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New ommatids from the Late Jurassic of western Liaoning, China (Coleoptera: Archostemata)

JING-JING TAN, DONG REN and MING LIU

College of Life Science, Capital Normal University, Beijing, China

Abstract A new genus *Amblomma* gen. nov. of fossil beetles is erected and can be assigned to the family Ommatidae because its two procoxal cavities are contiguous and the articulations of the abdominal ventrites are abutting. The new genus is similar to *Zygadenia* Handlirsch, 1906 (= *Notocupes* Ponomarenko, 1964), *Tetraphalerus* Waterhouse, 1901, *Rhobdocupes* Ponomarenko, 1966 and *Sinocupes* Lin, 1976, but can be distinguished from other genera according to the following characters: the second segment of antennae is shorter than the third one in length; the posterior tarsi with the basal segment is obviously shorter than the three following taken together in length; the antennae reach the posterior ridge of prothroax in length, and the sides of the prothroax with serrulate margin. Four new species of the new genus are described and figured: *Amblomma psilata* gen. *et* sp. nov., *Amblomma rudis* gen. *et* sp. nov., *Amblomma epicharis* gen. *et* sp. nov., and *Amblomma stabilis* gen. *et* sp. nov. A key to species within this new genus is provided. All the specimens are collected from the Late Jurassic Yixian Formation of western Liaoning and are now housed in the College of Life Science, Capital Normal University, Beijing, China.

Key words Ommatidae, Cupedidae, new genus, new species, Jurassic, Yixian Formation
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Introduction

Although the family Cupedidae was described in the 1900s, its phylogenetic position was poorly understood until the early part of the 20th century (Lawrence, 1999). In Lacordaire's major work, *Omma* (*Omma* Newman, 1839) was tentatively placed at the end of the Cucujides, while the family Cupesides (only including *Cupes* Fabricius, 1801) was placed between the Lymexylones and Ptiniores (Lawrence, 1999). On the basis of hind wing venation, Ganglbauer placed the cupedids in the suborder Adephaga, believing them to be a modified family of that group (Atkins, 1963). However, Kolbe (1908) considered the group to be a subdivision (Archostemata) of the suborder Symphiogastra. It was Forbes (1926) and Böving and Craighead (1930) who recognized the Archostemata as a suborder equivalent to Adephaga and Polyphaga, based on wing venation and larvae respectively, and considered that this suborder included Cupedidae and Micromalthidae.

The family Cupedidae includes some of the earliest known fossil beetles and some of the most primitive living beetles (Lawrence, 1999). This group is small, including only 25 extant and 9 extant genera (Neboiss, 1984), but it was abundant in the Permian and the Mesozoic (Lubkin, 2003). Consequently, the study of Mesozoic cupedids has been important in understanding their relationships.

Although a few fossil beeltes were described before the middle of the 20th century, the most abundant and complete specimens of Archostemata were not described until the 1960s. Ponomarenko (1969) defined Archostemata in a very broad sense to encompass the modern archostematan genera and all fossil taxa. He placed all of the typical cupedid-like samples from the Triassic to the Recent era in the family Cupedidae, which was subdivided into three subfamilies: Triadocupedinae, Cupedinae and Ommatinae.

The phylogenetic position of the subfamily Ommatinae

Correspondence: Dong Ren, College of Life Science, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100037, China. Tel & fax: +86 10 6898 0851; e-mail: rendong@mail.cnu.edu.cn

has been the subject of much controversy (Sharp & Muir, 1912; Ponomarenko, 1969; Lawrence, 1999). Based on the difference between *Omma stanleyi* Newman and *Tenomerga mucida* (Chevrolat) (as *Cupes clathratus* Solsky) in the aedeagus, Sharp and Muir (1912) first proposed Ommatidae. However, most subsequent workers continued to include *Omma* in the family Cupedidae. Lawrence (1999) found the enclosure of palpal sensillia in deep sensorial cavity on the apical palpomere was an additional character uniting *Omma* and *Tetraphalerus*; this cavity is absent in Cupedidae. Based on this fact, he discussed the relationships of Ommatidae and Cupedidae and thought that it would be preferable to elevate Ommatinae to Ommatidae and described the features of this family.

Up to now, a large fossil Archostematan assemblage has been found in the Mesozoic non-marine sedimentary strata from northern China (Lin, 1976; Hong & Wang, 1976; Hong, 1982, 1983, 1984, 1985, 1988, 1990, 1992a, 1992b; Ren *et al*., 1995; Wang & Liu, 1996; Zhang, 1997) and 16 extinct genera and 22 extinct species of Cupedidae have been assembled (Tan *et al*., 2004). Recently we recovered many well-preserved fossil cupedids from the Late Jurassic Yixian Formation in Chaomidian village, Beipiao City, Liaoning Province. The discovery of these fossils is very significant because most other Mesozoic cupedids in China are not complete which made studies on them confined solely on the basis of isolated elytron (Hong & Wang, 1976; Hong, 1982, 1983). So complete preservation enabled us to fix accurately the body characteristics of the ancient cupedids and to document the affinities of these species with existing and extinct groups.

This paper deals with one new genus and four new species of Archostemata from this assemblage. The dating of the Yixian Formation has proved to be contentious, and many biostratigraphical correlations and radiometric dates have been published that support the Yixian Formation being either Late Jurassic or Early Cretaceous in age (Chen, 1988; Chen *et al*., 1998; Wang, 1998; Swisher *et al*., 1999; Zhou *et al*., 2003). However, both Chen *et al*. (1998) and Ren *et al*. (1997) maintain that the samples analyzed by Swisher *et al*. (1999) came from intrusive volcanic rocks many millions of years younger, rather than from the fossil-bearing sediments deposited in the Upper Jurassic. We consider that ^{40}Ar-^{39}Ar dates of 124.6 $\pm$ 0.1 Myr obtained from tuff layers in the "Jianshangou beds" of the Yixian Formation by Swisher *et al*. (1999) is a date affected by secondly intrusive volcanics. The theropod dinosaur, *Sinosauropteryx*, from the lower part of this formation is comparable to *Compsognathus* from the Upper Jurassic (Tithonian) Solnhofen Beds in Germany (Chen *et al*., 1998). Also, a late Jurassic age is indicated by abundant fossil insect remains from the Yixian Formation which is similar to those known from the Upper Jurassic of both Kazakhstan and Solnhofen (Ren *et al*., 1997).

The specimens were examined with LAICA MZ12.5 dissecting microscope and illustrated with the aid of a drawing tube attached to a microscope. All the type specimens described here are deposited in the College of Life Science, Capital Normal University in Beijing, China.

Systematic paleontology

Order Coleoptera Linne, 1758

Family Ommatidae Lawrence, 1999

Subfamily Ommatinae Sharp *et* Muir, 1912

Genus *Amblomma* gen. nov.

Etymology. A combination of the Greek prefix *ambl*- (meaning "serrulate") and *Omma* (type genus of the family).

Type species. *Amblomma psilata* gen. nov. *et* sp. nov.

Diagnosis. Body subcylindrical; the head a little longer than wide; eyes large; mandible prominent and incurved; antennae filiform, 11-segment, nearly as long as the head and thorax taken together, the basal segment large, the second segment shorter than the third in length. Prothorax transverse, with a large elevation divided by a longitudinal line in the middle; the margin serrulate. Elytron with 11 rows of cells, gradually widening posteriorly then arcuately acuminated. Tarsi five-jointed, the posterior pair with the basal joint shorter than the three following taken together, abdomen with five visible sternites; the last sternite 2.5 times longer than the previous one.

Discussion. This paper tentatively follows the systematic arrangement of Lawrence (1999) at the familial level and have associated our Late Jurassic beetles with the Ommatidae on the basis of the following shared characteristics: mandible tridentate; propleuron almost reaching anterior edge of prothorax; procoxal cavities contiguous; elytron with 10 rows of cells on disc and one or more on the epipleuron; ventrites flattened and abutting one another not overlapping.

At present, this family includes three extant genera: *Omma* Newman, 1839, *Tetraphalerus* Waterhouse, 1901, and *Crowsoniella* Crowson, 1976 and ten previously described extinct genera: *Eurydictyon* Ponomarenko, 1969 (from the Jurassic of Kazakhatan), *Lithocupes* Ponomarenko, 1966 (from the Triassic to Jurassic of Kirghiz), *Zygadenia* Handlirsch, 1906 (from the Triassic of Kirghiz, the Jurassic and Cretaceous of Eurasia) (=*Notocupes* Ponomarenko, 1964), *Notocupoides* Ponomarenko, 1966 (from the Triassic of Kirghiz), *Rhobdocupes* Ponomarenko, 1966 (from the Triassic of Kirghiz), *Sinocupes* Lin, 1976 (from the Late Jurassic of China), *Monticupes* Ren, 1995 (from the Early Cretaceous

of China), *Forticupes* Hong, 1990 (from the Early Cretaceous of China), *Fuscicupes* Hong, 1990 (from the Early Cretaceous of China), *Picticupes* Hong, 1990 (from the Early Cretaceous of China) (Zhou, 1999; Carpenter, 1992; Ren *et al*., 1995; Hong, 1990; Ponomarenko, 2000).

The new genus is somewhat similar to the Late Triassic geneus *Zygadenia* Handlirsch, 1906 (Handlirsh, 1906; Ponomarenko, 1964, 1966, 1969, 1994, 2000), but differs from the latter by the second segment of antennae shorter than the third in length.

Amblomma gen. nov. is closely related to *Tetraphalerus* Waterhouse (Waterhouse, 1901; Crowson, 1962; Ponomarenko, 1964, 1969, 1997; Lin, 1976), but is distinguished from the latter by the basal joint of the posterior tarsi in *Amblomma* obviously shorter than the three following taken together in length.

Rhobdocupes Ponomarenko, 1966 (Ponomarenko, 1966, 1969) may be compared with our fossil beetles, but it is distinct from the new genus, for its antennae only reach the anterior ridge of the prothroax while the new one reaches the posterior.

The new genus also differs from *Sinocupes* Lin, 1976 by the sides of the prothroax with a serrulate margin while the latter is not.

Based on fossils described below, four new species of the new genus are established which are distinguished by the following key.

Key to species of *Amblomma*

1 Head with two circular tubercles dorsally .... *A. psilata* sp. nov.
Head with two butterfly-like tubercles 2
2 The cell is small, slight circular with 1−2 black-maculate, and the last sternite is 5 times as long as the previous one ..... *A. epicharis* sp. nov.
The cell is slight hexagon with 3−4 or 5 black-maculate, and last sternite is not 3 times longer than the precious one 3
3 Metasternum only with transverse suture, without longi tudinal suture ..... *A. rudis* sp. nov.
Metasternum with cross suture ..... *A. stabilis* sp. nov.

Amblomma psilata gen. *et* sp. nov. (Figs. 1−6)

Etymology. Name derived from Greek "*psilata*" = smooth, referring to the longitudinal ridges in elytron smooth and cell without black-maculate.

Holotype. A well preserved almost complete body with elytra, registration No. LB2004001.

Horizon and locality. Yixian Formation, Upper Jurassic, near Chaomidian Village, Beipiao City, Liaoning Province, China.

Description. Body subcylindrical and large; head little longer than wide, weakly narrowed frontally and with two circular tubercles dorsally; eyes somewhat prominent; basal part of head not narrowed behind the eyes; antennae filiform, 11-segment, nearly as long as the head and thorax taken together, the basal segment large, second shorter than third segment, third and fourth segment equal, the following joints smaller to apex (Fig. 4); mandible very prominent and tridentate. Prothorax transverse, 0.4 times as long as wide, strongly narrowed anteriorly, obviously wider than head; the disc of the pronotum bearing a large semicircular elevation divided by a longitudinal line in the middle, anterior edge slightly arcus, the posterior edge straight, the sides with serrulate margin (Fig. 2); notopleural suture straight and pleurosternal suture running oblique to coxa of forelegs. Tarsi five-jointed, the posterior pair with the basal joint shorter than the three following taken together in length (Fig. 5); cross suture developed on metasternum; the last sternite 3 times as long as the previous one, its apex is not tapered (Fig. 3).

Elytron with 10 rows of cell on disc and one on the epipleuron, 2.7 times as long as wide, elytra longer than the abdomen, dehiscent terminally, surface of elytra with 4 robust longitudinal striae, the two nearest to the suture united before the apex (Fig. 2); the cell hexagon without black-maculate (Fig. 6), elongated in the distal part of the elytron; approximately 25 cells form a row; the body rather evenly covered with tubercles.

Dimensions (mm). body length, 18−19; body width, 10; head and pronotum length, 4.7−5; abdomen length, 8; elytron length, 13−14.

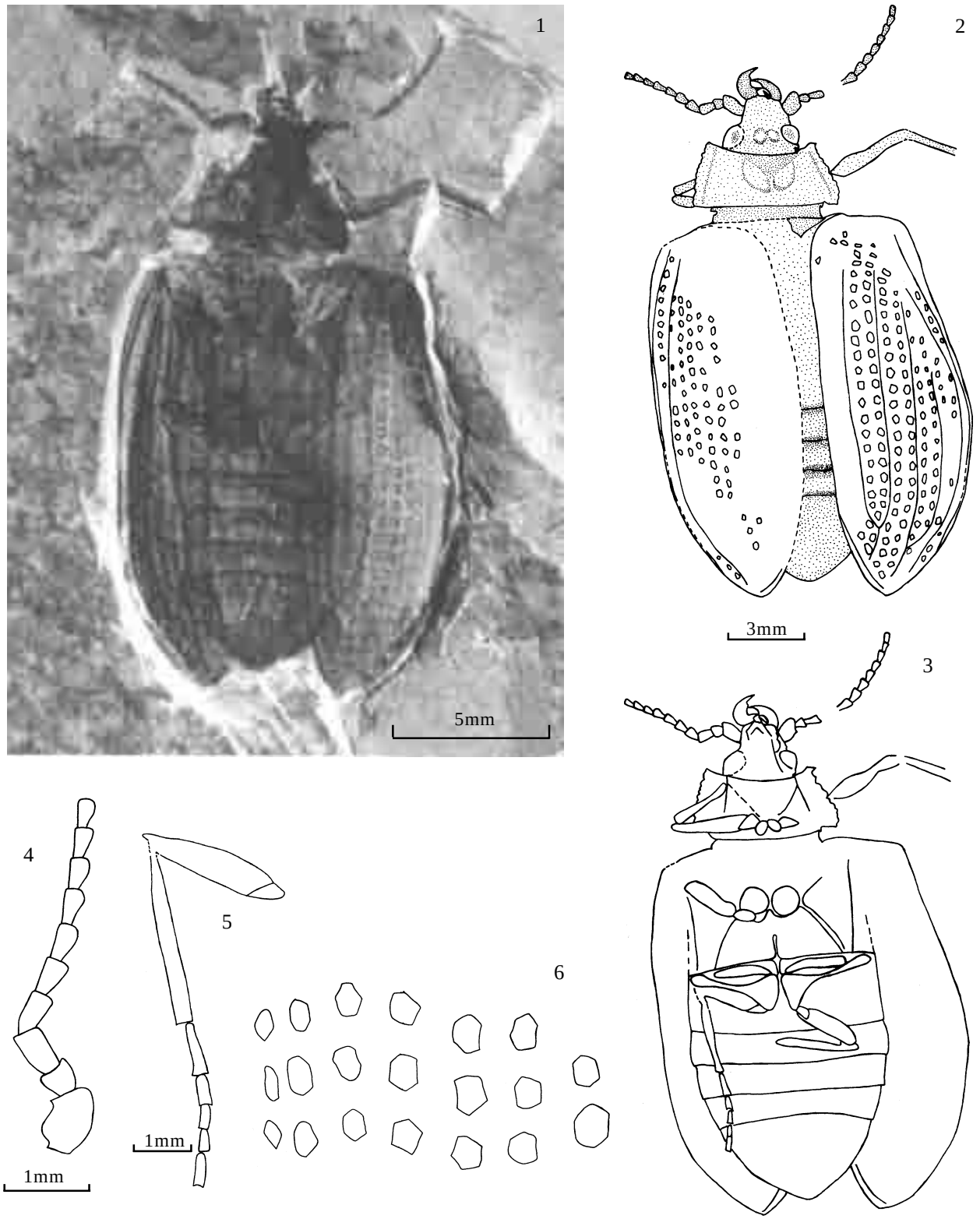
Amblomma epicharis gen. *et* sp. nov. (Figs. 7−10)

Etymology. Name derived from Greek "*epicharis*" = beautiful.

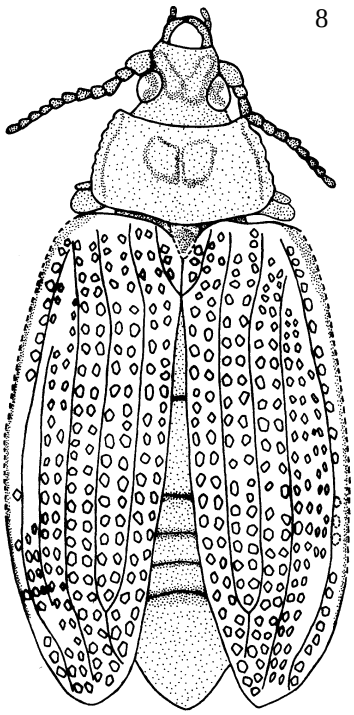
Holotype. A well preserved almost complete body with elytra, registration No. LB 2004002.

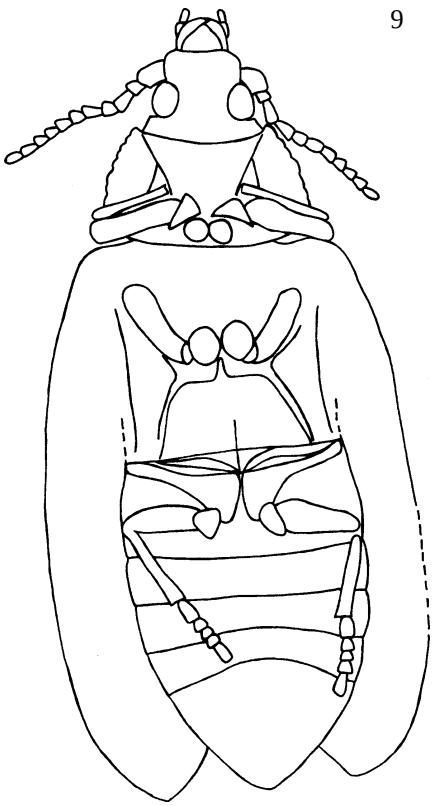
Horizon and locality. Yixian Formation, Upper Jurassic, near Chaomidian Village, Beipiao City, Liaoning Province, China.

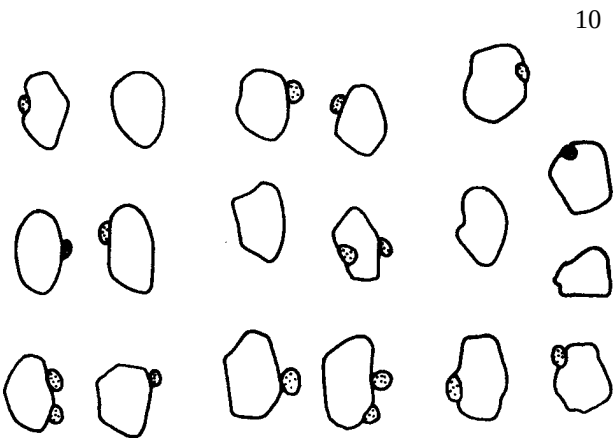
Description. Body subcylindrical, medium-sized; head as long as wide, weakly narrowed frontally, and with two butterfly-like tubercles dorsally; eyes prominent; basal part of head not narrowed behind the eyes; antennae filiform, 11-segment, nearly as long as the head and thorax taken together, the basal segment large, second shorter than third segment, third and fourth segments equal, the



Figs. 1–6 *Amblomma psilata* gen. *et* sp. nov. (holotype, No. LB2004001). 1. Photograph, holotype, LB2004001; 2. dorsal view; 3. ventral view; 4. antennae; 5. hind leg; 6. outline of cell.







Figs. 7–10 *Amblomma epicharis* gen. *et* sp. nov. (holotype, LB 2004002); 7. Photograph, holotype, LB2004002; 8. dorsal view; 9. ventral view; 10. outline of cell.

following segments smaller to apex, the mandibles prominent, maxillary palp with two visible joints. Prothorax transverse, 0.6 times as long as wide, obviously wider than head, the disc of the pronotum bearing a large rectangular elevation divided by a longitudinal line in the middle, anterior and posterior edge slightly arching, the sides with serrulate margin, and propleuron well developed (Fig. 8); pleurosternal suture apparently running oblique to coxa of fore legs. Tarsi five-jointed, the posterior pair with the basal joint shorter than the three following taken together; cross suture developed on metasternum; the last sternite 5 times as long as the previous one, its apex is tapered (Fig. 9).

Elytron with 10 rows of cells on disc and one on the epipleuron, 3 times as long as wide; elytra not longer than the abdomen, dehiscent terminally; surface of elytra with three robust longitudinal striae, the two nearest to the suture united before the apex; the cell small, slight circular with 1−2 black-maculate (Fig. 10), elongated in the distal part of the elytron; approximately 25 cells form a row; the body rather evenly covered with tubercles (Fig. 8).

Dimensions (mm). body length, 13; body width, 4; head and pronotum length, 4; abdomen length, 5−6; elytron length, 9.

Amblomma stabilis gen. *et* sp. nov. (Figs. 11−14)

Etymology. Name derived from Greek "*stabilis*" = firm.

Holotype. A well preserved almost complete body with elytra, registration No. LB 2004003.

Horizon and locality. Yixian Formation, Upper Jurassic, near Chaomidian Village, Beipiao City, Liaoning Province, China.

Description. Body subcylindrical and rather large; head longer than wide, similarly rectangular, with two butterfly-like tubercles dorsally; eyes somewhat prominent; basal part of head not slightly narrow behind the eyes; antennae filiform, 11-segment, nearly as long as the head and thorax taken together, the basal segment large, second shorter than third segment, and the following joints smaller to apex; the mandibles prominent. Prothorax transverse, 0.5 times as long as wide, obviously wider than head; the disc of the pronotum bearing a large rectangular elevation divided by a longitudinal line in the middle, the anterior edge slightly arching, the posterior edge straight, the sides with serrulate margin and propleuron well developed (Fig. 12); notopleural suture straight and parallel to the lateral edge of prothorax, pleurosternal suture running oblique to coax of forelegs; cross suture developed on metasternum; the last sternite 3 times as long as the previous one, its apex not tapered (Fig. 13).

Elytron with 10 rows of cells on disc and one on the epipleuron, 3 times longer than wide; elytron not longer than the abdomen, dehiscent terminally; surface of elytra with three robust longitudinal striae, the two nearest to the suture united before the apex; the cell slight hexagon with five black-maculate (Fig.14), elongated in the distal part of the elytron; approximately 28 cells form a row.

Dimensions (mm). body length, 24; body width, 7; head and pronotum length, 6; abdomen length, 11; elytron length, 17−18.

Amblomma rudis gen. *et* sp. nov. (Figs. 15−18)

Etymology. Name derived from Greek "*rudis*" = roughly.

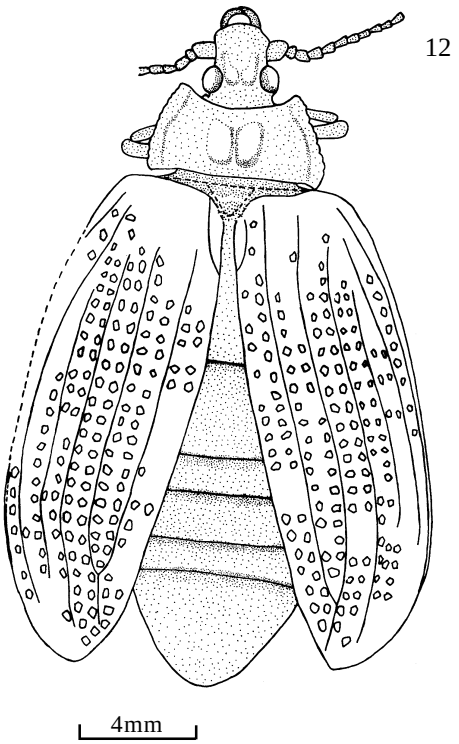
Holotype. A well preserved almost complete body with elytra, registration No. LB2004004.

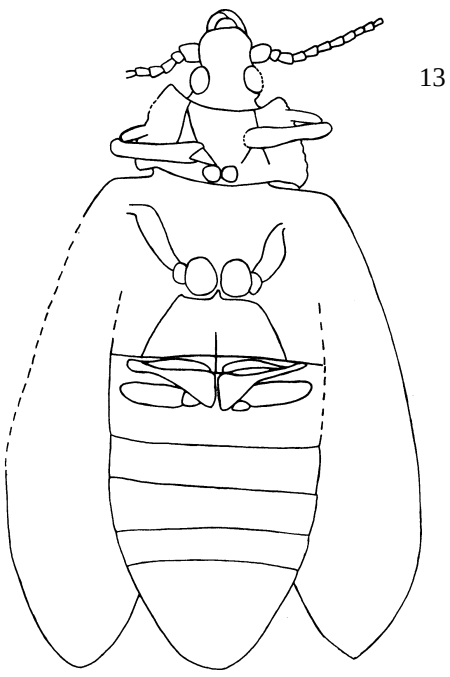
Horizon and locality. Yixian formation, Upper Jurassic, near Chaomidian Village, Beipiao City, Liaoning Province, China.

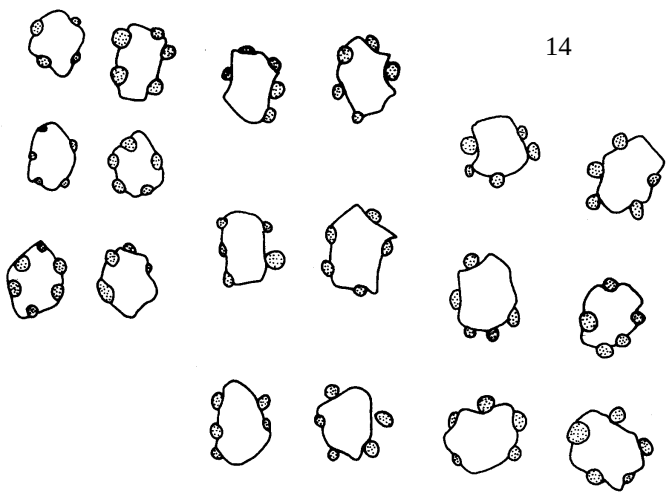
Description. Body subcylindrical, medium-sized; head as long as wide, nearly quadrate, and with two butterfly-like tubercles dorsally; eyes are somewhat prominent; basal part of head not slightly narrow behind the eyes; antennae filiform, 10 visible segments, nearly as long as the head and thorax taken together, the basal segment large, second shorter than third segment, and the following joints smaller to apex; the mandibles prominent. Prothorax transverse, 0.5 times as long as wide, obviously wider than head, the disc of the pronotum bearing a large rectangular elevation divided by a longitudinal line in the middle, the anterior edge slightly arcus, the posterior edge straight, the sides with serrulate margin and propleuron well developed (Fig. 16); notopleural suture straight and parallel to the lateral edge of prothorax; pleurosternal suture running oblique to coax of forelegs; tarsi five-jointed, the posterior pair with the basal joint shorter than the three following taken together in length; metasternum is without longitudinal suture; the last sternite 2.5 times as long as the previous one, its apex is round (Fig. 17).

Elytron with 10 rows of cells on disc and one on the epipleuron, 3 times as long as wide; elytra slightly longer than the abdomen, dehiscent terminally; surface of elytra with three robust longitudinal striae, the two nearest to the suture united before the apex; the cell slight hexagon with 3−4 black-maculate round its margin (Fig. 18), elongated in the distal part of the elytron; approximately 25 cells form a row; the body rather evenly covered with tubercles that are only larger in the forepart of each abdomenial sternite.

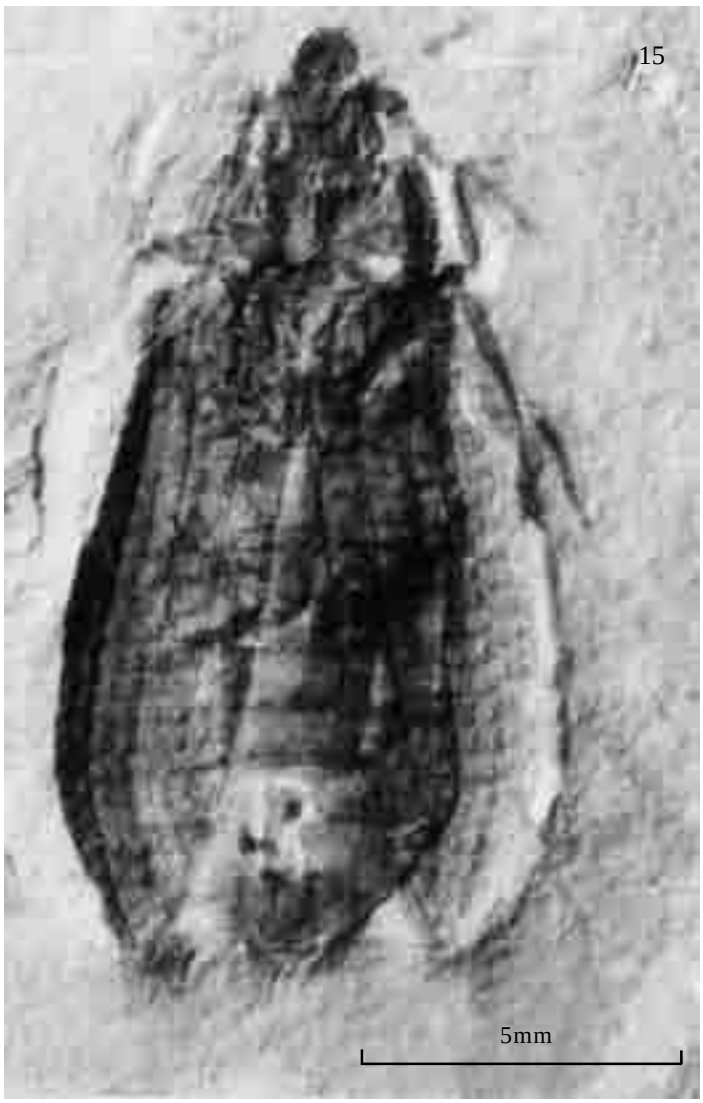
Dimensions (mm). body length, 14−15; body width, 5; head and pronotum length, 3−4; abdomen length, 6−7;

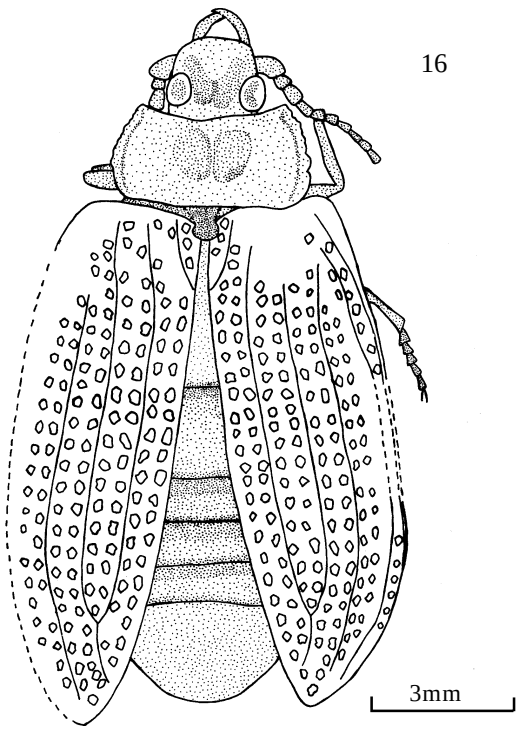


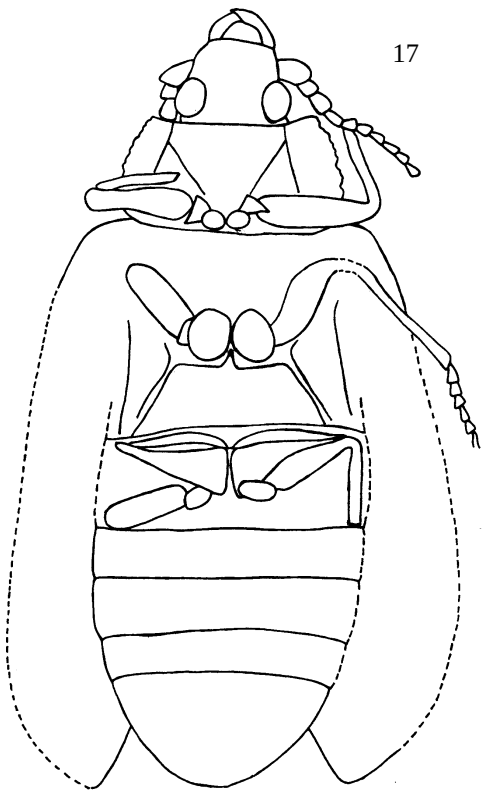


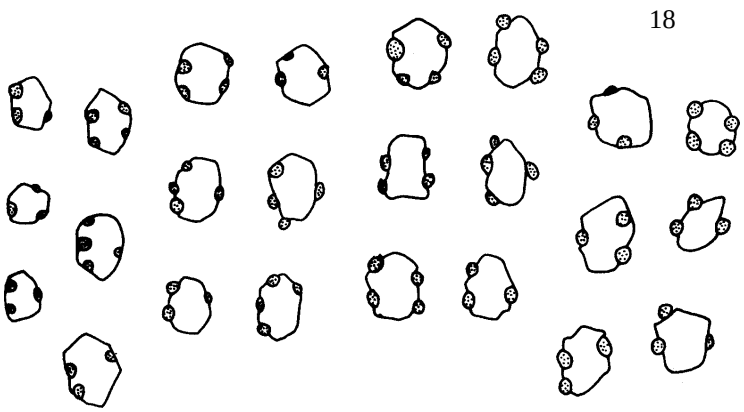


Figs. 11–14 *Amblomma stabilis* gen. *et* sp. nov. (holotype, LB 2004003); 11. Photograph, holotype, LB 2004003; 12. dorsal view; 13. ventral view; 14. outline of cell.









Figs. 15–18 *Amblomma rudis* gen. *et* sp. nov. (holotype, LB2004004); 15. Photograph, holotype, LB2004004; 16. dorsal view; 17. ventral view; 18. outline of cell.

elytron length, 10−11.

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