New spiders (Araneae: Palpimanoidea) from the Jurassic Yanliao Biota of China

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Several new spider specimens, belonging to the superfamily Palpimanoidea, are described from the Middle–Upper Jurassic Haifanggou Formation (early assemblage of the Yanliao Biota) of Inner Mongolia, China. Two new genera and species, and a new species in the genus Sinaranea Selden, Huang & Ren, 2008, are described. Caestaranea jurassica gen. et sp. nov. is described on the basis of several adult males, typified by boxing-glove shaped pedipalps, as well as females and juveniles. Onychopalpus thomisoides gen. et sp. nov. is the largest palpimanoid known, and its habitus resembles that of a crab spider (Thomisidae) in having large, laterigrade anterior legs with rows of macrosetae on the femora and a squat, rotund opisthosoma. However, the distinctive adult male pedipalp bears a pectinate claw, so the holotype specimen is a subadult male; the other specimens referred to this species are smaller juveniles. Three new specimens of Sinaranea metaxyostraca Selden, Huang & Ren, 2008, including two adult males, are described here, and the new species S. brevicrus sp. nov., which has shorter legs than the type species, is described from an adult male and an adult female. These new palpimanoids substantially increase the diversity of the superfamily in the Middle Jurassic, and the unusual Onychopalpus provides evidence for a different mode of life for these spiders.


Keywords: Arachnida; Callovian–Oxfordian; Fossil Lagerstätte; Haifanggou Formation

Introduction

The Fossil-Lagerstätte of Daohugou, Inner Mongolia, China, bearing the early assemblage of the Yanliao Biota, has provided palaeontologists with a wealth of exciting new finds of plants and animals from the Middle–Late Jurassic (Huang 2016; Xu et al. 2016). Until this century, the number of Jurassic spiders reported in the literature was meagre, but in the last few years several hundred specimens from the Daohugou locality have accumulated in collections in China, and several forms have been published (Selden et al. 2008, 2011, 2013, 2016; Selden & Huang 2010). The earliest of these publications described some palpimanoid spiders, including archaeids, and other specimens that could not be assigned to a modern family within the Palpimanoidae. Since then, a number of new specimens of palpimanoids from the Daohugou locality have been collected. Here, we describe these specimens, and reassess some from the original paper (Selden et al. 2008).

The first spider from the Mesozoic Era to be described was a single adult male specimen of an araneoid, Juraraneus rasnitsyni Eskov, 1984, from the Middle Jurassic Ichetuy Formation of Transbaikalia (redescribed by Selden 2012). Also in 1984, the first spider from the Middle Jurassic Jullongsan Formation of China was described as Mesarania hebeiensis Hong, 1984, and placed in Araneoidae (more likely, it belongs to the common cribellate genus Zhizhu Selden, Ren & Shih, 2016 from the Yanliao Biota, but the description and illustration are insufficient for identification and the holotype specimen is lost). Eskov described a single specimen of a female arachneid, Jurarchaea zherikhini Eskov, 1987, from the Upper Jurassic Karabastau Formation of Kazakhstan. During this century, many more specimens of spiders have been described from the Jurassic Haifanggou Formation of China (Selden et al. 2008, 2011, 2013, 2016; Selden & Huang 2010), including palpimanoids, plectreurids and deinopoids. Also, a possible uloborid was described from the Upper Jurassic Talbragar Fossil Fish Bed of New South Wales.
Australia, and a palpimanoid from the Early Jurassic (lower Toarcian) of Grimmen, Germany, was described by Selden & Dunlop (2014). This brings the number of described spider species from Jurassic strata to 10, though others await description from the Jurassic beds of China. Here, we describe three more palpimanoid spiders from the Yantiao Biota: Caestaranea jurassica gen. et sp. nov., Onychopalpus thomisoides gen. et sp. nov. and Sinaranea brevicrus sp. nov.

The superfamily Palpimanoidea was redefined by Forster & Platnick (1984) on the basis of peg teeth and glands opening on an elevated mound on the chelicera. Schütz (2000), in a study of the placement of Mimetiida Simon, 1881 within Palpimanoidea, pointed out that neither the gland mound nor the peg teeth are present in all members of Palpimanoidea sensu Forster & Platnick (1984), and that similar cheliceral structures occur in members of other superfamilies. Other studies have shown that the paraphaenoids, micropholocatales, holarchaeids and mimetids were misplaced in Forster & Platnick’s (1984) delimitation of Palpimanoidea (Rix et al. 2008; Blackledge et al. 2009; Dimitrov & Hormiga 2011; Dimitrov et al. 2012, 2017; Benavides et al. 2016). Despite the removal of numerous families placed in an expanded Palpimanoidea by Forster & Platnick (1984), the superfamily can still be recognized by a number of synapomorphies and general characteristics, enumerated by Wood et al. (2012, appendix 3). In the most recent molecular systematic analyses, e.g. Dimitrov et al. (2017), Wheeler et al. (2017) and Fernández et al. (2018), the superfamily is recovered as sister to Entelegyne. The clade currently encompasses the families Arachnidae Koch & Berendt, 1854, Huttoniidae Simon, 1893, Mecysmauchenidae Simon, 1895, Palpimanidae Thorell, 1870, and Stenochilidae Thorell, 1873, and the extinct Lagonomopidae Eskov & Wunderlich, 1995, Spantiatricidae Petrunkevitch, 1942, Micropalpimanidae Wunderlich, 2008b and Vetiatoridae Wunderlich, 2015.

Caestaranea jurassica gen. et sp. nov. is known from a suite of specimens, including adult and juvenile males and females, and is characterized by the male pedipalp superficially resembling a boxing glove. Onychopalpus thomisoides gen. et sp. nov. has a habitus reminiscent of the crab spiders (Thomisidae Sundevall, 1833), including large, laterigrade, anterior legs and a disc-shaped opisthosa. This is a novel mode of life for palpimanooids, and is perhaps a precursor, in behavioural terms, to the thomisid lifestyle. Though large in body size, the new species is known only from a subadult male (holotype) and juveniles, as evidenced by the pectinate tarsal claw on the male pedipalp of the holotype (see Discussion). New specimens of Sinaranea metaxyostraca Selden, Huang & Ren, 2008 are described here, and the new species S. brevicrus sp. nov., which has shorter legs than the type species, is described from an adult male and an adult female. The genus is characterized by the spiral structure of the adult male pedipalp.

Material and methods

Geological setting

The specimens described here come from finely laminated, pale grey tuffaceous shale near Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China (41°19′32″N, 119°14′35″E; see locality map in Selden et al. 2008). The Daohugou deposits consist of a basal synorogenic conglomerate and overlying grey tuff, tuffaceous shale and siltstones (Huang 2015a; Huang et al. 2015, 2018, fig. 1), indicative of lacustrine conditions in a volcanic region, and have yielded plants, insects, conchostracans, anostracans, arachnids (Selden et al. 2008, 2011, 2013, 2016; Huang et al. 2009; Selden & Huang 2010; Giribet et al. 2011; Huang 2015a, b, 2016) and vertebrates (Sullivan et al. 2014). The Daohugou beds form part of the Yantiao Biota, which originated before the Haifanggou Formation and extended into the Tiaojishan Formation (Huang 2019, fig. 4). The name Daohugou beds was first proposed by Wang et al. (2000), and they were initially attributed to the Tiaojishan Formation or the Jiulongshan Formation (Ren et al. 2002; Liu et al. 2006, 2012). However, they are now considered to belong to the Haifanggou Formation, based on lithological features, stratigraphical sequence, age and fossil content (Huang 2015b; Liao et al. 2017; Huang et al. 2018). The age of these beds has been controversial (e.g. He et al. 2004, 2005; Liu & Liu 2005; Chu et al. 2016). On present evidence (Huang 2019), the top of the Haifanggou Formation is c. 161 Ma, and the base c. 168 Ma, i.e. spanning a stratigraphical range from Bathonian to Oxfordian (Cohen et al. 2013). The approximate age of the beds which yielded the fossil spiders in this paper is 162–163 Ma, i.e. lowermost Oxfordian.

The spider fossils

The spiders (Figs 1–37) are preserved in slabs of grey, tuffaceous shale with abundant plant debris, but no conchostracans, which are typical of the middle and upper beds in the Daohugou sequence (Liao et al. 2017). The lower layers of the Daohugou beds are associated with many anostracans (Huang et al. 2018). The spider fossils are preserved as organic fragments on and within the rock matrix. All specimens are deposited in the collections of the Nanjing Institute of Geology and
Figure 1. *Caestranea jurassica* gen. et sp. nov., holotype male NIGP168480a,b, part, under ethanol. A, whole specimen. B, explanatory drawing of A. C, left leg I distal metatarsus and tarsus, showing poorly developed scopulae and pectinate paired tarsal claws. D, right leg I distal metatarsus and tarsus, showing poorly developed scopulae and tarsal claws. E, right leg II distal metatarsus and tarsus. F, left pedipalp tarsus and distal chelicera, showing peg teeth and fang. G, right pedipalp tarsus and distal chelicera, showing peg teeth and fang. Scale bar = 1 mm.
Figure 2. Caestaranca jurassica gen. et sp. nov., holotype male NIGP168480a,b, counterpart, under ethanol. A, whole specimen. B, explanatory drawing of A. C, right leg I metatarsus and tarsus, showing poorly developed scopulae. D, left pedipalp tarsus and distal chelicera, showing peg teeth and fang. E, right pedipalp tarsus and distal chelicera, showing peg teeth and fang. Scale bar = 1 mm.
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*Caestaranea jurassica* gen. et sp. nov. A series of specimens, including three that were originally described as possible juveniles of *Sinaranea metaxyostraca* by Selden et al. (2008), are here described as a new genus and species. The sclerotized area of the dorsal opisthosoma was originally called a scutum by Selden et al. (2012) but, since its edges are not clearly demarcated, it is perhaps better described as a sclerotized area.

The holotype NIGP168480a,b is preserved as part and counterpart; the part lacks only the distal parts of the posterior legs (Fig. 1), while the counterpart is almost complete (Fig. 2). Much of the cuticle is present, so details of the pedipalp and chelicerae are well preserved. This specimen and the paratypes are considered to be adult males because of their well sclerotized palpal cymbiaums (see Remarks). The allotype female NIGP168481a,b is preserved as part and counterpart, and almost complete, lacking only the tarsi of the fourth legs and parts of legs I (Figs 3, 4). The background matrix is rather dark and mottled, hence some of the morphology is difficult to see; however, the body is quite well preserved, showing traces of the coxal region and spinnerets. This specimen and other females of comparable size (Table 1) are considered to be adults. Paratype male NIGP168482 is preserved as the part only, and is almost complete, except for the tarsi of legs II (Fig. 5). The cuticle of leg I is particularly well preserved. Paratype male NIGP168483 is preserved as the part only. It is rather faint and lacks most of the tibiae-tarsi of the legs on the right side (Fig. 6). Nevertheless,
Figure 5. Caestaranea jurassica gen. et sp. nov., paratype male NIGP168482, under ethanol. A, whole specimen. B, explanatory drawing of A. C, left leg I metatarsus and tarsus, and right leg I tarsus, showing weak scopulae. D, left and right leg I tarsal claws. Scale bar = 1 mm.
the pedipalps and chelicerae are shown rather well. Paratype male NIGP168484a,b is preserved as part and counterpart and the cuticle remains over much of the part (Fig. 7), while the counterpart is fainter (Fig. 8). The pedipalps and chelicerae are preserved very well (Fig. 7E). An additional specimen, NIGP148238, possibly an adult female, was originally figured in Selden et al. (2012, figs 37, 38) and is shown here in Figure 9. It consists of the part only and lacks the distal parts of legs I and II, and right leg IV is folded over the opisthosoma. It shows a typical female pedipalp. Adjacent to the specimen are clutches of clam-shrimp eggs (see Shen & Huang 2008). Adult female? NIGP148239a,b, consisting of part and counterpart, was originally figured in Selden et al. (2012, figs 39, 40) and is reproduced in Figure 10. The specimen appears rather soft and the left side is a little shrivelled, so the measurements of legs I and II are probably shorter than they were in life. Nevertheless, it shows a typical female pedipalp. Specimen NIGP168485 consists of the part
Figure 7. Caestranacea jurassica gen. et sp. nov., paratype male NIGP168484a,b, part, under ethanol. A, whole specimen. B, explanatory drawing of A. C, left leg I metatarsus and tarsus, showing poorly developed scopulae and tarsal claws. D, left leg IV metatarsus and tarsus, showing fine bristles and tarsal claws. E, chelicerae showing peg teeth, fangs and remnants of stridulatory ridges, and pedipalps showing sclerotized tarsi with mesiolateral macroseta. Scale bar = 1 mm.
only and appears, from its size and the typical pedipalp, to be an adult female. Only a part of the animal is preserved; the remainder is lost due to cracks in the matrix (Fig. 11). The chelicerae are well preserved, as are the pedipalps and the coxosternal region (showing the elongate sternal shape well). Right leg I is complete, but only the proximal parts of other legs can be seen. The small specimen NIGP168486a,b, part and counterpart...
(Fig. 12), is likely a juvenile female, judging from its size and pedipalp. It appears soft, like NIGP148239a,b, and its legs are rather collapsed and lacking apparent stiffness, suggesting that this specimen may be a moult. The prosoma is preserved in a partly lateral view. The small specimen NIGP168487 consists of the part only and is preserved rather faintly, though almost completely, on the mottled matrix (Fig. 13). Like NIGP148239a,b, it also suffers from some shrivelling on the left side, making its podomere measurements rather tentative. Judging from its small size, and the slightly swollen pedipalp tarsus, this specimen is interpreted as a juvenile male. Specimen NIGP148236, part only, was figured by Selden et al. (2012, figs 33, 34), and is reproduced here in Figure 14. Though quite well sclerotized (it shows a well-defined sclerotized area on the opisthosoma) it is incomplete in lacking the left pedipalp, and most of legs II and III on the left. Its small size suggests it is a juvenile but the pedipalp is insufficiently preserved to determine its sex.

**Onychopalpus thomisoides gen. et sp. nov. holotype.** Almost the entire holotype, part and counterpart (NIGP168488a,b), is preserved, lacking only the distal tibia, metatarsus and tarsus of right leg I and the tip of the tarsus of right leg II. However, since the opposite appendage of all of these is preserved, details of the morphology of the animal are complete. The part (NIGP168488a) shows primarily dorsal features; for example, in low-angle light, the carapace is seen as an external mould; the opisthosoma and appendage features are dorsal. Conversely, the counterpart (NIGP168488b) shows mainly ventral features.

In the holotype, the anterior part of the carapace (caput) is distinctly demarcated, with wrinkled cuticle (taphonomically compressed) beyond the margins; the midline of the caput is not aligned with that of the posterior part of carapace but is skewed to the right (on the part), where a piece of carapace cuticle beyond the caput is seen to overhang the right edge of the carapace. This suggests that the caput has been compressed to the right during compaction and would have been raised in life. The anterior median part of the caput bears a circular feature at the anterior margin and a pair of circular features more posteriorly (Fig. 16A, B); these are interpreted as anterior and posterior median eyes. Lateral eyes are likely to be among the wrinkling of the lateral sides of the caput; note that eyes are rarely seen in fossil spiders in matrix preservation. The chelicerae are strongly directed forwards, though it is likely that, in life, they would have been at an angle of about 45° to the horizontal and have taken their present position through compaction. In other fossil spiders, where the chelicerae are smaller and directed vertically downwards, compaction normally results in compression, not rotation. The sternum is rather narrow in the fossil, although its shape may reflect incursion of the lateral coxae following compression; even if this is the case, it was clearly not wide in life. The labium, though not clearly demarcated, appears large, a little longer than wide, and clearly separating the lateral maxillae (pedipalp coxae), which do not converge in front of the labium.

The chelicerae are relatively large, two-thirds the length of the carapace, though not elongated. While immersion in ethanol and/or viewing in polarized light helps to enhance the contrast of the organic fragments against the rock background, some three-dimensional features show up better when the specimen is dry and

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**Figure 9.** *Caestaranea jurassica* gen. et sp. nov., female NIGP148238, dry. A, whole specimen. B, explanatory drawing of A. Scale bar = 1 mm.

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Figure 10. Caestaranea jurassica gen. et sp. nov., female NIGP148239a,b, under ethanol. A, part. B, counterpart. C, explanatory drawing of A. D, explanatory drawing of B. Scale bars = 1 mm.
illuminated with low-angle light. This is true of the patches of fine ridges seen in the postero-lateral parts of the ventral cheliceral paturon (Fig. 17A); they are interpreted as stridulatory in function, and such features are found in numerous spider families (Uhl & Elias 2011). Presumably, a corresponding pick is present on the pedipalp femur, but none is visible in the fossil. The numerous peg teeth extend along the promargin from near the base of the fang to the base of the paturon; particularly large peg teeth occur on both pro- and retromargins near the fang tip (Fig. 17B). A slight bump on the paturon mesial side could represent the cheliceral gland mound (Fig. 16A, B), but this is uncertain.

The tarsus of the right pedipalp is swollen (Fig. 18), which tells us that this specimen is a male. A pectinate claw is present on the pedipalp tarsus (Fig. 18). It is possible that a pair of claws were present because the disposition of the best-preserved claw of the right side (Fig. 18C) is offset to the left of the midline; the form of the associated setae of this pedipalp and the disposition of the setae on the pedipalp on the left side suggest that two claws may have been present. Pectination is typical of the paired claw, whereas the unpaired claw, if pectinate, generally has fewer teeth. On the other hand, spider pedipalp tarsi never show more than a single, median claw (see Remarks). A few large sockets near the tarsus tip (Fig. 18C) suggest that macrosetae were also present here. A large spine occurs disto-mesially (Fig. 18A, B) but its insertion is uncertain. Given the presence of a tarsal claw (absent in mature males), and the lack of any modifications of the tibia (usually adult males have apophyses on the tibia), it is most likely that this is a subadult male (see Remarks). The indications of structural detail within the tarsus suggest that the palpal organ is developed inside and ready to emerge at the next, final moult.

Legs I, II and III are rotated so that their anterior faces point upwards, and the legs are therefore latergrade. All femora bear a row of macrosetae which, on the anterior legs, are directed upwards. The scopula on
leg I runs from near the proximal end of the tibia, and along the whole of the metatarsus and tarsus. The tips of most of the scopular setae are broken off, but some show spatulate terminations (Fig. 20D). Tarsi bear three claws: pectinate paired claws and a non-pectinate unpaired claw, together with fimbriate accessory claws (sigmoid macrosetae with a ventral row of tiny spines). Such an arrangement is typical of a web-dwelling spider.

The opisthosoma is subcircular in outline; its central area appears more rigid than the lateral regions, though it shows no evidence of being a true sclerite. It appears to have been somewhat flattened in life because there is little evidence of compression apart from some wrinkling of the cuticle outside of the central area. Anteriorly, in the region of the pedicel, there is a triangular sclerite which appears concave on the part and raised on the counterpart; for this reason, it is assumed to be dorsal, and therefore a lorum (dorsal sclerite of the pedicel). Conversely, the larger, anterior spinnerets appear raised on the part and form depressions on the counterpart; these are, of course, ventral structures.

Additional specimens of Onychopalpus thomisoides gen. et sp. nov. Five additional specimens, NIGP148237, NIGP168490a,b, NIGP168489, NIGP168491a,b and NIGP168492, have been identified as belonging to Onychopalpus thomisoides gen. et sp. nov. They are all smaller than the holotype and have a pedipalp tarsus that is not swollen, and thus are presumed to be juveniles. Both NIGP148237 and NIGP168490a,b (Figs 23, 25, 26) consist of part and counterpart of complete specimens. They show the three tarsal claws (simple median claw and pectinate paired claws) and leg I scopulae particularly well. NIGP148237 shows evidence of the stridulatory file on the chelicera. NIGP168489 consists of the part only, showing the ventral side (Fig. 24). The proximity of the coxae to one another suggests a narrow sternum. There are spatulate setae on leg I tibia to tarsus, and the three tarsal claws are seen rather well. NIGP168491a,b consists of part and counterpart and shows the chelicerae with their characteristic peg teeth and some evidence of stridulatory file. NIGP168492 consists of part only, showing the ventral side (Fig. 29). This specimen shows only one chelicera, the pedipalp tarsus and only parts of the legs. Nevertheless, enough morphology is present to suggest it belongs to the same species.

New specimens of Sinaranea metaxyostraca. NIGP168494 (Fig. 34), part only, is squashed anteroposteriorly, so it looks like a frontal view of the animal. A squarish area marks the front part of the carapace, below which lie the chelicerae. Some setae mark where the pedipalps are likely to be, but there is no evidence to determine the sex of the animal. To each side, the legs are splayed out. There is no trace of the opisthosoma. NIGP168492a,b, part and counterpart, is an almost completely preserved adult male (Figs 30, 31). It is reasonably well sclerotized on a pale matrix so the features can be seen easily, including the shape of the opisthosoma (Figs 30A, 31A), the chelicerae and pedipalps (Fig. 30D), spinnerets (Fig. 31D) and leg podomeres, including the scopulae of spatulate setae (Figs 30C, 31C) and tarsal

![Figure 12. Caestaranea jurassica gen. et sp. nov., ?juvenile female NIGP168486a,b, under ethanol. A, part. B, counterpart. C, explanatory drawing of A. Scale bar = 1 mm.](image-url)
claws (Fig. 31C, E). Specimen NIGP168493a,b, part and counterpart, is another nicely preserved adult male (Figs 32, 33). It lies on the edge of a block, and so is missing the distal podomeres of legs I (patella-tarsus) and II (right distal tarsus, left metatarsus-tarsus) on the part. The part shows clear carapace features, pedipalps and chelicerae, including stridulating ridges, as well as the legs; the counterpart shows mostly ventral features, including the chelicerae and pedipalps.

Sinaranea brevicrus sp. nov. Two specimens, the holotype adult male NIGP168495 and the allotype adult female NIGP168496a,b, of this new species are known. NIGP168495 is almost entirely the part (Figs 35, 36); the counterpart is a tiny fragment bearing the counterpart metatarsus and tarsus of left leg IV (Fig. 36B). It is fairly complete, lacking only the tibia-tarsus of right leg IV and the patella-tarsus of the right pedipalp; however, their left counterparts are fully preserved. The caput region of the carapace is well delineated and the large chelicerae bear stridulating ridges laterally, and the pedipalp shows a spiral genital structure. NIGP168496a,b is poorly preserved overall (Fig. 37), but shows a very distinct scopula of spatulate setae on the anterior legs as well as the characteristic elongated patellae on leg I. Its overall morphology and dimensions and the simple pedipalp are evidence that it is the female of this species. The femora of this species are distinctly shorter than those of the type species, hence the new specific designation.

Methods

The specimens were prepared in parts with a fine chisel. They were studied and photographed dry, in both direct and low-angle light, and under ethanol (to enhance contrast) using a Leica M205C stereomicroscope, and photographed with Canon EOS 5D MkII and III cameras mounted on the microscope. Photographs were taken using DSLR Assistant (dslrassistant.com) and manipulated in Affinity Photo (affinity.serif.com). Older photographs were taken with Leica DFC 420C (Figs 1, 2, 5, 6, 13, 23, 24A, E–G, 25–28, 32D, 33, 35, 36), Nikon D1X (Figs 9, 10, 12, 14, 34, 37) or AxioCam HR3 (Fig. 24C, D, F) cameras mounted on Leica MZ microscopes using Nikon software and manipulated in Adobe Photoshop. Details of photographic methods can be found in Selden (2014). Drawings were made using Autodesk Graphic (graphic.com) from the photographs, with frequent checking back to the specimen. Measurements were made from the drawings using the analysis tools in Graphic.

Measurements of paired organs are averages of left and right of part and counterpart, i.e. maximally four measurements if all are preserved. Measurements were made only of complete podomeres, except where marked with \( \geq \) which is a minimum measurement of an incomplete podomere; measurements of coxae and trochanters are rather imprecise and uninformative. Length/width ratios are provided for carapace, opisthosoma, sternum and femora. Chelicera lengths include the fang. Leg total lengths are given as femur–tarsus; tarsus lengths include the claw. Leg formula (e.g. I > II > IV > III) indicates the length of each leg relative to the others, longest to shortest. Total body length excludes chelicerae and includes anal tubercle. Handedness of paired features refers to the position on the specimen, regardless of whether it may be ventral-side up, rather than the presumed position in life. All measurements are in mm.
Definitions of setae, macrosetae, spines and bristles are given in Selden et al. (2016); peg teeth are small macrosetae present on the pro- and/or retromargin of the chelicera in palpimanoid, mimetid and pararchaeine malkarid spiders, where true teeth (unsocketed) occur in other spiders (Forster & Platnick 1984). Trigger hairs are long setae that occur on the medial surface near the base of the chelicera paturon; in mecssmauchenidi and pararchaeine malkarids, whose chelicerae can lock open, stimulation of these setae causes the chelicerae to close (Wood et al. 2012, 2016).

Abbreviations

I, II, III, IV, leg numbers; as, anterior spinneret; at, anal tubercle; car, carapace; cx, coxa; ef, epigastric furrow; fe, femur; L, length; lb, labium; lo, lorum; mt, metatarsus; mx, maxilla; op, opisthosoma; pa, patella; Pd, pedipalp; sp, spinnerets; st, sternum; ta, tarsus; th, trigger hair; ti, tibia; tr, trochanter; ts, tracheal spiracle; W, width.

Phylogenetic methods

The new data were scored into the data matrix of Wood et al. (2012, appendix 2). Following the approach of this paper, we present a Bayesian analysis of this expanded version of the matrix. This was analysed using MrBayes v3.2.6 (parallel version; Ronquist et al. 2012), with two runs of four chains, three of which were heated. These ran for 5,000,000 generations, sampling every 500. 25% burn in was discarded. The analysis employed the Lewis (2001) discrete (morphology) model. We provide the NEXUS file, including MrBayes commands, in Supplementary Data. The tree presented here is a majority rule consensus generated by MrBayes, imported into R (R Core Team 2018). This was then plotted against a geological timescale using the package STRAP (Bell & Lloyd 2015), using the topology from MrBayes and branch lengths based on the fossil ages using the equal method. This was prepared for publication in Inkscape, and includes support values in the form of posterior probabilities for each clade.

Systematic palaeontology

Order **Araneae** Clerck, 1757
Suborder **Opisthothelae** Pocock, 1892
Infraorder **Araneomorphae** Smith, 1902
Superfamily **Palpimanoidea** sensu Thorell, 1870, Wood et al. (2012)

Diagnostic features. Palpimanoids are ecribellate spiders that share a combination of non-exclusive characters (see Wood et al. 2012, appendix 3). The most notable morphological characters seen in the fossils are the chelicera peg teeth, on both pro- and retromargin and clustered near the fang tip, the scopulae of spatulate setae on the tibia-tarsus of leg I, and the elevated cephalic region of the carapace. Other synapomorphies are discussed below.

**Caestaranae** gen. nov.

Type species. **Caestaranae jurassica** sp. nov.

Diagnostic. Palpimanoid with distinct male pedipalp tarsus resembling a boxing glove, bearing strongly sclerotized cymbium, subequant in outline; with relatively short legs (fe I/ch L ratio < 1.5 and leg I L/body L < 1.3); leg III not greatly shorter than leg I (mean ratio); legs lacking macrosetae except for few bristles on distal margin of metatarsi.
Derivation of name. Latin *caestus*, a battle glove, referring to the male pedipalp that resembles a boxing glove, and *aranea*, a spider.

Remarks. The new genus *Caestaranea* is placed in this superfamily because it shows a number of palpimanoid synapomorphies (see Wood et al. 2012, appendix 3). The enlarged, porrect chelicerae bearing peg teeth and stridulatory ridges are characteristic for the superfamily. The chelicerae are distinctly protrusive, though whether they emerge from a foramen is unclear. Peg teeth are known

Figure 16. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, anterior prosoma, under ethanol. A, part, carapace and chelicerae. B, explanatory drawing of A. C, counterpart, chelicerae showing peg teeth clustered near the tip of the fang and extending the length of the paturon edge. D, explanatory drawing of C.
to occur in non-palpimanoid families (e.g. Mimetidae, pararchaeine Malkaridae), but Caestaranea is quite unlike any of these; moreover, that the peg teeth occur on both pro- and retromargins of the chelicerae, and are clustered around the tip of the fang, is peculiar to Palpimanoidea. Stridulating ridges on the paturon occur in numerous families (see Uhl & Elias 2011 for a review) but, again, Caestaranea differs markedly from most of these. The scopula of spatulate setae on leg I is a distinctive feature of palpimanoids. In many palpimanoids, the pectinate paired claws on the tarsi are more comb-like on leg I while the teeth on the claws of leg IV are more widely spaced (Wood et al. 2012, fig. 7d, e). The same is true for Caestaranea. Also, trigger hairs, similar to those described for mecysmaucheniids and pararchaeine malkarids, are present on the chelicerae, suggesting some function in stimulating rapid closure of the chelicerae.

Caestaranea differs from other palpimanoids in its lower caput on the carapace, which is still clearly raised and well demarcated, the possible absence of a cheliceral foramen and lack of a sclerotized ring around the spinnerets. It differs from Sinaranea in the shape of the male pedipalp.

The new genus is defined by the male pedipalps, which resemble boxing gloves. These show a distinctive, well-sclerotized tarsal cymbium that completely covers the (presumed less well-sclerotized) bulb, embolus and other genitalia. Because the cymbium obscures the genital structures, these pedipalps give the appearance of being subadult males whose genital structures have not yet erupted. However, the cymbium is well sclerotized and distinctly enlarged. A number of specimens show a circular structure in the distal half, a median line, distal macrosetae, and a prominent retrolateral macroseta (e.g. Figs 1F, G, 2D, E, 6C, D, 7E, 8C), features that suggest a fully formed adult pedipalp. Interestingly, the genital structures of the pedipalps of the extant Huttoniidae (see, for example, Paquin et al. 2010, figs 18.4, 18.5) are concealed inside an enclosing cymbium, and those of Spatiatoridae and Vetiatoridae, extinct families of palpimanoids (see, for example, Petrunkevitch 1942, fig. 182; Wunderlich 2006, figs 2–4, 2008a, figs 1, 2, 2015, figs 283, 286, 287, 2017a, fig. 1, 2017b, fig. 202), are also simple and do not protrude beyond the cymbium. In this respect, the pedipalps of the new genus Caestaranea somewhat resemble those of Huttonia Pickard-Cambridge, 1879 figured by Paquin et al. (2010).

Caestaranea differs from Onychopalpus gen. nov. in that the holotype specimen of the latter shows a dentate claw on the male pedipalp, and its tarsus, while slightly inflated, lacks the sclerotization seen in Caestaranea, and hence Onychopalpus is considered to represent a subadult male (see below). No claw is seen on the male pedipalps of Caestaranea, which is further evidence that they belong to adults. Moreover, the leg I scopula is weak in Caestaranea males, in comparison to that on the Onychopalpus subadult male, suggesting that prey capture function is reduced in adult males while they search for females. The supposed adult females of Caestaranea are considered as such because of their larger size (mean body L of females 5.11, males 3.97) and simple palps; moreover, some structures are visible in the opisthosoma of the allotype specimen NIGP168481a,b (Fig. 4).

**Caestaranea jurassica** sp. nov.
(Figs 1–14)

2008 Sinaranea metaxyostraca: Selden, Huang & Ren additional specimen NIGP148236: 317, figs 33, 34.
2008 Sinaranea metaxyostraca: Selden, Huang & Ren
additional specimen NIGP148238: 317, figs 37, 38.
2008 Sinaranea metaxyostraca: Selden, Huang & Ren
additional specimen NIGP148239: 317, figs 39, 40.

Diagnosis. As for the genus (monotypic).

Derivation of name. After the Jurassic period during which the species was alive.

Material. Holotype: NIGP168480a,b adult male; allo-
type NIGP168481a,b adult female; paratypes NIGP168482,
NIGP168483, NIGP168484a,b, adult males; additional
specimens NIGP148238, NIGP148239a,b, NIGP168485,
adult? females, NIGP168486a,b, juvenile? female,
NIGP168487, juvenile male, NIGP148236, juvenile.

Occurrence. Jiulongshan Formation, Middle Jurassic;
Daohugou Village, Shantou Township, Ningcheng
County, Inner Mongolia, China.

Description of male. Based on holotype
NIGP168480a,b (Figs 1, 2) and paratypes NIGP168482
(Fig. 5), NIGP168483 (Fig. 6), NIGP168484a,b (Figs 7,
8) and NIGP168485 (Fig. 11). For specimen measure-
ments see Table 1. Body L 3.74–4.25. Carapace slightly
longer than wide, L 1.64–2.08, W 1.25–1.67, L/W ratio
1.14–1.31, with well-demarcated sub-semicircular caput
region (raised in life). Sternum longer than wide, scuti-
form, with gently scalloped border, L 0.56–0.69, W
0.40–0.42, L/W ratio 1.33–1.73 (Figs 1A, 2A, 8C).
Chelicera L 0.92–1.27, W 0.57–0.70, L/W ratio
1.56–1.81, with row of peg teeth along mesial edge of
paturon and on margins of cheliceral furrow, cluster of
large peg teeth near tip of fang; one or two long, thin
setae (trigger hairs) proximally (Figs 1F, G, 2D, F, 6A,
B, 7E, 8C); short, curved fang (L 0.38–0.55) situated
distally. Pedipalp tarsus of boxing-glove type, sub-oval
in outline, with longitudinal seam dorsally, bearing long
bristle mesiolaterally (Figs 1F, G, 2D, E, 6A, B); distal
subcircular foramen; total L (f) 1.75–2.19. Leg for-
"omula I > II > IV > III, legs I, II and IV approximately
equal in length, not greatly longer than leg III (ratio leg I
L/leg III L 1.43–1.50); tarsi shorter than metatarsi (mean
ta/mt ratio 0.53–0.78); legs lacking macrosetae except few
thin bristles at distal margin of metatarsi; scopulae on leg
I poorly developed (Figs 1C, D, 2C, D); tarsi with pecti-
nate paired claws, comb-like on leg I (Figs 1C, D, 2C, 5C,
D, 7C), sparser on other legs (Figs 1E, 7D). Leg lengths:
leg I 4.30–5.13, leg II 3.98–4.80, 4.80, leg III 2.61–3.48
and leg IV 3.58–4.53. Opisthosoma sub-circular in out-
line, L c. 2.20–2.41, W c. 1.87–2.25, L/W ratio c.
1.00–1.20, with darker (more sclerotized) central area, L
.88–1.14, W 0.76–1.04, L/W ratio 1.10–1.35. Spinnerets
subterminal (Figs 1A, B, 2A, B, 7A, B, 8A, B).

Description of female. Based on allotype
NIGP168481a,b (Figs 3, 4), and specimens

Figure 18. Onychopalpus thomisoides gen. et sp. nov., holotype NIGP168488a,b, pedipalps, under ethanol. A, part, pedipalp tarsus of left side, left arrow points to part of claw, right arrow to large spine. B, part, pedipalp tarsus of right side, spine arrowed. C, detail of claw and setae shown in B.
Carapace sub-oval, L 2.07

specimen measurements see

than leg III (ratio leg I L/leg III L 1.26

with small claw (L 0.55

Pedipalp bearing thin macrosetae on ti

(L 0.55

present at proximal end of peg tooth row (L 0.65) perpendicular to long axis of paturon. Pedipalp bearing thin macrosetae on ti–ta (> 3 on ta), ta with small claw (Fig. 11C); total L (fe–ta) 2.19–2.58. Leg formula I > II/IV > III, legs short, leg I somewhat longer than leg III (ratio leg I L/leg III L 1.26–1.74), few thin macrosetae e.g. c. 6 on distal mt; scopula on tibia–tarsus I; tarsi shorter than metatarsi (mean ta/mt ratio 0.56–0.84).

Leg lengths: leg I 4.42–5.96, leg II 3.72–4.67, leg III 3.29–3.51 and leg IV 4.80–4.91. Opisthosoma sub-circular in outline (sub-spherical in life), covered in bristles, L c. 2.72–3.01, W c. 2.27–2.73, L/W ratio c. 1.10–1.33; spinn

etrs c. one-third of the length of opisthosoma from posterior, semicircular structures on counterpart suggest presence of epigyne (Fig. 4).

Description of juveniles. For specimen measurements see Table 1. Juvenile female NIGP168486a,b (Fig. 12): description as for female, but smaller dimensions; leg formula I > II > IV > III, legs short, leg I somewhat longer than leg III (ratio leg I L/leg III L 1.27). Juvenile male NIGP168487 (Fig. 13): description as for male, but smaller dimensions; pedipalp with slightly expanded, more sclerotized tarsus; leg formula I > IV > II > III, legs short, leg I somewhat longer than leg III (ratio leg I L/leg III L 1.27), opisthosoma sub-circular in outline, covered in bristles. Juvenile specimen NIGP148236 (Fig. 14): small specimen, description as for female; pedipalp simple; leg formula I > II > IV > III, legs short, leg I not greatly longer than leg III (ratio leg I L/leg III L 1.49); tarsi nearly as long as metatarsi (mean ta/mt ratio 0.86); opisthosoma with darker (more sclerotized) central area, remainder of cuticle setose.

Onychopalpus gen. nov.

Type species. Onychopalpus thomisoides sp. nov.

Diagnosis. Palpimanoid with strong, laterigrade legs I–II with anterior surfaces facing upwards, scopula of spatulate setae along tibia, metatarsus and tarsus of leg I, femora with row of large macrosetae, subadult male pedipalp with pectinate claw.

Derivation of name. Latin onycho-, clawed (from Greek ὀνυχός, a claw), and Latin palpus, the palm of the hand, referring to the claws on the male pedipalp.

Remarks. Onychopalpus differs from other palpimanoids in its habitus: it is very large (holotype body length 9.75 mm, leg span c. 23 mm) – indeed, the largest palpimanoid known – and has laterigrade legs, thus resembling members of the Thomisidae (crab spiders). Onychopalpus is clearly not a thomisid because of its three tarsal claws (thomisids have two), lack of claw tufts and the peg teeth on the chelicerae (thomisid chelicerae generally lack teeth), and other characters of this family are lacking (see Benjamin 2011 for a review of Thomisidae).

Among the features of Onychopalpus is its rather elongated sternum, though the shape in the fossil may
reflect, to some extent, compression of the surrounding coxae onto the sides of the sternum (Figs 15B, D, F, 16C, D, 24A, B, 27A, B, E, 29A, B). A narrow sternum is uncommon in spiders, but is a characteristic of meso- theles, and occurs in elongate spiders, e.g. *Deinopis* MacLeay, 1839, *Miagrammopes* Pickard-Cambridge, 1870, some segestriids and salticids. It is rare in thom- sids (except the elongate *Monaeses* Thorell, 1869), but the palpimanoid *Eriauchenius* Pickard-Cambridge, 1881 (Arachaeidae) has a similar elongate sternum with impinging coxae (Petrunkevitch 1955, fig. 101.4c; Murphy & Roberts 2015, pl. 122) as *Onychopalpus*. The sternum is also longer than wide in *Caestaranea* gen. nov. (e.g. Figs 1A, B, 2A, B, 3, 6A, B, 7A, B).

A most unusual feature of the new genus is the presence of a pectinate claw on the male pedipalp tarsus (the cymbium in the mature pedipalp). The distribution of pedipalp claws among spider families is poorly studied (Jäger 2004). A single claw on the pedipalp of immatures of both sexes and of adult females is not uncommon, and this claw may be pectinate. A claw-like spine occurs on the adult male pedipalp of several species of the lycosid genera *Acantholycosa* Dahl, 1908, *Pardosa* Koch, 1847, *Trochosa* Koch, 1847, *Venatrix* Roewer, 1960 (Framenau & Vink 2001; Vink 2002; Framenau 2006, 2007) and *Ovia* Sankaran, Malamel & Sebastian, 2017. It is usually single, but up to three can occur at the tip of the cymbium in adult males of some species, e.g. *Pardosa truili* (Pickard-Cambridge, 1873) (Almqquist 2005, p. 230). Similar claw-like macrosetae occur on the male palps of several zodariid genera (Jocqué 1991), e.g. *Cavasteron* Baehr & Jocqué, 2000, *Diores* Simon, 1893, and some, such as *Dasmadiiores* Jocqué, 1987, *Heredida Simon*, 1893, *Palaestina* Pickard-Cambridge, 1872, *Palfuria* Simon, 1910, *Ranops* Jocqué, 1991 and *Tropizodium* Jocqué & Churchill, 2015, show dentate macrosetae as well as a claw-like macroseta at the cymbal tip. Female zodariids commonly have a well-developed, pectinate claw on the pedipalp tarsus, and a similar claw can occur on the pedipalp tarsus of the subadult male, e.g. in *Mallinus nitidiventris* Simon, 1893, the lectotype of which is a subadult male with a swollen palpal tarsus and a pectinate claw (Jocqué 1991). Determining the presence of so-called claws on the pedipalp of mature males is confusing because short macrosetae (spines) may also occur there. Almqquist (2005), in describing lycosids, distinguished between claws, macrosetae and spines (e.g. in *Alopecosa* Simon, 1885) on the tip of the cymbium. Harm (1931, figs 17–20) illustrated *Segestria bavarica* Koch, 1843 pedipalps with spines, claw and macrosetae on the developing male pedipalp. It has been supposed that the palpal organs of the male spider were derived from the apotele (the three tarsal claws and the base into which tendons are inserted) of the tarsus (Barrows 1925; Harm 1931), with the claws becoming the embolic division. Pedipalp tarsal claws co-exist with the developing palpal bulb, so there can be no direct homology (Coddington 1990). However, no male spider bears true claws on the adult cymbium; the claw-like features on the tip of the cymbium in lycosids and zodariids, described above, are almost certainly modified macrosetae. This was the opinion of Comstock (1910), but Chamberlin (1908) considered the (up to three) distal macrosetae in lycosids to be modified claws. For this reason, the pedipalp of *Onychopalpus* is considered to be that of a subadult male. It is unusual in being pectinate because median claws are usually simple – as, indeed, are those on the leg tarsus in this genus.

*Onychopalpus thomisoides* sp. nov. (Figs 15–29)

2008 *Sinaranea metaxyostraca* Selden, Huang & Ren: 317 (additional specimen NIGP148237), figs 35, 36.

Diagnosis. As for the genus (monotypic).

Derivation of name. Named after the general resemblance of the spider to members of the family Thomisidae.

Material. Holotype: NIGP168488a,b, subadult male. Other material: NIGP148237, NIGP168489, NIGP168490a,b, NIGP168491a,b and NIGP168492, all juveniles.

Occurrence. Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Description of subadult male. Specimen NIGP168488a,b (Figs 15–22). For measurements see Table 2. Body L (including anal tubercle) 7.90. Carapace slightly wider than long (L 3.11, W 3.27, L/W

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**Figure 20.** *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, legs, under ethanol. A, part, metatarsus and tarsus of leg I on left side, showing scopulae extending from base of metatarsus to tip of tarsus; circular pale patches on tarsus are artifacts of preparation. B, part, tibia, metatarsus and tarsus of leg II on left side, showing numerous setae, but not scopulae, along ventral metatarsus and tarsus, and macrosetae on tibia. C, part, tibia of leg I on left side, showing scopula. D, part, detail of scopulae on distal metatarsus and proximal tarsus of leg I on left side (see A); spatulate tips to setae are mostly missing, but can be seen in places (arrowed). E, part, patella-tibia of leg IV on left side. F, part, leg IV tibia of left side, showing trichobothria (arrowed). G, counterpart, leg III tibia of left side, showing trichobothria (arrowed). H, counterpart, leg III tibia of right side (i.e. same as G), showing trichobothria (arrowed). I, part, leg I tibia of right side, showing trichobothria (arrowed).
Figure 21. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, tarsi, under ethanol (except I). A, part, tip of tarsus of leg I on left side; circular pale patches are artifacts of preparation. B, part, tarsus of leg II on left side. C, part, tarsus of leg III on left side. D, counterpart, tarsus of leg III on left side, showing fimbriate accessory claw (arrowed). E, part, tarsus of leg IV on right side. F, part, tarsus of leg IV on left side. G, part, tarsal claws of leg I on left side (as A), showing pectinate paired claws and fimbriate accessory claws (arrowed). H, part, tarsal claws of leg IV on right side (as D), showing fimbriate accessory claw (arrowed). I, counterpart, tarsus of leg III on left side, showing fimbriate accessory claw (arrowed). J, counterpart, tarsus of leg III on left side (same as I), under ethanol (as D), showing non-pectinate unpaired claw (arrowed) and pectinate paired claws.
Figure 22. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, opisthosoma. **A**, part, showing lorum, more rigid central dorsal area, anterior spinnerets and anal tubercle, dry. **B**, counterpart, showing lorum, anterior spinnerets and anal tubercle, dry. **C**, part, opisthosomal bristles, under ethanol. **D**, part, anal tubercle, under ethanol. **E**, counterpart, spinnerets, under ethanol.
Description of juveniles. Based on specimens NIGP148237a,b (Fig. 23), NIGP168489 (Fig. 24), NIGP168490a,b (Figs 25, 26), NIGP168491a,b (Figs 27, 28) and NIGP168492 (Fig. 29). For specimen measurements see Table 2. Body L 3.10–6.00. Carapace slightly longer than wide, L 1.62–2.77, W 1.38–2.43, L/W ratio 1.01–1.17. Caput wider than long (L/W ratio 0.61–0.81), occupying nearly half of anterior carapace, with numerous, forward-pointing macrosetae (Figs 25A, C, 28A). Chelicera L 0.96–1.62, W 0.67–0.98, L/W ratio 1.29–1.65, with single row of peg teeth running from near base of paturon along mesial margin to near fang tip, cluster of larger peg teeth near fang tip, then continuing as rows along pro- and retromargins of cheliceral furrow (Figs 16C, D, 17); dorsal surface of paturon covered in bristles, ventral surface sparsely setose (no trigger hairs visible), with field of stridulating ridges occupying proximolateral quarter of paturon surface (Fig. 17A).

Pedipalp with inflated tarsus bearing pectinate claw (possibly one of a pair) with ≥7 blade-like teeth and stout spine distally on mesial side (Fig. 18), total L (fe–ta) ≥ 4.52. Leg formula I > II > IV > III; legs I (L 12.94) and II (L 11.28) considerably longer than leg III (L 7.47); femora of legs I, II and IV thicker (L/W ratios 3.71–3.72) than femur III (L/W ratio 2.83). Legs latergrade, estimated leg span 23. Leg I bearing scopula of thin setae with spatulate tips (Fig. 20A–D), extending along entire ventral surface of tibia, metatarsus and tarsus (ventral surface of leg is turned to face anterior). Patella I rather large (L 1.84) compared to patellae II–IV (L 1.47, 1.14, 0.99, respectively). Leg tarsi relatively short, mean ta/mt ratio 0.66, slightly constricted proximally, bearing three claws: paired claws pectinate with ≥7 blade-like teeth; median claw small, hooked, lacking teeth; at least two fimbriate accessory claws (Fig. 21G–J). Main (distal) tooth of paired claw becoming more elongate from leg I (Fig. 21A) to more posterior legs (Fig. 21D, J). Conspicuous row of macrosetae along anterior face of femora of legs I (≥7) and II (≥4) (these femora faced dorsally in life) (Fig. 19). Posterior surfaces of femora I and II (facing ventral in life) with longitudinal strip lacking setae; similar glabrous strip on ventral surfaces of femora III and IV. Other macrosetae on legs: ventral femora I and II, anterior femur III, dorsal femur IV; two rows, dorsal and anterior, on tibiae; numerous on metatarsi, especially ventrodistally and clustered at distal end (Fig. 21A–F). Few trichobothria in proximal half of dorsal tibia (Fig. 20F–I).

Opisthosoma sub-circular in outline, slightly wider than long: L 4.75, W 3.27, L/W ratio 0.96; dorsal median area sub-circular in outline: L 2.74, W 2.61, L/W ratio 1.05; dorsum covered in strong bristles (Fig. 22A–D). Triangular lorum present anteriorly, L 0.43, W 0.50, L/W ratio 0.86 (Fig. 22A, B). Anal tubercle situated at posterior of opisthosoma. Spinnerets six, subterminal, no sclerotized ring; anterior spinneret largest, two-segmented, others very small (Fig. 22D). Tracheal spiracle just anterior to spinnerets.

Figure 23. Onychopalpus thomisoides gen. et sp. nov., specimen NIGP148237, under ethanol. A, whole specimen, part. B, whole specimen, counterpart. C, explanatory drawing of A. D, explanatory drawing of B. E, part, chelicerae showing peg teeth, thin setae and remnants of stridulatory file on lateral edge of paturon of left chelicera, and palps showing distal tarsal macrosetae. F, part, leg I metatarsus and tarsus showing scopulae and tarsal claws, and leg II tarsus showing claws. G, part, left leg IV distal metatarsus showing ventrodistal macrosetae and tarsus showing claws. H, part, right leg IV distal metatarsus showing ventrodistal macrosetae and tarsus showing claws. I, part, left leg III distal metatarsus showing ventrodistal macrosetae and tarsus showing claws. Scale bar = 1 mm.

*Sinarannea* Selden, Huang & Ren, 2008

**Type species.** *Sinarannea metaxyostraca* Selden, Huang & Ren, 2008.

**Emended diagnosis.** Palpimanoids with a low but well-demarcated caput region of the carapace; male pedipalp bearing a spiral structure; macrosetae on walking legs (distally in *S. brevicrus*); lacking sclerotized ring around spinnerets.

**Remarks.** *Sinarannea metaxyostraca* was placed in Palpimanoidea incertae sedis by Selden et al. (2008) because of its obvious palpimanoid synapomorphies but without any particular characters that could place it within any described palpimanoid family. Now that a second species, *S. brevicrus*, of this genus has been discovered and more specimens of the type species, *S. metaxyostraca*, have been found, the genus has become more clearly recognizable. It is placed in Palpimanoidea.
Figure 25. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168490a,b, under ethanol. A, whole specimen, part. B, whole specimen, counterpart. C, explanatory drawing of A. D, explanatory drawing of B. Scale bar = 1 mm.
on account of the enlarged, porrect chelicerae, cheliceral peg teeth, stridulating ridges on the chelicerae, raised carapace caput, and scopula of spatulate setae on leg I tibia, metatarsus and tarsus. Cheliceral trigger hairs are present in *Sinaranea metaxyostraca*, and the superior claws of leg I in *Sinaranea brevicrus* appear to be more comb-like than those of leg IV. *Sinaranea* shows a characteristic male pedipalp with a small cymbium and spiral genital apparatus. The original diagnosis of the genus, “combination of elongate leg I 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” (Selden et al. 2008, 314), was too general to be useful; the emended diagnosis refers to features that are present on the holotype of the type species as well as the new species described herein. *Sinaranea* differs from other palpimanoids by apparently lacking the cheliceral foramen and the sclerotized ring around the spinnerets, and from *Caestaranea* and *Onychopalpus* by the form of the male pedipalp.

*Sinaranea metaxyostraca* Selden, Huang & Ren, 2008
(Figs 30–34)

2008 *Sinaranea metaxyostraca* Selden, Huang & Ren: 316, figs 25–32.
non 2008 *Sinaranea metaxyostraca*: Selden, Huang & Ren additional specimen NIGP148236: 317, figs 33, 34.
non 2008 *Sinaranea metaxyostraca*: Selden, Huang & Ren additional specimen NIGP148237: 317, figs 35, 36.
non 2008 *Sinaranea metaxyostraca*: Selden, Huang & Ren additional specimen NIGP148238: 317, figs 37, 38.
non 2008 *Sinaranea metaxyostraca*: Selden, Huang & Ren additional specimen NIGP148239: 317, figs 39, 40.

**Emended diagnosis.** *Sinaranea* with long legs (e.g. fe 1/car L > 1.7; fe 1/body L > 0.5; fe 1/ch L > 2.6), bearing macrosetae.

**Material.** Holotype: NIGP148830a,b (part and counterpart), adult male. Additional specimens: NIGP168493a,b (part and counterpart), adult male; NIGP168494 (part only), sex unknown; and NIGP168492a,b (part and counterpart), adult male. Specimens NIGP148236, NIGP148237, NIGP148238 and NIGP148239a,b, were referred to as additional specimens by Selden et al. (2008). NIGP148237 is here removed from *S. metaxyostraca* and placed in *Onychopalpus thomisoides* gen. et sp. nov. and NIGP148236, NIGP148238 and NIGP148239a,b, are removed from *S. metaxyostraca* and placed in *Caestaranea jurassica* gen. et sp. nov.

**Occurrence.** Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.
Remarks. In the original paper (Selden et al. 2008) four specimens in addition to the holotype were placed in *Sinaranea metaxyostraca* and were presumed to be juveniles. They differ from the holotype in numerous ways, and so have been reassigned. However, some additional specimens that are clearly conspecific with *S. metaxyostraca* have been identified and are described below. In this species, the cephalic area of the carapace
is noticeably demarcated, and presumably raised in life, but not elongated or with a neck. The opisthosoma bears a small, sub-circular dorsal dark area, previously called a scutum (Selden et al. 2008, figs 26, 28) though how sclerotized it was in life is not clear. The chelicera is robust but not elongated, bearing characteristic rows of leg teeth and a lateral stridulatory organ. The legs are relatively long, with leg I about twice the length of leg III, with the formula I > II > IV > III. The patella of leg I is noticeably elongated compared to those of other legs. All legs bear numerous macrosetae, especially distally, and there is a scopula of spatulate setae on leg I tibia to tarsus. The tarsi are relatively short compared to the metatarsi. The male pedipalp is distinctive, with a spiral structure (embolus?) distally.

NIGP168492a,b and NIGP168493a,b are adult males, while the sex of NIGP168494 is unknown. The last specimen is preserved head-on.

**Description.** Based on NIGP168492a,b (Figs 30, 31), NIGP168493a,b (Figs 32, 33) (adult males) and NIGP168494 (Fig. 34) (sex unknown). For specimen measurements see Table 3. Body L 4.96–5.42, Carapace L 2.31–2.45, W 2.19, L/W ratio 1.12. Row of semicircular objects along front of carapace of NIGP168493b suggestive of eyes (Fig. 32C, E). Chelicera L c. 1.32–1.47, W 0.75–0.85, L/W ratio 1.73–1.77, bearing row of peg teeth on proximal and retromargin of fang furrow, continuing as single row from fang tip towards base of paturon, few denticles adjacent to fang; short, curved fang (L 0.59) situated distally; stridulatory ridges on lateral sides of paturon. Pedipalp with spiral structure (Figs 30D, 33A), total L 3.14–3.51. Legs relatively long, leg I about twice length of leg III, fe/ch L ratio 2.90–3.08; leg formula I > II > IV > III; macrosetae numerous on femora, tibiae and metatarsi, especially distally; tarsi about half length of metatarsi (mean ta/mt ratio 0.44–0.53), with three claws, paired claws pectinate, fimbriate accessory claws (Figs 31C, 32D, 33B, C). Tibiae with trichobothria. Leg lengths: leg I 12.02–12.34, leg II 9.96–10.95, leg III 6.24–7.04 and leg IV 7.05–8.52. Opisthosoma sub-circular in outline, slightly longer than wide, L c. 2.90–2.96, W 2.37–2.90, L/W ratio c. 1.00–1.25. At least two pairs of spinnerets subterminal in compact group (Fig. 31D).
Sinaranea brevicrus sp. nov.
(Figs 35–37)

Diagnosis. Sinaranea with shorter legs than S. metaxyostraca (fe I/car ratio c. 1 or less, cf. > 1.7 in S. metaxyostraca; FeI/body L ratio < 0.5 cf. > 0.5 in S. metaxyostraca); scopula present on legs I and II in female.

Derivation of name. Latin brevis, short, and crus, a leg, referring to the shorter legs of this species compared to the type species.
Figure 30. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168492a,b, part. A, whole, dry. B, explanatory drawing of A. C, left leg I tibia-tarsus, showing macrosetae, scopulae and tarsal claws, under ethanol. D, chelicerae and palps, under ethanol. Scale bar = 1 mm.
Figure 31. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168492a,b. A, counterpart, whole, dry. B, explanatory drawing of A. C, part, right leg I tibia-tarsus, showing macrosetae, scopulae, tarsal claws and fimbriate accessory claws (arrow), under ethanol. D, part, spinnerets and anal tubercle, under ethanol. E, counterpart, distal metatarsi and tarsi of legs IV, showing macrosetae and tarsal claws. Scale bar = 1 mm.
Figure 32. *Sinaranea metaxyostra*ca Selden, Huang & Ren, 2008, specimen NIGP168493a,b, under ethanol. **A,** part, whole. **B,** explanatory drawing of **A.** **C,** explanatory drawing of **E.** **D,** part, leg IV tarsi showing claws. **E,** counterpart, whole. Scale bar = 1 mm.
Material. Holotype NIGP168495 (part only), adult male; allotype NIGP168496a,b (part and counterpart), adult female.

Occurrence. Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Description of adult male. Based on holotype NIGP168495 (Figs 35, 36). For detailed measurements see Table 3. Body length / eye 4.18. Carapace longer than wide, L 2.11, W 1.65, L/W ratio 1.27, cephalic region clearly demarcated (likely raised in life), L 0.93. Chelicerae large, L 1.37, W 0.75, L/W ratio 1.83, robust, peg teeth along both sides of cheliceral furrow, stridulating ridges on lateral surface of paturon, fang L 0.59. Pedipalp short, with spiral genital structure (embolus?) on tarsus, total L 2.12. Leg formula I > II > IV > III, legs I and II approximately equal in length, podomeres slender, patella I longer (0.85) than patellae II–IV (0.52, 0.44, 0.48, respectively); macrosetae thin, sparse, mainly on distal ends of podomeres, especially metatarsi (Fig. 36B), no large macrosetae on femora or tibiae; weak scopula of thin, clavate setae on tibia, metatarsus and tarsus of leg I; tarsi about half length of metatarsi (mean ta/mt ratio 0.53), with simple median claw and pectinate paired claws bearing ≥ 6 teeth, comb-like on leg I (Fig. 36C), becoming more elongated and talon-like on posterior leg tarsi. Leg lengths: leg I 6.63, leg II 6.45, leg III 4.42 and leg IV 5.65. Opisthosoma outline not clear, L ≥ 2.0, W ≥ 1.67, L/W ratio 1.20, covered in bristles; median darker region (sclerotized in life) subtriangular (Fig. 35).

Description of female. Based on allotype NIGP168496a,b (Fig. 37). For detailed measurements see Table 3. Carapace about as long as wide, cephalic region clearly demarcated (likely raised in life), L 2.67, W 2.53, L/W ratio 1.06. Chelicerae large, robust, bearing peg teeth, L 1.88, W 1.07, L/W ratio 1.76 (Fig. 37C). Pedipalp simple, ta claw not visible. Podomere lengths: pa 0.56, ti 1.21, ta 1.03. Leg formula I > II > IV > III; patella of leg I elongated; scopulae of spatulate setae on leg I ti and mt, and leg II mt (Fig. 37E), macrosetae only at distal ends of podomeres (Fig. 37D); paired tarsal claws pectinate (Fig. 37D). Leg lengths: leg I 10.26 and leg II 9.71. Opisthosoma outline not clear, covered in bristles.

Family Archaeidae Koch & Berendt, 1854

Patarchaea Selden, Huang & Ren, 2008

Type species. Patarchaea muralis Selden, Huang & Ren, 2008.
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 (after Selden et al. 2008).

Patarchaea muralis Selden, Huang & Ren, 2008

Material. Holotype: NIGP148828a,b (part and counterpart), adult female; allotype: SIM2005003-1 and SIM2005003-2 (part and counterpart), adult male; additional specimen NIGP148829, adult female.

Remarks. Since its original description in 2008, no additional specimens showing new features have been discovered.

Discussion

Phylogenetic placement
In order to discover where the taxa described here fit into the existing cladogram of palpimanoids, we added the new data into the matrix of Wood et al. (2012, appendix 2). Many of the characters used the analysis of Wood et al. (2012, appendix 1) could not be scored.
Figure 35. *Sinaranea brevicrus* sp. nov., holotype male NIGP168495, part, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. Scale bar = 1 mm.
because they are not visible in the fossils (e.g. characters 92–98, relating to female genitalia, and 101–108, relating to male genitalia), so these were treated as ?.

The modified matrix is present as a NEXUS file in Supplementary Data. Some important characters that could be scored are discussed below.

Character 15, sternum border: absent (0), present (1); a distinct line outlining the sternum is present in Caestaranea jurassica (Figs 8C, 11A), so this was scored as 1 for this species and ? for the others.

Character 23, pars cephalica (caput): unelevated (0), elevated (1); this was scored as 1 for all species because they all show a distinctly demarcated cephalic region.

Character 30, leg III metatarsus with distal comb or brush of setae or spines: all of the species described here show macrosetae distally on the posterior metatarsi (III and IV), but no true comb, so they are scored as 0 for this character.

Character 35, scopula on leg I position: Caestaranea shows a single row of scopula setae (1), while Onychopalpus (Figs 23F, 24D, 26B, D, E, 28C, D) and Sinaranea (Figs 26E, 31C, 37E) show scopulae on both sides of the leg (2). Where there are scopulae on both sides of the leg, the spatulate setae may be shaped differently, e.g. Sinaranea brevicrus allotype female (Fig. 37E) and S. metaxyostraca adult male (Fig. 31C). Similarly, Eriauchenius workmani Pickard-Cambridge, 1881 (Griswold et al. 2005, fig. 134D) shows two kinds of scopula setae. Character 37, scopula on leg II: this is absent in Caestaranea (0), but present (1) in the other taxa.

Character 39, relative length of patella and tarsus I: in all taxa described here, the patella is greater than or equal to the tarsus (1). Character 40, relative shape and size of superior tarsal claws I and IV: similar (0); in some taxa, e.g. palpimanids, huttoniids and mecysmaucheniids (Wood et al. 2012), the paired tarsal claws of leg I are comb-like, while those of leg IV more talon-like, with fewer teeth (1); and in some, e.g. mecysmaucheniids and archaeids (Wood et al. 2012), the paired claws of leg I are distinctly smaller than those of leg IV. The superior claws of leg I in Caestaranea (Figs 1C, 7C vs Fig. 7D) and Sinaranea brevicrus (Fig. 36B vs Fig. 36C) appear to be more comb-like (1), while those of Onychopalpus (Fig. 21) are barely different (0). Character 51, leg spination reduced or not: Caestaranea shows very sparse leg spination (1) whereas macrosetae occur on the legs of the other taxa described here (0). Characters 56 and 57,
chelicera trigger hairs: long setae in distinct follicles can be seen on the chelicerae at the proximal end of the peg-tooth row in Caestaranea (Figs 3, 6C, D, 11B, C) and Sinaranea metaxyostraca (Fig. 30D). These are scored as present (1) for character 56, and in one row (1) for character 57. No trigger hairs are visible on Onychopalpus or S. brevicrus, so these are scored as ? for both characters. Characters 58–60, cheliceral peg teeth, presence, on pro- and/or retromargins, and number of rows: these occur in all the taxa described, on both margins, and in numerous rows, hence they score 1 for all these characters. Characters 62 and 63, presence of cheliceral stridulatory ridges and their morphology: they occur on all the fossils described (1) and consist of uniform, densely spaced fingerprint ridges (0). Characters 65 and 66, peg teeth straight and all of same length on
Table 1. *Caestaranea jurassica* gen. et sp. nov., specimen measurements. Italics denote uncertain measurements.

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<tr>
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<td>0.56</td>
<td>0.67</td>
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<td>0.66</td>
<td>0.64</td>
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<td>1.05</td>
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</tr>
<tr>
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<tr>
<td>Leg III ti L</td>
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<td>0.75</td>
<td>0.65</td>
<td>0.83</td>
<td>0.91</td>
<td>0.84</td>
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<td>0.56</td>
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<td>0.70</td>
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(Continued)
the matrix of Wood et al. (2012) was used as a basis. So, the boxing-glove type of pedipalp characteristic of Caestaranea is also echoed in Onychopalpus and might suggest a closer relationship between these taxa. However, numerous other characters (e.g. scopulae) separate these taxa. Despite the new taxa being sister group to the remaining Palpimanoidea, they are not in any sense primitive. While they lack some extreme morphologies, e.g. the neck structures seen in archaeids, the new fossils do show specializations for different modes of prey capture to those seen in modern palpimanoid families.

**Modes of life**

Living palpimanoids are obligate or facultative araneophages, a feeding speciality shared with the Mimetidae, the jumping spider genus *Portia* Karsch, 1878, and many other species belonging to diverse families (e.g. Pekar et al. 2012; Pekar & Toft 2014). In nearly all palpimanoids and mimetids, this mode of feeding is highly derived and reflected in functional morphological adaptations. Both of these groups have peg teeth on the chelicerae (and they were, at one time, united phylogenetically: Forster & Platnick 1984). In the archaeids, for example, a greatly elongated neck, supporting an enlarged cephalic region of the carapace from which long, slender chelicerae emerge through a foramen, is adapted for capturing and restraining their dangerous spider prey (Wood et al. 2012). Fossil archaeids show similar morphologies, e.g. the Jurassic *Jurarchaea zherikhini* Eskov, 1987 and *Patarchaea muralis* Selden, Huang & Ren, 2008. Other fossil palpimanoids do not
Figure 38. Phylogeny of palpimanoid spiders and their outgroups from Bayesian analysis of morphological data, plotted against geological time using fossil dates and equal branch lengths (see methods). Numbers at nodes represent posterior probabilities. Based on the matrix of Wood et al. (2012, appendix 2) with the addition of the fossil taxa described here. † denotes fossil taxa. Compare with Wood et al. (2012, fig. 4).
show such exaggerated features – but neither do some modern palpimanoid families, e.g. Palpimanidae, yet they are also araneophagous predators (Pékár et al. 2011). For example, there is an undescribed palpimanid from the Cretaceous of Brazil (Selden & Penney 2017, fig. 16), and the palpimanoid Seppo koponeni Selden & Dunlop, 2014, from the Jurassic of Germany, which do not show extreme adaptations. Palpimanids avoid defensive reactions from their high-risk spider prey by having a thick cuticle, and another family of predominantly spider predators, the mimetids, bear long, strong macrosetae on leg I that are used to hold prey firmly (Pékár et al. 2011). Among fossil palpimanoids, the Cretaceous Lagonomegopidae, characterized by their large, laterally or anterolaterally directed anterior median eyes, show a wide range of morphologies that

Table 2. *Onychopalpus thomisoides* gen. et sp. nov., specimen measurements. Italics denote uncertain measurements.

<table>
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<th>168490a,b</th>
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<td>juv.</td>
<td>juv.</td>
<td>juv.</td>
<td>juv.</td>
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<td>4.64</td>
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<td>6.00</td>
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<td>1.62</td>
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<td>2.18</td>
<td>2.77</td>
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</tr>
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<td>0.59</td>
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</table>
suggest varied modes of life. Some, such as *Picturmegops* Wunderlich, 2015 (see Wunderlich’s fig. 255) resemble thomisids with good lateral vision, while others, e.g. *Koreamegops* Park, Nam & Selden, 2019, show a remarkable resemblance to salticids with their short legs, squat bodies and enlarged anterior median eyes in an anterolateral position.

The large *Onychopalpus thomisoides* shows a remarkable convergence with some crab spiders (Thomisidae).

Features of *Onychopalpus* that resemble those of many thomisids include the laterigrade stance, with leg I rotated and bearing macrosetae (in addition to scopulae) to act as a grasping appendage, the probable prominent eyes on the carapace (Fig. 16A, B) and the rotund opisthosoma. There are differences, however, in that thomisids generally carry grasping spines on the tibia-tarsus of leg I, rather than the femur, as in *Onychopalpus*; nevertheless, the functional anatomy is

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Table 3. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008 and *S. brevicrus* sp. nov., specimen measurements. Italics denote uncertain measurements.

<table>
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<th>S. metaxyostraca 168493a,b</th>
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<td>δ</td>
<td>?</td>
<td>δ</td>
<td>δ</td>
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<tr>
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<td>0.50</td>
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similar. Also, thomisids generally have small chelicerae. The overall impression of *Onychopalpus* is that of a pal-
palmimanoid spider convergent on the mode of life of a thomisid. So, we could expect that *Onychopalpus* was a sit-and-wait predator, lurking on vegetation for passing prey (possibly other spiders), which it then grabbed with its outstretched forelegs. Alternatively, prey could be caught by the large chelicerae and then gripped in a safe position by the scopulae and the femoral macrosetae.

In contrast to *Onychopalpus*, *Caestaranea* lacks strong femoral macrosetae on leg I, and its scopulae are much more poorly developed. Its legs are not laterigrade and leg I is not particularly longer than other legs (mean Leg I L/Leg III L ratio for *Caestaranea* = 1.49, for *Onychopalpus* = 1.72). Nevertheless, *Caestaranea* shows good palpimanoid characters, with enlarged, porrect cheli-
cerae arising from a raised, strongly demarcated caput region of the carapace, and bearing peg teeth in the standard arrangement. *Sinanareanae* shows better developed scopulae and also macrosetae on the legs, though not especially more developed on leg I. In contrast to *Caestaranea* and *Onychopalpus*, the legs of *Sinanareanae* are slender and either quite long (*S. metaxyostraca*) or shorter (*S. brevicrus*). They also show typical palpimanoid characters. In Mecysmauchenidae and pararchaeine Malkaridae, the chelicerae snap shut following stimulation of long, so-called trigger hairs, equivalent to those found in trap-jaw ants, *Odontomachus* Latreille, 1804 (Wood *et al.* 2012, 2016). Similar long setae have been reported from the Burmese amber *Lacuvaueninesis* Wunderlich, 2008b, and can be seen in *Caestaranea* and *Sinanareanae metaxyostraca*. In these fossils the chelicerae are commonly preserved splayed out at a wide angle, indicating they might have had some sort of trap-jaw mechanism triggered by stimulation of these setae. The identity of their prey can only be speculated upon, though araneophagy, as in most palpimanoids, is possible.

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**Supplemental material**

Supplementary material for this article can be accessed here: [https://doi.org/10.1080/14772019.2019.1584831](https://doi.org/10.1080/14772019.2019.1584831).

**References**


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