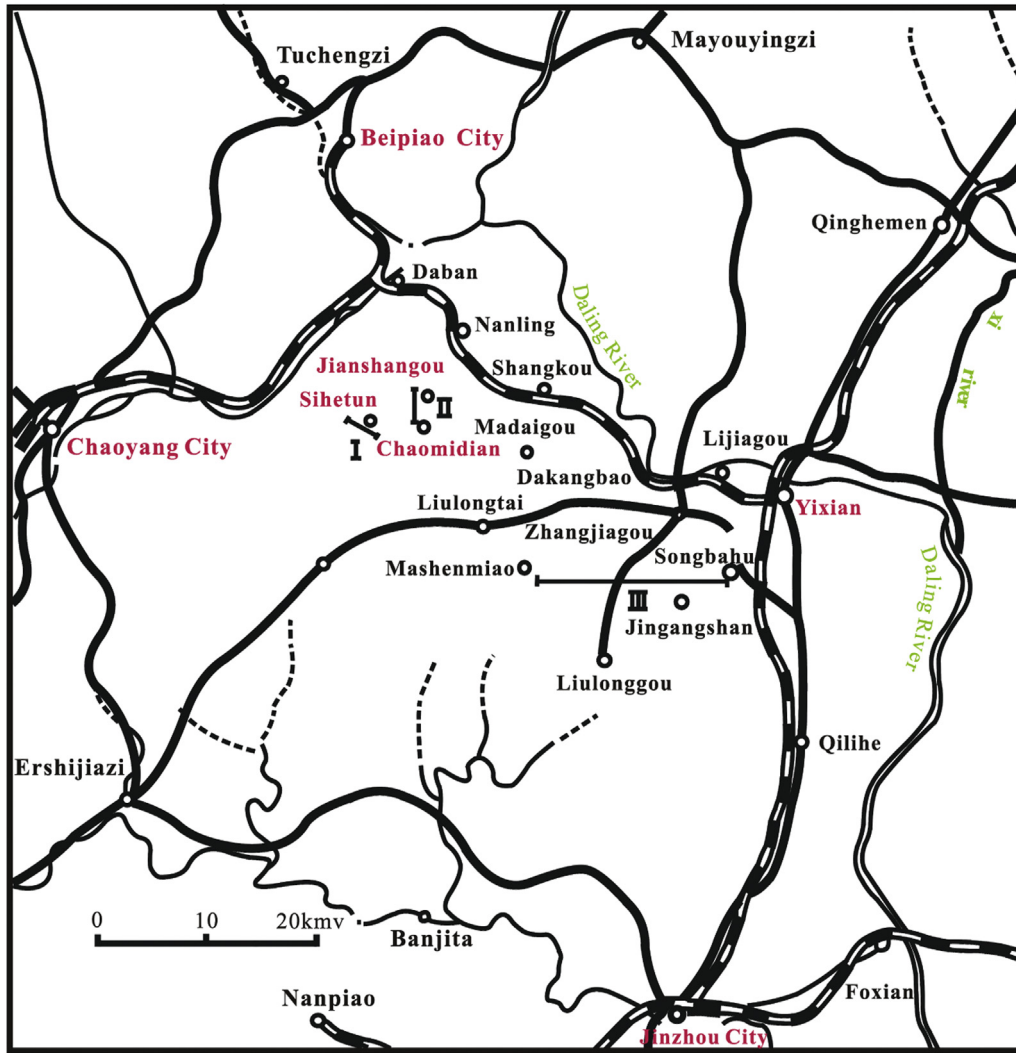


Fig. 1. Index map showing section localities of the Yixian Formation in Jinzhou – Yixian area, western Liaoning (after Ren et al., 1997) I. Sihetun section; II. Jianshangou section; III. Mashenmiao – Songbahu section.

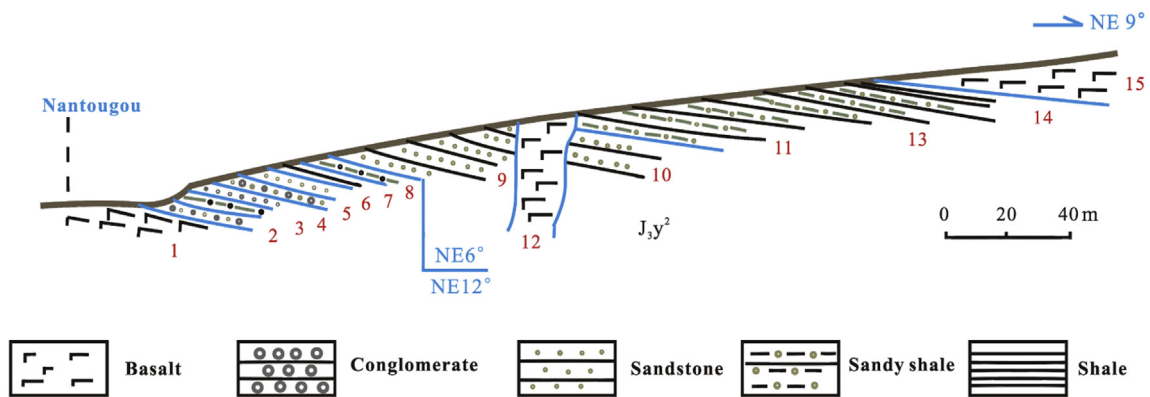


Fig. 2. Stratigraphic section measured at the base part of Yixian Formation near Jianshangou, Chaomidian (after Ren et al., 1997).

ethanol using a Nikon D90 camera with Nikkor 105 mm lens. We used the ocular index of Campbell and Marshall (1964) in the description.

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758.

Superfamily Tenebrionoidea Latreille, 1802.

Family Tenebrionidae Latreille, 1802.

Subfamily Alleculinae Laporte de Castelnau, 1840.

Tribe Cteniopodini Solier, 1835.

Genus *Platycteniopus* gen. nov.

Type species, *Platycteniopus diversoculatus* sp. nov.

Etymology. The name of the new genus is derived from the Greek word “πλάτύς” – wide and the Latin generic name *Cteniopus* Solier, 1835 (Tenebrionidae: Alleculinae, Cteniopodini).

Composition. The type species only.

Diagnosis. Body large (20 mm), elongate. Head nearly oval. Eyes round dorsally and transverse ventrally. Antennae serrate, first four antennomeres weakly transverse or with subequal width and length. Mandibles bifid. Pronotum bell-shaped, not narrower than humeral angles of elytra; posterior angles distinct, almost straight. Elytra wide, with broadly rounded lateral margins, narrowed to apex, densely and finely punctate. Mesoventrite process between mesocoxal cavities apically acute. Abdominal ventrite 6 (sternite VIII) with wide deep emargination. Abdominal ventrite 5 with straight apical margin. Fore and mid legs not long, profemora and mesofemora not protruding beyond pronotum and elytra. Hind legs longer, visibly protruding beyond elytra. Protibia straight, metatibia weakly bent. Tarsi narrow, filiform, their penultimate segment without membranous lobe. Protarsomere 1 equal in length to protarsomeres 2–4. Metatrochanters small, much shorter than metafemora. Male genitalia: basal piece long, apical piece short, outwardly curved.

Platycteniopus diversoculatus gen. et sp. nov. (Figs. 3 and 4)

Etymology. The name of the new genus is derived from the Latin words “diversi” (masculine, plural) – different and “oculatus” – having eyes.

Holotype. Registration number is 41HII0137 PC (P: Part; C: Counterpart). Right antenna is absent, left antenna has 4 antennomeres on part and 6 antennomeres on counterpart. Left mesotibia is partly visible only on counterpart. Metatarsi are absent.

Locality and horizon. The holotype was collected from 2nd Bed of Yixian Formation in Huangbanjigou, near Chaomidian Village, Shangyuan County, Beipiao City, Liaoning Province (Fig. 2). Coordinates: N 41.6148, E 120.8341. Early Cretaceous, 125Ma (Swisher et al., 1999).

Description. Male. Body length 20 mm, width 8 mm. Body elongate, robust (Fig. 3A and B). Anterior margin of clypeus emarginate. Head widest at level of eyes. Eyes dorsally (part) large, round (Fig. 3C), ventrally (counterpart) strongly transverse (2.5 times as wide as long) (Fig. 3F). The ‘ocular index’ dorsally – 20, ventrally – 23.6. Mandibles clearly visible, elongate, with long distance between apical and inner teeth. Antennae serrate, 2nd antennomere longitudinal, other ones subequal in length and width (Figs. 3A and B, 4).

Pronotum transverse (1.8 times as wide as long), bell-shaped, widest near base, 2.25 times as wide as head. Ratio of pronotum width at base and anterior margin 7: 2.2. Lateral margins almost straight and parallel in basal third, strongly oblique and straight in anterior 2/3. Anterior margin emarginate, base widely rounded in middle, bisinuate. Anterior angles obtuse, narrowly rounded at apex, posterior angles almost right, with distinct apex. Width of pronotum 6 mm.

Scutellum rhombic. Elytra elongate, 13 mm wide (each elytron about 3 times as long as wide), narrowed to apex, widest a just before the middle, 1.3 times as wide and 3.2 times as long as pronotum, 3 times as wide as head. Elytral width 8 mm. Surface of elytra with fine and dense punctation and recumbent short setae. Apex of each elytron rounded. Epipleura wide at base (1.7 times as wide as mesepimera), strongly narrowed to apex.

Mesoventral process between mesocoxae sphenoid, acute. Inner margin of mesocoxal cavities straight. Mesoventral process and

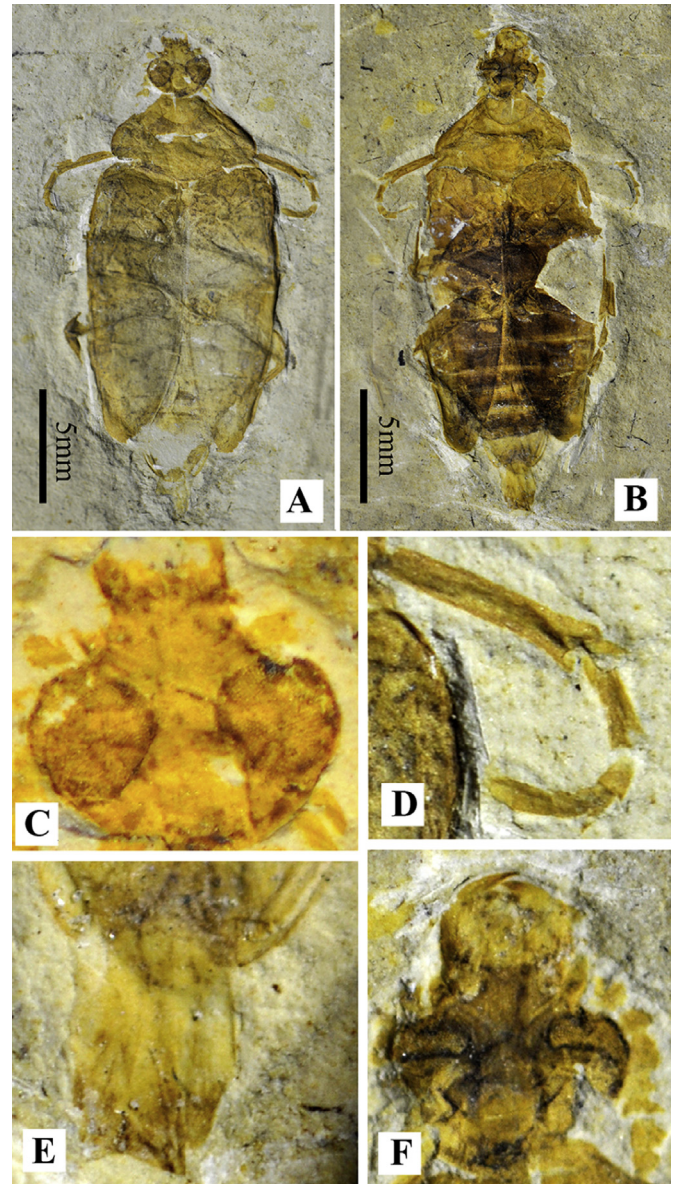


Fig. 3. Comb-clawed beetle *Platycteniopus diversoculatus* gen. et sp. nov. from Lower Cretaceous (Yixian Formation, Laoning, China), holotype, male. A, B – general view; C – head dorsally; D – protarsi; E – male terminalia; F – head, ventral view.

anterior margins of mesocoxal cavities distinctly bordered. Metaventrite twice as wide (including metepisterna) as long. Metepisterna long, 3.8 times as long as wide (ratio of maximal length and width).

Abdomen with 6 ventrites, rather narrowed to apex. Ventrite 1 with wide, distinct triangular process between metacoxae. Ventrite 6 (sternite VIII) with deep triangular emargination in the middle and more sclerotized than lateral margins. Membranes between ventrites 3, 4 and 5 distinct.

Legs. Protibiae narrow, straight, profemora obviously short and not extended beyond margins of pronotum. Protarsomeres not broadened, simple, protarsomere 4 without lobes. Protarsomeres 1 and 5 clearly wider than other ones, Protarsomeres 2 and 3 combined (Figs. 3D and 4B). Mesofemora extended beyond elytral margins. Mesotibiae (only apical half of left mesotibia preserved on counterpart) wider than protibiae. Mesotarsomeres (only tarsomeres 1–3 visible on counterpart) elongate, with subequal length.

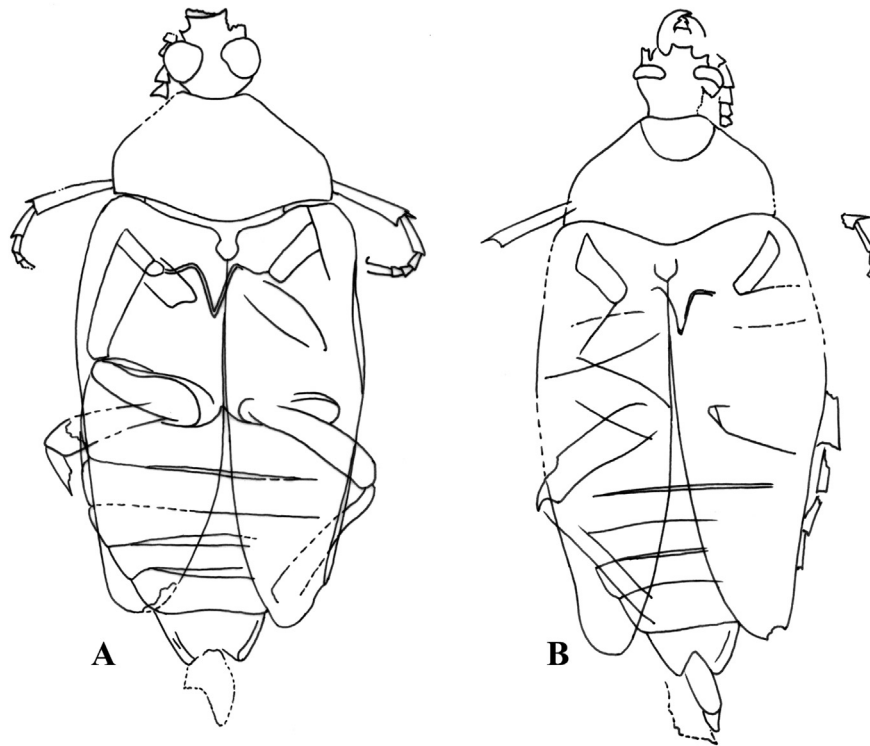


Fig. 4. Comb-clawed beetle *Latoctenipous diversoculatus* gen. et sp. nov. from Lower Cretaceous (Yixian Formation, Laoning, China), holotype, male, reconstruction. A – habitus, part; B – habitus, counterpart.

Metacoxae large, transverse, widened from outer to inner margin. Metafemora weakly bent and long, visibly extended beyond elytra. Metatibia straight, of same length as metafemora.

Genitalia (Figs. 3E and 4B). Counterpart with exposed male terminalia: long basal piece and short and weakly bent apical piece.

3.1. Comparison

Synapomorphies, allowing including to the new genus in the family Tenebrionidae:

1. Antennae inserted under lateral expansions of frons which conceal at least base of scape dorsally.
2. External membranes between abdominal sternites 3, 4, and 5 and accordingly presence of abdominal glands. Nearly perfect correlation between the presence of glands and external membranes between abdominal sternites 3, 4, and 5 was established by Doyen (1972).
3. Normal position of aedeagus (not inverted aedeagus). With one known exception, Tenebrionidae with the aedeagus inverted lack defensive glands, while species with the aedeagus in the normal position possess them (Doyen, 1972; Watt, 1974). Accordingly Doyen (1972) “the tenebrionid subfamily Tenebrioninae, together with the Alleculidae, Lagriidae and Nilionidae possess defensive glands and external abdominal membranes and have the aedeagus in the normal position”.

Doyen (1972) treated Tenebrioninae, Alleculinae, Lagriinae and Nilioninae as subfamilies in the family Tenebrionidae considering two last correlation differences.

Unfortunately Alleculinae apomorphy “pectinate tarsal claws” is not visible on the part and counterpart. But complex of other characters (see below), including six visible abdominal ventrite (the unique character of Cteniopodini) allows to include the new genus

in the subfamily Alleculinae.

The new genus has distinct characters allowing us to include it in the tribe Cteniopodini: six visible abdominal ventrites (ventrite 6 corresponds to sternite VIII), in contrast to other Alleculinae, having five abdominal ventrites; epistomal canthus of eyes not emarginate; anterior margin of abdominal ventrite 1 not bordered. From all recent representatives of the tribe the new genus differs in the follows characters: eyes very large, round dorsally and strongly transverse ventrally; serrate antennae not typical for Cteniopodini. The body form of *Platycteniopus diversoculatus* sp. nov. is similar to recent species of the genera *Podonta* Solier, 1835, *Heliotaurus* Mulsant, 1856 and *Gastrhaema* Jacquelin du Val, 1863, from which the new genus additionally differs in the very large eyes, structure of protarsi (protarsomeres 1–4 in *Podonta* spp. are short, with subequal length; protarsomeres 1 and 5 in *Platycteniopus diversoculatus* sp. nov. are markedly longer than each of other ones) and larger body. Moreover, anterior margin of abdominal ventrite 1 is not bordered in *Platycteniopus* unlike *Podonta* and the close genera *Podontinus* Podontinus Seidlitz, 1896 and *Cistolomorpha Redtenbacher*, 1867. The new fossil species has also bifid mandibles in contrast with other Cteniopodini. The oldest representative of the tribe has combination of characters of tribes Alleculini and Cteniopodini.

4. Discussion

Comb-clawed beetles (the subfamily Alleculinae of the family Tenebrionidae) are a widespread and diverse group of Tenebrionidae, which is well represented in the fossil record. Thirty two fossil taxa of Alleculinae have been described up to the present time (Kirejtshuk, Merkl, & Kernegger, 2008; Ponomarenko & Kirejtshuk, 2015), four of them are known from the Mesozoic. The oldest representative of comb-clawed beetles *Cistelites insignis* was described from the Upper Jurassic (Heer, 1865), formation

Insektenmergel, Schambelen, Aargau. It should be noted, that the original description of the genus *Cistelites* Heer, 1865 (and the type species *Cistelites insignis*) and subsequent redescriptions with figures (Scudder, 1885: Fig. 1016) raise doubt that the genus belongs to tenebrionid beetles. Another probable representative of comb-clawed beetles *Wuhua jurassica* is known from the Middle Jurassic of Daohugou, China (Wang & Zhang, 2011). The authors left the family attribution of this species unsolved noting only that it belongs to the superfamily Tenebrionoidea. However *Wuhua jurassica* may belong to the comb-clawed beetles based on some characters including pectinate tarsal claws. The oldest comb-clawed beetle *Jurallecula grossa* with distinct alleculoid characters was described by L. Medvedev (1969) from the Upper Jurassic of Karatau (Kazakhstan). This species was included in the tribe Alleculini. A fourth Mesozoic alleculine species *Cistelites sachalinensis* Heer, 1878 was described from the Upper Cretaceous (Santonian of Sakhalin) (Heer, 1878), but, as is the case with other descriptions of Heer, doubt remains as to whether this species belongs to Alleculinae. Thus, information about Mesozoic Alleculinae is very scarce, and descriptions are often uninformative. Recently a new alleculid genus and species of the tribe Gonoderini was described from the Yixian Formation (Nabozhenko et al., in litt.). This genus differs from known genera of Gonoderini by its long hind spurs on the metatibia, equal to half of the metatarsomere I. Other characters of the genus are very similar to characters of recent genera of Alleculinae (the tribe Gonoderini).

Platycteniopus diversoculatus sp. nov. combines characters common to the tribe Cteniopodini (6 abdominal ventrites, anterior margin of eyes not sinuate, anterior margin of first abdominal ventrite not bordered) with characters usual for other comb-clawed beetles (tribes Alleculini, Gonoderini, Xystopodini) (serrate antennae, not bifid mandibles). According to Ogloblin and Znojko (1950) Cteniopodini (interpreted as the subfamily Omophlinae of the family Alleculidae) differs from the alleculoid branch (the subfamily Alleculinae of the family Alleculidae sensu Ogloblin and Znojko) in the follows characters of adults: mandibles is not bifid; abdomen (at least in females) with six abdominal ventrites (excluding *Podonta*, *Cistelomorpha* and *Podontinus*); metacoxae with rounded posterior margin, which are above the level of the abdominal ventrites (excluding *Podonta* and *Cistelomorpha*); head with short genae and anterior margin of eyes not widely sinuate.

Recent representatives of Cteniopodini are widespread in the Palaearctic (more, than 300 species) (Novák, 2008), Indomalayan region, Madagascar, and the Nearctic (two genera) (Ogloblin & Znojko, 1950). Fossil representatives (genera *Cteniopus* and *Cteniopinus*) are known from Baltic Amber (Klebs, 1910; Larsson, 1978; Hieke & Pietrzeniuk, 1984; Kirejtshuk et al., 2008). Ogloblin and Znojko (1950) supposed that Cteniopodini is a young group in comparison with Alleculini, because of highly specialized structures of its adults and larvae and the narrow distribution of this tribe. The first record of Cteniopodini in the Lower Cretaceous significantly corrects this opinion. However, the combination of characters similar to those in different groups in *Platycteniopus* gen. n. indicates that Cteniopodini may have originated somewhat later than Alleculini, typical representatives of which are known from the Upper Jurassic. Recent representatives of Cteniopodini are associated with flowers of angiosperms, while other groups of Alleculinae, especially Gonoderini and Alleculini are mainly saprophagous and lichenophagous. Age of *Platycteniopus* finding coincides with the beginning of the angiosperms heyday.

The oldest species of Tenebrionidae demonstrate that in the Upper Jurassic and Lower Cretaceous this family was represented by forms that were rather similar to the recent ones (Kirejtshuk et al., 2011; Nabozhenko & Kirejtshuk, 2014). This supports the concept of a presumably early Jurassic diversification of the

superfamily Tenebrionoidea (Medvedev, 1969).

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