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A new fossil genus in Pamphiliidae (Hymenoptera) from China

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A new genus with two new species, *Scabolyda orientalis* gen. et sp. nov. and *Scabolyda incompleta* sp. nov., assigned to the subfamily Juralyinae in the family Pamphiliidae are described and illustrated. They were collected from the Middle Jurassic Jiulongshan Formation and the Lower Cretaceous Yixian Formation in northeastern China. They represent the first fossil pamphiliids described from China.

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Key words: Pamphiliidae, Middle Jurassic, Early Cretaceous, Jiulongshan Formation, Yixian Formation, China.

PAMPHILIOIDEA includes two extant families, Pamphiliidae and Megalodontesidae (Taeger *et al.* 2010), which have been considered sister groups amongst extant Hymenoptera by some researchers (Vilhelmsen 2001, Schulmeister 2003, Ronquist *et al.* 2012). In addition, two extinct families (Praesiricidae and Xyleyidae) also belong to this superfamily and they possibly form a grade or a stem group of the superfamily (Rasnitsyn 1988, 2002, Ronquist *et al.* 1999, Grimaldi & Engel 2005).

There are three subfamilies in Pamphiliidae. Pamphiliinae and Cephalciinae have both extant and extinct members, and subfamily Juralyinae includes only extinct (Mesozoic) representatives. Pamphiliidae consists of 13 extant genera with over 136 species and three extinct genera: *Juralyda* Rasnitsyn, 1977, in the subfamily Juralyinae, from the Upper Jurassic of Transbaikalia (Rasnitsyn 1977); *Tapholyda* Rasnitsyn, 1983, in Cephalciinae, from the uppermost Eocene of Colorado and Upper Miocene of Khabarovsk Territory (Rasnitsyn 1983; age of Florissant and equivalent deposits of Colorado after Evanoff *et al.* 2001); and *Atocus* Scudder, 1892, in Pamphiliinae, from the uppermost Eocene of Colorado (Scudder 1892, Rasnitsyn 1983).

We report four pamphiliids in Juralyinae (two of which are preserved with part and counterpart). Three of these specimens were collected from the Jiulongshan Formation of late Middle Jurassic age near Daohugou Village and belong to the Yanliao Biota (Gao & Ren 2006). The other derives from the Yixian Formation of Early Cretaceous age near Chaomidian Village and belongs to the famous Jehol Biota (Ren *et al.* 1997). These localities have yielded numerous excellently preserved insect fossils (Ren *et al.* 2010a). Among these are Mecoptera (Ren *et al.* 2009, 2010b, Wang, Labandeira *et al.* 2012), Odonata (Li *et al.* 2012), Coleoptera (Yue *et al.* 2010), Hymenoptera (Gao & Ren 2008, Gao *et al.* 2009, 2010, 2011, Wang, Shih *et al.* 2012, 2013, Li *et al.* 2013), Siphonaptera (Gao *et al.* 2012, 2013, Huang *et al.* 2012, 2013) and Neuroptera (Wang *et al.* 2010, Shi *et al.* 2011).

Materials and methods

The specimens are housed in the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China. They were examined using a Leica MZ 16.5 stereomicroscope (Leica, Wetzlar, Germany). Line drawings were prepared with Adobe Illustrator CS2 software. The images of the specimens were taken with a camera system connected to the Leica MZ 16.5. For some images we covered the specimen in 95% ethanol

to obtain clearer results. The wing venation nomenclature used in this paper is modified from Rasnitsyn (1969, 1980).

Systematic palaeontology

Order HYMENOPTERA Linnaeus, 1758

Superfamily PAMPHILIOIDEA Cameron, 1890

Family PAMPHILIIDAE Cameron, 1890

Subfamily JURALYDINAE Rasnitsyn, 1977 emend.

Type genus. *Juralyda* Rasnitsyn, 1977

Emended subfamily diagnosis. Antennae with *ca* 12 segments (where visible); third antennal segment distinctly thicker than following segments, twice to three times as long as the fourth antennal segment or equal to combined length of fourth–seventh antennal segments. Forewing with 1-RS about half as long as, or slightly longer than, half of 1-M; M+Cu without cu-a stub at angulation or, at most, with extremely short stub present; cell 1mcu shorter than length of pterostigma; cell 2r much wider than cell 2rm, and 3r-m separated from apex of cell 3r by nearly its own length.

Remarks. The type genus (*Juralyda*) was described based on a right forewing (Rasnitsyn 1977). With new morphological information and data from the five well-preserved fossils attributed to Juralyinae in this paper, we have added diagnostic characters of the antennae and forewings to the subfamily. Furthermore, we no longer consider the shortened and diminished forewing vein SC as diagnostic.

We propose to transfer *Atocus* from Pamphiliinae to Juralyinae despite its young age (latest Eocene), based on the putative synapomorphy of a very short antennae with 12 segments and its symplesimorphies shared with Juralyinae: third antennal segment long and thick (nearly as long as the next four segments), and forewing with 1-RS long and M+Cu without an extra vein at its angulation (i.e., cu-a).

The apomorphic nature of the oligomeric antennae is implied from the polymeric state, which is characteristic of the more basal pamphilioid family, Xyelydidae (Rasnitsyn 1983). The long and thick third antennal segment, long 1-RS and absence of a supernumerary crossvein cu-a are the ground plan character states of the grade ‘Suborder’ Symphyta (Rasnitsyn 1988, Ronquist *et al.* 2012).

Genera included. *Juralyda* Rasnitsyn, 1977, *Scabolyda* gen. nov. and *Atocus* Scudder, 1892.

***Scabolyda* gen. nov.**

Type species. *Scabolyda orientalis* sp. nov.

Etymology. The generic name is a combination of the Latin prefix ‘scab-’ (meaning coarse) and *Lyda* Fabricius, a junior synonym of *Pamphilius* (Springate 1999, Taeger *et al.* 2010) often used as a suffix for generic

names in Pamphiliidae (e.g., *Acantholyda*, *Juralyda*). The gender of the name is feminine.

Diagnosis. Antennae with third antennal segment at least twice as long as the fourth. Mesoscutellum small, nearly as large as mesoprescutum. Forewing with pterostigma long and narrow, completely sclerotized. In forewing, SC well developed and bifid, RS+M at least 1.3 times as long as 1-M, 2-M about 0.8–0.9 times as long as RS+M, angle between 1-M and 1-Cu over 90°, cell 1mcu at least 1.3 times as long as wide, 2r-rs near apex of pterostigma, and 3r-m oblique and inclined toward wing apex.

Remarks. *Scabolyda* is attributed to Pamphiliidae based on the following characters: forewing with SC developed, R sinuate and not straight before RS base, M+Cu angularly bent rather than arcuate or straight, and third antennal segment not several times thicker than the fourth. The new genus is further assigned to Juralyinae, based on having 1-RS long and M+Cu lacking a supernumerary cu-a (vein stub at the angulation).

Scabolyda gen. nov. differs from *Juralyda* and *Atocus* in having a complete SC (vs rudimentary, weak SC lacking an apical fork in *Juralyda*, or with only 1-SC lost in *Atocus*). It also differs from *Juralyda* in having a clearly oblique 3r-m (vs an almost vertical 3r-m in *Juralyda*). It further differs from *Atocus* in its narrow pterostigma, with 2r-rs near its apex, and the posterobasal angle of cell 1mcu being obtuse (vs *Atocus* with a much wider pterostigma, 2r-rs located far from the pterostigmal apex, and the posterobasal angle of cell 1mcu being acute).

***Scabolyda orientalis* sp. nov.** (Figs 1, 2)

Material. Holotype, CNU-HYM-NN2012108 (part and counterpart; Fig. 1A–C); Paratypes, CNU-HYM-NN2012109 (Fig. 2A); CNU-HYM-NN2012110 (part and counterpart; Fig. 2B, C); and specimen NND0117 kept at the Nanjing Institute of Geology and Palaeontology CAS, illustrated by Rasnitsyn & Zhang (2004, pl. 1, fig. 6).

Locality, unit and age. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.979’N, 119°14.318’E); Jiulongshan Formation; late Middle Jurassic.

Etymology. The species name is a Latin adjective, meaning oriental.

Diagnosis. In addition to the generic diagnosis, RS+M shorter than 1.5 times length of 2-M.

Description

Holotype. Sex unknown. Surface sculpture coarsely punctate, especially on head and thorax (Fig. 1A, B). Head and thorax preservational colour dark, pterostigma, hind femora and abdomen less dark, antenna and

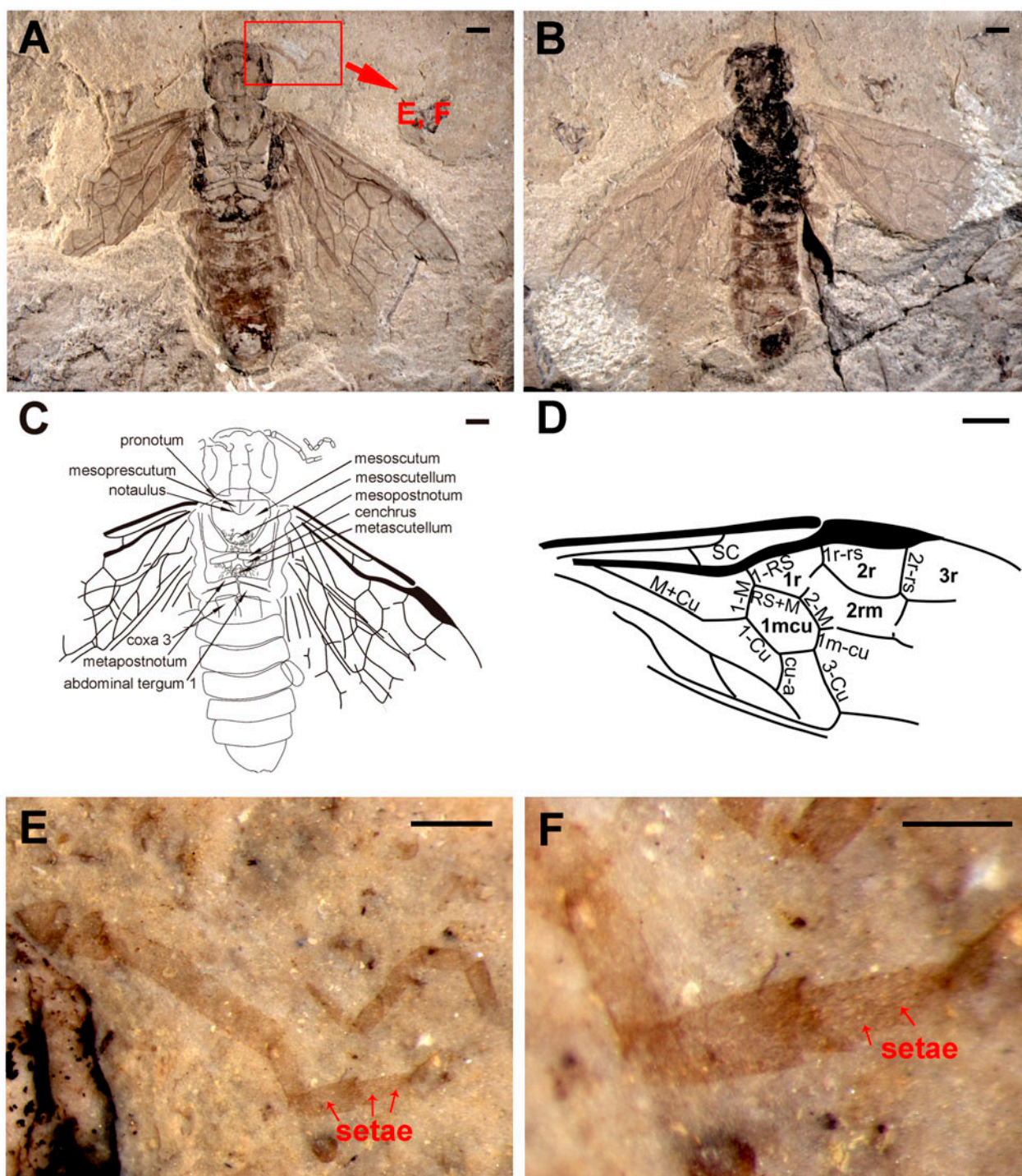


Fig. 1. *Scabolyda orientalis* gen. et sp. nov., holotype, CNU-HYM-NN2012108 (part and counterpart). A, Photo of part; B, Photo of counterpart; C, Line drawing of part; D, Line drawing of right forewing of part; E, Antenna of part; F, Setae on antenna. Scale bars = 1 mm in A–D; 0.5 mm in E; 0.5 mm in F. Venation symbols: SC, R, RS, RS+M, M, Cu, M+Cu—main (longitudinal) veins; 1-RS, 1-M etc.—sections of these veins; 1r-rs, 2r-rs, 2r-m, etc.—crossveins; 1r, 2rm, 1mcu, etc.—cells.

hind tibia (basally) pale, wing membrane is slightly darkened towards wing base.

Head massive and subcircular, length nearly equal to width. Mandible long and narrow, oral cavity isolated from occipital foramen by hypostomal bridge. Antennae approximately 1.7 times as long as head width, densely covered with short setae (Fig. 1E, F); scape incompletely preserved, more than twice as wide as pedicel; pedicel

0.2 times as long as third antennal segment, and 1.2 times as wide as third segment basally, and third antennal segment nearly three times as long, and 1.5 times as wide, as the fourth. Nine or ten additional cylindrical segments present apically, becoming shorter toward apex.

Thorax slightly narrower than the head. Pronotum trapezoid, at least four times as wide as long. Mesonotum with median mesoscutellar sulcus and notauli present

(Fig. 1A, B), mesoscutellum short. Metanotum with cenchri and metascutellum comparatively narrow.

Legs poorly preserved, with hind coxae trapezoidal. Abdomen with eight segments preserved, wider than mesonotum, sterna short, parallel-sided, with fore margin indented medially. Genitalia poorly preserved thus preventing sex determination.

Forewing with pterostigma sclerotized (Fig. 1D). R bent strongly near RS base, sinuous before RS; 1-RS short and inclined toward wing apex, nearly half as long as 1-M. Cell 2r widened strongly, 2r-m inclined toward wing base, located somewhat distally of 2r-rs. RS+M just 1.4 times as long as 1-M, vertical to 1-M, 1-M meeting 1-Cu nearly at 125° , M+Cu bending sharply anteriorly after its mid-point, no stub (supernumerary cu-a) present. Vein 2-M about 0.8 times as long as RS+M. Cell 1mCu about 1.45 times as long as wide, with cu-a near its apex. Hind wings not observable.

CNU-HYM-NN2012109 (Fig. 2A). Surface sculpture and colour pattern similar to holotype, except that abdomen and wing somewhat paler. Head large, 1.2 times as wide as long. Antennae with nearly 12 complete segments preserved on right side; scape 4.1 times as long as and 1.5 times as wide as pedicel; pedicel short, 0.2 times as long as and 1.3 times as wide as third antennal segment; third antennal segment 3.4 times as long as the fourth, and nearly equal to following three segments combined. Thorax 1.1 times wider than head. Abdomen 0.9 times as wide as thorax, becoming narrower towards apex. Forewing with pterostigma sclerotized; SC bifid; R sinuate before RS; 1-RS short and inclined toward wing tip, nearly 1.2 times longer than half of 1-M. Cell 2r widened strongly; 2r-m meeting RS slightly beyond 2r-rs, nearly in a line. RS+M meeting 1-M at about 100° , and just 1.3 times as long as 1-M; 1-M meeting 1-Cu nearly at 117° ; M+Cu bending sharply (anteriorly) after its mid-point, with no stub (supernumerary cu-a) present. Vein 2-M about 0.8 times as long as RS+M. Cell 1mCu about 1.42 times as long as wide, with cu-a near its apex. Hind wings not observable.

CNU-HYM-NN2012110 (part and counterpart) (Fig. 2B, C). Head huge and rounded, 1.2 times as wide as long, mandible short, 0.6 times as long as head width. Eyes reniform, 2.4 times as long as wide, and occupying 0.4 of head's side. Antennae not preserved. Thorax about 1.1 times as wide as head. Mesoprescutum about 0.3 times as long as mesonotum, and equal to length of mesoscutellum. Metanotum with cenchri and metascutellum comparatively narrow, and nearly equal in width. Abdomen 1.1 times as wide as thorax, equal in width. Forewing with pterostigma sclerotized completely; SC bifid; R sinuate before RS; 1-RS short and inclined toward wing apex, nearly 0.8 times as long as 1-M. Cell 2r widened moderately; 2r-m meeting RS slightly beyond 2r-rs. RS+M meeting 1-M at about 92° , and 1.5 times as long as 1-M; 1-M meeting 1-Cu nearly at 116° ; M+Cu bending sharply (anteriorly) after its mid-

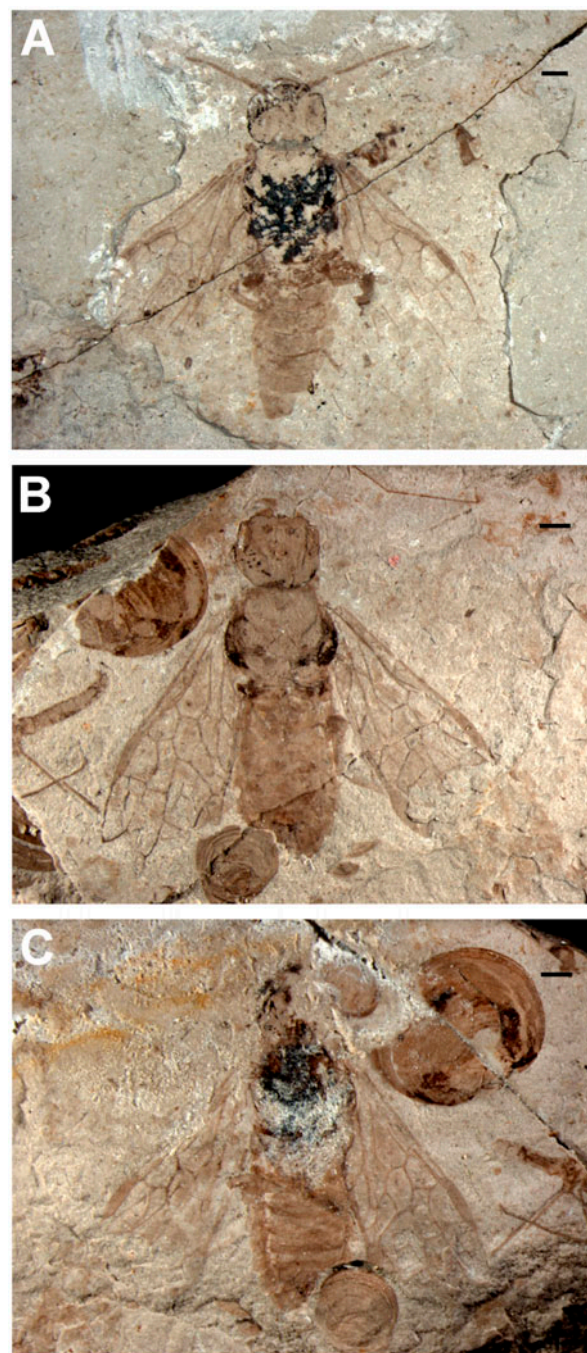


Fig. 2. Photos of paratypes of *Scabolyda orientalis* gen. et sp. nov. A, CNU-HYM-NN2012109; B, CNU-HYM-NN2012110 (part); C, CNU-HYM-NN2012110 (counterpart). Scale bars = 1 mm.

point, and no stub (supernumerary cu-a) present. Vein 2-M about 0.8 times as long as RS+M. Cell 1mCu about 1.48 times as long as wide, with cu-a near its middle. Hind wings not observable.

NND0117 (cf. Rasnitsyn & Zhang 2004, pl. 1, fig. 6). Sex indeterminate. Surface sculpture not apparent, colour pattern similar to holotype. Head nearly round, 1.3 times as wide as long, eyes large, reniform. Antennae not preserved. Thorax about as wide as head. Mesopseudosternum 0.4 times as wide as mesothorax.

Forewing with pterostigma sclerotized completely, SC two-branched, 1-RS short and inclined toward wing apex, RS+M meeting 1-M at about 97° , and 1.45 times as long as 1-M, 1-M meeting 1-Cu nearly at 124° , M+Cu bending sharply anteriorly after its mid-point, and no stub (supernumerary cu-a) present. Cell 1mcu about 1.3 times as long as wide, with cu-a beyond its middle. Hind wings not observable.

Dimensions (in mm). CNU-HYM-NN2012108 (p/c): body length (excluding antenna) 15.7; head width 3.0, length 2.7; third antennal segment as preserved 3.1; forewing length up to end of cell 3r 11.2. CNU-HYM-NN2012109: body length (excluding antenna) 13.4; head as preserved: width 3.3, length 1.7; forewing length as preserved 9.7. CNU-HYM-NN2012110 (p/c): body length (excluding antenna) 13.6; head width 3.2, length without mandibles 2.7, mandible length 1.8; forewing length up to end of cell 3r 10.3.

Scabolyda incompleta sp. nov. (Fig. 3)

Etymology. From the Latin *incompletus*, meaning incomplete.

Locality, unit and age. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China; Yixian Formation; Early Cretaceous.

Material. Holotype, CNU-HYM-LB2012111 (Fig. 3A, D).

Diagnosis. In addition to generic diagnosis, cell 1mcu long, with RS+M about two times as long as 2-M (vs both cell 1mcu and vein RS+M shorter in *S. orientalis*).

Description. Head massive and subcircular, widest nearly at mid-length, about as long as wide. Mandibles bent, sickle-shaped, with subapical tooth, reaching base of opposite mandible when closed (Fig. 3A). Antennae incompletely preserved; scape 1.75 times as wide as pedicel; third antennal segment nearly twice as thick as the fourth (Fig. 3B); rest of antennal segments thinner and longer, cylindrical; fourth antennal segment thicker and shorter than the fifth, narrowing towards base.

Thorax poorly preserved. Abdomen slightly wider than thorax (Fig. 3A), with eight segments, and first segment barely discernible.

Forewing with pterostigma sclerotized (Fig. 3C, D). 1-SC not bent towards C except at very apex, meeting

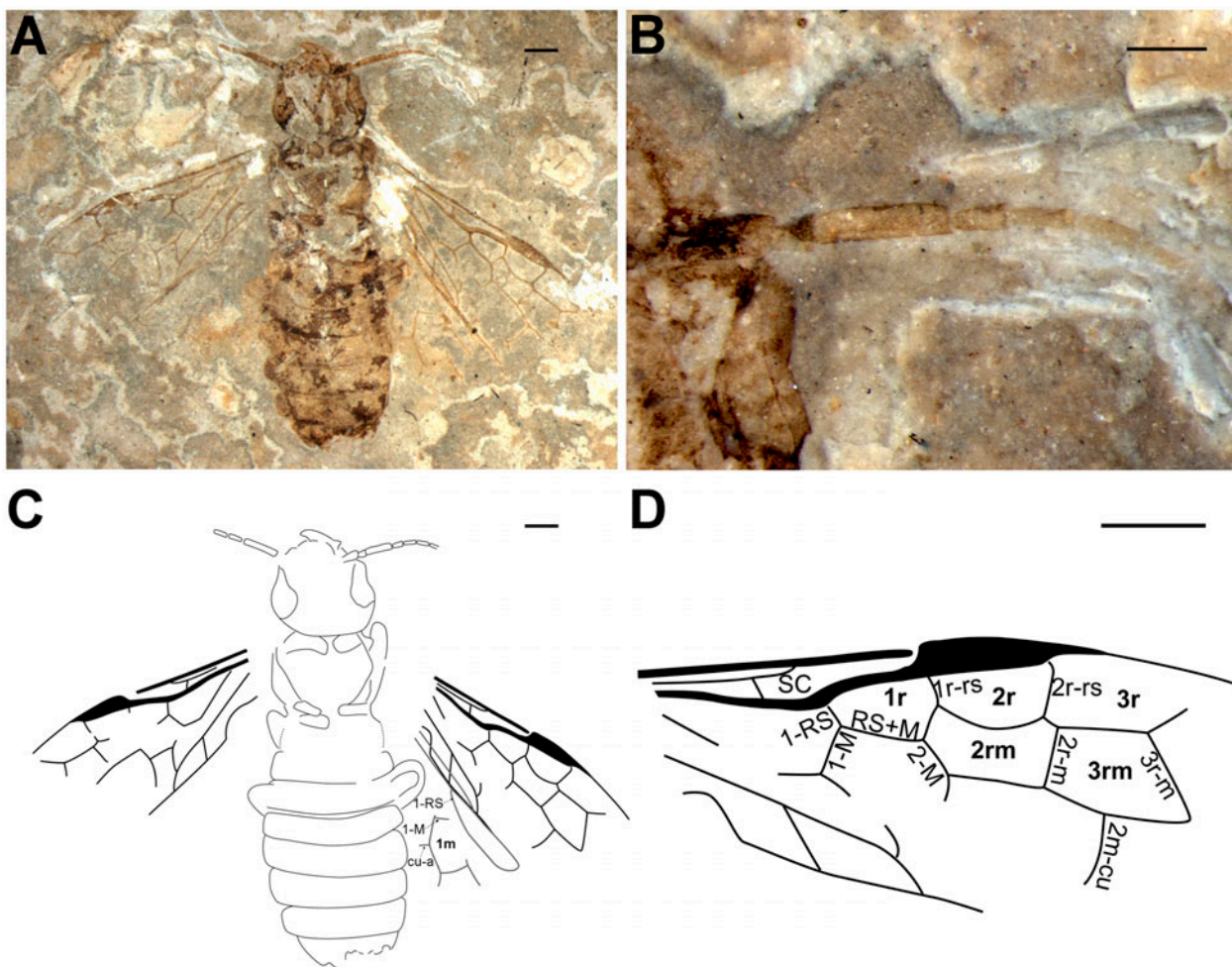


Fig. 3. *Scabolyda incompleta* sp. nov., holotype, CNU-HYM-LB2012111. A, Photo of habitus; B, Photo of antenna; C, Line drawing; D, Line drawing of right forewing. Scale bars = 1 mm in A, C and D, 0.5 mm in B.

C before RS base. 1-RS short and inclined towards wing apex, shorter than half of 1-M. 1r-rs inclined towards wing apex, and 2r-rs inclined towards wing base, with 1r-rs nearly half as long as 2r-rs. 2r-m parallel to 2r-rs and located distad to it. 2m-cu at middle of cell 3m. RS+M meeting 1-M at about 104°, nearly 1.6 times as long as 1-M, 1-M meeting 1-Cu at about 105°. M+Cu bending anteriorly sharply after mid-length, lacking cu-a stub. Vein 2-M about half as long as RS+M. Cell 1mcu about 1.85 times as long as wide (Fig. 3D). Hind wing partially preserved, with 1-RS slightly longer than 1-M, and cu-a located at middle of cell 1m (Fig. 3C).

Dimensions (in mm). Holotype, CNU-HYM-LB2012111: body 14.3 long with mandibles (excluding antenna); head width 3.3, length 3.5; third antennal segment 1.2 as preserved; forewing length up to end of cell 3r 8.3.

Remarks. We differentiate *Scabolyda orientalis* and *S. incompleta* mainly on wing venation, especially the relative length of RS+M, which is shorter than 1.5 times length of 2-M in the former species and almost twice as long as 2-M in the latter. Also, cell 1mcu is 1.5 times as long as wide in the former, and almost twice so in the latter. Furthermore, in *S. orientalis*, the third antennal segment is three times as long as the fourth; the fourth antennal segment is thinner than the fifth, and of equal length; the fifth antennal segment gradually thickens (narrower at the base), and subsequent segments are cylindrical and nearly as long and thick as the fourth. In contrast, in *S. incompleta*, the third antennal segment is nearly 2.5 times as long as the fourth; the fourth is thicker and shorter than the fifth; and subsequent segments are thinner and longer than the fourth.

Discussion

Until recently, Pamphiliidae was considered essentially a Cenozoic family, with just one aberrant specimen described from the upper Lower or lower Middle Jurassic of Transbaikalia (Rasnitsyn 1983). Rasnitsyn & Zhang (2004) reported two additional fossils from the Middle Jurassic of Daohugou that appeared less aberrant, but they did not describe them. We have found more material from the same stratum since then and, based on the description above, it is justifiable to conclude that the specimen illustrated by Rasnitsyn & Zhang (2004, pl. 1, fig. 6) is sufficiently similar to *Scabolyda orientalis* sp. nov. in characters of the head, thorax and especially wing venation to be assigned to this new species.

In Pamphiliidae, the extant subfamilies Cephalciinae and Pamphiliinae are clearly differentiated by characters such as pretarsal claws either with a small inner tooth (in Cephalciinae) or bifid at the apex (in Pamphiliinae), and the wing membrane being either coriaceous

(in Cephalciinae) or corrugated at the apex (in Pamphiliinae) (Benson 1945). However, these characters are rarely visible in fossils. Fortunately, it is possible to differentiate the extinct subfamily Juralydinae from both the extant subfamilies using the palaeontologically more appropriate venational characters (see Diagnosis above). Furthermore, we consider that the more important taxonomic characters are the difference in the number of antennal segments, which is about 12 in Juralydinae, but 17 or more in Cephalciinae and Pamphiliinae. Compared with the venational characters, morphological differences in antennae are more reliable if the antennae are sufficiently well preserved.

The importance of the antennal morphology of *Scabolyda* gen. nov. is based on the observation that the basal pamphilioids (Xyelydidae and Praesiricidae) have the hymenopteran ground plan of antennae with a much enlarged, compound third antennal segment (Rasnitsyn 1996, 2006). In view of this, the character states observed in Juralydinae can be interpreted as intermediate between the basal grade (represented by Xyelydidae and Praesiricidae) and the derived extant taxa (Pamphiliinae and Cephalciinae), which have secondarily simplified antennae, with the third segment less different in size from the following ones (Wang *et al.* 2013). At the same time Juralydinae also has autapomorphies, such as the oligomeric antennae (with only 12 segments), and can be interpreted as the sister group of the extant subfamilies.

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