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

Evgeny V. Yan, Bo Wang, Alexander G. Ponomarenko, Haichun Zhang

A S T R A C T

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 is 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.

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1. Introduction

Beetles in the family Jurodidae are an amazing example of “living fossils”, alongside the famous coelacanth Latimeria smithi, 1939 or coniferous redwood Metasequoia, 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; Hörschemeyer, 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.
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* Pononarenko, 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* Pononarenko, 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 Sikholtealinidae. *Sikholtealinia* 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 Sikholtealinidae are closer to Archostemata and some Adephaga (Eodromeinae and Dytiscoidae), 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). For the first time, mentioned three ocelli on the *Sikholtealinia* head — a unique character in the whole of the order, Coleoptera and placed Sikholtealinidae in the suborder Archostemata, but abstained from a more precise attribution (Fig. 2C, F).

Only after about three years, Kirejtshuk (1999), following Pononarenko’s suggestion, revealed strong morphological similarities and phylogenetic affinities between Jurassic *Jurodes* and recent *Sikholtealinia*, and transferred the latter to Jurodidae and both of them to Archostemata respectively. Kirejtshuk (1999, 2013) showed that recent *Sikholtealinia* 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...
and further proved that both result of postmortal deformation and detachment of the abdomen, and 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 uncoupled 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 genitita), 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 = Sikhotealiniiidae Lafer, 1996

<table>
<thead>
<tr>
<th>Jurodes daohugouensis sp. nov.</th>
<th>J. pygmeus sp. nov.</th>
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<tr>
<td>NIGP154969</td>
<td>NIGP154971</td>
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<tr>
<td>Body</td>
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<td>Elytron</td>
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<td>Hindleg length</td>
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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. Body length less than 4 mm; inner margins of eyes (on dorsal side) only slightly curved
   – Body length more than 5 mm; inner margins of eyes (on dorsal side) curved, S-shaped

3. Alacristae on metanotum parallel-sided; undersides of elytra without transverse ridges
   "Jurodes minor" Ponomarenko, 1990

Fig. 3. *Jurodes dao hugouensis* 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.
Genus *Jurodes* Ponomarenko, 1985

*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).

*Jurodes 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.

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**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; ep1 proepisternum; fmr1 profemur; fn frons; gen genae; lbr labrum; lts laterosternite; mbr membranous joint; mnd mandible; ocl ocelli; pdc pedicellus; scl2 mesoscutellum; scp scapus; s. fg fronto-genal suture; s.int interpleural suture; tib1 protibia. Scale bar equals 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 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, 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 fronto-ocular 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 (Fig. 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, 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
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).
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 mesotibial length. Mesofemur and mesotibia almost at the middle of its length, closer to its posterior portion of scutum to its hind margin. Scuto-scutellar suture crossing towards prescutum. Alacristae X-shaped, long and distinct, with exes. 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. Mesotarsus 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 tibiae). Maximal lengths of metacoxae are equal to length of sternites 1–4; metatrochanter oval-shaped, its basal third narrowed, separated by thin sulcus. Metatarsus 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 sub-trapezoidal, 1.5 times longer than each of antenomeres 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 semi-oval, 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 membranous connections between all tergites distinct and rather wide, at least tergite 2–5 with attached laterosternites.

Measurements
See Table 1.
Remarks

Fig. 7. _Jurodes daohugouensis_ sp. nov. NIGP154971, counterpart. Line drawing of the paratype. Label abbreviations: scl2 — mesocutellum; sc2 — mesoscutum; Its — laterosternites. Scale bar equals 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 polyphagan beetles (Ponomarenko, 2002). Thus, it is very likely that the occurrence of three ocelli in both Jurodidae and Lestevia 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 wing venation of *Sikhotealinia* was believed to be very advanced and attributed to the “cantharoid” subtype, so it could be placed in the superfamilies Scirtoidea or Scarabaeoidea (Lafer, 1996; Fedorenko, 2009). Our results show 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 mesosomal 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. zhiltzovae* 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 trachanition of all coxae, elytra with rows of punctures, and wing venation. These key characters of
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 12100006) and the Russian Foundation for Basic Research (Project No. 11-04-01712).

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

Fig. 11. Jurodes pygmaeus sp. nov. NIGP154972. Line drawing of the holotype. A, dorsal view; B, ventral view; C, Mesos- and metanotum. Label abbreviations: alc alacrista; clp clypeus; epm1 proepimeron; ep1 proepisternum; gen gena; lts laterosternites; pn3 metapostnotum; psc3 metaprescutum; sc3 metascutum; sc12/3 meso-/metascutellum; s1nt interpleural suture; sss metathoracic scutoscutellar suture; tg1 first abdominal tergite. Scale bars equal to 1 mm.

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