

The oldest known scoliid wasps (Insecta, Hymenoptera, Scoliidae) from the Jehol biota of western Liaoning, China



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The earliest known scoliid wasps (Insecta: Hymenoptera: Scoliidae) from the Yixian Formation (latest Jurassic or early Early Cretaceous) of Beipiao, western Liaoning Province, China are described. *Protoscolia sinensis* gen. et sp. nov., *P. normalis* sp. nov. and *P. imperialis* sp. nov. belong to Archaeoscoliinae, which were previously known from the Barremian (Early Cretaceous) to the Oligocene (late Paleogene).

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KEY WORDS: Hymenoptera; Scoliidae; taxonomy; latest Jurassic; Early Cretaceous; China.

1. Introduction

The Scoliidae, a small family of aculeate wasps, belongs to the superfamily Scolioidea (Rasnitsyn, 1988) and is subdivided into three subfamilies: Scoliinae, Proscoliinae and Archaeoscoliinae (Rasnitsyn, 1977, 1993). The Scoliinae, including about 500 extant species (Brothers, 1975; Rasnitsyn, 1993), has a poorly known history. Only a few fossil species referred to the subfamily have been discovered in the Middle Miocene succession of Shandong Province, China (Zhang, 1989) and in the Upper Miocene of Oeniggen, Germany (Heer, 1865). The Proscoliinae embraces just two genera: the extant genus *Proscolia* Rasnitsyn with two closely related species (Rasnitsyn, 1977; Day *et al.*, 1981; Osten, 1987) and the Lower Cretaceous (Aptian or Albian) genus *Cretaproscolia* Rasnitsyn & Martínez-Delclòs with a single species (Rasnitsyn & Martínez-Delclòs, 1999). The Archaeoscoliinae includes seven fossil species within three genera from the Barremian of Spain, Aptian of central Mongolia, Cenomanian of northeast Siberia, Turonian of Kazakhstan and Lower Oligocene of Colorado (Rasnitsyn, 1993; Rasnitsyn & Martínez-Delclòs, 1999, 2000; Table 1).

Recently one of us (ZH) has collected three archaeoscoliine wasps from the uppermost Jurassic or lower Lower Cretaceous 'Jianshangou Bed' in the lower part of the Yixian Formation of Huangbanjigou

Village near the town of Shangyuan, 28 km south-east of Beipiao, western Liaoning Province, China (Figure 1).

2. Stratigraphy

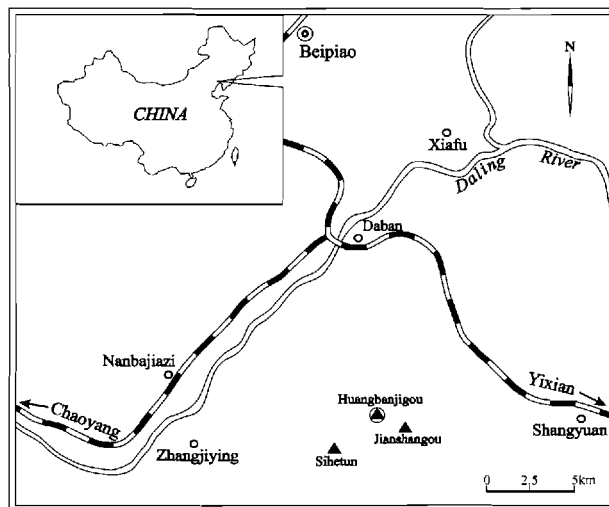
The Yixian Formation is more than 2000 m thick, and consists of layers of volcanic rocks sandwiched between sedimentary deposits (Chen *et al.*, 1980). The Jianshangou Bed, named by Chen *et al.* (1980) and well developed in the Shangyuan area of Beipiao, western Liaoning, is the lowest part of the Yixian Formation. The thickness of the bed varies from 20 to 150 m (Chen *et al.*, 1980; Wang *et al.*, 1998). It can be divided into three parts: a lower part of coarse clastic rocks, a middle part of intermediate-basic volcanic rocks and an upper part of fossil-bearing, fine-grained, clastic rocks. The upper part, which is the most important component of the bed, yields abundant fossils and can be subdivided into five subunits. In ascending order, these are: First Horizon consisting of bivalve-bearing sandstone (Bed 4); Second Horizon of (lower) fossil-bearing mudstone and shale (Bed 5); Third Horizon of siltstone and sandstone (Bed 6); Fourth Horizon of (upper) fossil-bearing mudstone and shale (Beds 7 and 8); and Fifth Horizon of turtle-bearing tuffaceous sandstone (Bed 9) (Figure 2).

Table 1. Geographical distribution of the known taxa of Archaeoscoliinae of Scoliidae.

AGE			TAXON	LOCALITY
Pg	OLIGOCENE		<i>Floriscolia relict</i> Rasnitsyn, 1993	Florissant, Colorado, USA
	EOCENE			
	PALEOCENE			
K	K ₂	Maastrichtian		
		Campanian		
		Santonian		
		Coniacian		
		Turonian	<i>Cretoscolia patiens</i> Rasnitsyn, 1993	Kzyl-Zhar Hill, Karatau, Kzyl-orda, Kazakhstan
		Cenomanian	<i>Cretoscolia promissiva</i> Rasnitsyn, 1993	Obeshchayushchiy Stream, Magadan, Siberia
	K ₁	Albian		
		Aptian	<i>Archaeoscolia senilis</i> Rasnitsyn, 1993	Bon Tsagan, Bayanhongor, Mongolia
		Barremian	<i>Archaeoscolia hispanica</i> Rasnitsyn & Martínez-Delclòs, 1999 <i>Cretoscolia conquensis</i> Rasnitsyn & Martínez-Delclòs, 2000	Las Hoyas, Serranía de Cuenca, Spain
			<i>Cretoscolia montsecana</i> Rasnitsyn & Martínez-Delclòs, 1999	La Cabrera, Montsec Range, Lleida, Spain
		Hauterivian		
		Valanginian		
Berriasian	<i>Protoscolia sinensis</i> gen. et sp. nov. <i>Protoscolia normalis</i> gen. et sp. nov. <i>Protoscolia imperialis</i> gen. et sp. nov.	Huangbanjigou Village, Beipiao, Liaoning Province, China		
J	J ₃	Tithonian		

Abbreviations: J, Jurassic; J₃, Late Jurassic; K, Cretaceous; K₁, Early Cretaceous; K₂, Late Cretaceous; Pg, Paleogene.

The Jianshangou Bed yields abundant fossils including macroplants, palynomorphs, bivalves, gastropods, conchostracans, ostracods, shrimps,

**Figure 1.** Map showing the locality yielding the insect fossils.

insects, fish, amphibians, turtles, lizards, crocodiles, pterosaurs, dinosaurs, birds and mammals (Chen *et al.*, 1998). Beipiao City has become famous for its fossil localities, such as Sihetun, Huangbanjigou, Jianshangou, yielding early birds, feathered dinosaurs and the earliest angiosperm. All have come from the Jianshangou Bed (Hou *et al.*, 1995; Ji *et al.*, 1998; Chen *et al.*, 1998; Sun *et al.*, 1998). The wasps dealt with in this paper were collected from the Fourth Horizon of the bed, in particular from Bed 7 of the Huangbanjigou composite section (Figure 2), from which many insects have been reported (Zhang, 1999; Zhang & Zhang, 2000a–c, 2001; Zhang *et al.*, 2001).

The age of the Jianshangou Bed is still debated. It is considered by various authors to be Late Jurassic, Early Cretaceous, or Late Jurassic–Early Cretaceous (e.g., Hou *et al.*, 1995; Chen *et al.*, 1998; Sun *et al.*, 1998; Ji *et al.*, 1999; Swisher, 1999; Lo *et al.*, 1999; Zhang, 1999; Jiang *et al.*, 2000). The insect assemblage from the Yixian Formation can be roughly correlated with the extensive assemblage that includes the giant mayfly *Ephemeropsis* Eichwald in Siberia and Mongolia (Zherikhin, 1978; Ponomarenko, 1990;

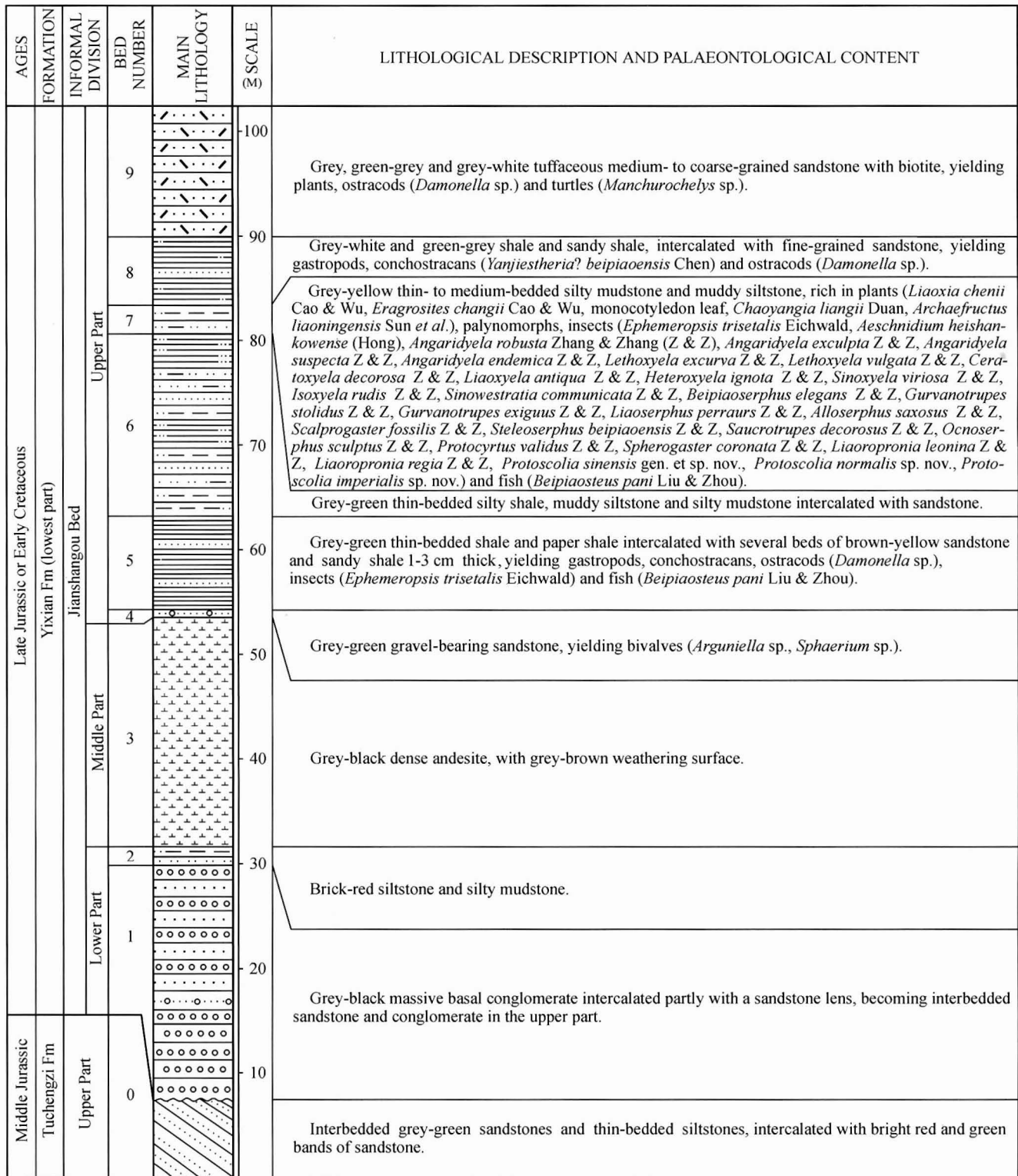


Figure 2. Composite columnar section of the Jianshangou Bed measured at Huangbanjigou Village in the Shangyuan area, Beipiao, western Liaoning, China.

Sinitshenkova, 1999). More detailed correlation is possible using the composition of the hymenopteran assemblage with a high representation of Proctotrupidae (nine of 65 hymenopteran specimens in total, or 14%) and comparatively low abundance of Angarosphecinae (Sphecidae) (five or more specimens among ten aculeate wasps other than Scoliididae, i.e., 8–15% of all hymenopterans). This is indicative of the proctotrupid (earlier) subtype of the baissine (mainly Early Cretaceous) type of hymenopteran assemblages (Rasnitsyn *et al.*, 1998). This subtype is characteristic of numerous fossil sites in Transbaikalia (Eastern Siberia) and Mongolia as well as of Purbeck (both Lulworth and Durlston formations) of southern England. The Berriasian (earliest Cretaceous) age of the insectiferous deposits of Purbeck is rarely questioned now (Rasnitsyn *et al.*, 1998). Hence the record of Archaeoscoliinae and of Scoliididae from western Liaoning in general is the oldest worldwide: the earliest previous records are from assemblages of the angarosphecine subtype of Bon-Tsagan (Aptian, Mongolia), Ceará (Aptian or Albion, Brazil) and Montsec (Barremian, Spain) (Rasnitsyn & Martínez-Delclòs, 2000).

3. Systematic palaeontology

Order: Hymenoptera Linnaeus, 1758
 Suborder: Apocrita Gerstaecker, 1867
 Superfamily: Scoliioidea Latreille, 1802
 Family: Scoliididae Latreille, 1802
 Subfamily: Archaeoscoliinae Rasnitsyn, 1993

Genus *Protoscolia* gen. nov.

Etymology. Greek adjective *protos*, primal, and the generic name *Scolia*; gender feminine.

Type species. *Protoscolia sinensis* Zhang, Rasnitsyn & Zhang, sp. nov.; uppermost Jurassic or lowest Cretaceous, Yixian Formation, Liaoning, China.

Species included. Three monotypic species described herein.

Diagnosis. Female (male unknown). Body slender, with head, thorax and metasoma basally more or less infuscated, metasomal apex pale. Head lacking tubercle or shelf associated with antennal base. Clypeus narrow, with fore margin straight or concave. Labrum large, semicircular. Mandible rather long, pointed, with irregular, low serration instead of subapical teeth. Notauli and medial lines long, percurrent, adlateral lines present. Propodeum with

delimited U-shaped area reminiscent of propodeal enclosure of Apoidea instead of two sublateral lines. Legs short, moderately stout, femora lacking tibial plates, tibiae without strong (fossorial) spines, tarsi very long. Forewing with rudiment of 1r-rs or at least with RS angular at its position; RS meeting 2r-m proximad of 2r-rs; apex of 3r rounded near fore margin of wing and much proximad of apex of 3rm; 2-3r-m both oblique and strongly bent outwards; 3rm higher than wide; 1m-cu meeting cell 2rm midway; cu-a distinctly postfurcal, cell 2cua angular posteroapically. Hindwing with cu-a postfurcal.

Comparison. Only three genera, namely *Archaeoscolia* Rasnitsyn, 1993, *Cretoscolia* Rasnitsyn, 1993 and *Floriscolia* Rasnitsyn, 1993, are known to be included in the subfamily Archaeoscoliinae (Rasnitsyn, 1993; Rasnitsyn & Martínez-Delclòs, 1999, 2000). The new genus differs from all of these in its forewing with a vestige of 1r-rs present, 2rm petiolate, 2r-rs connected to cell 3rm, cu-a postfurcal, and 2cua angular posteroapically, and in the presence of the enclosed area on the propodeal dorsum.

Remarks. A vestigial 1r-rs is known for *Protoscolia sinensis* sp. nov. and *P. normalis* sp. nov. (*P. imperialis* sp. nov. lacks 1r-rs but has the geniculate RS indicating its position). Vein 1r-rs is present in *Proscolia* Rasnitsyn (Proscoliinae) but lost in Archaeoscoliinae other than *Protoscolia*, which altogether lack the RS angulation at the former place of 1r-rs (Rasnitsyn, 1993; Rasnitsyn & Martínez-Delclòs, 1999, 2000). The presence of 1r-rs is considered primitive because this condition is present in Symphyta and some Apocrita. The same holds true for the postfurcal position of cu-a and posteroapical angulation of 2cua. Petiolate 2rm and 2r-rs connected to 3rm instead of 2rm are unique to *Protoscolia* within the Scoliididae and are known among various other scattered aculeate wasps (e.g., Sphecidae: *Alysson* spp., *Brachystegus* spp.): it is an apomorphy of *Protoscolia*. The enclosed propodeal area is another autapomorphy which is absent from other scoliid wasps as well as from lower hymenopterans. It is not known whether it is a true propodeal enclosure (enlarged metapostnotum) or just a secondarily delimited part of the propodeum. Quite unusual, and a doubtless apomorphy, is the mandible structure and narrow clypeus of *Protoscolia*. The phylogenetic status of the large, semicircular labrum is obscure. In general, these oldest known scoliid wasps show a mixture of primitive and derived traits. Of their characters, only the complete set of lines and sutures of the mesonotum and, possibly, the

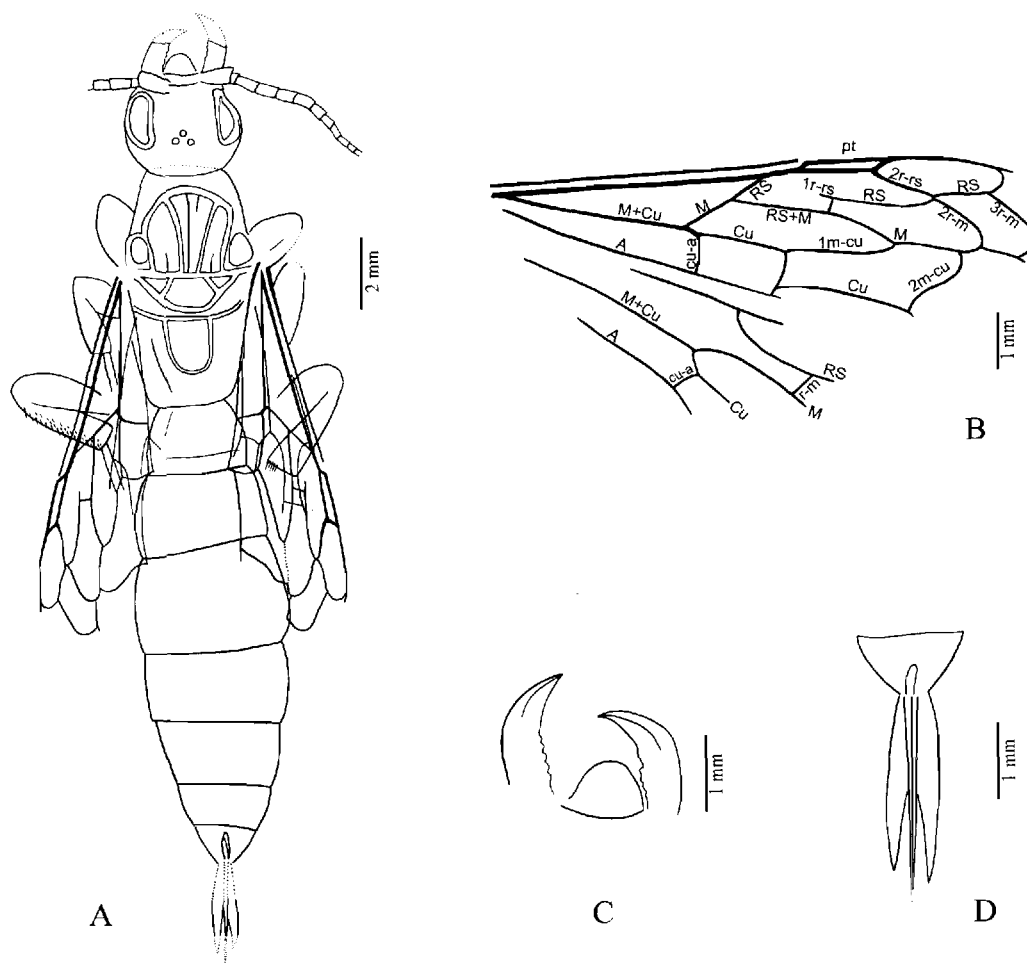


Figure 3. *Protoscolia sinensis* sp. nov. A, body, dorsal aspect, camera lucida drawing of LBSH98064b. B, forewing and hindwing, camera lucida drawing of LBSH98064b. C, mandibles and labrum, camera lucida drawing of LBSH98064a. D, sting, camera lucida drawing of LBSH98064a.

less modified coxal structure (see *P. imperialis* for details) may be currently added to the family ground-plan.

Protoscolia sinensis sp. nov.

Figures 3, 4A, B

Etymology. Latin, *sinensis*, of China.

Material. Holotype LBSH98064/NIGP133154 (female), part and counterpart, from Huangbanjigou Village, Beipiao, Liaoning Province, China; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Description. Female (male unknown). Head length 3.3 mm, mesosoma 6.6 mm, metasoma 12.5 mm; forewing length, as preserved, 10.3 mm, width

3.1 mm; hindwing length, as preserved, 6.0 mm, width 2.0 mm. Body and flagellum rather evenly infuscated except metasomal segments 5–7 pale; legs pale. Head medium-sized and suboval; eyes large, kidney-shaped, distant from head hind margin; ocelli small with hind ones separated from each other by about their width, and distant from fore ocellus by less than their width; clypeus short, with concave fore margin. Antennae short with 12 segments preserved; scape enlarged; pedicel small; first flagellomere twice as long as wide, slightly thinner than pedicel basally and about as wide as pedicel apically; second, third and fourth flagellomeres as long as first and as wide as first apically; following segments gradually decreasing in size but maintaining proportions. Mesosoma large; pronotum short medially; scutellum inversely trapezoidal; metanotum short; propodeum broad with convex U-shaped 'enclosure'. Foreleg short; midleg similar to foreleg, with slender tarsus; hindleg with

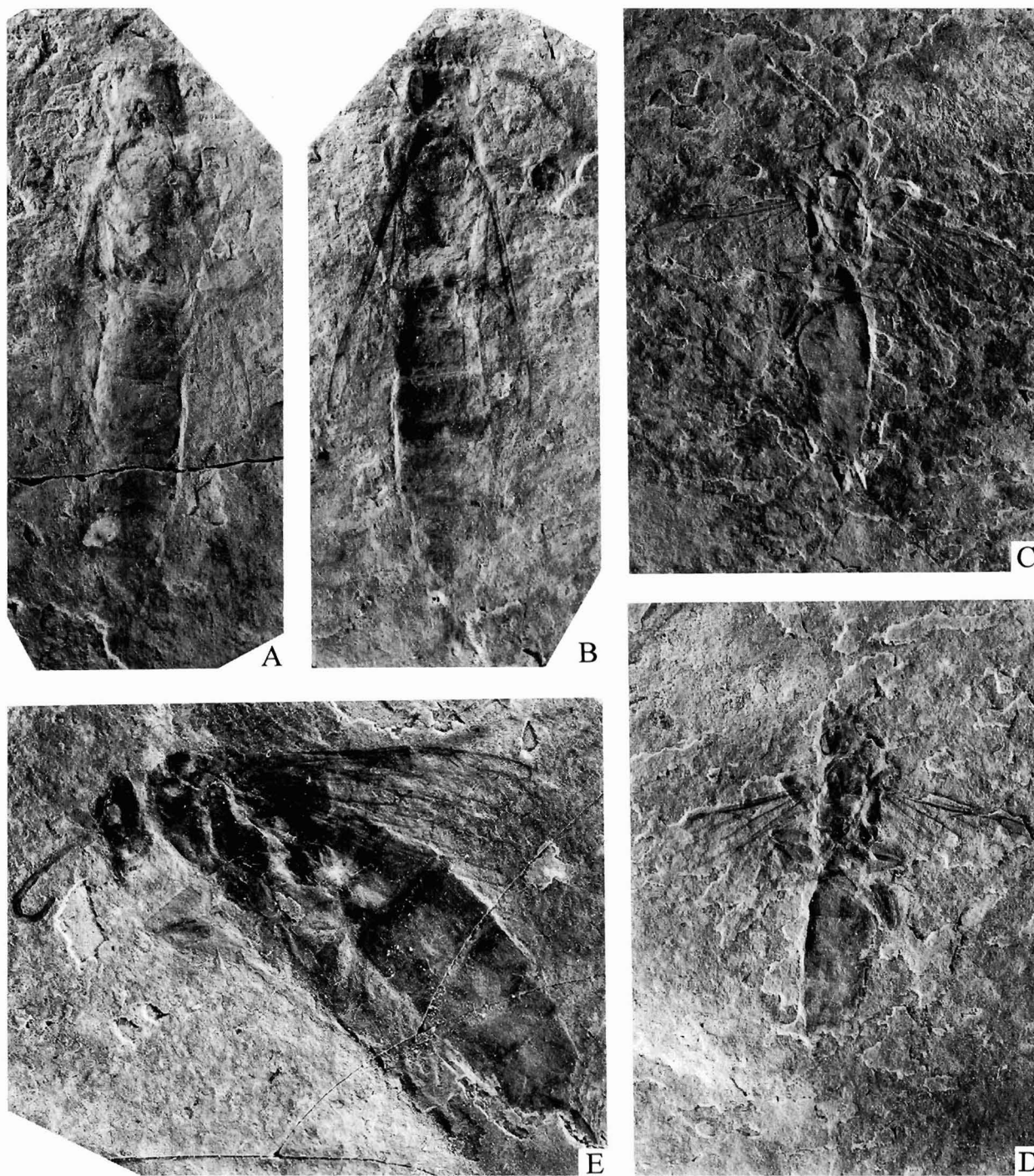


Figure 4. A, *Protoscolia sinensis* sp. nov., LBSH98064a; $\times 4$. B, *Protoscolia sinensis* sp. nov., LBSH98064b; $\times 4$. C, *Protoscolia normalis* sp. nov., LBSH98065a; $\times 3$. D, *Protoscolia normalis* sp. nov., LBSH98065b; $\times 3$. E, *Protoscolia imperialis* sp. nov., LBSH98066a; $\times 3$.

femur and tibia slightly thicker and longer; tibia with thin spines on outer surface; tarsus slender. Forewing with pterostigma narrow, widened apicad, slightly sclerotised; basal section of RS slightly shorter than that of M; vestigial 1r-rs short, parallel to RS+M; RS

angular at junction with 1r-rs; petiole between cells 3r and 2rm point-like, connected to cell 3r at its midlength; cell 3r 1.5 times as long as pterostigma, and 3.5 times as long as wide; 2m-cu joining cell 2rm well before its end; cu-a postfurcal by almost half

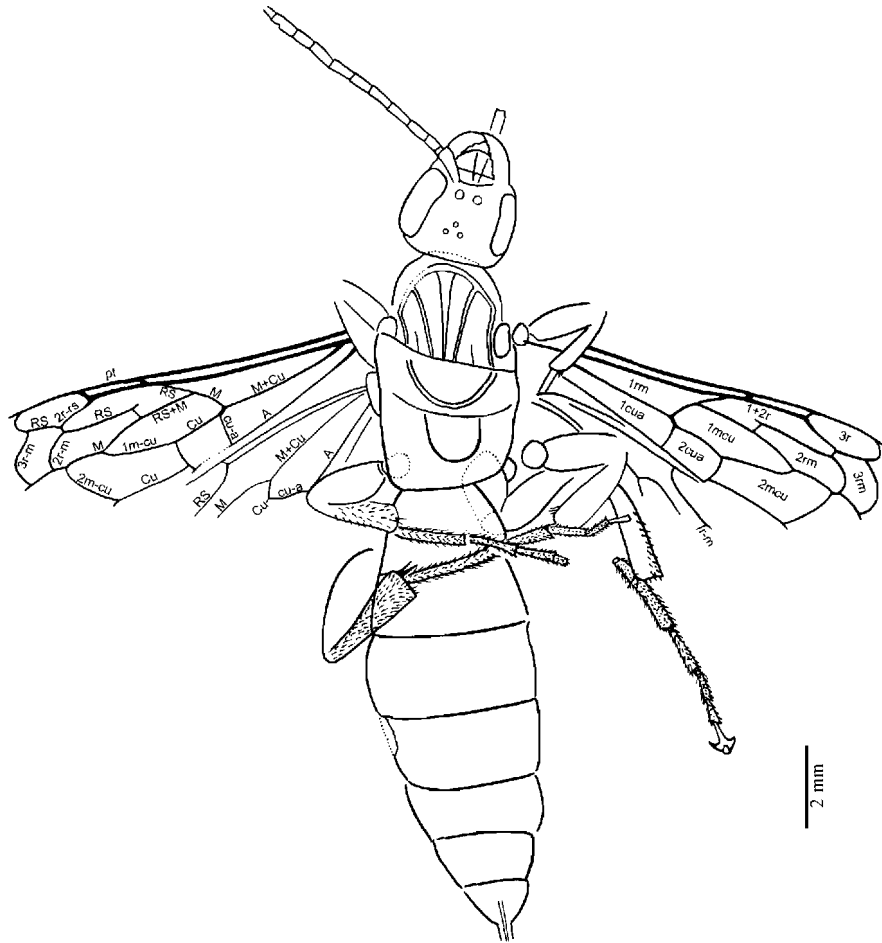


Figure 5. *Protoscolia normalis* sp. nov., dorsal aspect, camera lucida drawing of LBSH98065a.

its length, slightly shorter than basal section of M; cell 2cu-a nearly parallel-sided, with sides arcuate. Hindwing with RS short beyond r-m; r-m short and subvertical to M; cu-a postfurcal, comparatively short and subvertical to A. Metasoma long (much longer than head and thorax combined), somewhat constricted between 1st and 2nd segments. Sting as long as mesonotum and scutellum combined; sheaths apparently entire and acuminate.

Protoscolia normalis sp. nov.
Figures 4C, D, 5

Etymology. Latin, *normalis*, normal.

Material. Holotype LBSH98065/NIGP133155 (female), part and counterpart, from Huangbanjigou Village, Beipiao, Liaoning Province, China; housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Description. Female (male unknown). Head length 2.8 mm, mesosoma 5.6 mm, metasoma 10.5 mm; forewing length, as preserved, 10.3 mm, width 2.4 mm; hindwing length, as preserved, 4.5 mm, width 1.7 mm. Body yellowish-brown with antennae, legs and wings slightly damaged; antenna light, head and thoracic infuscation patchy, metasomal terga 1–4 with darker lateral spots. Head medium-sized, wider than long, widened basad; eyes large, kidney-shaped, nearly reaching hind margin of head; ocelli, clypeus and labrum similar to those in *P. sinensis* except that fore margin of clypeus is straight, mandibles slightly smaller. Antennae thin; scape enlarged; pedicel small; first flagellomere slightly longer than wide; second to ninth flagellomeres as thick as first and twice as long as wide, with third to seventh slightly widened apicad; tenth distinctly thinner. Mesosoma suboval; pronotum short, arcuate; scutellum semi-circular; metanotum short; U-shaped propodeal ‘enclosure’ no longer than wide. Foreleg with trochanter small, oval; femur short; tibia and tarsus thin. Midleg obviously

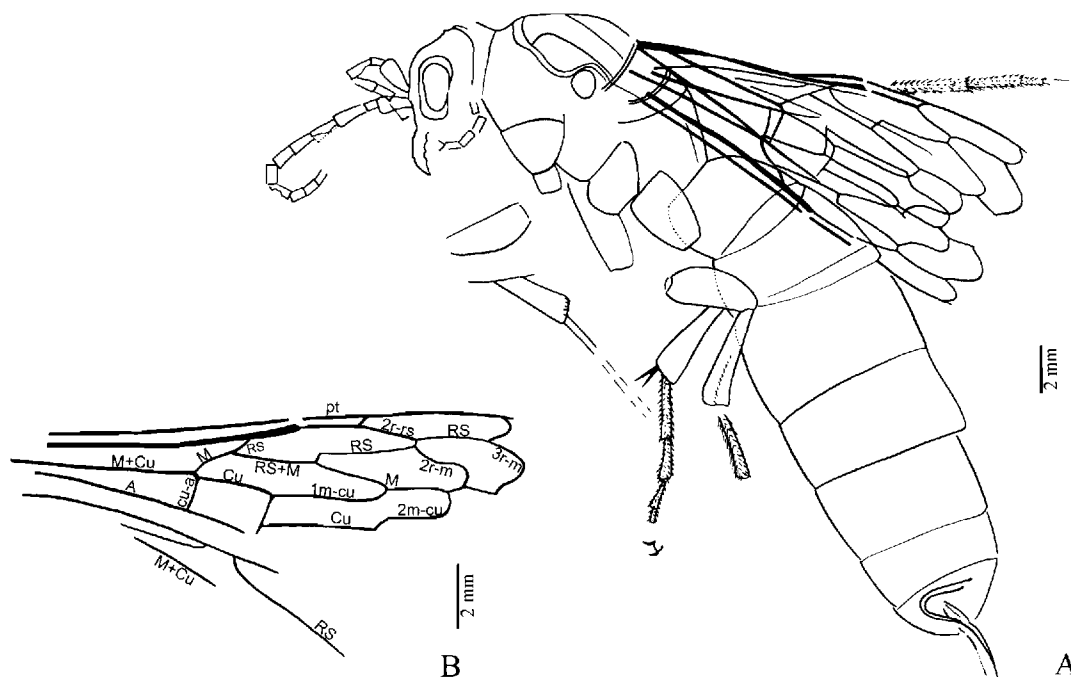


Figure 6. *Protoscolia imperialis* sp. nov. A, body, lateral aspect, camera lucida drawing of LBSH98066a. B, forewing and hindwing, camera lucida drawing of LBSH98066a.

thicker than foreleg with trochanter rounded and narrow; femur thick and short; tibia slightly longer than femur, setose on outer surface; tarsus slender and elongate, setose, with basitarsus only slightly shorter than tibia. Hindleg slightly thicker and longer than midleg; tibia densely setose, with two short, subequal apical spurs; tarsus about twice as long as tibia, densely setose, with all segments elongate, basitarsus slightly shorter than tibia; claws simple. Forewing with pterostigma narrow, slightly sclerotised, widened apicad; basal section of RS slightly shorter than that of M; vestigial 1r-rs present at angulation of RS, short and parallel to RS+M; petiole between cells 3r and 2rm distinct, meeting cell 3r at its midlength; cell 3r broad and short, 2.5 times as long as wide; 2m-cu joining cell 2rm close to its end; cu-a moderately postfurcal, as long as basal section of M; cell 2cua nearly rectangular. Hindwing with RS short beyond r-m; r-m short; cu-a postfurcal, long, sinuate. Metasoma longer than head and thorax combined, lacking evident intersegmental constrictions.

Comparison. Similar to *P. sinensis* except head tapering forward and with eyes longer, antenna longer, not tapering apicad before apical segment, and with first flagellomere short, propodeal 'enclosure' wider, forewing cell 2rm with distinct petiole and 2m-cu meeting M close to 2r-m, hindwing with cu-a longer

and more oblique, and metasoma apparently lacking intersegmental constrictions.

Protoscolia imperialis sp. nov.

Figures 4E, 6

Etymology. Latin, *imperialis*, imperial.

Material. Holotype LBSH98066/NIGP133156 (female), part and counterpart, from Huangbanjigou Village, Beipiao, Liaoning Province, China; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Description. Female (male unknown). Head length 2.5 mm, mesosoma 9.3 mm, metasoma 20.4 mm; forewing length, as preserved, 15.8 mm, width 4.2 mm; hindwing length, as preserved, 10.5 mm. Distal half of antenna, head, thorax and bases and, to a lesser extent, apices of metasomal segments infuscated (much less so toward metasomal apex), legs pale. Head small; eyes large, kidney-shaped, distant from head hind margin; temple wide; mandibles possibly typical of genus (not properly seen). Antennae thin and not long, with 11 segments preserved; scape enlarged; pedicel small; first flagellomere 2.5 times as long as wide, basally as wide

as pedicel, apically wider; following flagellomeres decreasing in size gradually, second to sixth similar to first in form, those following subcylindrical. Pronotum short with short collar. All coxae very large [possibly they (particularly the mid pair) are not perfectly level with the thoracic venter, as is characteristic of Scoliinae and Proscoliinae; however, the data so far seem inconclusive in this respect]. Foreleg with trochanter small, quadrate; femur short; tibia and tarsus thin. Midleg with tarsus slender, densely setose. Hindleg with femur short, comparatively thick; tibia thin, slightly longer than femur, with a row of short setae on outer surface and two moderately short, subequal apical spurs; tarsus slender, densely setose, about twice as long as tibia; claws short, simple. Forewing with basal section of RS slightly shorter than that of M; 1r-rs lost but RS geniculation present in its place; pterostigma hardly sclerotised, nearly linear; cell 2rm with distinct petiole meeting cell 3r before its midlength; 3r narrow, five times as long as wide; 2m-cu joining cell 2rm distant from its end; cu-a slightly postfurcal, as long as basal section of M; cell 2cu-a nearly rectangular. Hindwing incomplete with RS long. Metasoma almost twice as long as head and thorax combined (possibly because of postmortem distension), with at least ventral constriction between first two segments. Sting short (as long as mesonotum before scutellum), slightly bent downwards; sheaths not complete, looking entire.

Comparison. Differs from the above two species in its larger size, enlarged scape, basal half of flagellum serrate below, long 3r cell, and lost 1r-rs vestige.

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