

Palpimanoid spiders from the Jurassic of China

Paul A. Selden¹: The Paleontological Institute, University of Kansas, Lindley Hall, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA; and Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

Huang Diying¹: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, 210008, P. R. China

Ren Dong: College of Life Science, Capital Normal University, Beijing 100037, P. R. China

Abstract. Only two specimens of spiders have been described from Jurassic strata, so the recovery of some 400 new specimens from rocks of middle Jurassic age from China signals a dramatic increase in information on fossil spiders of this period. Here, new spiders belonging to the superfamily Palpimanoidea *sensu* Forster & Platnick 1984, from the locality of Daohugou, Inner Mongolia, are described. *Pataarchaea muralis* n. gen., n. sp. is a true archaeid, represented by both an adult male and female. *Sinaranea metaxyostraca* n. gen., n. sp., represented by an adult male and juveniles, is a palpimanoid similar to Palpimanidae and Huttoniidae, but is not placed in a modern family.

Keywords: Archaeidae, Palpimanoidea, Middle Jurassic, Daohugou, China

Only two specimens of spiders have been described from rocks of Jurassic age (ca 145–200 mya): *Jurarchaea zherikhini* Eskov 1987 from Kazakhstan, which has been described as an archaeid, pararchaeid, or holarchaeid (Eskov 1987), and the araneoid *Juraneus rasnitsyni* Eskov 1984 from Transbaikalia. A third, from the Jurassic of Grimmen, Germany, has been figured but not yet formally described (Ansorge 2003; preliminary investigation by the senior author suggests this may be a palpimanoid). Recently, more than 400 new specimens have become available for study from beds of Middle Jurassic age at Daohugou, Nincheng County, Inner Mongolia, China (Huang et al. 2006). Most belong to Uloboridae and will be the subject of another publication; the specimens described here belong in the superfamily Palpimanoidea *sensu* Forster & Platnick 1984, due to the presence of peg-teeth on the promargin of the chelicera.

The family Archaeidae Koch & Berendt 1854 is unique in that it was first described from fossils in Baltic amber (Koch & Berendt 1854), and some 25 years later living representatives were discovered in Madagascar (Pickard-Cambridge 1881). In the following century, living species have been described from other parts of Gondwana, and fossils described from strata of Mesozoic age: Cretaceous (Penney 2003) and Jurassic (Eskov 1987). The original family Archaeidae was divided into four families by Forster & Platnick (1984): Mecysmaucheniidae Simon 1895, Holarchaeidae Forster & Platnick 1984, and Pararchaeidae Forster & Platnick 1984, in addition to the type family. Archaeidae consists of small to medium-sized haplogyne ecribellate araneomorphs that are distinguished from other spiders by the character combination of peg-teeth on the promargin of the chelicera and an abdomen–petiole stridulatory system (Forster & Platnick 1984). Other features of the family, shared by some related families, are: stridulatory ridges on the lateral side of the chelicera, a raised cephalic region of the carapace, and chelicerae arising from a foramen in the clypeus, which is fully sclerotized ventrally in adults (Forster &

Platnick 1984). These authors expanded the concept of the superfamily Palpimanoidea from its original size (formerly only Palpimanidae Thorell 1870, Stenochilidae Thorell 1873, and Huttoniidae Simon 1893) by the addition of three families, Mimetidae Simon 1881, Tetricellidae Hickman 1945, and Micropholcommatidae Hickman 1944, previously placed in the Araneoidea Latreille 1806, as well as the four families in the original Archaeidae. Later, Platnick & Forster (1986) placed Tetricellidae as junior synonym of Micropholcommatidae, and Platnick & Forster (1987) added Malkaridae Wunderlich 1986 to the Palpimanoidea. Two cheliceral characters were proposed as synapomorphies for the enlarged superfamily Palpimanoidea by Forster and Platnick (1984): the presence of peg teeth (modified setae) on the promargin of the cheliceral furrow, and the presence of an elevated cheliceral gland mound. The occurrence of peg teeth in other, unrelated, Araneomorphae were regarded as convergent features. In addition to these extant families, the fossil families Lagonomegopidae Eskov & Wunderlich 1995 and Spatiatoridae Petrunkevitch 1942 were included in Palpimanoidea by Eskov & Wunderlich (1995) and Wunderlich (1986), respectively.

Since the controversial expansion of the Palpimanoidea by Forster & Platnick (1984), several authors have studied the relationships of families within the superfamily. Schütt (2000, 2003) showed that the micropholcommatids and tetricellids have spigots more similar to symphytognathids and that Mimetidae, Pararchaeidae, and Malkaridae should be removed from Palpimanoidea and placed in Araneoidea. The study of entelegyne spider phylogeny by Griswold et al. (2005) indicated that the extended Palpimanoidea was likely paraphyletic, with numerous families more probably belonging in Araneoidea. Most likely, the haplogyne palpimanoid families Archaeidae, Huttoniidae, Palpimanidae, and Stenochilidae really do belong in that superfamily, while the entelegyne palpimanoids, Holarchaeidae, Pararchaeidae, and Mimetidae are araneoids. Wunderlich (2004) recognized a number of palpimanoid families within his newly defined and expanded Eresoidea. The fossils described here do not provide evidence for any of these hypotheses, but they can be accommodated

¹ Corresponding authors. E-mail: paulselden@mac.com; huangdiying@sina.com

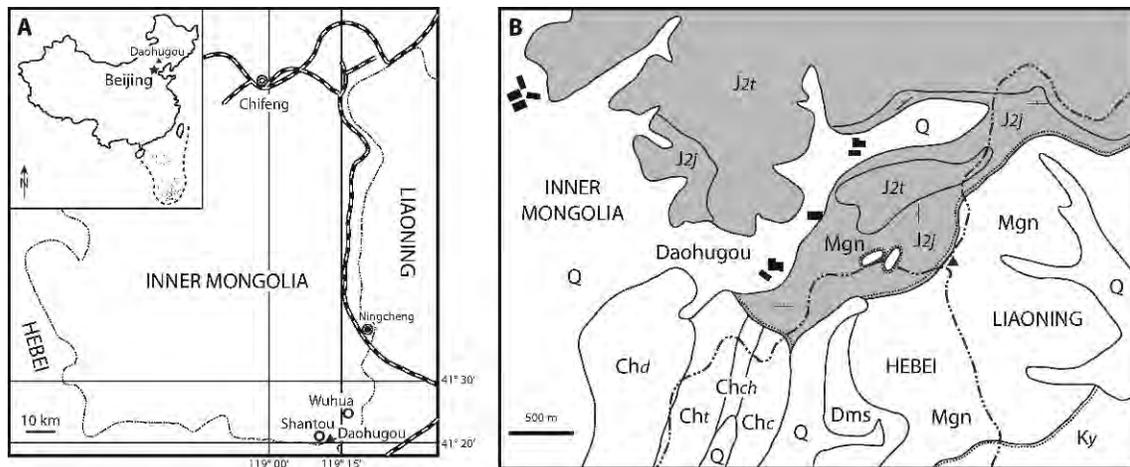


Figure 1.—Location and geological maps of the Daohugou locality. A. Location map of Daohugou village in Inner Mongolia and (inset) within China. B. Simplified geological map of the Daohugou area at the junction of three provinces. Dashed lines = province boundaries; solid lines = geological boundaries (solid + dotted line = unconformity between Precambrian and Mesozoic strata); shaded area = Jurassic (with strike/dip symbols). Precambrian formations: Mgn = Maanshan gneiss, Dms = Dalaiyingtu metamorphic series, Chc = Changchougou Fm., Chch = Chuanlinggou Fm., Chd = Dahongyu Fm., Cht = Tuanshanzi Fm.; Mesozoic Formations: J2j = Jiulongshan Fm., J2t = Tiaojishan Fm., Ky = Yixian Fm., Q = Quaternary. After Ren et al. (2002) and Gao & Ren (2006).

within the Palpimanoidea *sensu stricto*. *Patarchaea muralis* n. gen., n. sp., belongs in Archaeidae, and *Sinaranea metaxyostraca* is a palpimanoid with similarities to Palpimanidae and Huttoniidae.

Among the palpimanoid families (s.l.), Malkaridae and Stenochilidae have no fossil record. *Jurarchaea*, from the Jurassic of Kazakhstan, has been described as a possible holarchaeid or pararchaeid (see Penney 2003); these families would otherwise have no fossil record. Mimetidae is known from Baltic and Ukraine amber (Wunderlich 2004), and the strictly fossil family Spatiatoridae occurs in Baltic amber (Petrunkevitch 1942; Wunderlich 2006). Another wholly fossil family, Lagonomegopidae, is known from Cretaceous ambers from Siberia (Eskov & Wunderlich 1995), Canada (Penney 2004), New Jersey (USA) and Myanmar (Penney 2005), and Spain (Penney 2006). A huttoniid has been described from Cretaceous Canadian amber (Penney & Selden 2006). Palpimanidae has been described from the Oligocene of Aix-en-Provence, France (Gourret 1888) and Miocene Dominican amber (Wunderlich 1988). Micropholcommatidae has recently been described from Eocene amber of France (Penney et al. 2007), and the first fossil mecysmaucheniid has been described from Cretaceous amber of France (Saupe & Selden in press). Penney (2003) listed *Baltarchaea conica* (Koch & Berendt 1854), from Eocene Baltic amber, as a mecysmaucheniid following a suggestion by Eskov (1987); however, the specimen has been lost, so its identity cannot be checked. First described from Eocene Baltic amber (Koch & Berendt 1854), archaeids have a fossil record that extends from the Recent back to the Jurassic (Eskov 1987; this paper). Within this range, archaeids are known from sub-Recent Madagascan copal (Lourenço 2000), many in Cenozoic Baltic amber (Wunderlich 2004) and Cretaceous Burmese amber (Penney 2003), but not Dominican amber – the specimen reported as Archaeidae by Wunderlich (1999), supposedly a fossil in Dominican amber, is actually a subfossil preserved in Madagascan copal (Wunderlich 2004; Penney & Langan 2006)

METHODS

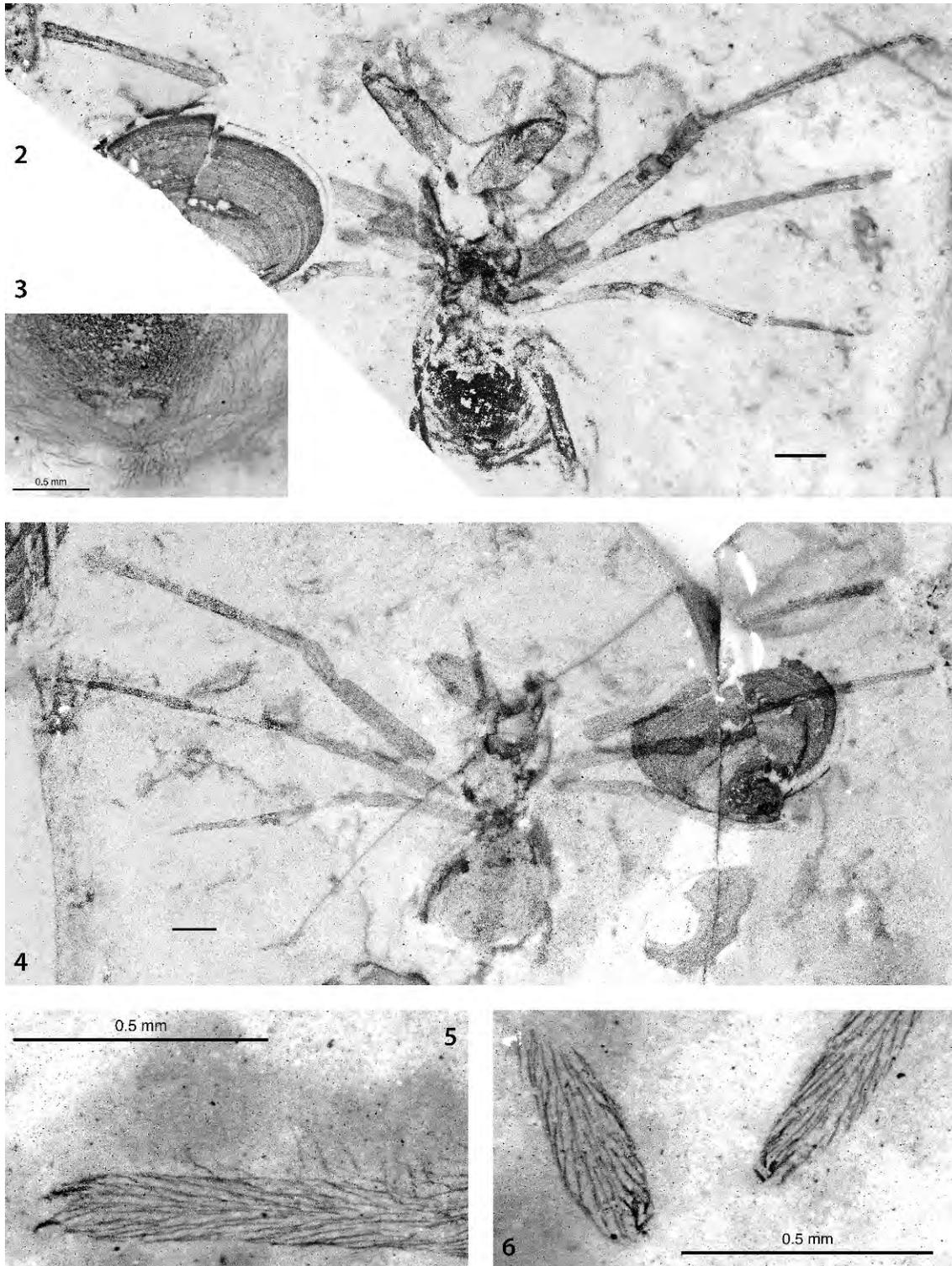
Material.—The spiders are preserved in a finely laminated, pale gray siltstone which represents a lacustrine deposit. On many bedding planes, the matrix is characteristically crammed with conchostracans and insects. The spiders are preserved as brown material compressed within the siltstone. Locality details are shown in Figure 1, and can be found in Ren et al. (2002). Recent evidence, which places the strata in the Jiulongshan Formation, and discussion of its age, is given in Chen et al. (2004) and Gao & Ren (2006). Eight specimens are described here, seven of which (prefixed NIGP) are held in the collections of the Nanjing Institute of Geology and Palaeontology, the other (prefixed SIM) is in the collections of the College of Life Science, Capital Normal University, Beijing. PAS is responsible for the arachnological studies; the other authors discovered the specimens and provided study facilities for PAS in China.

Methods.—The preparation of most of the spiders (NIGP specimens) was carried out by Huang Diying using a small chisel and a sharp knife. An aroonneedle (Selden 2003) was used to prepare specimen SIM2005003. Photomicrographs were made using a Nikon D1X digital camera on Leica MZ microscopes and manipulated in Adobe Photoshop. Drawings were prepared using a drawing tube on the microscope and also by tracing from photographs with Adobe Illustrator. All measurements are in mm, and were made using Carnoy 2.1 (Schols et al. 2002) for *Patarchaea*, and measuring tools in Photoshop CS3 Extended for *Sinaranea*.

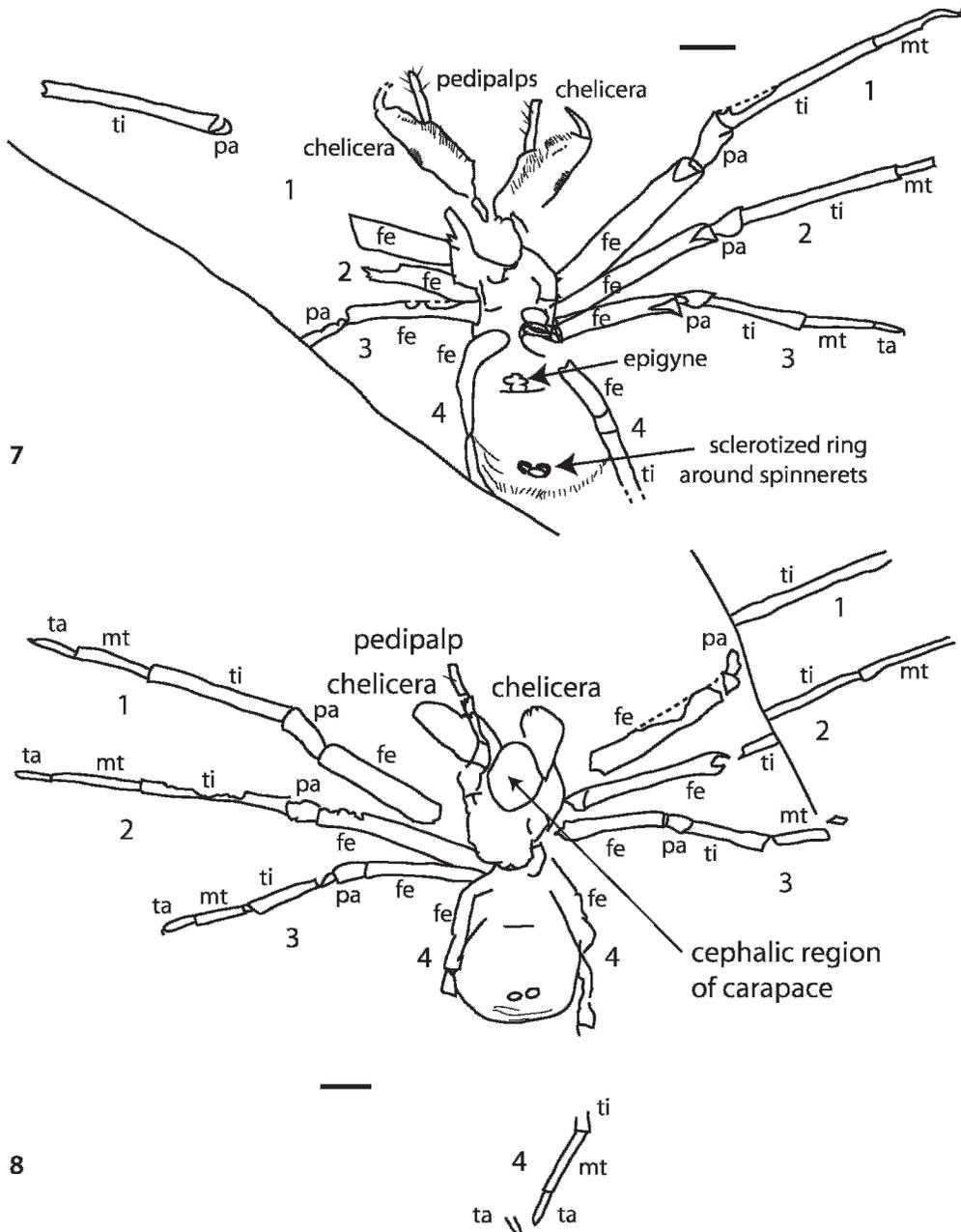
Abbreviations used in the Figures.—1, 2, 3, 4 = leg numbers, conch = conchostracan, cx = coxa, e & c = embolus and conductor, fe = femur, mt = metatarsus, pa = patella, st = sternum, strid. file = stridulatory file, ta = tarsus, te = tegulum, ti = tibia.

INTERPRETATION OF THE FOSSILS

The cephalic region of the carapace of the holotype of *Patarchaea* was presumed to have been raised in life because the fossils show a ring of cuticle infilled with a white mineral; thus the head region is preserved inside the rock matrix. The



Figures 2–6.—*Patarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part) and NIGP148828b (counterpart), Jurassic of China. 2. Part, whole; 3. Spinnerets of part; 4. Counterpart whole (except leg 4 tarsi); 5. Counterpart left tarsus 1; 6. Counterpart left and right tarsi 4. Scale = 1.0 mm unless stated otherwise.



Figures 7, 8.—*Pataarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part) and NIGP148828b (counterpart), Jurassic of China. 7. Camera lucida drawing of part, explanatory drawing for Figure 2; 8. Camera lucida drawing of counterpart, explanatory drawing for Figure 4. Scale = 1.0 mm.

fossil has suffered some compression so that the chelicerae are divergent on the bedding plane. In all of the fossils, there is evidence, in the form of crumpling and skewing, that the head region was raised, but without an elongated neck.

An interesting feature in NIGP148238 is the presence of two patches of small, circular objects which have been identified here as conchostracan ova (Shen & Huang 2008).

TAXONOMY

Superfamily Palpimanoidea *sensu* Forster & Platnick 1984

Family Archaeidae Koch & Berendt 1854

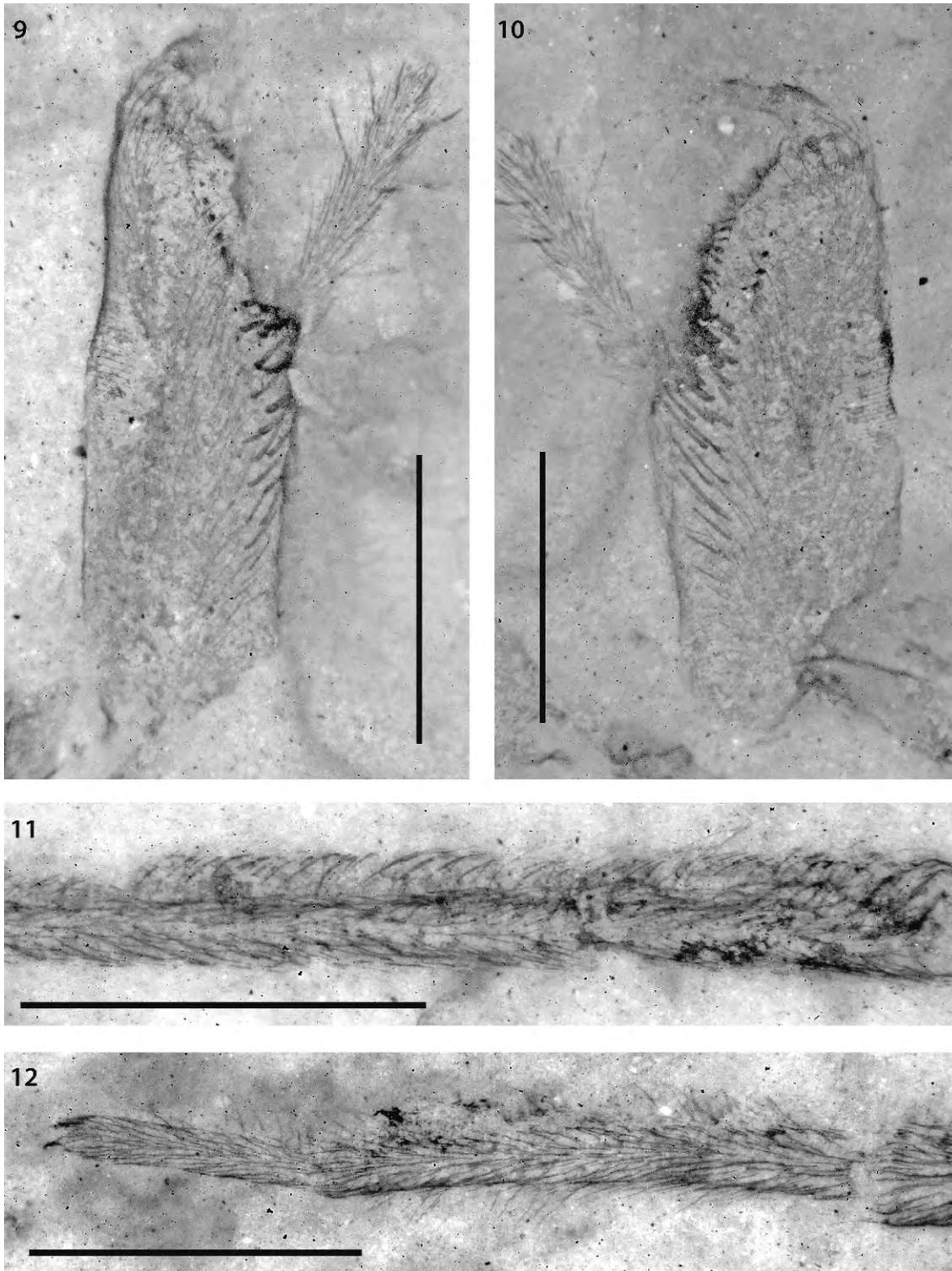
Pataarchaea new genus

Type species.—*Pataarchaea muralis* new species

Diagnosis.—Archaeid with pair of sclerotized lunules round anterior side of spinnerets, rather than completely encircling spinnerets; male pedipalp with large, thick spine arising from cymbium.

Etymology.—Greek *patos*, a beaten path, and *Archaea*, the type genus of Archaeidae.

Remarks.—*Pataarchaea* can be referred to the family Archaeidae on account of the long, slender legs lacking macrosetae; leg 1 being especially longer and stouter than the others, with a conspicuously long patella and spatulate setae on the tibia and metatarsus; three tarsal claws; long, slender



Figures 9–12.—*Patarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part) and NIGP148828b (counterpart), Jurassic of China. 9. Left chelicera of part; 10. Right chelicera of part; 11. Right tibia 1 of part, showing curved, spatulate setae; 12. Left metatarsus and tarsus 1 of counterpart (i.e., same leg as in Figure 11). Scale = 1.0 mm.

chelicerae with peg-teeth on the promargin extending back down much of the length of the paturon, true teeth on the retromargin, short, curved fang, cheliceral gland mound near the fang tip, stridulatory ridges; and sclerotized semicircles in

front of the spinnerets. Closely related families differ in the following ways. In Pararchaeidae leg 1 is not markedly slender and lacks scopulae, the first leg patella is not conspicuously long; the chelicerae have peg-teeth on the promargin but the

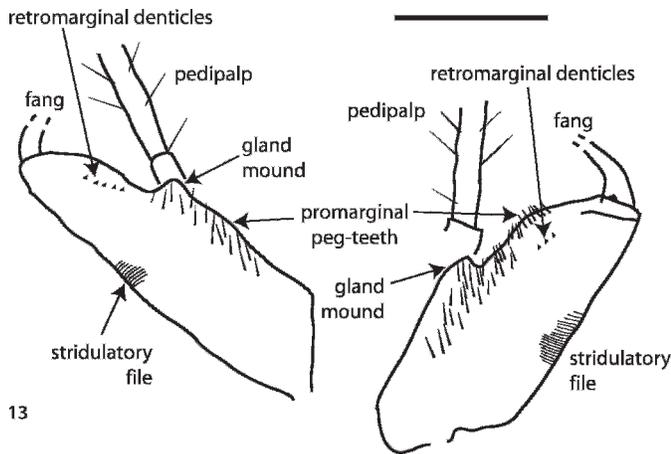


Figure 13.—*Patarchaea muralis* new genus and species. Holotype adult female, NIGP148828a (part), Jurassic of China, camera lucida drawing of chelicerae, explanatory drawing for Figures 9–10.

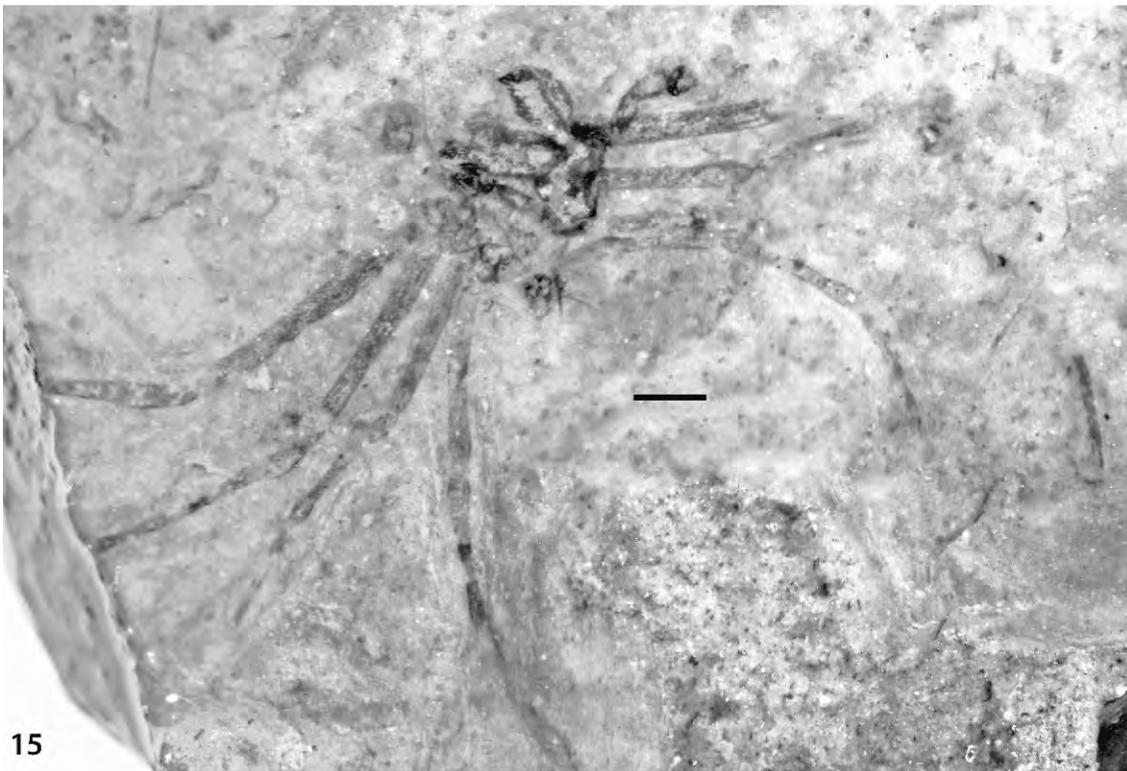
retromargin lacks teeth or denticles; there is a pronounced keel down the ventral side of the paturon beyond the fang tip; and there is no sclerotized ring around the spinnerets. Holarchaeids are minute; leg 1 lacks scopulae and the tarsi of legs 1 and 2 are swollen and have a patch of modified setae; patella 1 is not conspicuously long; the chelicerae lack peg-teeth though there are a few slender teeth on the promargin; there are no stridulatory ridges on the chelicerae nor a sclerotized ring around the spinnerets. The first legs in Mecysmaucheniidae lack scopulae and the patella is not especially elongate; the peg-teeth on the cheliceral promargin do not extend down the paturon and there are no teeth on the retromargin; there is no sclerotized ring around the spinnerets in modern forms.

There are three described extant genera of Archaeidae: *Afrarchaea* Forster & Platnick 1984, *Austrarchaea* Forster & Platnick 1984, and *Eriauchenius* O. Pickard-Cambridge 1881 (Lotz 2006). Wunderlich (2004) listed six fossil genera, all from Baltic amber. The Jurassic *Jurarchaea* Eskov 1987, from the Jurassic of Kazakhstan, which Wunderlich (2004) considered to be too poorly preserved to be identified as an archaeid, most likely belongs close to Pararchaeidae and Holarchaeidae, where it was placed by Eskov (1987) (Penney 2003). Eskov (1992) described *Mimetarchaea gintaras* from Baltic amber from a specimen that supposedly possesses key apomorphies of the families Archaeidae *sensu lato* (modified chelicerae and carapace) and Mimetidae (metatarsal macrosetal brush), and he placed *Mimetarchaea* close to Pararchaeidae or Holarchaeidae. Eskov (1990) had suggested that Mimetidae and Archaeidae form a sister pair within the Palpimanoidea, and thus more closely related than was suggested by Forster & Platnick (1984). However, Wunderlich (2004) concluded that the holotype of *Mimetarchaea gintaras* was a subadult male, not an adult, and that the embolus described by Eskov (1992) was the margin of the palpal tarsus. Wunderlich placed the specimen in Mimetidae, even considering it to belong to the extant genus *Mimetus* and stated that Eskov's speculations regarding the relationships between Archaeidae and Mimetidae were invalid. In any case, *Patarchaea* does not possess the characteristic mimetid-like spines on the metatarsi of legs 1 and 2. Eskov (1992) erected the genus *Baltarchaea* Eskov 1992

for the Baltic amber *Archaea conica* Koch & Berendt 1854; the type specimen of which is lost, but Wunderlich (2004, photos 66, 67) figured specimens which he considered belong in this genus. *Baltarchaea* is characterized by a squat carapace with a pair of posterior cephalic projections and short legs and chelicerae, and was placed in Mecysmaucheniidae by Eskov (1992). *Archaea* differs from *Patarchaea* by its stridulating file being in the proximal half of the chelicera (Wunderlich 2004) and the more elongated head region. The genus *Eoarchaea* Forster & Platnick 1984 was erected for the very small species *Archaea hyperoptica* Menge, in Koch and Berendt 1854 from Baltic amber which lacks the elongated head region of other archaeids. Forster & Platnick (1984) suggested that the genus was known only from juveniles, and Eskov (1992) synonymized *Eoarchaea* with *Archaea* on this basis. However, Wunderlich (2004) considered the genus to be valid and the specimens (more of which are now available in both Baltic and Bitterfeld amber) to be small females due to their general proportions and the fact that many specimens of the same size have been found; no genital organs, nor males, have been found. Regardless of whether the genus is a valid one, it differs from *Patarchaea* by the very short carapace; in *Patarchaea*, while the head region is unlikely to be strongly elongated, the total carapace length is about twice that of the head region. *Myrmecarchaea* Wunderlich 2004 was erected for a group of archaeids with an extremely elongated petiolus and, thus, a general resemblance to ants. *Saxonarchaea* Wunderlich 2004 differs from *Patarchaea* by its more greatly elongated anterior legs and chelicerae and small cymbium in the male.

Eriauchenius was the first living archaeid to be described (Pickard-Cambridge 1881), albeit as a theridiid. The genus was placed in synonymy with *Archaea* Koch & Berendt 1854 by Forster & Platnick (1984), but removed from this synonymy by Wunderlich (2004) on the basis of the position of the stridulating file on the chelicera: it is in the distal half in *Eriauchenius* (and *Austrarchaea*), the proximal half in *Archaea*. Eskov (1992) synonymized *Archaea* and *Afrarchaea* but this synonymy was not accepted by later workers (Penney 2003; Lotz 2006). Wunderlich synonymized *Afrarchaea* and *Eriauchenius*, on the basis of similarity in the male palps, a decision not followed by Lotz (2006). *Afrarchaea* has a much lower head region without a constricted neck, in comparison with *Archaea* and *Eriauchenius* (Lotz 2006).

Of all archaeid genera, *Patarchaea* most resembles *Afrarchaea* on the following characters. The head region is not greatly elongated, the position of the stridulating file is in the distal half of the chelicera, the presumed large cheliceral gland mound resembles the triangular process on the male chelicera of the type species *Afrarchaea godfreyi* (Hewitt 1919) (Lotz 1996, fig. 6). *Patarchaea* differs from *Afrarchaea* in its longer carapace, as well as in the diagnostic features listed above. Although not mentioned by the authors in the text, a distinct bend in the fourth femur can also be seen in *Afrarchaea* and *Eriauchenius*: *Afrarchaea royalensis* Lotz 2006 (Lotz 2006, fig. 8), *A. woodae* Lotz 2006 (Lotz 2006, fig. 11), *A. grimaldii* Penney 2003 (Penney 2003, fig. 1), *Eriauchenius cornutus* (Lotz 2003) (Lotz 2006, fig. 1), *E. gracilicollis* Millot 1948 (Wunderlich 2004, fig. 44; pls. 81, 82). In a recent paper on the *Eriauchenius gracilicollis* group from Madagascar the distinctly curved fourth femur is listed in the genus description and



Figures 14, 15.—*Patarchaea muralis* new genus and species. Allotype adult male, SIM2005003-1 (part) and SIM2005003-2 (counterpart), Jurassic of China. 14. Counterpart, whole; 15. Part, whole. Scale = 1.0 mm.

illustrated (Wood 2008: fig. 7D). In correspondence, Wood (February 2008) provided the information that the curved fourth femur is pronounced in archaeids and also occurs, to a lesser extent, in mecysmaucheniids. Its function may be to aid in closely adressing the leg against the rotund abdomen when at rest.

Patarchaea muralis new species

Figs. 2–24

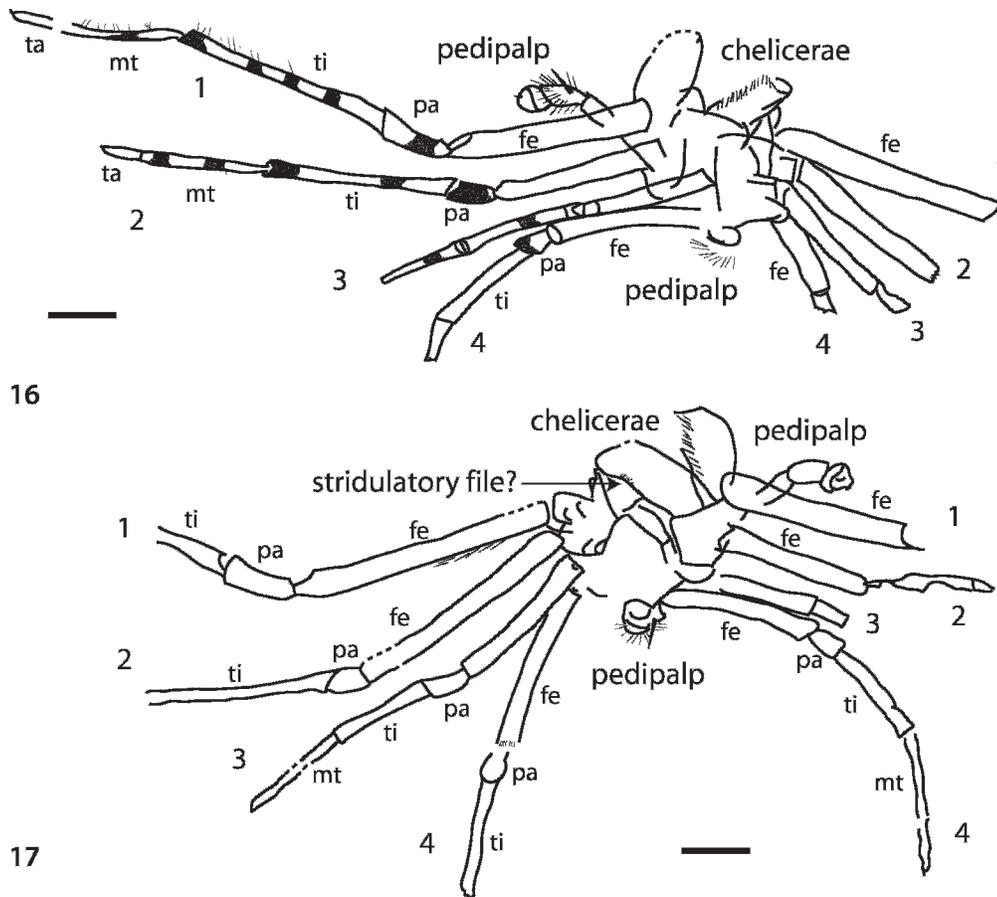
Material examined.—Holotype: NIGP148828a, b (part and counterpart), adult female, from laminated siltstones of the Middle Jurassic Jiulongshan Formation, Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China

(41°19.532'N, 119°14.589'E). Allotype: SIM2005003-1 and SIM2005003-2 (part and counterpart), adult male, from the same locality. Additional specimen NIGP148829, adult female, from the same locality.

Diagnosis.—As for the genus.

Etymology.—Latin *murus*, a wall; in combination with the prefix to the genus name, in memory of a wonderful day in great company walking along the Great Wall of China.

Description of holotype, NIGP148828a,b (Figs. 2–13).—Adult female. Carapace with raised cephalic area; eyes not seen. Carapace length 2.51, width 1.98; head region length 1.37, width 1.07. At least two thorns on carapace lateral margin. Chelicera long (paturon length 2.33) with prominent



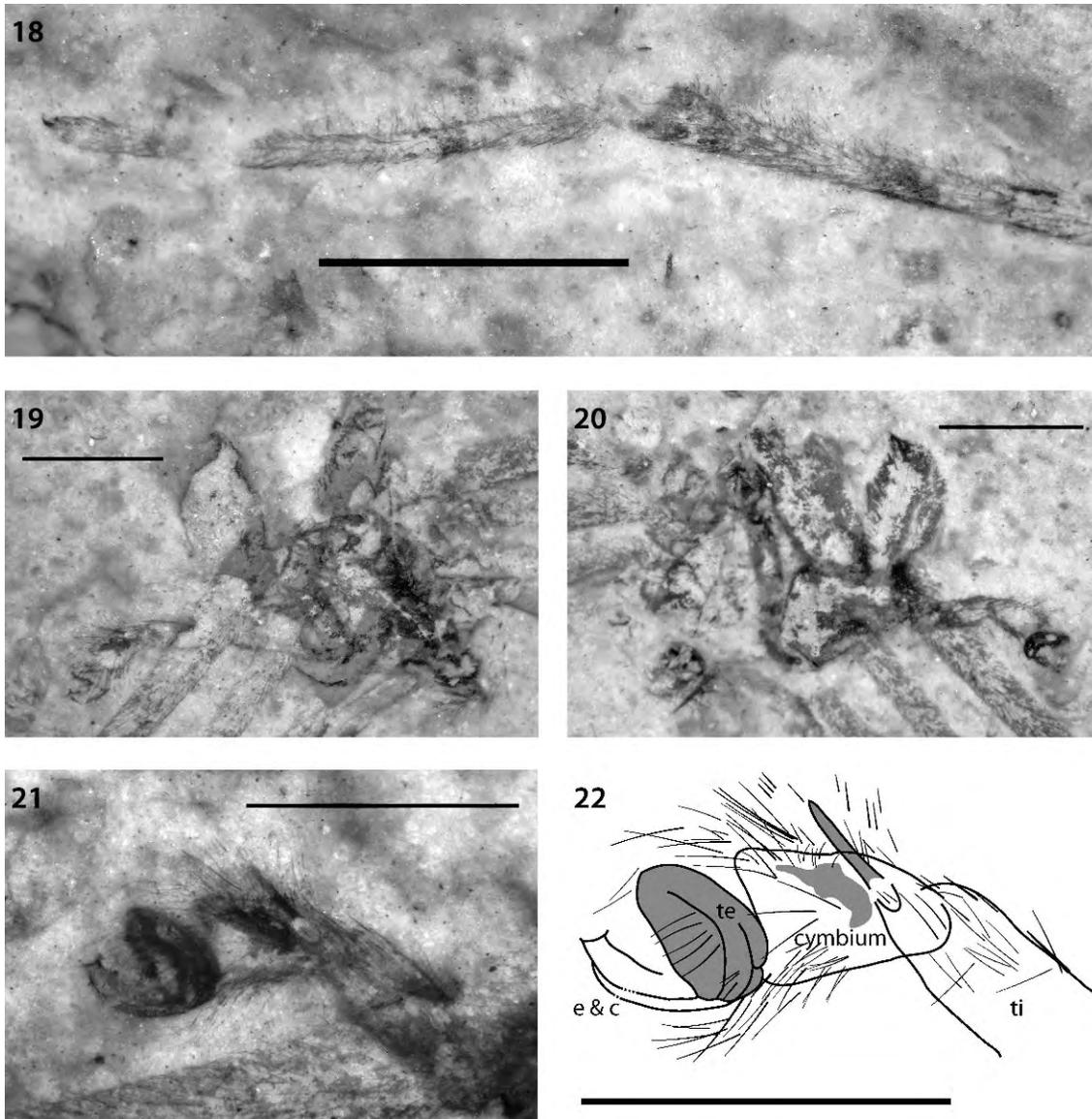
Figures 16, 17.—*Pataarchaea muralis* new genus and species. Allotype adult male, SIM2005003-1 (part) and SIM2005003-2 (counterpart), Jurassic of China. 16. Camera lucida drawing of counterpart, explanatory drawing for Figures 14 and 19; 17. Camera lucida drawing of part, explanatory drawing for Figures 15 and 20. Scale = 1.0 mm.

cheliceral gland mound just less than half cheliceral length from base of fang. Cheliceral groove with at least five retromarginal denticles and many promarginal peg-teeth extending from near base of fang to near base of paturon (c. $\frac{3}{4}$ length of paturon). Normal setae also present. Stridulatory file situated mid-way between base of fang and base of chelicera, on ectal margin (approximately on opposite side of paturon from cheliceral gland mound). Fang thickened at base. Pedipalp at least as long as chelicera, with at least six macrosetae on tarsus. Leg formula 1243. Podomere lengths: leg 1 femur 3.44, patella 1.07, tibia 3.12, metatarsus 1.46, tarsus 0.99; leg 2 femur 3.21, patella 0.67, tibia 2.97, metatarsus 1.76, tarsus 0.72; leg 3 femur 2.27, patella 0.60, tibia 1.72, metatarsus 1.30, tarsus 0.68; leg 4 femur 3.09, patella 0.43, tibia 2.07, metatarsus 1.35, tarsus 0.74. Leg 1 noticeably longer and more robust than other legs: femur thicker, patella longer and more robust, and tibia longer. Leg 4 femur distinctly bent. All leg podomeres lack macrosetae; leg 1 with scopula of curved, spatulate setae on tibia, continues with fine, erect setae on metatarsus and tarsus. Three tarsal claws. Opisthosoma pyriform in dorsal aspect, with blunt posterior margin; length 3.54, width 2.39 at widest point close to posterior margin. Epigynum subtriangular, apex pointing anterior, posterior corners each with a distinct c-shaped ?receptaculum. Ventral cuticle between epigynum and spin-

nerets rugose. Pair of curved, sclerotized ridges in anterolateral part of spinneret region.

Description of allotype, SIM2005003-1/2 (Figs. 14–22).—Adult male. Carapace not preserved. Chelicera 1.47 long; many promarginal peg-teeth extending from near base of fang to near base of paturon. Pedipalp tibia elongate; cymbium with massive, straight macroseta arising from base; large bulb (tegulum) with distal embolus and conductor. Leg formula 1243. Podomere lengths: leg 1 femur 3.44, patella 1.13, tibia 3.26, metatarsus 1.84, tarsus 0.78; leg 2 femur 2.93, patella 0.64, tibia 2.82, metatarsus 1.92, tarsus 0.58; leg 3 femur 2.00, patella 0.49, tibia 1.61, metatarsus 1.47; leg 4 femur 2.37, patella 0.49, tibia 1.65, metatarsus 1.33, tarsus 0.80. Leg 1 noticeably longer and more robust than other legs; patella longer and stouter, metatarsus slightly curved. Leg 4 femur distinctly curved. Legs annulated: at least patella, tibia, and metatarsus with up to three dark annulae. All leg podomeres lack macrosetae; leg 1 with sparse scopula of fine, erect setae on tibia, metatarsus, and tarsus. Opisthosoma not preserved.

Description of additional specimen, NIGP148829 (Figs. 23, 24).—Adult female. Carapace very poorly preserved; outline of raised head region with subcircular cross-section, ≤ 1.58 long; outline of carapace subparallel-sided, 3.62 long, 2.26 wide. Chelicera ≥ 2.41 long; left chelicera shows few promarginal peg-teeth distally, stridulating file. Pedipalp



Figures 18–22.—*Patarchaea muralis* new genus and species. Allotype adult male, SIM2005003-1 (part) and SIM2005003-2 (counterpart), Jurassic of China. 18. Left distal tibia, metatarsus and tarsus of leg 1 of counterpart; 19. Detail of body showing chelicerae and pedipalps of counterpart, see Figure 16; 20. Detail of body showing chelicerae and pedipalps of part, see Figure 17; 21. Photograph combining left palp of counterpart superimposed on right palp of part; note massive, straight macroseta on tibia; 22. Explanatory drawing for Figure 21. Scale = 1.0 mm.

slender, left pedipalp tarsus with claw. Only proximal leg segments preserved. Podomere lengths: leg 1 femur 4.43, patella 1.28; leg 2 femur 3.77, patella 1.01; leg 3 femur 2.72, patella \geq 0.80; leg 4 poorly preserved but femoral curve visible. Leg 1 noticeably longer and more robust than other legs. All visible podomeres lack macrosetae. Opisthosoma not preserved.

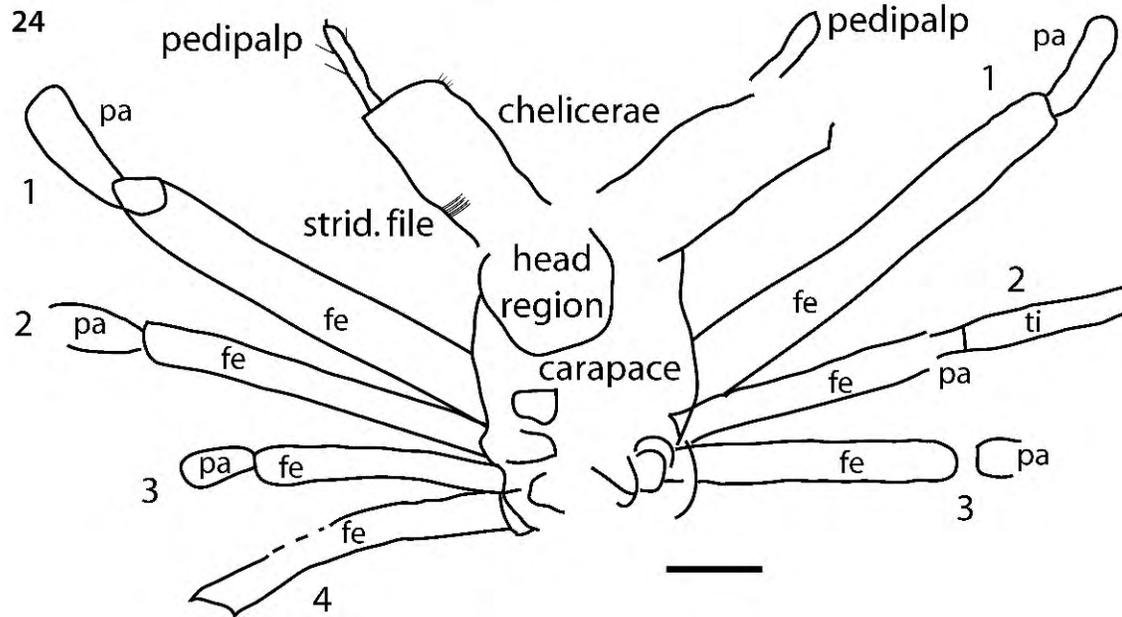
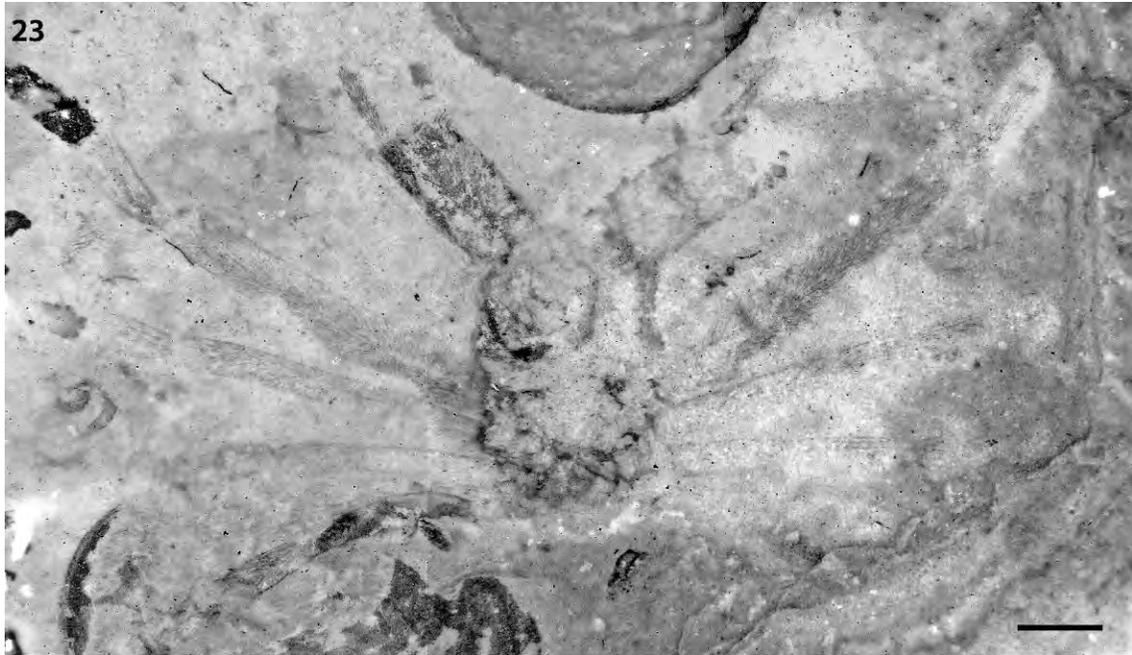
Family unknown
Sinaranea new genus

Type species.—*Sinaranea metaxyostraca* new species

Diagnosis.—Palpimanoid with a combination of elongate leg 1 patella and short leg 2 patella; carapace with raised cephalic area (cf. Huttoniidae) but apparently lacking rugose or tuberculate ornament (cf. Palpimanidae); scutum on dorsal opisthosoma.

Etymology.—Latin *Sinae* (after ancient Arabic *Sin*), China, and *aranea*, a spider.

Remarks.—*Sinaranea* can be referred to the Palpimanoidea on the basis of the cheliceral peg-teeth. The carapace is not diamond-shaped like in Stenochilidae, and has no greatly elongated neck as in Archaeidae, but it has a raised cephalic region, unlike the Huttoniidae; it seems to lack the strong sclerotization of Palpimanidae. The chelicerae are large, but not elongated, and the fang is short and transverse to the long axis of the cheliceral paturon, as in Palpimanidae and Huttoniidae. No stridulating ridges can be seen on the chelicerae in the fossils. The holotype is missing the distal podomeres of leg 1, so it is impossible to tell whether spatulate setae are present, but they seem to occur in NIGP148237, a probable juvenile. Overall, the genus resembles Palpimanidae



Figures 23, 24.—*Patarchaea muralis* new genus and species. Adult female, NIGP148829, Jurassic of China. 23. Photograph; 24. Camera lucida drawing, explanatory drawing for Figure 23. Scale = 1.0 mm.

and Huttoniidae more than other Palpimanoidea, but is not sufficiently well defined to be placed with certainty in either of these modern families. Indeed, it is possible that it could be ancestral, so no familial placement is proposed.

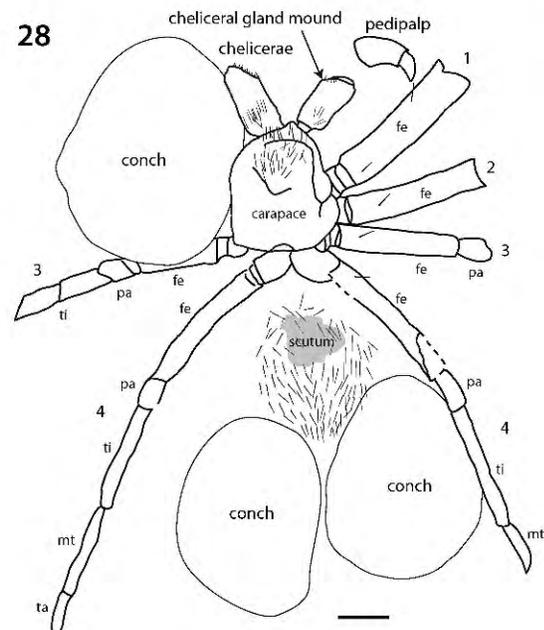
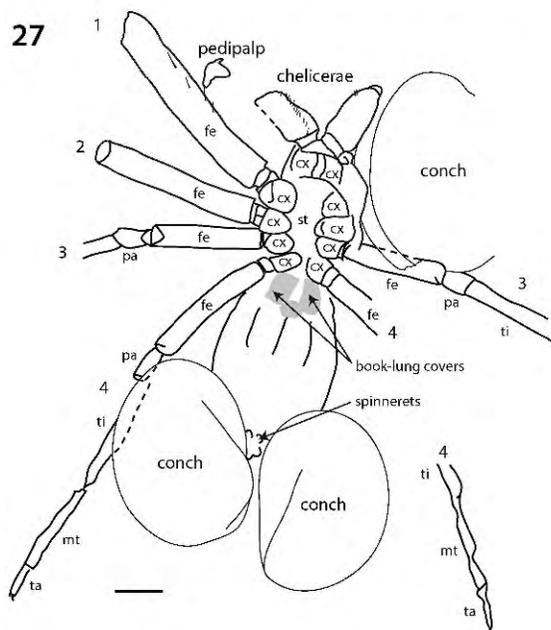
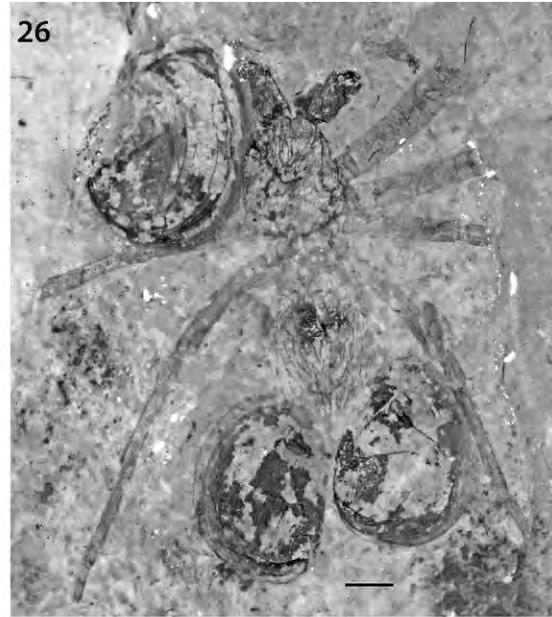
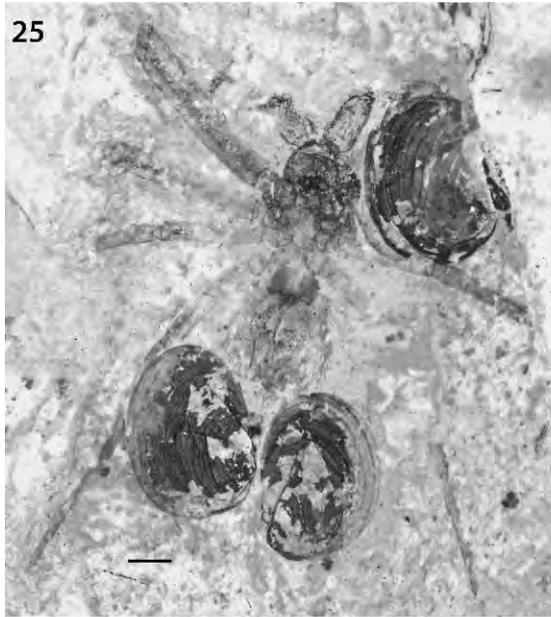
Sinaranea metaxyostraca new species
Figs. 25–40

Material examined.—Holotype: NIGP148830a,b (part and counterpart), adult male, from laminated siltstones of Middle Jurassic Jiulongshan Formation, Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China (41°19.532'N, 119°14.589'E).

Diagnosis.—As for the genus.

Etymology.—Greek *metaxy*, between, and *ostraca*, shells, in reference to the occurrence of the holotype between a number of conchostracan shells.

Remarks.—These five specimens are placed together in *Sinaranea metaxyostraca* on account of their similar habitus. The cephalic area of the carapace is noticeably raised, but not elongated or with a neck; the opisthosoma bears a small, subcircular dorsal scutum; the legs are short, with the formula 1243, and the patella of leg 1 is noticeably long, while that of leg 2 is distinctly short; the femur of leg 4 is not curved. Apart from the holotype, the specimens are preserved on the bedding



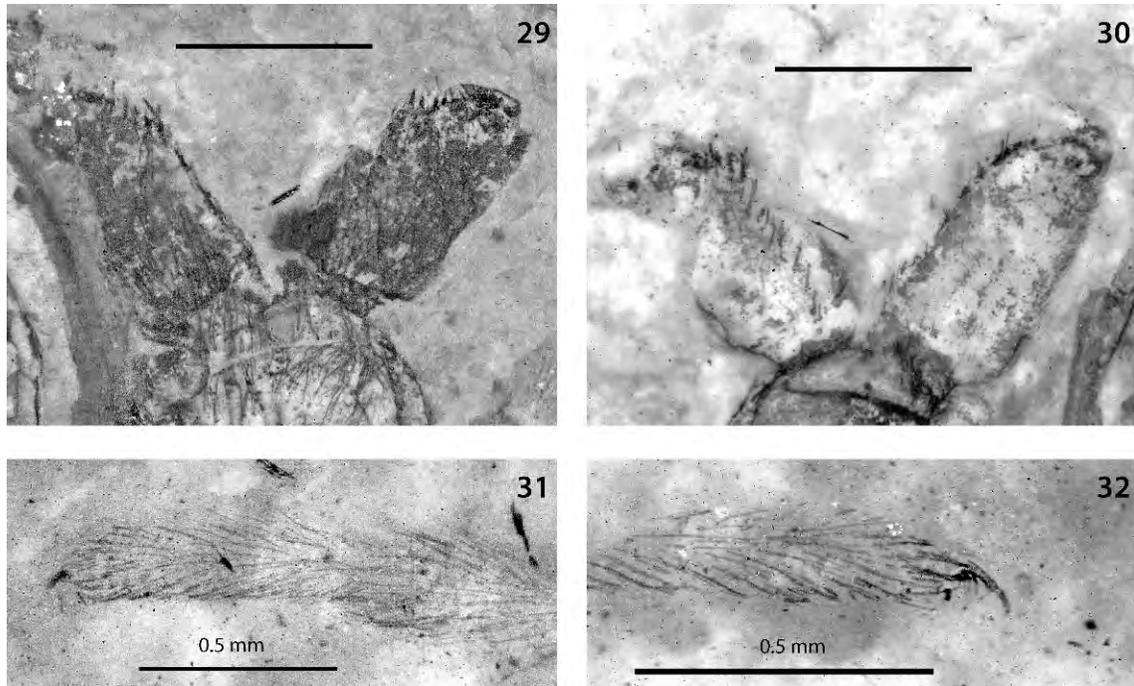
Figures 25–28.—*Sinaranea metaxyostraca* new genus and species. Holotype adult male, NIGP148830a (part) and NIGP148830b (counterpart), Jurassic of China. 25. Part, whole; 26. Counterpart, whole; 27. Camera lucida drawing of part, explanatory drawing for Figure 25; 28. Camera lucida drawing of counterpart, explanatory drawing for Figure 26. Scale = 1.0 mm.

planes of whitish-gray tuff at Xiayingzi in Daohugou Village. This fossil bed is easily recognized because it lacks the familiar conchostracans present on bedding planes with *Pataarchaea*, but has anostracans and ova. The paleoecological significance of this not clear, but the two new genera reported here may not have lived in the same habitat.

The holotype is somewhat larger than the rest, and is probably an adult male because of the fragment of pedipalp, its larger size (hence likely mature), longer legs, and lack of an epigynum. The other specimens are most likely juveniles because adult female spiders are normally larger than adult

males, and they show no sign of the development of modified palps, nor epigyna.

Description of holotype, NIGP148830a,b (Figs. 25–32).—Adult male. Carapace length 2.48, width 2.17, subrectangular, broadly recurved posterior margin, subparallel-sided, procurved anterior margin; distinctly demarcated anterior cephalic area, length 1.07, presumably raised in life. Chelicera subrectangular, somewhat elongated and robust, distal margin at right angle to ectal edge for first half of width, then turns c. 30° angle to meet mesal edge; fang extends across distal edge and along mesal angle; many peg-teeth extend from distal edge



Figures 29–32.—*Sinaranea metaxyostraca* new genus and species. Holotype adult male, NIGP148830a (part) and NIGP148830b (counterpart), Jurassic of China. 29. Counterpart, chelicerae; 30. Part, chelicerae; 31. Counterpart tarsus of left leg 4; 32. Part tarsus of right leg 4 (i.e., same tarsus as is Figure 31). Scale = 1.0 mm.

down full length of mesal edge; stridulatory organ (if present) not visible. Pedipalp poorly preserved but some sclerotization preserved at distal tip of right pedipalp suggests a modified male organ. Leg formula (based on femora) 1243. Podomere lengths: leg 1 femur 4.54; leg 2 femur 3.56; leg 3 femur 2.29, patella 0.70, tibia 1.69; leg 4 femur 2.85, patella 0.72, tibia 2.62, metatarsus 1.99, tarsus 0.90. Leg 4 femur curved but without distinct bend-point. Tarsus 4 with distinctly elongate paired claws, pectinate with at least 3 teeth basally; hook-like third claw. Opisthosoma suboval, length 3.68, width 2.50; dorsal scutum (NB: dark area between rear of book-lung covers on NIGP148830a (ventral), which superficially resembles an epigynum, is most likely the anterior part of the dorsal scutum cuticle superimposed on the ventral counterpart, as are patches of cuticle posterior to it). Spinnerets subterminal.

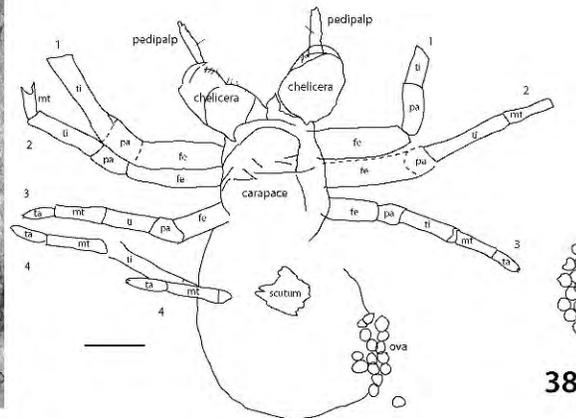
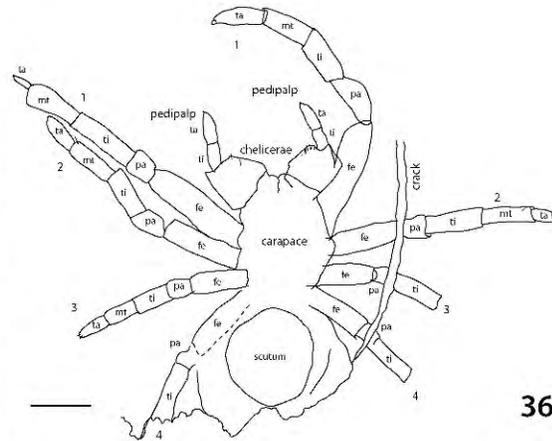
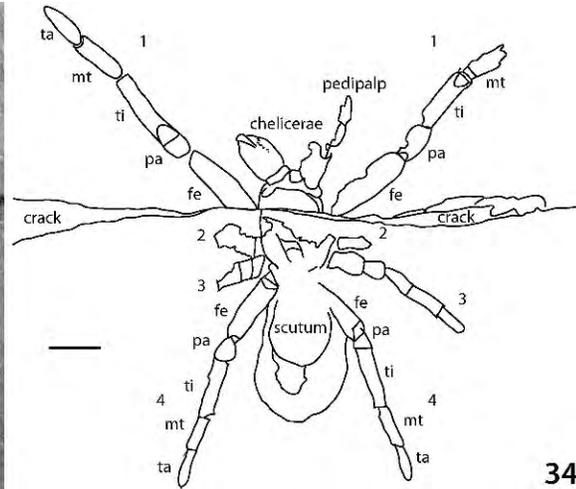
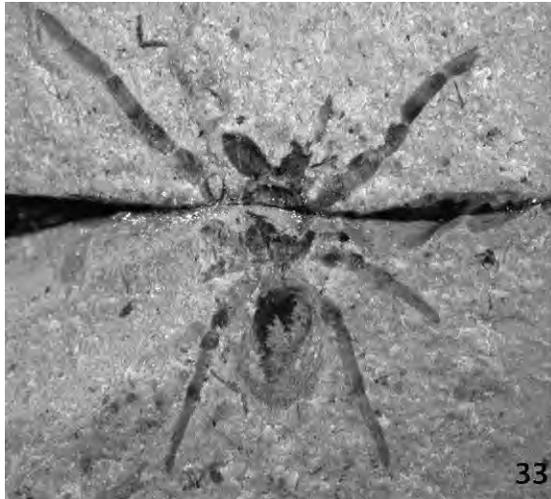
Description of additional specimen, NIGP148236 (Figs. 33, 34).—Juvenile? Carapace length 1.95, width 1.26, subrectangular to broadly suboval, raised head region clearly demarcated, 1.09 long. Chelicerae large, robust, with row of many peg-teeth extending from distal edge down length of mesal edge; length 1.18; curved fang visible on left side. Pedipalp poorly preserved on right side, clearly not bulbous. Legs short; leg formula 1243. Podomere lengths: leg 1 femur 1.81, patella 0.78, tibia 1.41, metatarsus 1.03, tarsus 0.98. Leg 2 poorly preserved. Leg 3 femur ≥ 0.69 , patella 0.42, tibia 0.64, metatarsus 0.73, tarsus 0.60 (incl. claws). Leg 4 femur 1.33, patella 0.48, tibia 1.18, metatarsus 0.78, tarsus 0.78 (incl. claws). Opisthosoma length 2.85, width 1.80; scutum covers most of dorsal surface, remainder of cuticle setose. Spinnerets not preserved.

Description of additional specimen NIGP148237 (Figs. 35, 36).—Juvenile? Carapace length 1.75, width 1.60. Chelicerae

large, robust, with peg-teeth extending from distal edge down length of mesal edge; length 0.96. Pedipalps on both sides not bulbous, tarsus with claw; tarsal length 0.55 (incl. claw). Legs short; leg formula 1243. Leg 1 right preserved in lateral aspect, palpimanid-like, apparently with scopulae on tibia–tarsus. Podomere lengths: leg 1 femur 1.73, patella 0.85, tibia 1.00, metatarsus 0.87, tarsus 0.87 (incl. claws). Leg 2 femur 1.40, patella 0.50, tibia 0.90, metatarsus 0.84, tarsus ≥ 0.64 . Leg 3 femur 1.01, patella 0.37, tibia 0.66, metatarsus 0.53, tarsus 0.53 (incl. claws). Leg 4 femur 1.37, patella 0.33, tibia 0.82. Opisthosoma dimensions difficult to measure; scutum (length 1.67, width 1.59) on dorsal surface. Spinnerets not preserved.

Description of additional specimen NIGP148238 (Figs. 37, 38).—Juvenile? Carapace length ca 2.35, width 1.84. Chelicerae large, robust, with peg-teeth extending from distal edge down length of mesal edge; fang perpendicular to long axis of paturon; length 1.50. Pedipalps on both sides not bulbous, with thin spines; tarsus 0.56. Legs short; leg formula 1243. Podomere lengths: leg 1 femur 1.80, patella long 0.87, tibia 1.35, metatarsus 1.24, tarsus 0.87. Leg 2 femur 1.68, patella short 0.66, tibia 1.30, metatarsus ≥ 0.88 . Leg 3 femur 0.96, patella 0.47, tibia 0.93, metatarsus 0.70, tarsus 0.58 (incl. claws). Leg 4 tibia 1.23, metatarsus 0.99, tarsus 0.61 (incl. claws). Opisthosoma length c. 3.23, width c. 2.79; scutum (length ≥ 1.00 width ≥ 0.96) on dorsal surface. Spinnerets not preserved.

Description of additional specimen NIGP148239a,b (Figs. 39, 40).—Juvenile? Carapace length 2.28, width 1.65, cephalic region width 1.12. Chelicerae large, robust; fang perpendicular to long axis of paturon; length 1.30. Pedipalps on both sides not bulbous; length ≥ 1.55 , tibia 0.56, tarsus 0.60. Legs short; leg formula 1243. Podomere lengths: leg 1 femur 1.73, patella

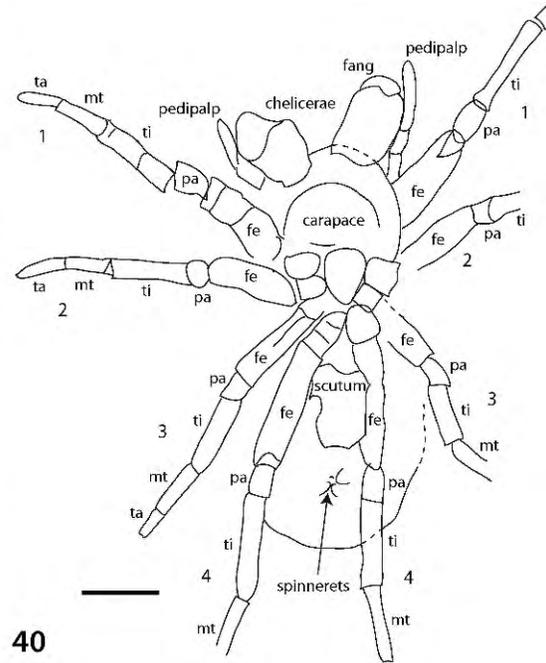


Figures 33–38.—*Sinaranea metaxyostraca* new genus and species. Juveniles? 33. Photograph of NIGP148236; 34. Camera lucida drawing of NIGP148236, explanatory drawing for Figure 33; 35. Photograph of NIGP148237; 36. Camera lucida drawing of NIGP148237, explanatory drawing for Figure 35; 37. Photograph of NIGP148238; 38. Camera lucida drawing of NIGP148238, explanatory drawing for Figure 37; Scale = 1.0 mm.

long 0.61, tibia 1.20, metatarsus 0.69, tarsus 0.56. Leg 2 femur 1.15, patella short 0.33, tibia 1.10, metatarsus 0.63, tarsus 0.50 (incl. claws). Leg 3 femur 1.15, patella 0.43, tibia 1.06, metatarsus 0.82, tarsus \geq 0.32. Leg 4 femur 1.46, patella 0.45, tibia 1.61, metatarsus 0.93. Opisthosoma length 3.02, width 2.16; scutum (length \geq 1.04 width \geq 0.77) on dorsal surface. Spinnerets on ventral surface ca $\frac{1}{4}$ of length of opisthosoma from posterior.

DISCUSSION

The presence of palpimanoids, and especially archaeids, in strata of Jurassic age confirms the geological age of the Palpimanoidea, and the presence of identifiable palpimanoid families in the Jurassic suggests an even earlier origin for the superfamily. The presence of the group in the Jurassic of China is especially interesting because it extends the geo-



Figures 39, 40.—*Sinaranea metaxyostraca* new genus and species. Juvenile? 39. Photograph of NIGP148239a; 40. Camera lucida drawing of NIGP148239a, explanatory drawing for Figure 39; Scale = 1.0 mm.

graphic range of the superfamily. Today, spiders of the superfamily Palpimanoidea are widespread throughout tropical and subtropical areas of the world, but most constituent families have more limited distributions. Living archaeids are known from Australia, South Africa and Madagascar, a classic Gondwanan distribution. Fossil archaeids, however, are known from the Jurassic of Kazakhstan (Eskov 1987), China (this paper), the Cretaceous of Myanmar (Penney 2003), Baltic amber (Wunderlich 2004), and Madagascan copal (Lourenço 2000). The Kazakhstan and North China plates form a part of eastern Laurasia which had accreted by late Devonian times; the part of Myanmar which produces Cretaceous amber (Grimaldi et al. 2002) was situated on the Sibamisu terrane, which formed the northern shore of the Tethys ocean in the late Cretaceous (Metcalf 2005). The origin of Baltic amber lies in western Laurasia. The presence of archaeids in the eastern Laurasian part of Pangaea in the Mesozoic and western Laurasia in the Cenozoic appears at first to contradict the present-day Gondwanan distribution of the family. Archaeids are small, litter-inhabiting spiders, and their dispersal abilities are probably low. The present disjunct distribution of the family suggests a geological history that pre-dates the break-up of Gondwana in Jurassic times and the fossil occurrences suggests a cosmopolitan distribution in the Mesozoic. The lack of Mesozoic fossils in the Gondwana area can be explained by the rarity of suitable fossil sites there. The Cretaceous Myanmar archaeid was referred by Penney (2003) to the modern genus *Afrarchaea*, which today occurs in southern Africa. This genus must, therefore, have occurred from the northern shores of the Tethys Ocean down to the central Gondwana area at that time. Fossil evidence thus demonstrates that the present-day distribution of archaeids probably results from a reduction in the former range of the family (the theory of ousted relics: Eskov & Golovatch 1986;

Eskov 1987, 1992), perhaps as a consequence of Neogene climate cooling (Grimaldi & Engel 2004).

ACKNOWLEDGMENTS

We thank Dr. Shih Chung-Kun, Infineum Beijing, for kindly presenting the allotype specimen of *Patarchaea* for study. This research is supported by the National Natural Science Foundation of China (grants no. 40672013, 40632010 and 30430100), the Major Basic Research Projects of MST of China (2006CB806400), the State Key Laboratory of Palaeobiology and Stratigraphy (NIGPAS, no. 073101), and the Beijing Natural Science Foundation (No. 5082002).

LITERATURE CITED

- Ansorge, J. 2003. Insects from the Lower Toarcian of Middle Europe and England. *Acta Zoologica Cracoviensia* 46 (Supplement – Fossil Insects):291–310.
- Chen, W., Q. Ji, D. Liu, Y. Zhang, B. Song & X. Liu. 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* 23:1165–1169. [In Chinese, English summary].
- Eskov, K.Y. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1984:645–653.
- Eskov, K.Y. 1987. A new archaeid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called “Gondwanan” ranges of recent taxa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175:81–106.
- Eskov, K.Y. 1990. Spider palaeontology: present trends and future expectations. *Acta Zoologica Fennica* 190:123–127.
- Eskov, K.Y. 1992. Archaeid spiders from Eocene Baltic amber (Chelicerata: Araneida: Archaeidae) with remarks on the so-called “Gondwanan” ranges of Recent taxa. *Neues Jahrbuch für Geologie und Paläontologie* 185:31–328.

- Eskov, K.Y. & S.I. Golovatch. 1986. On the origin of trans-Pacific disjunctions. *Zoologische Jahrbücher. Abteilung für Systematik, Oekologie und Geographie der Tiere* 113:265–285.
- Eskov, K.Y. & J. Wunderlich. 1995. On the spiders from Taimyr ambers, Siberia, with the description of a new family and with general notes on the spiders from the Cretaceous resins. *Beiträge zur Araneologie* 4:95–107.
- Forster, R.R. & N.I. Platnick. 1984. A review of the archaeid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). *Bulletin of the American Museum of Natural History* 178:1–106.
- Gao, K.-Q. & D. Ren. 2006. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou beds. *Acta Geologica Sinica* 80:42–45.
- Gourret, M.P. 1888. *Recherches sur les arachnides Tertiaires d'Aix en Provence*. *Recueil Zoologique Suisse* 1888:431–496.
- Grimaldi, D.A. & M.S. Engel. 2004. *Evolution of the Insects*. Cambridge University Press, Cambridge, UK. 755 pp.
- Grimaldi, D.A., M.S. Engel & P.C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361:1–71.
- Griswold, C.E., M.J. Ramírez, J.A. Coddington & N.I. Platnick. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 56:1–324.
- Hewitt, J. 1919. Description of new South African spiders and solifuge of the genus *Chelypus*. *Records of the Albany Museum* 3:196–215.
- Hickman, V.V. 1944. On some new Australian Apneumonomorphae with notes on their respiratory system. *Papers and Proceedings of the Royal Society of Tasmania* 1943:179–195.
- Hickman, V.V. 1945. A new group of apneumone spiders. *Transactions of the Connecticut Academy of Arts and Sciences* 36:135–157.
- Huang, D.-Y., A. Nel, Y.-B. Shen, P.A. Selden & Q.-B. Lin. 2006. Discussions on the age of Daohugou fauna — evidence from invertebrates. *Progress in Natural Science (Special Issue)* 16:308–312.
- Koch, C.L. & G.C. Berendt. 1854. *Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt*. Edwin Groening, Berlin. 1(2):1–124.
- Latreille, P.A. 1806. *Genera crustaceorum et insectorum*. Tome 1. Paris. [Araneae, pp. 82–127].
- Lotz, L.N. 1996. Afrotropical Archaeidae (Araneae): 1. New species of *Afrarchaea* with notes on *Afrarchaea godfreyi* (Hewitt, 1919). *Navorsing van die Nasionale Museum Bloemfontein* 12:142–159.
- Lotz, L.N. 2003. Afrotropical Archaeidae: 2. New species of the genera *Archaea* and *Afrarchaea* (Arachnida: Araneae). *Navorsing van die Nasionale Museum Bloemfontein* 19:221–240.
- Lotz, L.N. 2006. Afrotropical Archaeidae: 3. The female of *Eriauchenius cornutus* and new species of *Afrarchaea* (Arachnida: Araneae) from South Africa. *Navorsing van die Nasionale Museum Bloemfontein* 22:113–127.
- Lourenço, W.R. 2000. Premier cas d'un sub-fossile d'araignée appartenant au genre *Archaea* Koch & Berendt (Archaeidae) dans le copal de Madagascar. *Comptes Rendus. Académie des Sciences, Paris, Sciences de la Terre et des Planètes* 330:509–12.
- Metcalf, I. 2005. Asia: South-East. Pp. 169–198. *In* *Encyclopedia of Geology*. Volume 1. (R.C. Selley, L.R.M. Cocks & I.R. Plimer, eds.). Elsevier Academic Press, Amsterdam.
- Millot, J. 1948. Faits nouveaux concernant les *Archaea* [Aranéides]. *Mémoires de l'Institut scientifique de Madagascar* 1(A1):3–14.
- Penney, D. 2003. *Afrarchaea grimaldii*, a new species of Archaeidae (Araneae) in Cretaceous Burmese amber. *Journal of Arachnology* 31:122–130.
- Penney, D. 2004. Cretaceous Canadian amber spider and the palpimanoidean nature of lagonomegopids. *Acta Palaeontologica Polonica* 49:579–584.
- Penney, D. 2005. The fossil spider family Lagonomegopidae in Cretaceous ambers with descriptions of a new genus and species from Myanmar. *Journal of Arachnology* 33:438–443.
- Penney, D. 2006. The oldest lagonomegopid spider, a new species in Lower Cretaceous amber from Alava, Spain. *Geologica Acta* 4:377–382.
- Penney, D., M. Dierick, V. Cnudde, B. Masschaele, J. Vlassenbroeck, L. van Hoorebeke & P. Jacobs. 2007. First fossil Micropholcommatidae (Araneae), imaged in Eocene Paris amber using X-Ray Computed Tomography. *Zootaxa* 1623:47–53.
- Penney, D. & A.M. Langan. 2006. Comparing amber fossil assemblages across the Cenozoic. *Biology Letters* 2:266–270.
- Penney, D. & P.A. Selden. 2006. First fossil Huttoniidae (Arthropoda: Chelicerata: Araneae), in late Cretaceous Canadian amber. *Cretaceous Research* 27:442–446.
- Petrunkovitch, A. 1942. Amber spiders in European collections. *Transactions of the Connecticut Academy of Arts and Sciences* 41:97–400.
- Pickard-Cambridge, O. 1881. On some new genera and species of Araneidea. *Proceedings of the Zoological Society of London* 1881:765–775.
- Platnick, N.I. & R.R. Forster. 1986. On *Teutoniella*, an American genus of the spider family Micropholcommatidae (Araneae, Palpimanoidea). *American Museum Novitates* 2854:1–9.
- Platnick, N.I. & R.R. Forster. 1987. On the first American spiders of the subfamily Sternodinae (Araneae, Malkaridae). *American Museum Novitates* 2894:1–12.
- Ren, D., K. Gao, Z.J.S. Guo, J. Tan & Z. Song. 2002. Stratigraphic division of the Jurassic in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* 21:584–591. [In Chinese, English summary].
- Saupe, E.E. & P.A. Selden. In press. First fossil Mecysmaucheniidae (Arthropoda: Chelicerata: Araneae), from Lower Cretaceous (Upper Albian) amber of Charente-Maritime, France: *Geodiversitas*.
- Schols, P., S. Desein, C. D'hondt, S. Huysmans & E. Smets. 2002. Carnoy: a new digital measurement tool for palynology. *Grana* 41:124–126.
- Schütt, K. 2000. The limits of the Araneoidea. *Australian Journal of Zoology* 48:135–153.
- Schütt, K. 2003. Phylogeny of Symphytognathidae s.l. (Araneae, Araneoidea) *Zoologica Scripta* 32:129–151.
- Shen, Y.-B. & D.-Y. Huang. 2008. Extant clam shrimp egg morphology: taxonomy and comparison with other fossil branchiopod eggs. *Journal of Crustacean Biology* 28:342–350.
- Selden, P.A. 2003. A new tool for fossil preparation. *The Geological Curator* 7:337–339.
- Simon, E. 1881. *Les Arachnides de France*. Tome 5. 1 ère partie contenant les familles des Epeiridae (supplément) et des Theridionidae (commencement). Librairie encyclopédique de Roret, Paris. 1–180.
- Simon, E. 1893. *Histoire naturelle des Araignées*. Tome 1, Fascicule 1. Second édition. Librairie encyclopédique de Roret, Paris. Pp. 257–488.
- Simon, E. 1895. *Histoire naturelle des Araignées*. Tome 1, Fascicule 4. Second édition. Librairie encyclopédique de Roret, Paris. Pp. 761–1084.
- Thorell, T. 1870. On European spiders. *Nova Acta Regia Societas Scientiarum Upsalaensis*. Series 3, Volume 7:109–242.
- Thorell, T. 1873. Remarks on synonyms of European spiders. Part IV, Uppsala. Pp. 375–645.
- Wood, H. 2008. A revision of the assassin spiders of the *Eriauchenius gracilicollis* group, a clade of spiders endemic to Madagascar

- (Araneae: Archaeidae). Zoological Journal of the Linnaean Society 152:255–296.
- Wunderlich, J. 1986. Spinnenfauna gestern und heute: Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten. Quelle & Meyer, Wiesbaden. 283 pp.
- Wunderlich, J. 1988. Die fossilen Spinnen im Dominikanischen Bernstein. Beiträge zur Araneologie 2:1–378.
- Wunderlich, J. 1999. Two subfamilies of spiders (Araneae, Linyphiidae: Erigoninae and Anapidae: Mysmeninae) new to Dominican amber—or falsificated amber? Estudios del Museo Ciencias Naturales de Álava 14(Número Especial 2):167–72.
- Wunderlich, J. 2004. Fossil spiders in amber and copal. Beiträge zur Araneologie 3A–B:1908 pp.
- Wunderlich, J. 2006. *Spatiator martensi* n. sp., a second species of the extinct spider family Spatiatoridae in Eocene Baltic amber (Araneae). Zootaxa 1325:313–318.

Manuscript received 10 December 2007, revised 20 May 2008.