Gondwana Research xxx (2013) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Gondwana Research

journal homepage: www.elsevier.com/locate/gr

The most mysterious beetles: Jurassic Jurodidae (Insecta: Coleoptera) from China

Evgeny V. Yan [a,b], Bo Wang [a,*], Alexander G. Ponomarenko [b], Haichun Zhang [a]

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Rd., Nanjing 210008, China
[b] Paleontological Institute, Russian Academy of Sciences, 123 Profsoyuznaya Str., Moscow 117647, Russia

ARTICLE INFO

Article history:
Received 7 January 2013
Received in revised form 1 April 2013
Accepted 6 April 2013
Available online xxxx

Handling Editor: M. Santosh

Keywords:
Coleoptera
Paleogeography
Jurassic
Daohugou
China

ABSTRACT

Jurodidae are thought to be some of the world's most mysterious beetles and display an intriguing mixture of characters occurring in three different suborders. Hitherto, all known fossil and extant Jurodidae were extremely rare and restricted to Russian Siberia and the Far East. Here we describe two new species, *Jurodes daohugouensis* sp. nov. and *Jurodes pygmaeus* sp. nov. from the Middle Jurassic of Daohugou, China. A key to all species of Jurodidae and their research history are given, and the detailed morphology of fossil Jurodidae is also presented. Our results confirm the presence of three ocelli in fossil Jurodidae, and reveal that hind wings of *J. pygmaeus* sp. nov. possess well developed radial and oblong cells, and are very similar to those of extant Jurodidae (*Sikhotealinia zhiltzovae*). Male genitalia of fossil Jurodidae were described herein for the first time, showing a basal trilobate structure. The presence of exposed propleuron, three pairs of external trochantins, metanepisterna with ridges, primitive characters of wing venation further support the probable placement of Jurodidae in the suborder Archostemata. *J. daohugouensis* and *J. pygmaeus* are very similar to *S. zhiltzovae* in having the big protruding eyes, elevated median portion of frons bearing three ocelli, pubescent body, contiguous procoxae, exposed trachantion of all coxae, elytra with rows of punctures, and wing venation. Our results show that these key characters of extant Jurodidae can be traced back to the Middle Jurassic, revealing that the family has been in a period of evolutionary stasis for at least 160 million years. Furthermore, our discoveries widen the paleogeographic distribution of fossil Jurodidae from Russian Siberia to northern China.

1. Introduction

Beetles in the family Jurodidae are an amazing example of "living fossils", alongside the famous coelacanth *Latimeria* Smith, 1939 or coniferous redwood *Metasequoia* Miki, 1941, where fossil representatives were discovered before their recent descendants. As usual for "living fossils", both extant and fossil jurodids are very rare; all fossils belong to the type genus with two species *Jurodes ignoramus* Ponomarenko, 1985 and *Jurodes minor* Ponomarenko, 1990 from Russian Transbaikalian localities, Novospasskoe (Lower–Middle Jurassic) and Unda (Upper Jurassic) respectively (Fig. 1). A single recent species *Sikhotealinia zhiltzovae* Lafer, 1996, represented by only one specimen, was found on the western slopes of Sikhote-Alin mountain in the Russian Far East (Lafer, 1996). Nothing is known about the original area of distribution, the habitat, the biology and the immature stages of this species (Beutel et al., 2009). Up to now, the family Jurodidae comprised only these three species.

Jurodidae completely deserve their status as the "most mysterious representatives of beetles" (Kirejtshuk, 1999) and "a phantom in beetle evolution" (Beutel et al., 2009), because even at subordinal level their taxonomical placement within the Coleoptera has remained uncertain for a long time. It was previously assigned to the Adephaga (Ponomarenko, 1985, 1990), Polyphaga (Lafer, 1996), or Archostemata (Kirejtshuk, 1999; Beutel et al., 2008; Hörnschemeyer, 2009). The reason for such taxonomical difficulties is a mixture of morphological characters which can be found in three out of four major beetle suborders. This family may represent an important piece in the subordinal puzzle, and an intensive investigation of the taxon may greatly contribute to the understanding of basal branching events in Coleoptera in the future (Kukalová-Peck and Lawrence, 2004; Beutel et al., 2009; Ge et al., 2011).

A systematic study of Jurodidae has been hindered by the rarity of fossil and extant specimens. In addition, a critical comparison between extant and fossil Jurodidae is lacking, partly because the known fossils give very limited morphological information. Studies of the fossil record are very important for the reconstruction of beetle evolution and contribute valuable information on the time of origin and extinction, and provide a means of estimating paleodiversity (Beutel et al., 2008). Furthermore, ancestral Jurodidae retain numerous primitive characters and are very important for revealing trends in the evolution of the morphological traits. Herein, we report two new species of the type genus *Jurodes* based on six well-preserved specimens from the Middle Jurassic of Daohugou Lagerstätte, China. These fossils pave the way for a detailed morphological study of fossil Jurodidae.

* Corresponding author. Tel.: +86 25 83282176.
E-mail addresses: yanevgeny@gmail.com (E.V. Yan), savantwang@gmail.com (B. Wang).

1342-937X/$ – see front matter © 2013 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.gr.2013.04.002

Fig. 1. Global paleogeographic reconstruction for the Late Jurassic with a plot of the distribution of fossil and extant Jurodidae localities. Modified after Blakey (2005). 1, Novospasskoe; 2, Unda; 3, Daohugou; 4, southern Primorsky Territory. Yellow stars represent fossil localities, and the red circle shows distribution of extant Jurodidae.

Some important taxonomic characters, e.g., head, thorax, elytra, hind wing and male genitalia, are described in detail for the first time, and shed light on the early evolution of these mysterious beetles.

2. Research history

Starting from the original description of *J. ignoramus* Ponomarenko, 1985, its morphological characters become the subject of controversial taxonomic interpretations (Fig. 2B). This species was attributed to the suborder Adephaga on the basis of big metacoxal plates and the presence of the second (i.e., first visible) abdominal sternite (Ponomarenko, 1985). Although external propleuron and a closed oblongum cell on the hindwing seem to support this systematic placement, jurodids share these characters with representatives of the suborder Archostemata. However, their unusual appearance with short prosternum and contiguous, prominent procoxae make them look like the primitive adephagan Triaplidae; and their head and shape of the antennae resemble those of Rhysodidae (from which the family name "*Jurodidae*" was partly formed) (Ponomarenko, 1985). The later discovery of *J. minor* Ponomarenko, 1990 only added some extra morphological data, e.g., the structure of the meso- and metanotum, wing venation. Six years later, Lafer (1996) independently described the new recent monotypic family Sikhotealiniidae. *Sikhotealinia* possess quite a number of plesiomorphic characters, such as wide metacoxae, which laterally reach the epipleura, mesocoxal cavities partly closed by metanepisterna, caraboid wing venation, retained notopleural and interpleural sutures on the pronotum. These characters imply that Sikhotealiniidae are closer to Archostemata and some Adephaga (Eodromeinae and Dytiscoidea), but the presence of ocelli, together with wide metacoxae and characteristic closure of the mesocoxal cavities, make them resemble some polyphagan beetles e.g., the family Derodontidae (Lafer, 1996). Lafer (1996), for the first time, mentioned three ocelli on the *Sikhotealinia* head — a unique character in the whole of the order, Coleoptera and placed Sikhotealiniidae in the suborder Archostemata, but abstained from a more precise attribution (Fig. 2C, F).

Only after about three years, Kirejtshuk (1999), following Ponomarenko's suggestion, revealed strong morphological similarities and phylogenetic affinities between Jurassic *Jurodes* and recent *Sikhotealinia*, and transferred the latter to Jurodidae and both of them to Archostemata respectively. Kirejtshuk (1999, 2013) showed that recent *Sikhotealinia* only slightly differed from its Mesozoic ancestors in the length and thickness of the antennae, the length of the pronotum, the proportions of tarsomeres, with the main

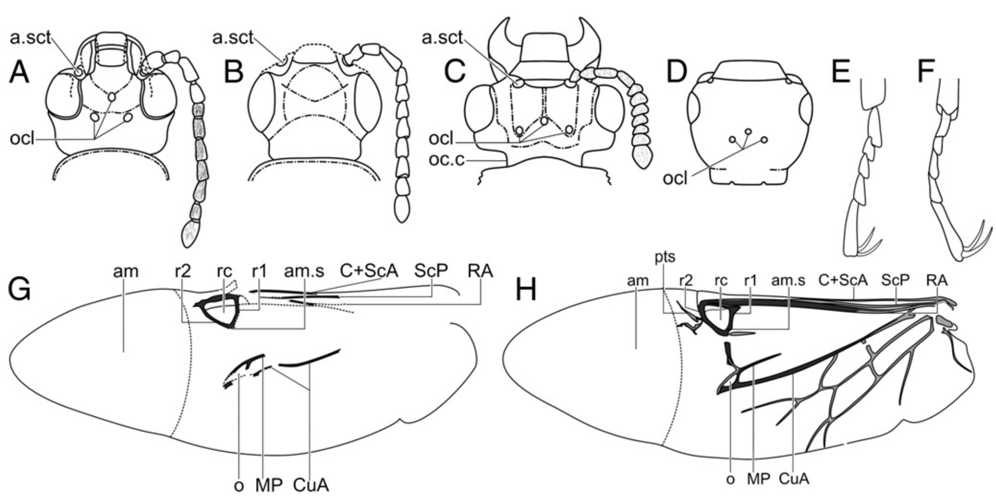

Fig. 2. A, Head reconstruction of *Jurodes daohugouensis* sp. nov.; B, head reconstruction of *Jurodes pygmaeus* sp. nov.; C, head of *Sikhotealinia zhiltzovae* (redrawn after Lafer, 1996 with changes); D, scheme of staphylinoid head (redrawn after Naomi, 1987 with changes); E, *J. daohugouensis* sp. nov., reconstruction of metatarsus; F, *S. zhiltzovae* metatarsus; G, *J. pygmaeus* sp. nov. reconstruction of the hind wing; H, *S. zhiltzovae* line drawing of the hind wing. Shaded areas represent different states of vein sclerotization. Label abbreviations: a.sct antennal socket; oc.c occipital constriction (neck); ocl ocellus. Wing structures: am apical membrane; am.s anteromedial sclerotization; C + ScA costa fused with anterior branch of subcosta; CuA cubitus anterior; CuA2 cubitus anterior, second branch; MP media posterior; o oblongum cell; pts pterostigma; r1 cross-vein r1; r2 cross-vein r2; RA radius anterior; rc radial cell; ScP subcosta, posterior branch.

difference being in number and density of elytral punctate rows. He also pointed out that some similarities occurred between *Jurodes* and the rest of modern Archostemata in configuration of thoracic sclerites, structure of abdominal ventrites, and presence of short sharp ridge between metacoxae (Kirejtshuk, 1999). He considered that the enlarged "adephagan metacoxal plates" of *Jurodes* were the result of postmortal deformation and detachment of the abdomen, and further proved that both *S. zhiltzovae* and *J. ignoramus* are males (Kirejtshuk, 1999). He also mentioned that *Sikhotealinia* have nearly polyphagan venation and folding pattern, and suggested an intermediate position of Jurodidae between clades Cupedidae–Ommatidae and Crowsoniellidae–Micromalthidae (Kirejtshuk, 1999). The placement of *Sikhotealinia* in Archostemata was supported in subsequent papers (Hörnschemeyer, 2005; Beutel et al., 2008), who further performed several cladistic analyses. Beutel et al. (2008) showed that jurodids obviously differed from the "typical" archostematan beetles by lacking the cuticular tubercles and the window punctures on elytra, but they possess some archostematan characters in having exposed six abdominal segments and the wings without oblongum, constricted neck, and paired protuberances on head. In addition, *Sikhotealinia* has preserved an array of archostematan plesiomorphic features, such as the transverse ridge on the mesoventrite, the membranous joint between meso- and mesoventrites, non-enlarged metacoxal plates, and a median ridge on the first abdominal ventrite (Beutel et al., 2008). *Sikhotealinia*, therefore, clusters with *Jurodes*, and becomes the sister group to all other archostematan beetles (Beutel et al., 2008).

3. Material and methods

The material studied comes from the Jurassic deposits of the Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia of China. The Daohugou deposits, consisting of gray tuff, tuffaceous siltstone and mudstone, are now considered to be one of the most important insect Lagerstätten (Rasnitsyn and Zhang, 2004). The fossil insects described here are commonly preserved as compressions in gray tuffaceous siltstones, together with small freshwater conchostracans (Wang et al., 2009). The Daohugou fossil-bearing strata consist of mainly grayish white tuff, tuffaceous sandstone, tuffaceous siltstone and shale, with a tuffaceous conglomerate at the base and a thick rhyolitic breccia together with andesite at the top (Chen et al., 2004; Liu et al., 2006). The age of the fossil-bearing strata is thought to be late Middle Jurassic or early Late Jurassic (Liu et al., 2006; Wang et al., in press). The Daohugou Biota has yielded not only insects and spiders, but also other invertebrates including bivalves, conchostracans, pterosaurs, salamanders, mammals and macroplants (Zhang, 2006). Fossil insects at Daohugou are particularly diverse and numerous, belonging to 25 orders. The coleopteran assemblage is the most diverse in this fauna, and more than 10 families have been described and more fossils (especially in the suborder Polyphaga) await description (Kirejtshuk et al., 2010; Wang et al., 2012). The paleoclimate in Daohugou during mid-Jurassic times was warm temperate (Rees et al., 2000; Zhang, 2006).

The specimens were examined dry and under alcohol using a Nikon SMZ1000 stereomicroscope and a Zeiss Discovery V20 microscope; preparation was done using a PaleoTools Micro-Jack 3. The photographs were prepared using an attached digital camera DXM1200 (on the Nikon) and an AxioCam HRc (on the Zeiss Discovery). Line drawings were prepared on photographs using image-editing software (CorelDRAW X4 and Adobe Photoshop CS). Fossil beetles in the Daohugou Lagerstätten are preserved as complete bodies with several collapsed layers of cuticle, so that the dorsal and ventral surfaces are usually visible on the same imprint; for the convenience of morphological interpretation here, dorsal and ventral characters for each specimen are given on two separate figures (except Fig. 7). Drawing conventions are: solid line, distinct margin; dashed, indistinct and structures overlapping each other; dashed and dotted, fold; dark gray, wing veins; light gray, sclerotized wing membrane. The holotype of *Jurodes daohugouensis* sp. nov. was analyzed uncoated in detail using a scanning electron microscope (SEM) at variable voltages. Micro-surface information was obtained under the low vacuum mode (100 Pa in a sample chamber) of an LEO1530VP SEM with the accelerating voltage 5–20 kV. The SEM analyses were performed in the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). The following measurements were recorded (depending on the state of preservation): total body length (including length of everted abdominal sternites and genitalia), body width; length and width of elytra, head, pronotum, abdomen; for legs only length was specified; tarsal length excluded length of claws (see Table 1). Abbreviations for wing venation are after those of Fedorenko (2009). All fossils are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

4. Systematic paleontology

Order Coleoptera Linnaeus, 1758

Family Jurodidae Ponomarenko, 1985 = Sikhotealiniidae Lafer, 1996

Table 1
Measurements of all specimens (all in mm).

	Jurodes daohugouensis sp. nov.					*J. pygmaeus* sp. nov.
	NIGP154969	NIGP154971	NIGP154973	NIGP154974	NIGP154975	NIGP154972
Body						
Length/width	7.6/3.1	6.1/3	>5.5/3.1	>5/~	7.2/2.9	3.6/~
Elytron						
Length/width	4.4/1.6	4.1/1.5	3.6/1.5	~/1.3	4.6/1.4	2.6/1.2
Head						
Length/width	1.1/1.4	0.8/1.1	~/1.1	~/~	0.7/1	0.7/0.8
Pronotum						
Length/width	1/1.4	1/1.3	1/1.3	0.7/1.1	1.1/1.1	0.7/0.8
Abdomen						
Length/width	4.2/2.5	2.6/2.1	~/~	~/~	3/2.4	1.2/~
Foreleg length						
Femur/tibia/tarsus	1.1/1.1/0.5	~	0.7/~/~	~	~	~
Middle leg length						
Femur/tibia/tarsus	1.3/1.3/0.6	~	~	~	1.2/1/~	~
Hindleg length						
Femur/tibia/tarsus	1/1.2/1.1	1.2/1.1/~	~	~	~	~

Please cite this article as: Yan, E.V., et al., The most mysterious beetles: Jurassic Jurodidae (Insecta: Coleoptera) from China, Gondwana Research (2013), http://dx.doi.org/10.1016/j.gr.2013.04.002

Key to species of Jurodidae

1. Antennae as long as head; antennomeres 5–10 strongly transverse; antennal sockets located on anterior margin of frons; head with distinct occipital constriction (neck); elytra with 11 rows of punctures ....*Sikhotealinia zhiltzovae* Lafer, 1996
   – Antennae twice longer than head; antennomeres 5–10 longer than wide, or square-shaped; antennal sockets located on genae; head narrowing posteriorly, but lacking occipital constriction (neck) and distinct temples; elytra with not less than 15 rows of punctures..2
2. Body length less than 4 mm; inner margins of eyes (on dorsal side) only slightly curved...3
   – Body length more than 5 mm; inner margins of eyes (on dorsal side) curved, S-shaped..4
3. Alacristae on metanotum parallel-sided; undersides of elytra without transverse ridges.............*Jurodes minor* Ponomarenko, 1990

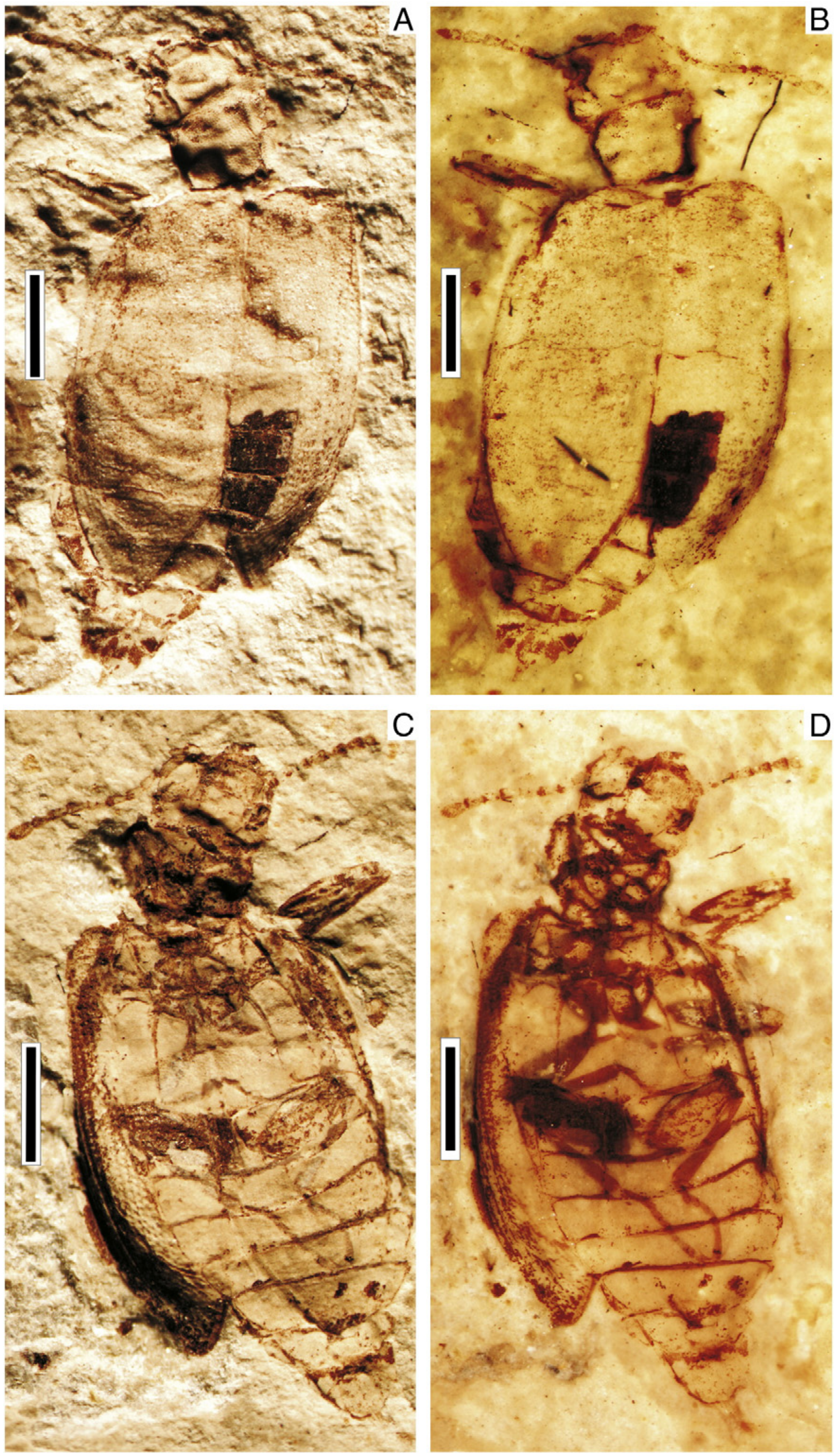

Fig. 3. *Jurodes daohugouensis* sp. nov. NIGP154969, habitus photos of the holotype, part and counterpart: A and C, dry; B and D, wetted with ethanol. Scale bars equal 1 mm.

– Alacristae on metanotum X-shaped; undersides of elytra with transverse ridges in distal thirds…………..…*J. pygmaeus* sp. nov.

4. Pronotum shorter than head; antennomere 10 0.7 times as wide as apical one; antennomere 9 bead-shaped, its length and width subequal………………………..……*J. ignoramus* Ponomarenko, 1985

– Pronotum as long as head; antennomere 10 half as wide as apical one; antennomere 9 elongate-rectangular, twice as long as wide……………………………………*J. daohugouensis* sp. nov.

Genus *Jurodes* Ponomarenko, 1985

Type species

Jurodes ignoramus Ponomarenko, 1985; by original designation.

Type horizon and locality

Lower–Middle Jurassic; Novospasskoe, Transbaikalia, Russia.

Revised diagnosis

Small, flattened beetles. Head quadrangular, length equal to maximal width at eyes midlength, narrowing anteriorly and posteriorly. Eyes big, oval, weakly protruding laterally. Clypeus and labrum well defined; frons with wide, flat median elevation. Antennal insertions located on genae, in front of eyes; antennae not reaching base of elytra, apical antennomere egg-shaped, two times longer and wider than penultimate one. Pronotum shorter than head, much shorter than wide, with rounded sides, narrowed anteriorly and posteriorly. Prosternum not longer than procoxae. Scutellum small, narrowing posteriorly to widely rounded apex. Elytra with not less than 15 rows of punctures, distance between two nearest punctures in a row equal to diameter of one puncture. Metaventrite almost twice longer than mesoventrite, paracoxal suture strongly shifted to metaventrite posterior margin. Metanepisterna big, roundly widening before anterior margin and narrowing posteriorly. Abdomen egg-shaped, narrowing posteriorly from base.

Included species

Four species: *Jurodes ignoramus*; *J. minor* Ponomarenko, 1990 from the Upper Jurassic of Unda, Russia; *J. daohugouensis* sp. nov. and *J. pygmaeus* sp. nov. from the Middle Jurassic of Daohugou, China.

Remarks

Jurodes can be distinguished from *Sikhotealinia* in having antennae twice as long as head, antennomeres 5–10 longer than wide, antennal sockets located on genae, head without occipital constriction (neck), elytra with not less than 15 rows of punctures, wing with comparatively bigger radial and oblong cells, and apical metatarsomere shorter than summarized lengths of previous three (Fig. 2).

J. daohugouensis sp. nov. and *J. pygmaeus* sp. nov. are placed in the genus *Jurodes* by the following characters: moniliform antennae, with enlarged egg-shaped apical antennomere; elevated median portion of frons; small, rounded pronotum; contiguous procoxae; elytra with more than 15 rows of punctures; and metanepisterna widened anteriorly.

Jurodes daohugouensis sp. nov. (Figs. 3–8)

Etymology

After the type locality "Daohugou".

Holotype

NIGP154969, male, part and counterpart; Middle Jurassic, Daohugou.

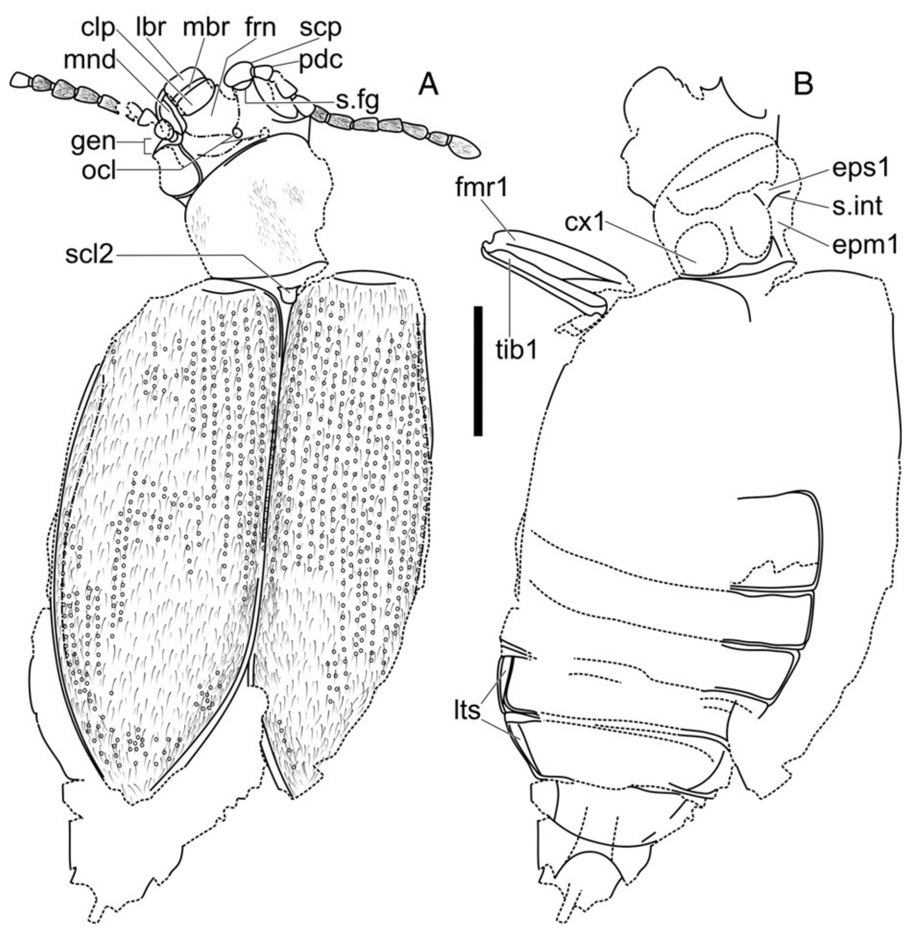

Fig. 4. *Jurodes daohugouensis* sp. nov. NIGP154969, counterpart. Line drawings of the holotype, A, dorsal view; B, ventral view. Label abbreviations: clp clypeus; cx1 procoxa; epm1 proepimeron; eps1 proepisternum; fmr1 profemur; frn frons; gen genae; lbr labrum; lts laterosternite; mbr membranous joint; mnd mandible; ocl ocelli; pdc pedicellus; scl2 mesoscutellum; scp scapus; s. fg frontogenal suture; s.int interpleural suture; tib1 protibia. Scale bar equals 1 mm.

Please cite this article as: Yan, E.V., et al., The most mysterious beetles: Jurassic Jurodidae (Insecta: Coleoptera) from China, Gondwana Research (2013), http://dx.doi.org/10.1016/j.gr.2013.04.002

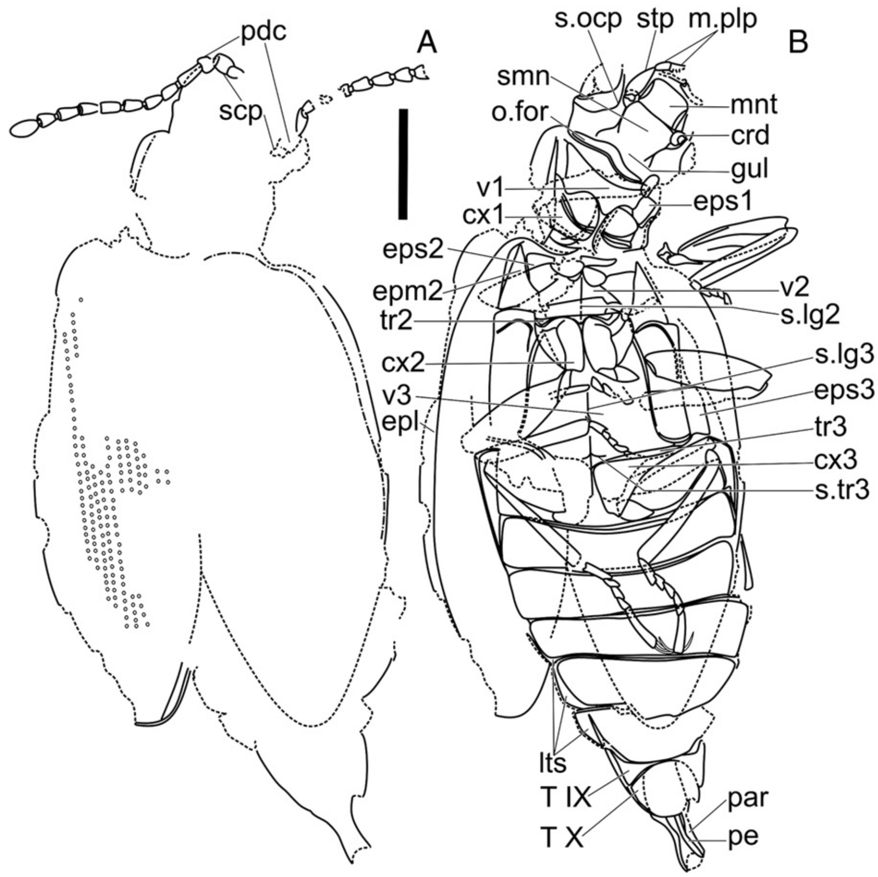

Fig. 5. *Jurodes daohugouensis* sp. nov. NIGP154969, part. Line drawings of the holotype, A, dorsal view; B, ventral view. Label abbreviations: crd cardo; cx1/2/3 pro-/meso-/metacoxae; epm 2 mesepimeron; epl epipleura; eps1/2/3 pro-/meso-/metepisternum; gul gula; lts laterosternite; mnt mentum; m.plp maxillar palpomeres; o.for occipital foramen; par paramere; pdc pedicellus; pe penis; scp scapus; s.lg2/3 longitudinal suture on meso/metaventrite; smn submentum; s.ocp occipital suture; stp stipes; s.tr3 transverse suture on metaventrite; T IX, X tergite 9 and 10 (proctiger); tr2/3 meso-/metatrochantine; v1/2/3 pro-/meso-/metaventrite. Scale bar equals to 1 mm.

Paratypes

NIGP154971, NIGP154973, NIGP154974 (strongly deformed), NIGP154975, all males; all specimens with part and counterpart; Middle Jurassic, Daohugou.

Diagnosis

Body length more than 5 mm; inner margins of eyes (on dorsal side) curved, S-shaped; pronotum as long as head; scutellum very small, narrower than 1/5 of elytron base; metepisterna with thick arcuate ridge on their upper half; antennomere 10 half as wide as apical one; antennomere 9 elongate-rectangular, twice as long as wide.

Description

Head of medium size, 1/5 of body length, almost quadrangular, its width only exceeds length by 1/5 becoming abruptly depressed behind eyes, sunken into pronotum on level of posterior margins of eyes (Fig. 2A). Mandibles with roundly curved outer- and almost straight inner margins, half of head length. Labrum only slightly shorter than clypeus, broad, 2.5 times as wide as long; its anterior margin rounded, separated from clypeus by wide membrane, as long as half of labrum itself. Clypeus transverse, with straight anterior and curved posterior margins. Frons with concave anterior margin, its anterior angles distinctly tapering forward. Genae glabrous, with antennal sockets in middle, separated from rest of frons by fine frontogenal sulci (Fig. 9D). Median portion of frons between eyes elevated, anteriorly restricted by pair of grooves from base of mandibles to median ocellus, and posteriorly by another bisinuate groove. Front ocelli situated at midlength level of eyes, closer to inner margins of eyes than to each other (Figs. 2A, 9A). At least antennomeres 5–11 are covered with short, fine pubescence. Scapus of elongate-oval shape, 1.8 times longer and 1/3 thicker than subtrapezoidal pedicellus; antennomeres 3 and 4 subtrapezoidal, 1/3 longer than pedicellus; antennomeres 5–9 are of elongate-rectangular shape, only slightly widening anteriorly. Penultimate antennomere 1/3 shorter than each of previous 6–9 antennomeres, 0.5 times as wide as egg-shaped apical one. Each antennomere with very narrow short base, separated by thin groove. Eyes very big, 1/2 of head length, thinly edged; ventral portion of eyes 1/2 of dorsal. Head (excluding genae) uniformly covered with deep punctures.

Anterior margin of gular plate enveloping submentum, so its anterior angles are strongly protruded anteriorly. Submentum subtrapezoidal. Cardo rounded, two times shorter than drop-shaped stipes; first two maxillar palpomeres elongate-oval. Mentum rectangular, 1.7 times as wide as long, with rounded anterior margin and anterior angles, its sides ridged. Dorsal and ventral portions of head divided by distinct occipital sutures. Ventral side of head covered with dense deep punctures, often big, with hair attachments in middle, located along inner margins of eyes.

Pronotal length and width equal to those of head; pronotum widened anteriorly, thickly carinated, anterior angles and sides rounded; its surface uniformly covered with deep punctures which are of the same size and density as on frons. Prosternum very short (including length of triangular intercoxal process), 0.3 times as long as pronotum. Proepisternum rectangular, about same length as prosternum; interpleural suture distinct, proepimeron well developed.

Scutellum very small, 1/5 of basal elytral width, its anterior margin twice as wide as rounded posterior, anterior angles pointed, protruding anterolaterally.

Elytron of elongate-oval, 2.4 times longer than wide, elytral disc strongly convex, with flattened outer margin, edged, with at least

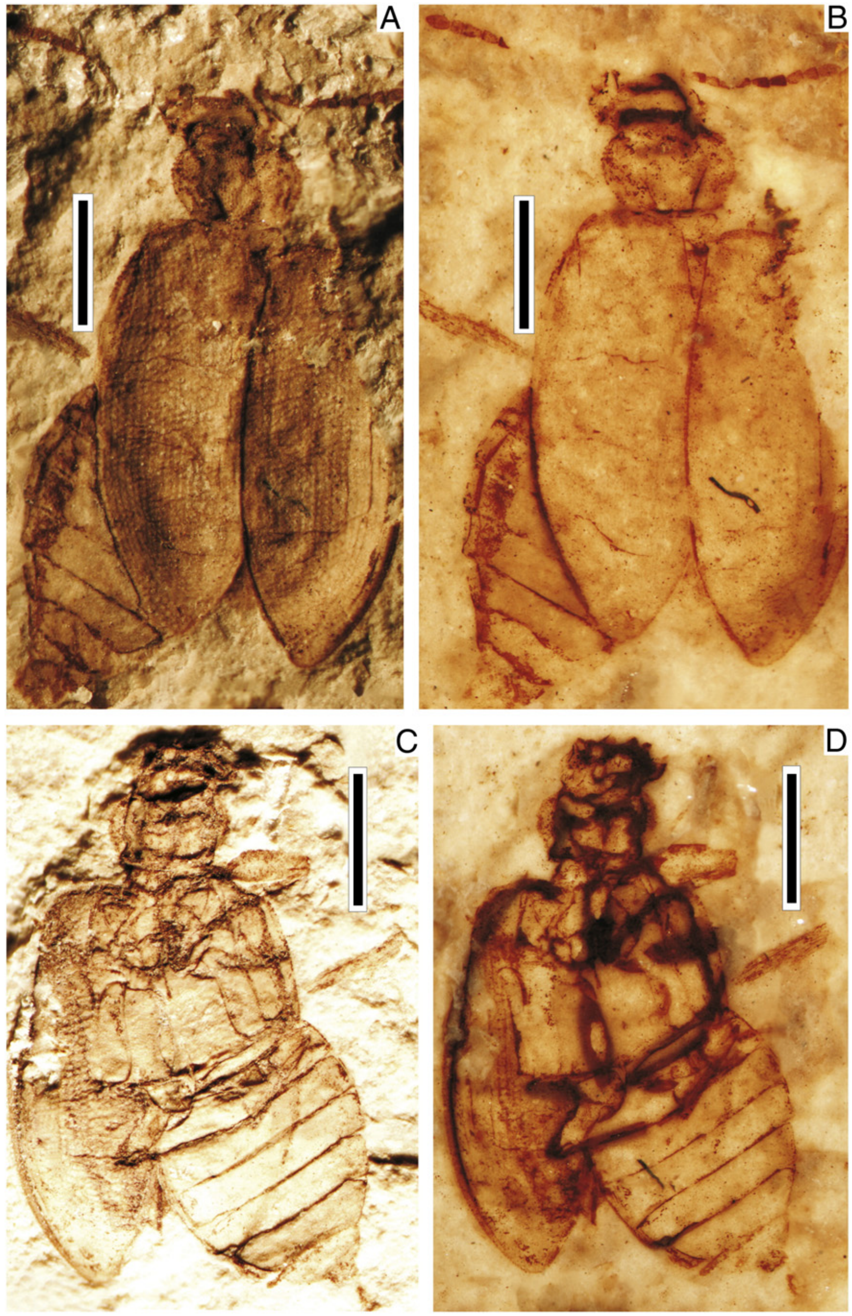

Fig. 6. *Jurodes daohugouensis* sp. nov. NIGP154971, habitus photos of the paratype, part and counterpart. A and C, dry; B and D, wetted with ethanol. Scale bars equal 1 mm.

20 rows of punctures, distance between two nearest punctures in a row is equal to diameter of one puncture; near elytral apex rows draw closer, so it looks uniformly punctate.

Mesoventrite narrowing anteriorly, its posterior margin twice as wide as anterior, length same, with contiguous, transverse mesocoxae; anterior process of mesoventrite sharp, flattened, equal to 1/4 of mesoventrite length; posterior process very short, not longer than 1/6th of mesoventrite length; longitudinal suture goes all along sclerites' length. Mesepisterna and mesepimeron trapezoidal, covered with deep, oblique short furrows.

Metaventrite posterior margin twice wider than anterior, its anterior angles weakly protruding forward; anterior intercoxal process 1/3 as long as mesocoxae, almost not narrowing to wide blunt apex; posterior intercoxal process rather short, triangular, shorter than 1/3 of metacoxal length. Posterior angles of metaventrite protruding laterally and enveloping 1/3 of metepisternal posterior margins. Longitudinal suture present, transverse suture strongly shifted to posterior margin. Metepisterna elongate-rectangular, slightly widened anteriorly, with semiarcuate ridge which starts near sclerites anterior margin and ends in basal fifth. Metaventrite and metepisterna covered with dense big punctures, about the same size as on pronotum.

First visible abdominal sternite with long, wide triangular intercoxal process, which divides metacoxae at 3/4 of their length; sternites 1–4 of same lengths, starting from 5th sternites become 1/5 longer than previous one, with longest, triangular 6th sternite. Contact margins of sternites thickened. Sixth visible abdominal sternite not covered by elytra. Abdominal apex with visible tergites IX and X (proctiger) in paratype NIGP154975 (Fig. 9F). Aedeagus of trilobate type, parameres slightly curved medially, penis as long as parameres, parallel-sided (Fig. 9B).

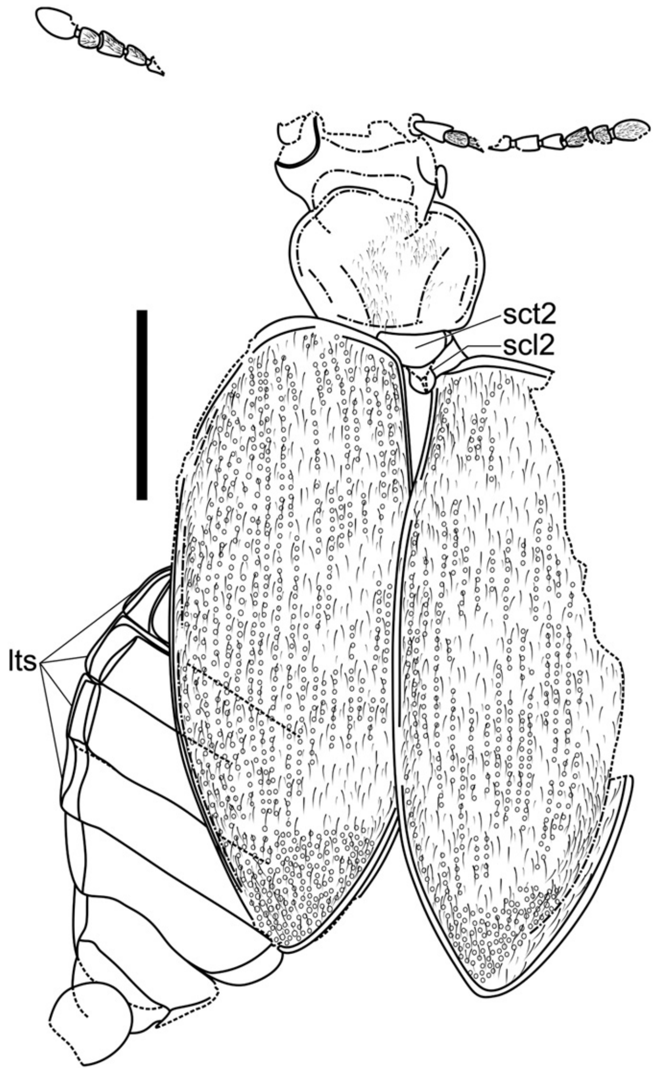

Fig. 7. *Jurodes daohugouensis* sp. nov. NIGP154971, counterpart. Line drawing of the paratype. Label abbreviations: scl2 — mesoscutellum; sct2 — mesoscutum; lts — laterosternites. Scale bar equals 1 mm.

Coxae of all legs very broad with exposed trochantins. Procoxae big, makes almost 1/2 of pronotal length. Protrochanters long, half of profemoral length, Profemur with several longitudinal ridges, as long as protibia which has only single ridge. Protarsi with elongated tarsomeres 1 and 5, 2nd is 1/3 longer than 3rd or 4th, which are of the same size and shape. Profemur covered with punctures on pronotum. Mesocoxae as long as mesoventrite. Mesotrochanter elongated, with pointed apex, 1/3 of mesofemoral length. Mesofemur and mesotibia 1/5 longer than prolegs. Mesotibial spurs very short and thin, 1/2 of first mesotarsomere length. Mesotarsi thin and long, not shorter or thinner than 1/2 of mesotibial length or width. Mesotarsomeres of elongate-rectangular shape; tarsomere 1 equal to combined length of tarsomeres 2 and 3, only slightly longer than penultimate one. Middle and hindlegs are of the same size (at least femora and tibias). Maximal lengths of metacoxae are equal to length of sternites 1–4; metatrochanter oval-shaped, its basal third narrowed, separated by thin sulcus. Metatarsi as long as metatibiae, only 1/3 thinner. Tarsomeres 1–4 of the same proportions as protarsi, length of apical tarsomere equal to combined lengths of previous three; claws weakly curved, long and thin, longer than half of 5th tarsomere length (Figs. 2E, 9E).

Measurements

See Table 1.

Remarks

The front ocellus is very clear in the holotype. The right ocellus is visible, but the left ocellus is unclear in the holotype (Fig. 9A). In Fig. 5B there are paired dotted lines separating the procoxae which are actually the margins of the coxal cavities, covered above by the big procoxae, so the procoxae are contiguous. In the same figure, the oval-shaped structure on the anterior margin of the pronotum looks like a cervical sclerite (a typical polyphagan character), but this structure is actually a protrochanter.

Jurodes pygmaeus sp. nov. (Figs. 10, 11)

Etymology

After Latin "pygmaeus", due to the miniature size.

Holotype

NIGP154972, counterpart; Middle Jurassic, Daohugou.

Diagnosis

Body length less than 4 mm; inner margins of eyes (on dorsal side) only slightly curved; eyes only 1.5 times shorter than head length excluding labrum and mandibles; elytra with transverse ridges underneath, located at the elytral apical 1/3.

Description

Head quite big, 1/5 of body length, not shorter than pronotum, distinctly narrower behind eyes, sunken into pronotum at half the length of the parietals. Clypeus not shorter than genae, its posterior margin straight. Genae glabrous, ridged, separated from the rest of the frons by fine sulci, with antennal sockets in the middle. Median portion of frons elevated, bordered laterally, divided in the middle by a V-shaped groove at anterior 1/3 of eye length. Scapus of elongate-rectangular shape, only slightly longer than pedicellus; antennomeres 3 subtrapezoidal, 1.5 times longer than each of antennomeres 4–10, equal in length, but 0.5 times as wide as the apical egg-shaped antennomere. Rest of antennomeres, i.e., 4–10, are of subtrapezoidal shape and equal in size. Frontal region (excluding genae) uniformly covered with fine punctures.

Pronotum thickly carinated, anterior angles completely absent, sides rounded. Pronotum uniformly covered with deep punctures which are of the same size and density as on frons. Proepisternum rectangular, slightly wider than proepimeron, interpleural suture distinct.

Scutellum very small, less than 1/6 of basal elytral width, its anterior margin deeply emarginated so the anterior angles become heavily protruded forward.

Elytron of elongate-oval shape, 2.5 times longer than wide, elytral disc very convex, with flattened outer margin; elytron edged, with at least 25 rows of punctures, distance between two nearest punctures in a row is equal to the diameter of one puncture; near apex rows draw closer, so elytral apices look uniformly punctate.

Hind wing with big, triangular radial cell (rc), wing membrane around it thickly sclerotized; oblong cell (o cell) rather big, triangular, oblique, apical membrane (am) long.

Metanotum with prescutum represented by narrow anteriorly oriented sclerites. Anterolateral portion of scutum sharply deflected towards prescutum. Alacristae X-shaped, long and distinct, with expanded posterior arms, extending from anterior margin of horizontal part of scutum to its hind margin. Scuto-scutellar suture crossing alacristae almost at the middle of its length, closer to its posterior half. Scutellum semioval, with weakly curved anterior and posterior margins. Metapostnotum large, 1.5 times longer than metascutellum, divided into a median and lateral portion by short but distinct longitudinal ridges, and into a cranial and caudal part by a transverse ridge; connected with metepimeron by a distinct, but narrow, ventrolaterally directed triangular extension.

Abdominal tergite 1 shortest, 0.5 times as long as each of tergites 2–6 which are of the same length; intersegmental membranose connections between all tergites distinct and rather wide, at least tergites 2–5 with attached laterosternites.

Measurements

See Table 1.

Remarks

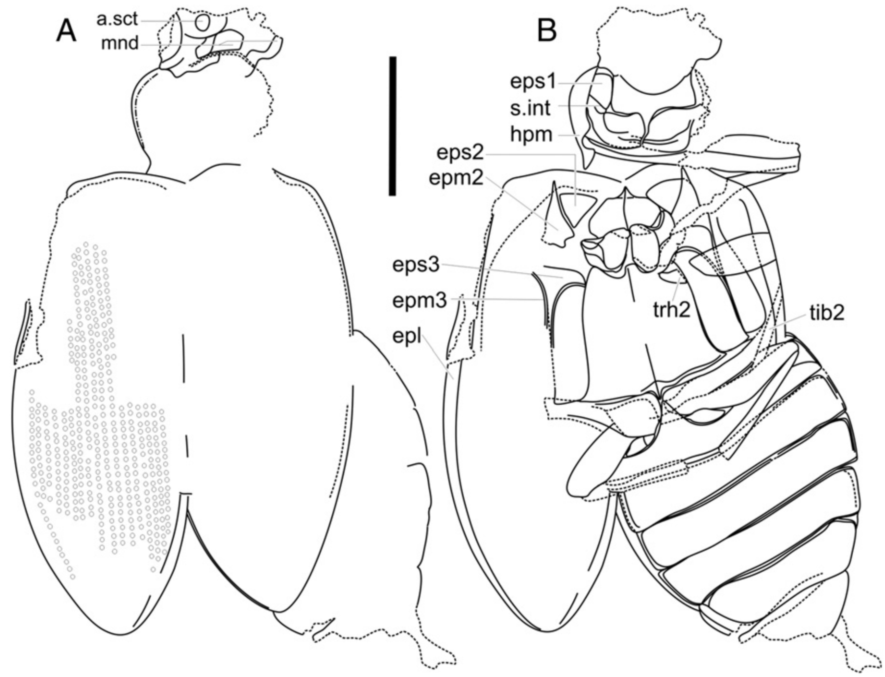

Fig. 8. *Jurodes daohugouensis* sp. nov. NIGP154971, part. Line drawings of the paratype. A, dorsal view; B, ventral view. Label abbreviations: a.sct antennal socket; epm2/3 mes-/metepimeron; epl epipleura; eps1/2/3 pro-/meso-/metepsternum; hpm hypomeron; mnd mandibles; s.int interpleural suture; tib2 mesotibia; thr2 mesotrochanter. Scale bar equals to 1 mm.

Costal bar of the left wing of *J. pygmaeus* (Fig. 11A) is overturned, so its posterior margin is facing forward. In the reconstruction (Fig. 2G), the wing of *S. zhiltzovae* from Fedorenko (2009) was used as a model to show the wing outline and vein positions (Fig. 2H).

5. Discussion

The extant specimen of Jurodidae possesses three ocelli in triad on its forehead (Leschen and Beutel, 2004). The ocelli in *J. ignoramus* and *J. minor* were unknown so far; Kirejtshuk (1999) did not mention this structure, and the state of their preservation leaves only a small chance of finding such fine structures. The preservation of Daohugou insects is usually quite exquisite, in detail so fine that ocelli and even fine setae can be discerned clearly on tiny specimens such as the Jurodidae. We carried out a detailed SEM investigation on the well preserved dorsal part of the head of Daohugou Jurodidae (Fig. 9A). Our results confirm the presence of three ocelli in Mesozoic Jurodidae, and imply that Jurodidae retain this apomorphy over a period of 160 million years from the Middle Jurassic to Recent. Three ocelli are probably also present in *J. ignoramus* (see photos in Kirejtshuk, 2013), but a re-examination of this specimen is needed to confirm it. Ocelli, one or two, can be found in some families of Polyphaga, but their internal structure is strongly simplified compared with other groups of Insecta (Leschen and Beutel, 2004). The presence of three ocelli may be a feature in the ground-plan of Coleoptera (Crowson, 1981; Leschen and Beutel, 2004). There is an exception, however, to this rule: Naomi (1987) found a teratological individual of the genus *Lesteva* Latreille, 1797 (Polyphaga: Staphylinidae: Omaliinae) with three ocelli which form exactly the same pattern as in Jurodidae: one ocellus between the compound eyes, and two behind them (Fig. 2D). Previous fossils reveal that ocelli are absent extensively in Permian and Triassic stem groups of archostematan beetles (Ponomarenko, 2002). Thus, it is very likely that the occurrence of three ocelli in both Jurodidae and *Lesteva* is an atavism (Naomi, 1987; Leschen and Beutel, 2004).

The wing venation of *Sikhotealinia* was previously considered to be a good reason to place Jurodidae within Polyphaga (Lafer, 1996). The venation in *Sikhotealinia* was believed to be very advanced and attributed to the "cantharoid" subtype, so it could be placed in the superfamily Scirtoidea or Scarabaeoidea (Lafer, 1996; Fedorenko, 2009). Our results shows that the venation of *J. pygmaeus*, at least on the remigium (Figs. 2G, 9C, 11A), is very similar to that of *Sikhotealinia* (Fig. 2H). Both their wings are not of the typical archostematan ground plan, because they lack carpal cells and oblong cells and decreased in size. Nevertheless, the oblong cell of *J. pygmaeus* is comparatively much bigger and less reduced, and its posterodistal border is well developed, compared with *Sikhotealinia*. There is also a remnant pterostigma on the wings of *Sikhotealinia*, which is also not typical for Polyphaga. The presence of an oblong cell, unmodified anal venation (known only for *Sikhotealinia*), and remnant pterostigma allows us to put Jurodidae neither in Scirtoidea nor in Scarabaeoidea.

In Lafer's description (1996), *Sikhotealinia* was compared with representatives of the polyphagan family Derodontidae, which has mesocoxal cavities partly closed by metepisterna, a character usually found in Archostemata (Friederich et al., 2009). Now it is clearly visible that the wing venation, contiguous procoxae and exposed pleural parts of the pronotum of Jurodidae do not match the diagnosis of the Derodontidae, which appears to be an advanced family (Ge et al., 2007). The male genitalia in *J. daohugouensis* (Figs. 5B, 9B) is the first discovery of such a structure in this family. In original description, *S. zhitzovae* was supposed to be a female (Lafer, 1996). Our results show Jurodidae has an archaic trilobate structure, and further support the assumption of Kirejtshuk (1999) that the only one known sample of *Sikhotealinia* is a male because it shows an anal sclerite, which is also observable in the *J. daohugouensis* holotype and paratypes ("tergite X" in Fig. 5B).

In conclusion, there are a lot of morphological similarities among *J. daohugouensis*, *J. pygmaeus* and *S. zhiltzovae* in the big protruding eyes, elevated median portion of frons bearing three ocelli, pubescent body, contiguous procoxae, exposed trachantion of all coxae, elytra with rows of punctures, and wing venation. These key characters of

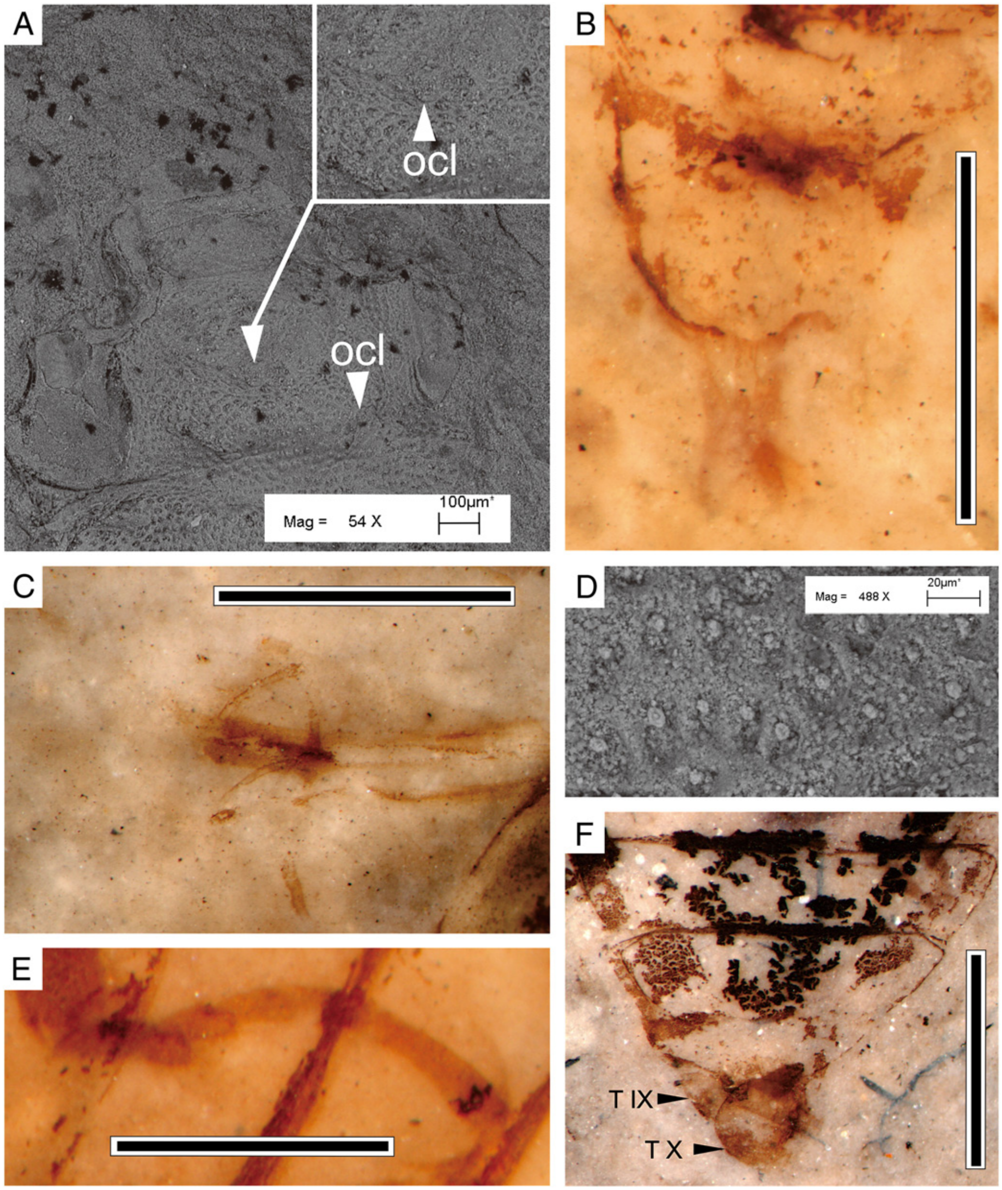

Fig. 9. Morphological details of *Jurodes daohugouensis* sp. nov., the holotype NIGP154969 (A; B; D; E) and paratype NIGP154975 (F), and *Jurodes pygmaeus* sp. nov. NIGP154972, the holotype (C). A, frons with ocellus (ocl); B, aedeagus; C, left wing; D, microsculpture of the genae; E, metatarsus; F, abdominal apex with visible tergites IX and X (proctiger). Scale bars (excluding A and D) equal to 1 mm.

extant Jurodidae can be traced back to the Middle Jurassic, which therefore reveals that the family has been in a period of evolutionary stasis for at least 160 million years. The family Jurodidae represents a group of beetles with unusual morphology. The presence of exposed propleuron, three pairs of external trochantins, metanepisterna with ridges (as in some Cupedidae), trilobate aedeagus, and primitive characters of wing venation of *Jurodes* species described herein and *Sikhotealinia*, further support the probable attribution of Jurodidae to Archostemata.

Our discoveries widen the paleogeographic distribution of fossil Jurodidae from Russian Siberia to northern China (Fig. 1). Jurodidae were probably widespread in temperate zones during the Mesozoic and also present in other Mesozoic insect Lagerstätten, but were neglected or unrecognized because of their tiny size and poor preservation. *Sikhotealinia* was only known from the southern Primorsky Territory of Far Eastern Russia which is a refugium of the Mesozoic and Tertiary insect faunas (Lafer, 1996; Lelej and Storozhenko, 2010). Given the previous distribution of fossil Jurodidae, more extant specimens of Jurodidae may be found in some Asian refugia.

Acknowledgments

We thank Mr. Chenyang Cai (NIGPAS) for providing useful discussions, and Prof. E.A. Jarzembowski for improving the English language of the manuscript. We also thank three anonymous reviewers for reviewing the manuscript and for their constructive criticisms, and Prof. M. Santosh for his helpful editorial comments. This research was financially supported by the National Basic Research Program of China (Grant No. 2012CB821900), the China Postdoctoral Science Foundation funded project (No. 2012M511808), the National Natural Science Foundation of China (Grant Nos. 41002006 and J1210006) and the Russian Foundation for Basic Research (Project No. 11-04-01712).

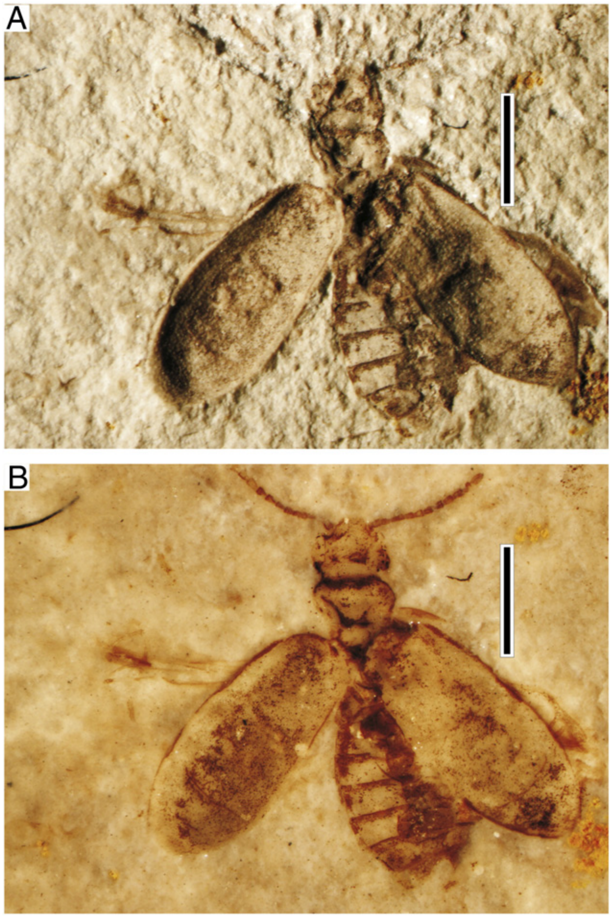

Fig. 10. *Jurodes pygmaeus* sp. nov. NIGP154972, habitus photos of the holotype. A, dry; B, wetted with ethanol. Scale bars equal to 1 mm.

References

Beutel, R.G., Ge, S.Q., Hörnschemeyer, T., 2008. On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. Cladistics 24, 270–298.

Beutel, R.G., Friedrich, F., Leschen, R.A.B., 2009. Charles Darwin, beetles and phylogenetics. Naturwissenschaften 96, 1293–1312.

Blakey, R., 2005. Global Paleogeographic Views of Earth History — Late Precambrian to Recent. http://jan.ucc.nau.edu/rcb7 ([online] (Last accessed October 2012)).

Chen, W., Ji, Q., Liu, D.Y., Zhang, Y., Song, B., Liu, X.Y., 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. Geological Bulletin of China 23, 1165–1169.

Crowson, R.A., 1981. The Biology of Coleoptera. Academic Press, London (802 pp.).

Fedorenko, D.N., 2009. Evolution of the Beetle Hind Wing, with Special Reference to Folding (Insecta, Coleoptera). Pensoft Publishers, Sofia-Moscow (335 pp.).

Friederich, F., Farrell, B., Beutel, R.G., 2009. The thoracic morphology of Archostemata and the relationships of the extant suborders of Coleoptera (Hexapoda). Cladistics 25, 1–37.

Ge, S.Q., Beutel, R.G., Yang, X.K., 2007. Thoracic morphology of adults of Derodontidae and Nosodendridae and its phylogenetic implications (Coleoptera). Systematic Entomology 32, 635–667.

Ge, S.Q., Hörnschemeyer, T., Friedrich, F., Beutel, R.G., 2011. Is *Crowsoniella relicta* really a cucujiform beetle? Systematic Entomology 36, 175–179.

Hörnschemeyer, T., 2005. Archostemata Kolbe, 1908. In: Kristensen, N.P., Beutel, R.G. (Eds.), Coleoptera, Vol. I. Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga Partim). Handbook of Zoology Vol. IV, Arthropoda: Insecta. De Gruyter, Berlin, New York, pp. 157–182.

Hörnschemeyer, T., 2009. The species-level phylogeny of archostematan beetles — where do *Micromalthus debilis* and *Crowsoniella relicta* belong? Systematic Entomology 34, 533–558.

Kirejtshuk, A.G., 1999. *Sikhotealinia zhiltzovae* Lafer, 1996 — recent representative of the Jurassic coleopterous fauna (Coleoptera, Archostemata, Jurodidae). Proceedings of the Zoological Institute RAS, 281 21–26.

Kirejtshuk, A.G., 2013. Most Mysterious Representative of beetles — *Sikhotealinia zhiltzovae* Lafer, 1996. http://www.zin.ru/Animalia/Coleoptera/rus/sikhot06.htm (http://www.zin.ru/Animalia/Coleoptera/eng/jurodesk.htm [online] (Last accessed March 2013)).

Kirejtshuk, A.G., Ponomarenko, A.G., Prokin, A.A., Chang, H., Nikolajev, G.V., Ren, D., 2010. Current knowledge of Mesozoic Coleoptera from Daohugou and Liaoning (Norteast China). Acta Geologica Sinica 84, 783–792.

Kukalová-Peck, J., Lawrence, J.F., 2004. Relationships among coleopteran suborders and major endoneopteran lineages, evidence from hind wing characters. European Journal of Entomology 101, 95–144.

Lafer, G.S., 1996. Family Sikhotealiniidae. In: Ler, P.A. (Ed.), Key to the Insects of the Russian Far East, vol. III, part 3. Dal'nauka, Vladivostok, pp. 390–396.

Latreille, P.A., 1797. Précis des Caractères Génériques des Insectes, Disposés dans un Ordre Naturel. Dufart, Paris (Brive: F. Bourdeaux. xiv. +201 +7).

Lelej, A.S., Storozhenko, S.Y., 2010. Insect taxonomic diversity in the Russian Far East. Entomological Review 90, 372–386.

Leschen, R.A.B., Beutel, R.G., 2004. Ocellar atavism in Coleoptera: plesiomorphy or apomorphy? Journal of Zoological Systematics and Evolutionary Research 42, 63–69.

Linnaeus, C., 1758. Systema Naturae per regni tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentius Salvius, Stockholm ((10th revised ed.) 1: iv + 824 pp.).

Liu, Y.Q., Liu, X.Y., Ji, S.A., Yang, Z.Q., 2006. U–Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. Chinese Science Bulletin 51, 2634–2644.

Miki, S., 1941. On the change of flora in Eastern Asia since Tertiary Period (I). The clay or lignite beds flora in Japan with special reference to the *Pinus trifolia* beds in Central Hondo. The Journal of Japanese Botany 11, 237–304.

Naomi, S.I., 1987. Comparative morphology of the Staphylinidae and the allied groups (Coleoptera, Staphylinoidea). Japanese Journal of Entomology 55, 450–458.

Ponomarenko, A.G., 1985. Coleoptera. In: Rasnitsyn, A.P. (Ed.), Jurassic Insects of Siberia and Mongolia. : Trudy paleontologicheskogo instituta akadamii nauk SSSR. Nauka, Moscow, pp. 47–87.

Ponomarenko, A.G., 1990. Beetles. Scarabaeida. In: Rasnitsyn, A.P. (Ed.), Late Mesozoic Insects of Eastern Transbaikalia. : Trudy paleontologicheskogo instituta akadamii nauk SSSR. Nauka, Moscow, pp. 39–87.

Ponomarenko, A.G., 2002. Superorder Scarabaeidea Laicharting, 1781. Order Coleoptera Linné, 1758. The beetles. In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), History of Insects. Kluwer Academic Publisher, Dordrecht, pp. 164–176.

Rasnitsyn, A.P., Zhang, H.C., 2004. Composition and age of the Daohugou Hymenopteran assemblage from Inner Mongolia, China. Palaeontology 47, 1507–1517.

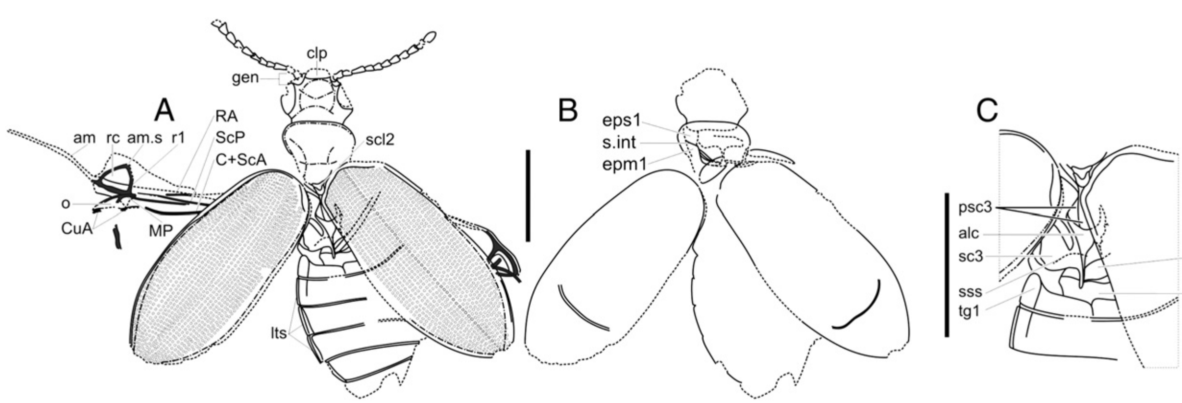

Fig. 11. *Jurodes pygmaeus* sp. nov. NIGP154972. Line drawing of the holotype. A, dorsal view; B, ventral view; C, Meso- and metanotum. Label abbreviations: alc alacrista; clp clypeus; epm1 proepimeron; eps1 proepisternum; gen gena; lts laterosternites; pn3 metapostnotum; psc3 metaprescutum; sc3 metascutum; scl2/3 meso-/metascutellum; s.int interpleural suture; sss metathoracic scutoscutellar suture; tg1 first abdominal tergite. Scale bars equal to 1 mm.

Rees, P.M., Ziegler, A.M., Valdes, P.J., 2000. Jurassic phytogeography and climates: new data and model comparisons. In: Huber, B.T., MacLeod, K.G., Wing, S.L. (Eds.), Warm Climates in Earth History. University of Cambridge Press, Cambridge, England, pp. 297–318.

Smith, J.L.B., 1939. A living fish of Mesozoic type. Nature 143, 455.

Wang, B., Li, J.F., Zhang, H.C., Fang, Y., 2009. Preliminary elemental analysis of fossil insects from the Middle Jurassic of Daohugou, Inner Mongolia and its taphonomical implications. Chinese Science Bulletin 54, 783–787.

Wang, B., Zhang, H.C., Ponomarenko, A.G., 2012. Mesozoic Trachypachidae (Insecta: Coleoptera) from China. Palaeontology 55, 341–353.

Wang, B., Zhang, H.C., Jarzembowski, E.A., Fang, Y., Zheng, D.R., 2013. Taphonomic variability of fossil insects: a biostratinomic study of Palaeontinidae and Tettigarctidae (Insecta: Hemiptera) from the Jurassic Daohugou Lagerstätte. Palaios (in press).

Zhang, J.F., 2006. New winter crane flies (Insecta: Diptera: Trichoceridae) from the Jurassic Daohugou Formation (Inner Mongolia, China) and their associated biota. Canadian Journal of Earth Sciences 43, 9–22.