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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.

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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 Palpimanoidea. 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, *Jurararaneus 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 Jiulongshan Formation of China was described as *Mesarania hebeiensis* Hong, 1984, and placed in Araneoidea (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 archaeid, *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,

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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 Yanliao 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. Schütt (2000), in a study of the placement of Mimetidae 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 pararchaeids, micropholocomatines, 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 Entelegynae. The clade currently encompasses the families Archaeidae Koch & Berendt, 1854, Huttoniidae Simon, 1893, Mecysmaucheniidae Simon, 1895, Palpimanidae Thorell, 1870, and Stenochilidae Thorell, 1873, and the extinct Lagonomegopidae Eskov & Wunderlich, 1995, Spatiatoridae 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 opisthosoma. This is a novel mode of life for palpimanoids, 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 Yanliao 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

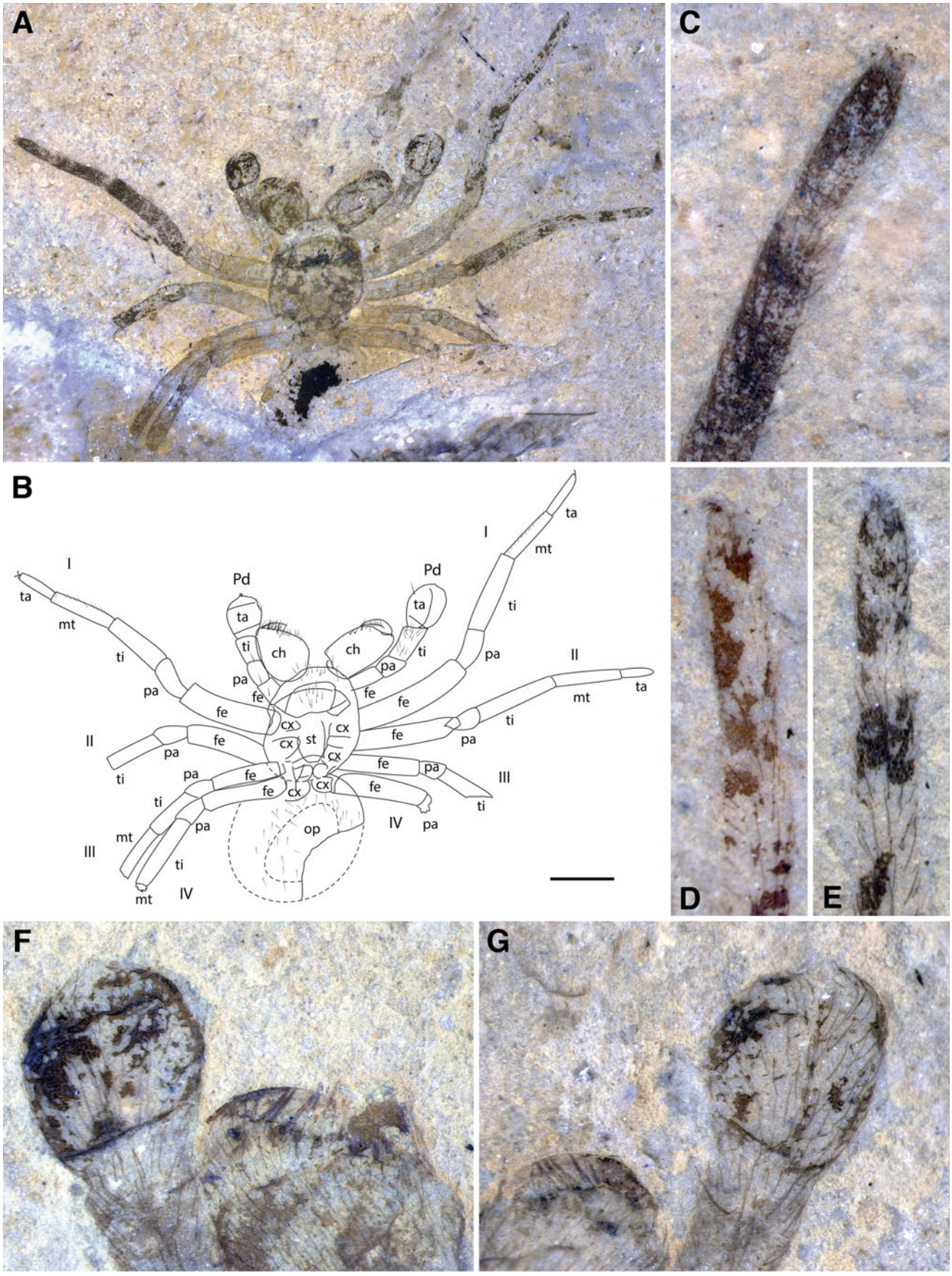

Figure 1. *Caestaranea jurassica* gen. et sp. nov., holotype male NIGP168480a,b, part, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** left leg I distal metatarsus and tarsus, showing poorly developed scopulae and pectinate paired tarsal claws. **D,** right leg I distal 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.

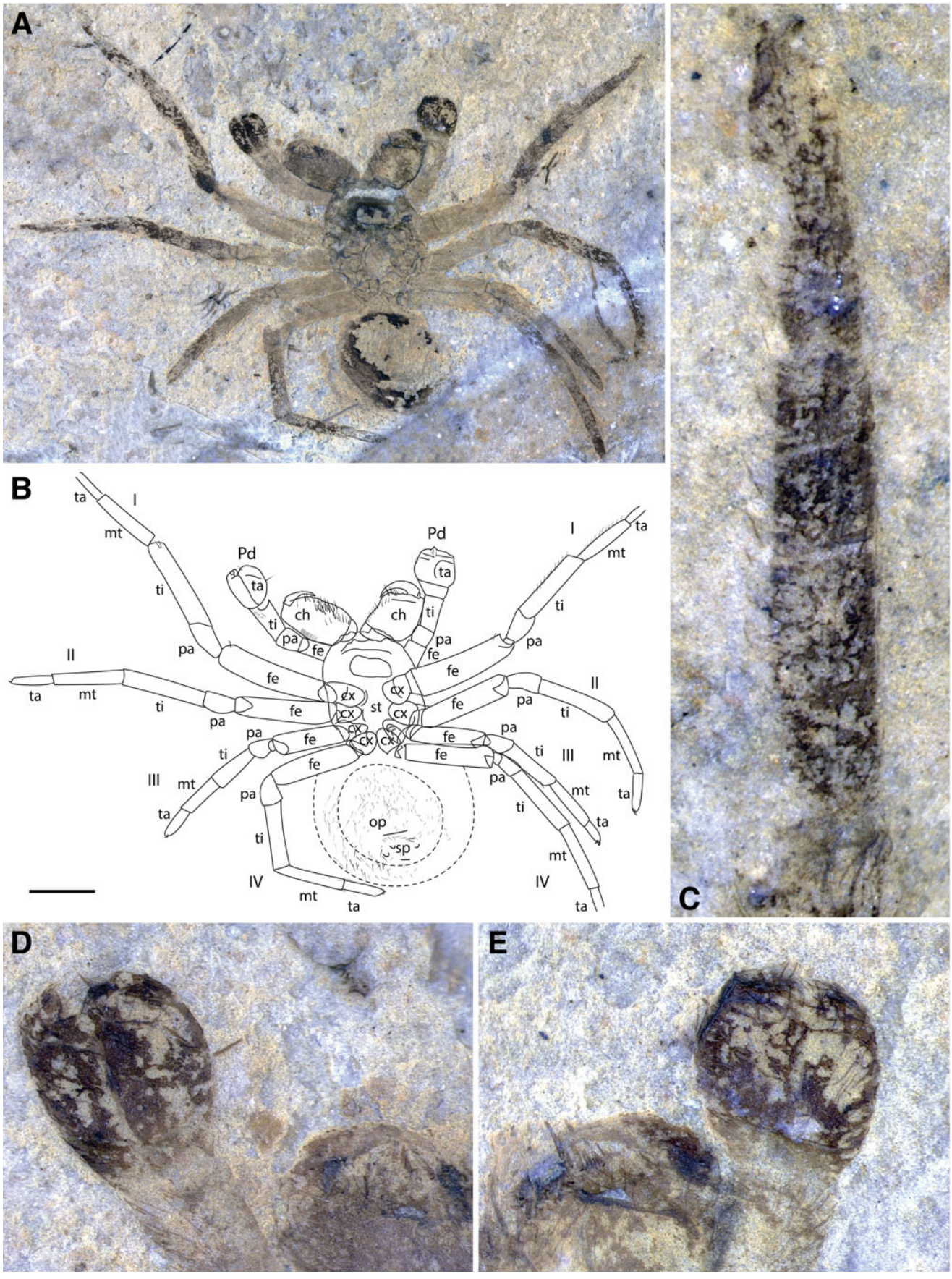

Figure 2. *Caestaranea jurassica* gen. et sp. nov., holotype male NIGP168480a,b, counterpart, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** right leg I metatarsus and tarsus, showing poorly developed scopulae. **D,** left pedipalp tarsus and distal chelicera, showing peg teeth and fang. **E,** right pedipalp tarsus and distal chelicera, showing peg teeth and fang. Scale bar = 1 mm.

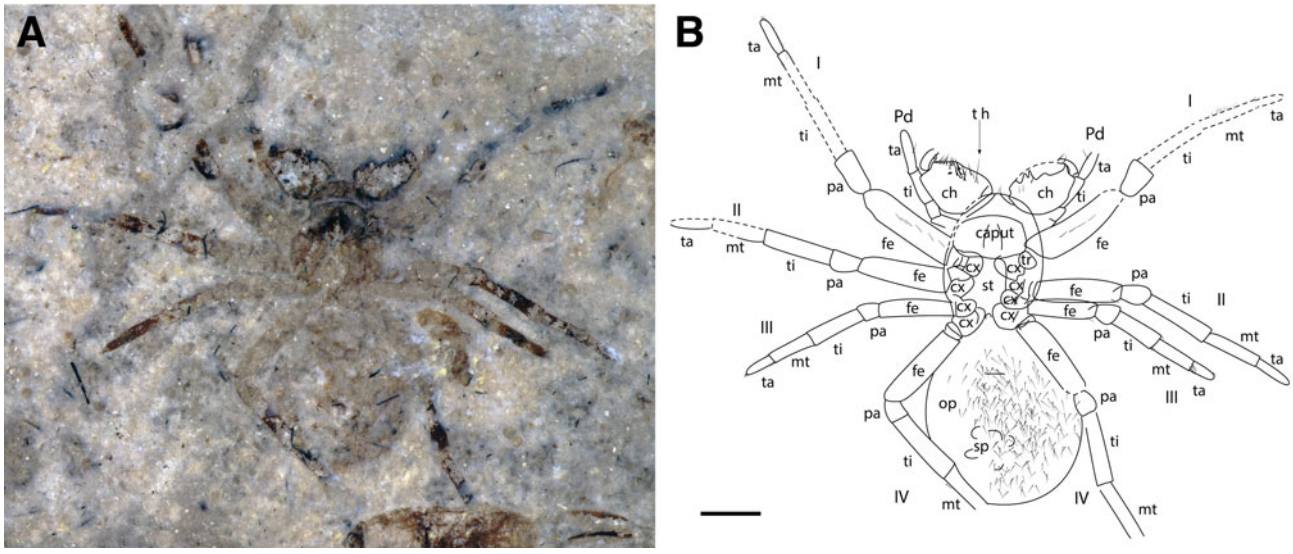

Figure 3. *Caestaranea jurassica* gen. et sp. nov., allotype female NIGP168481a,b, part, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. Scale bar = 1 mm.

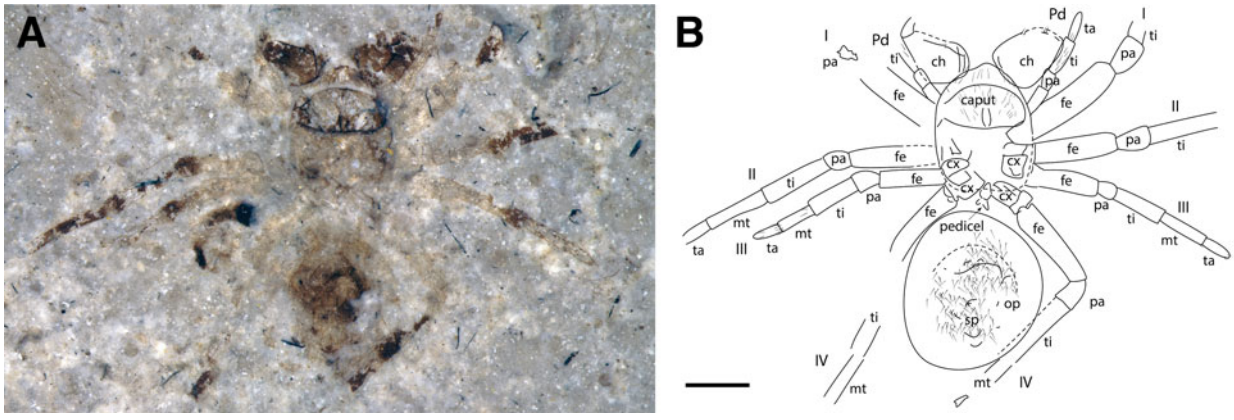

Figure 4. *Caestaranea jurassica* gen. et sp. nov., allotype female NIGP168481a,b, counterpart, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. Scale bar = 1 mm.

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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 cymbiums (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,

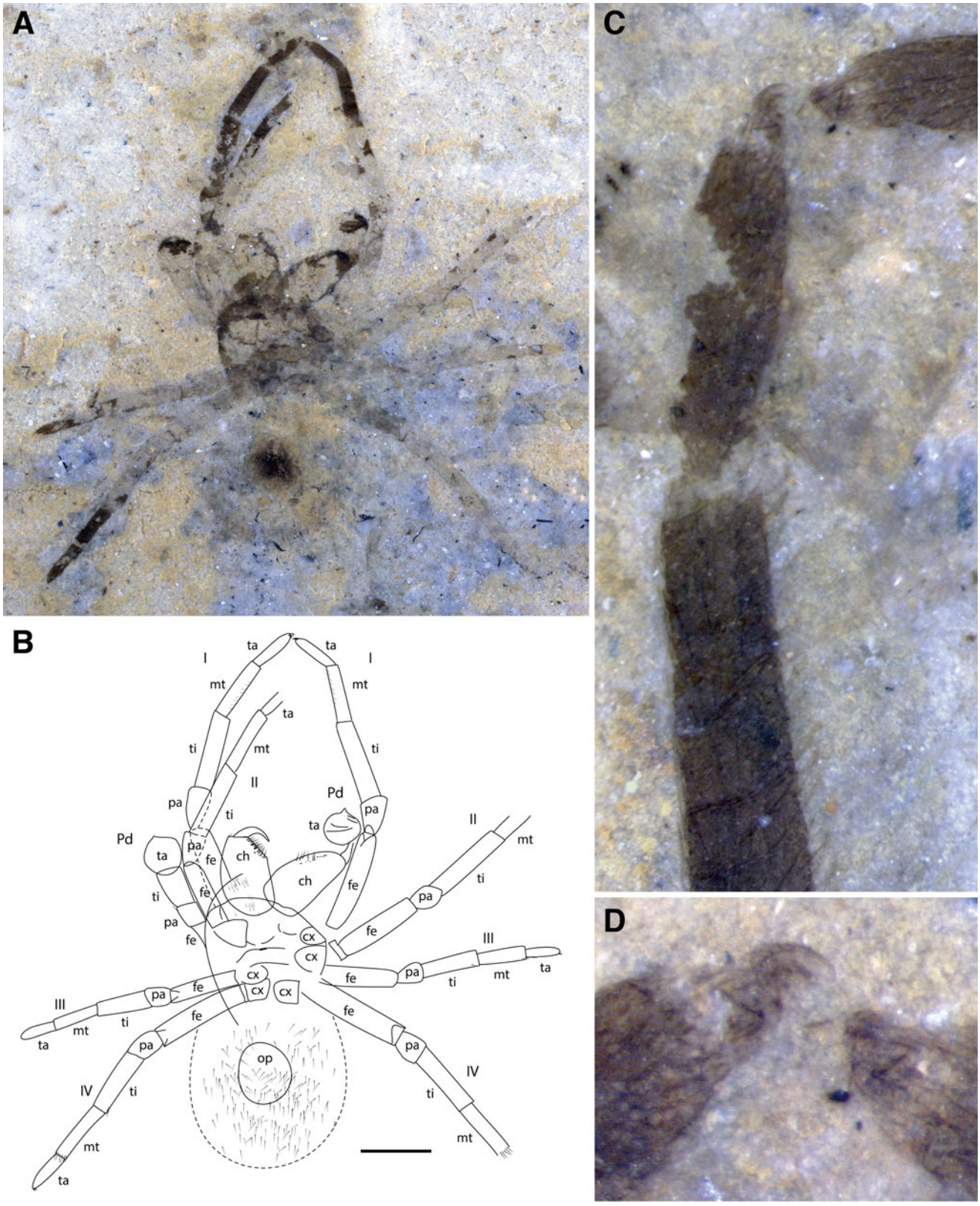


Figure 5. *Caestaranea jurassica* gen. et sp. nov., paratype male NIGP168482, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** left leg I metatarsus and tarsus, and right leg I tarsus, showing weak scopulae. **D,** left and right leg I tarsal claws. Scale bar = 1 mm.

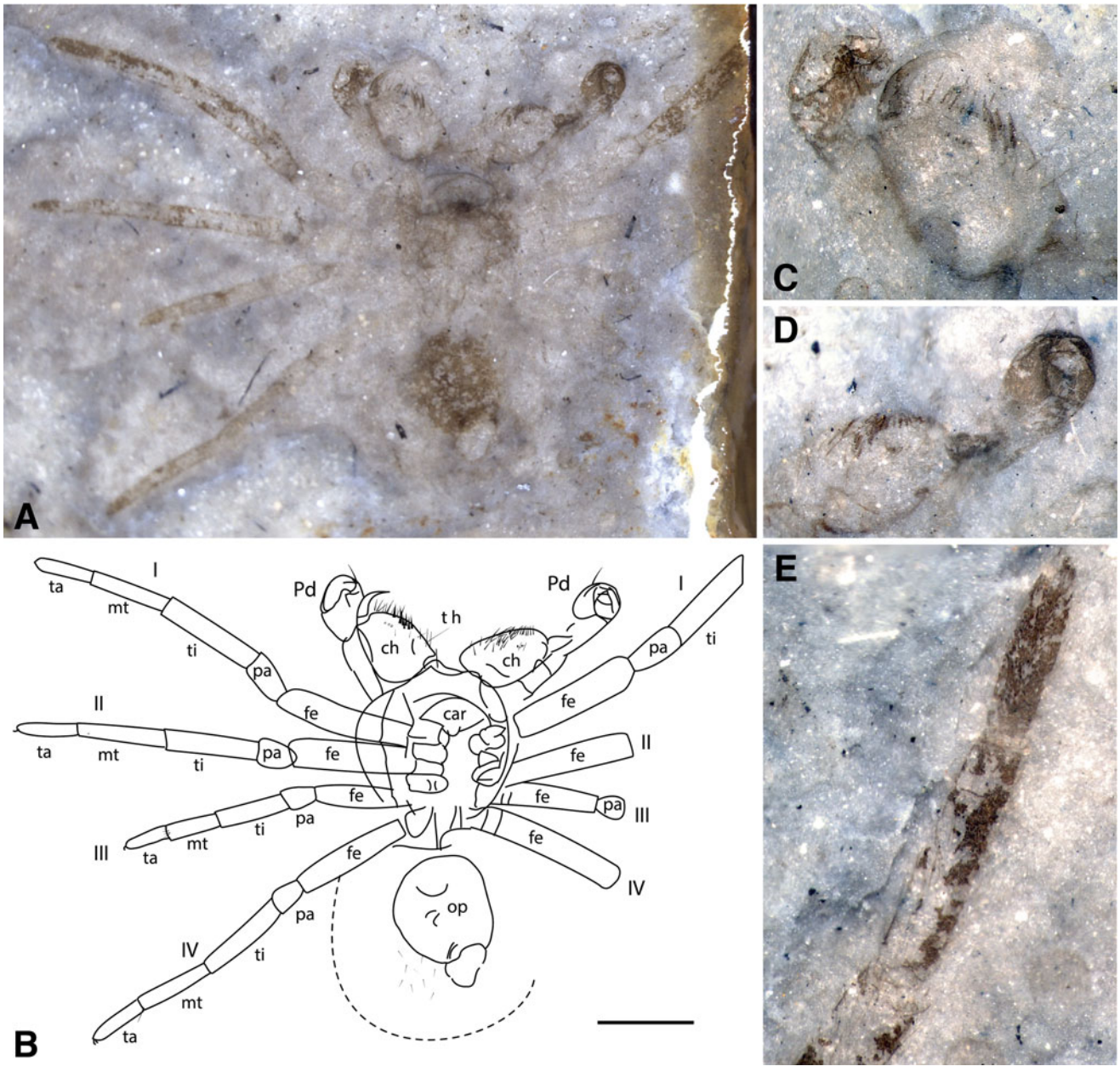


Figure 6. *Caestaranea jurassica* gen. et sp. nov., paratype male NIGP168483, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** left chelicera and pedipalp. **D,** right chelicera and pedipalp. **E,** left leg I metatarsus and tarsus showing poorly developed scopulae. Scale 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

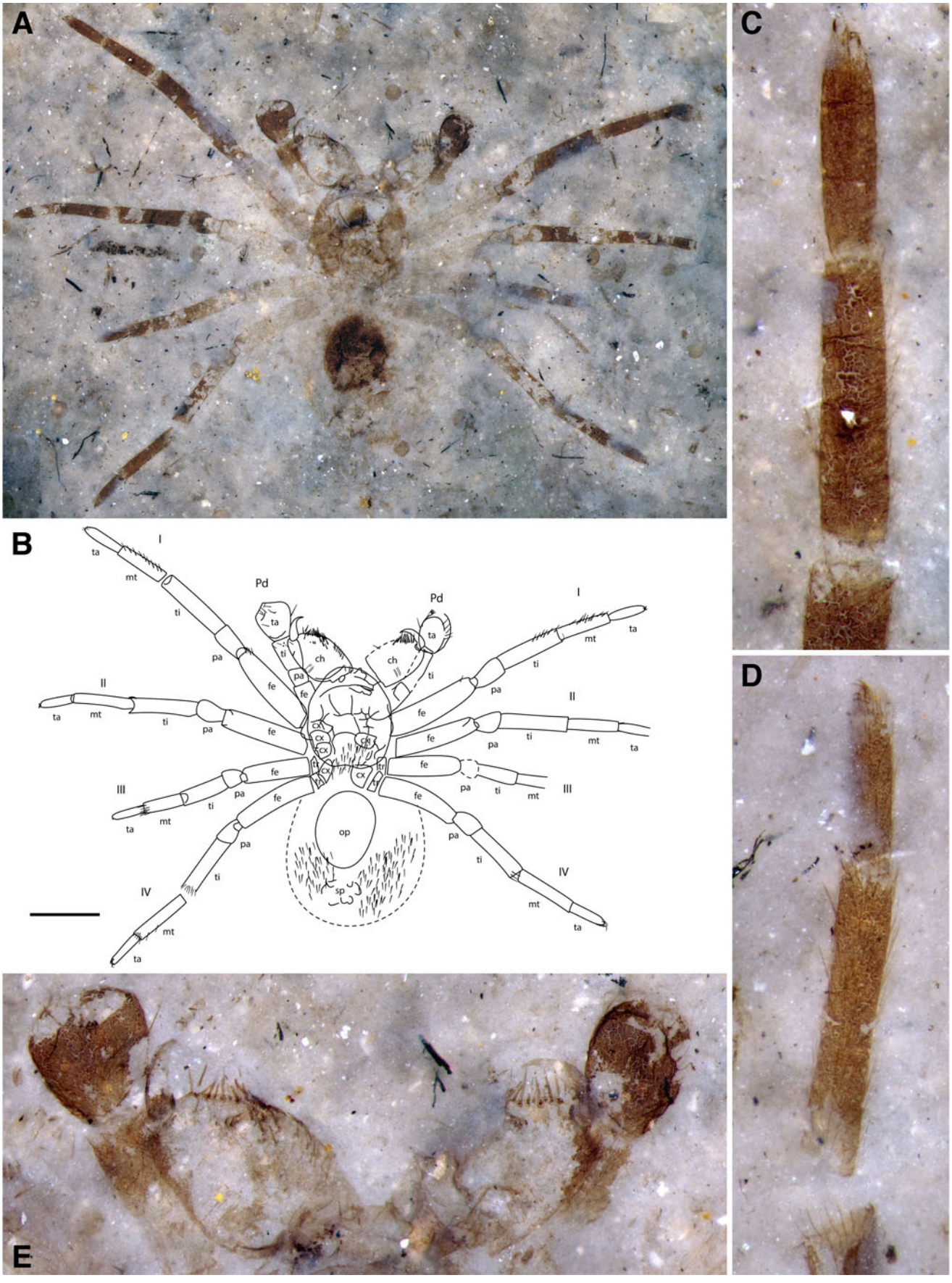


Figure 7. *Caestaranea jurassica* gen. et sp. nov., paratype male NIGP168484a,b, part, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** left leg I metatarsus and tarsus, showing poorly developed scopulae and tarsal claws. **D,** left leg IV metatarsus and tarsus, showing 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.

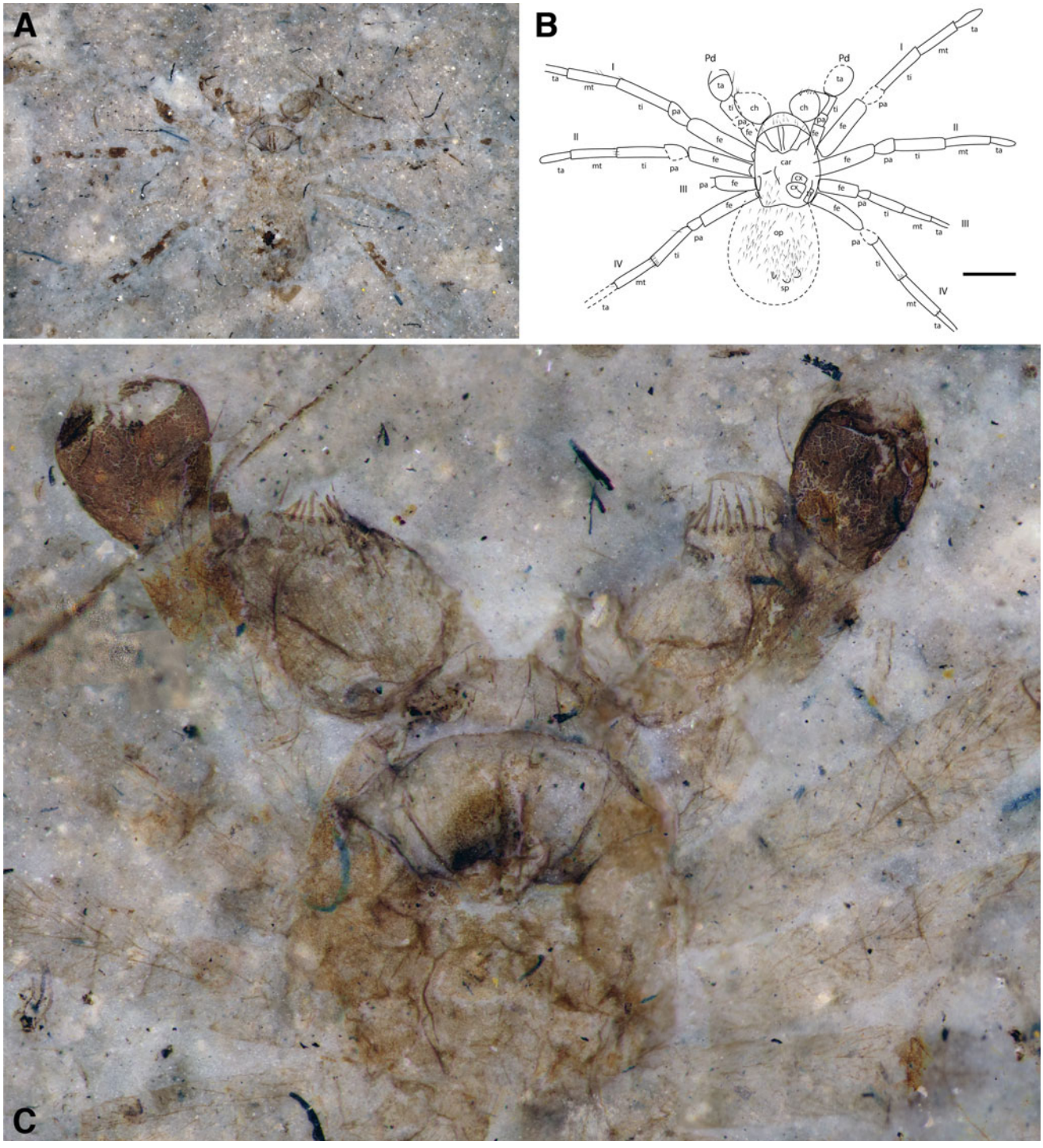


Figure 8. *Caestaranea jurassica* gen. et sp. nov., paratype male NIGP168484a,b, counterpart, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** part and counterpart superimposed, showing chelicerae, pedipalps and central prosoma (with carapace and ventral features superimposed) showing caput region, coxae and elongate, scutiform sternum. 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

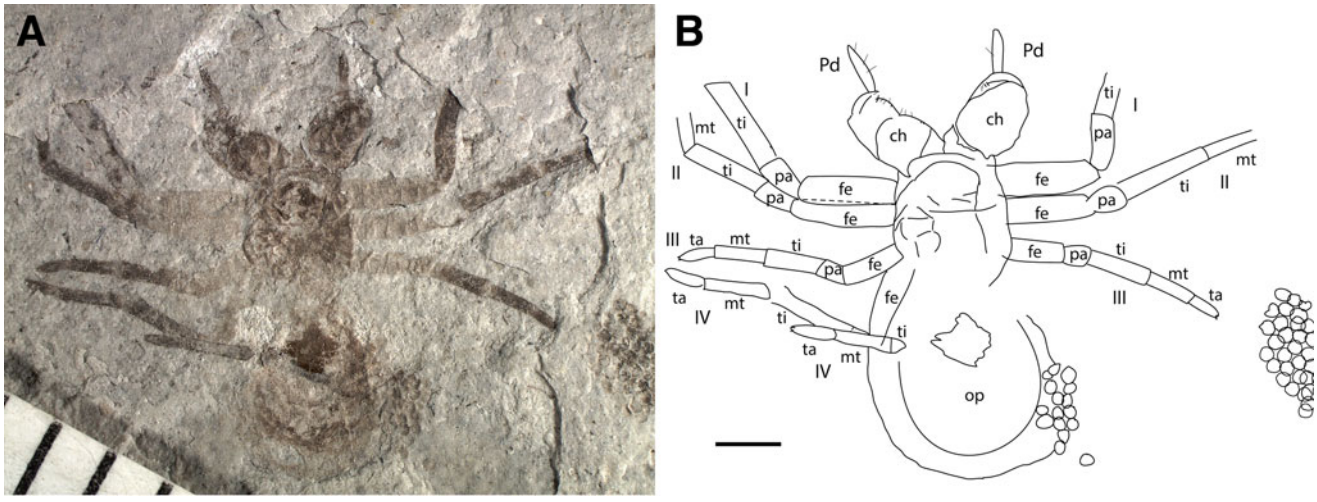


Figure 9. *Caestaranea jurassica* gen. et sp. nov., female NIGP148238, dry. **A,** whole specimen. **B,** explanatory drawing of A. Scale bar = 1 mm.

(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

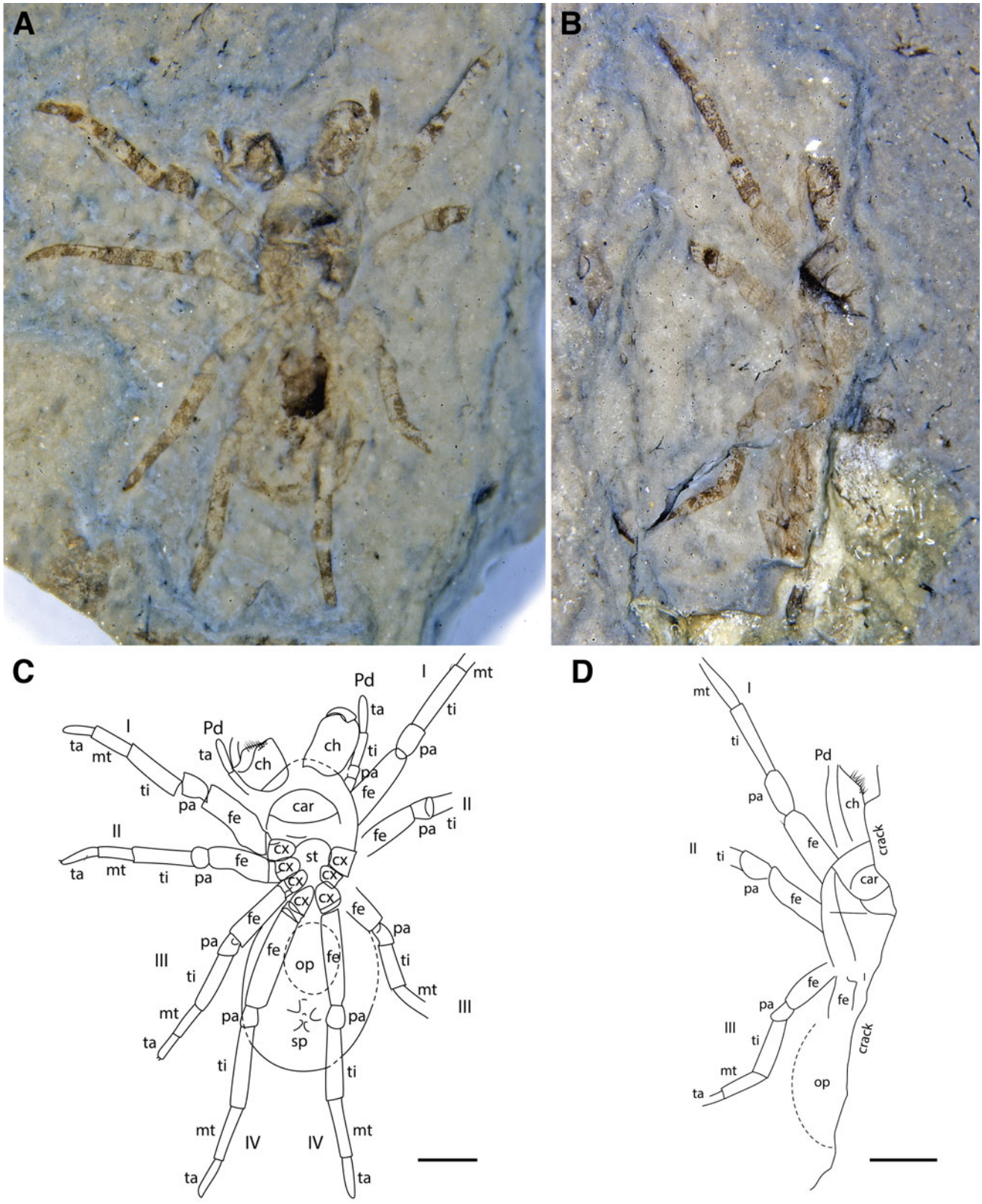


Figure 10. *Caestaranea jurassica* gen. et sp. nov., female NIGP148239a,b, under ethanol. **A,** part. **B,** counterpart. **C,** explanatory drawing of A. **D,** explanatory drawing of B. Scale bars = 1 mm.

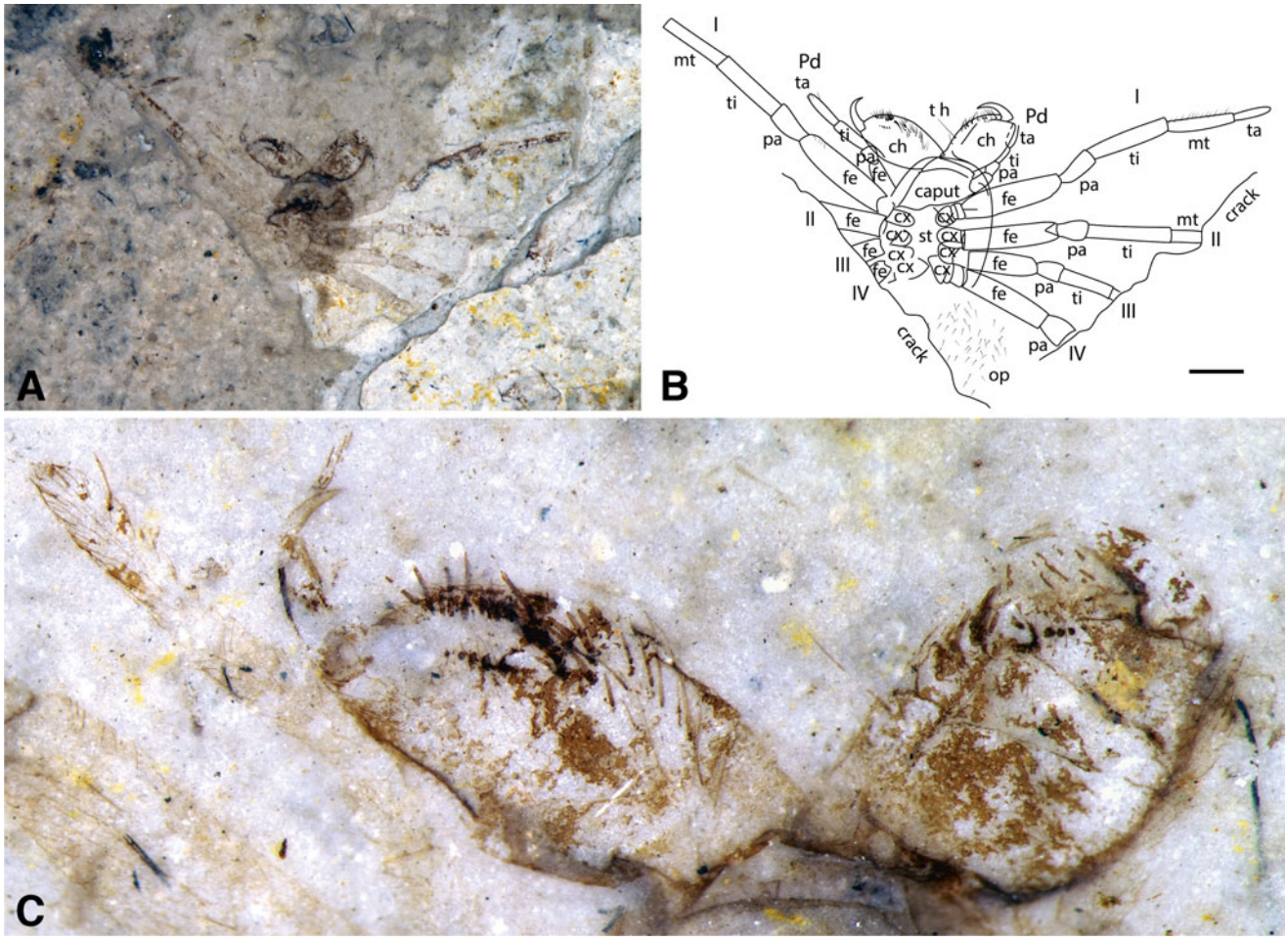


Figure 11. *Caestaranea jurassica* gen. et sp. nov., female NIGP168485, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** chelicerae showing arrangement of peg teeth and fang, and left pedipalp showing distal curved bristles. Scale bar = 1 mm.

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 laterigrade. All femora bear a row of macrosetae which, on the anterior legs, are directed upwards. The scopula on

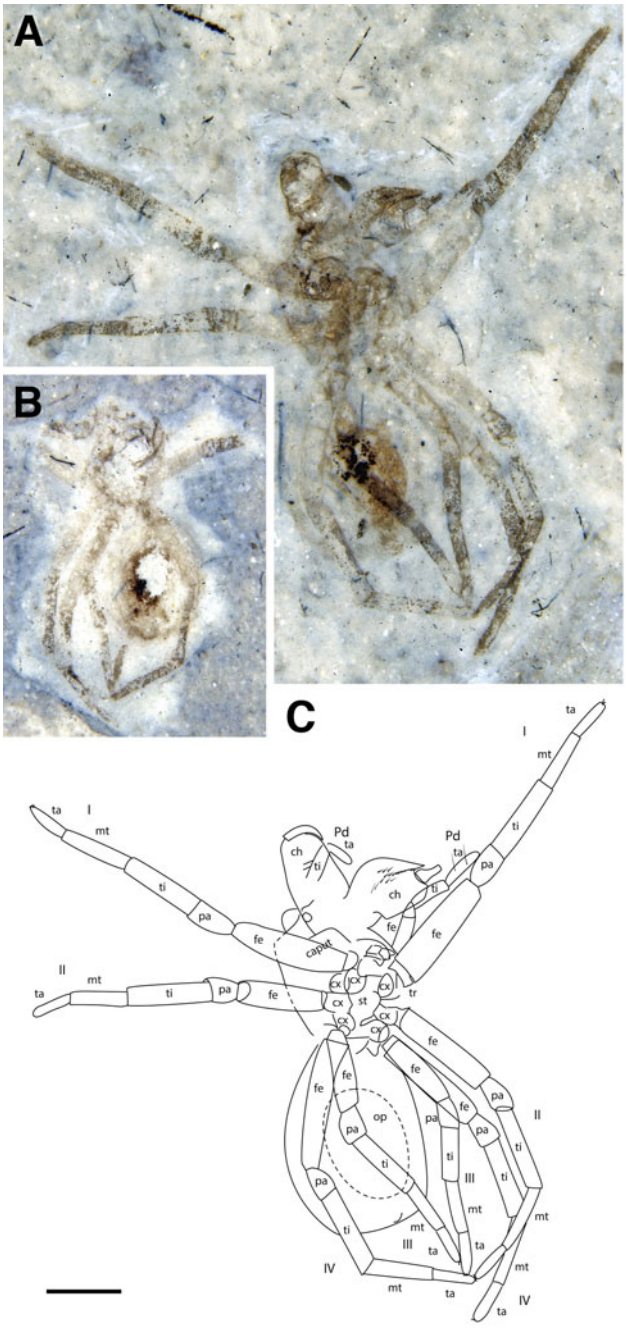


Figure 12. *Caestaranea jurassica* gen. et sp. nov., ?juvenile female NIGP168486a,b, under ethanol. **A,** part. **B,** counterpart. **C,** explanatory drawing of A. Scale bar = 1 mm.

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

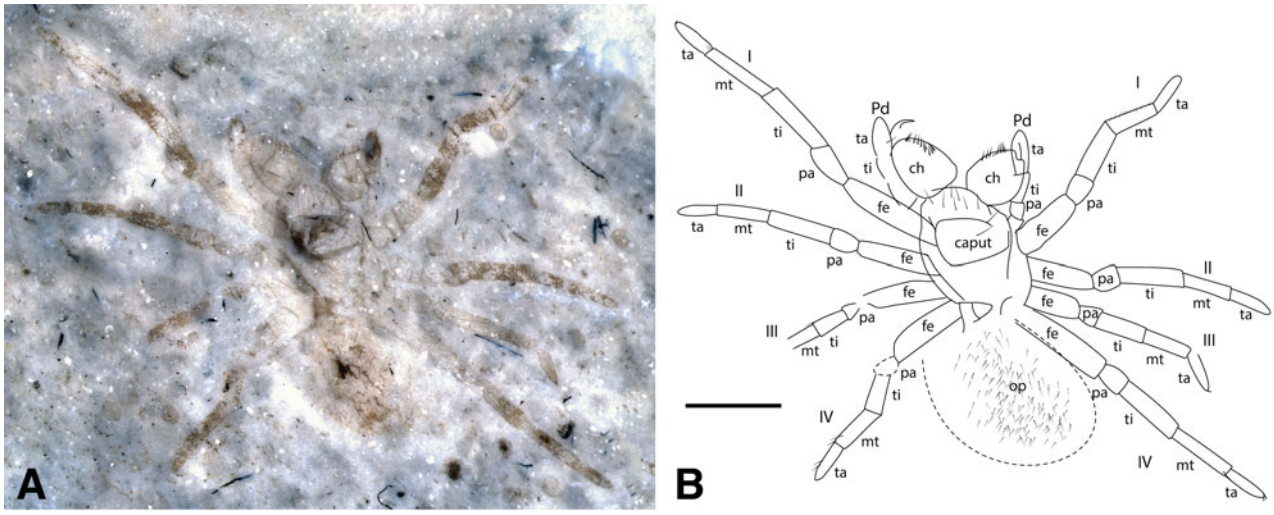


Figure 13. *Caestaranea jurassica* gen. et sp. nov., ?juvenile male NIGP168487, under ethanol. **A,** part. **B,** explanatory drawing of A. Scale bar = 1 mm.

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 ≥ 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.

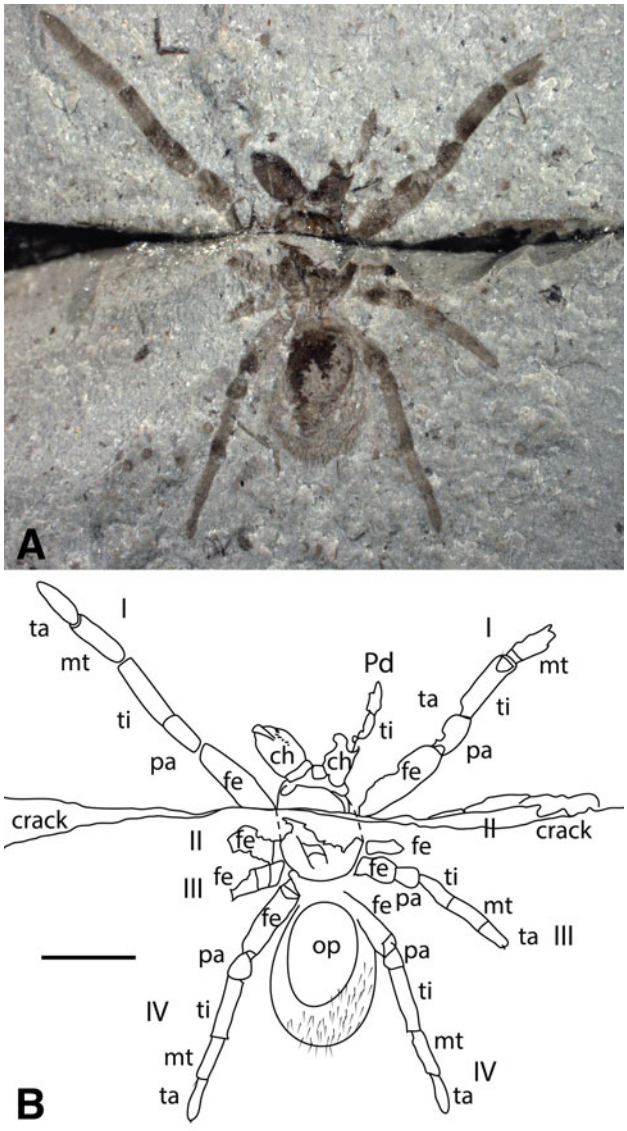


Figure 14. *Caestaranea jurassica* gen. et sp. nov., ?juvenile NIGP148236, dry. **A,** whole specimen. **B,** explanatory drawing of A. Scale bar = 1 mm.

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 mecysmaucheniids 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 chelicerae peg teeth, on both pro- and retromargins 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.

Caestaranea gen. nov.

Type species. *Caestaranea jurassica* sp. nov.

Diagnosis. 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.

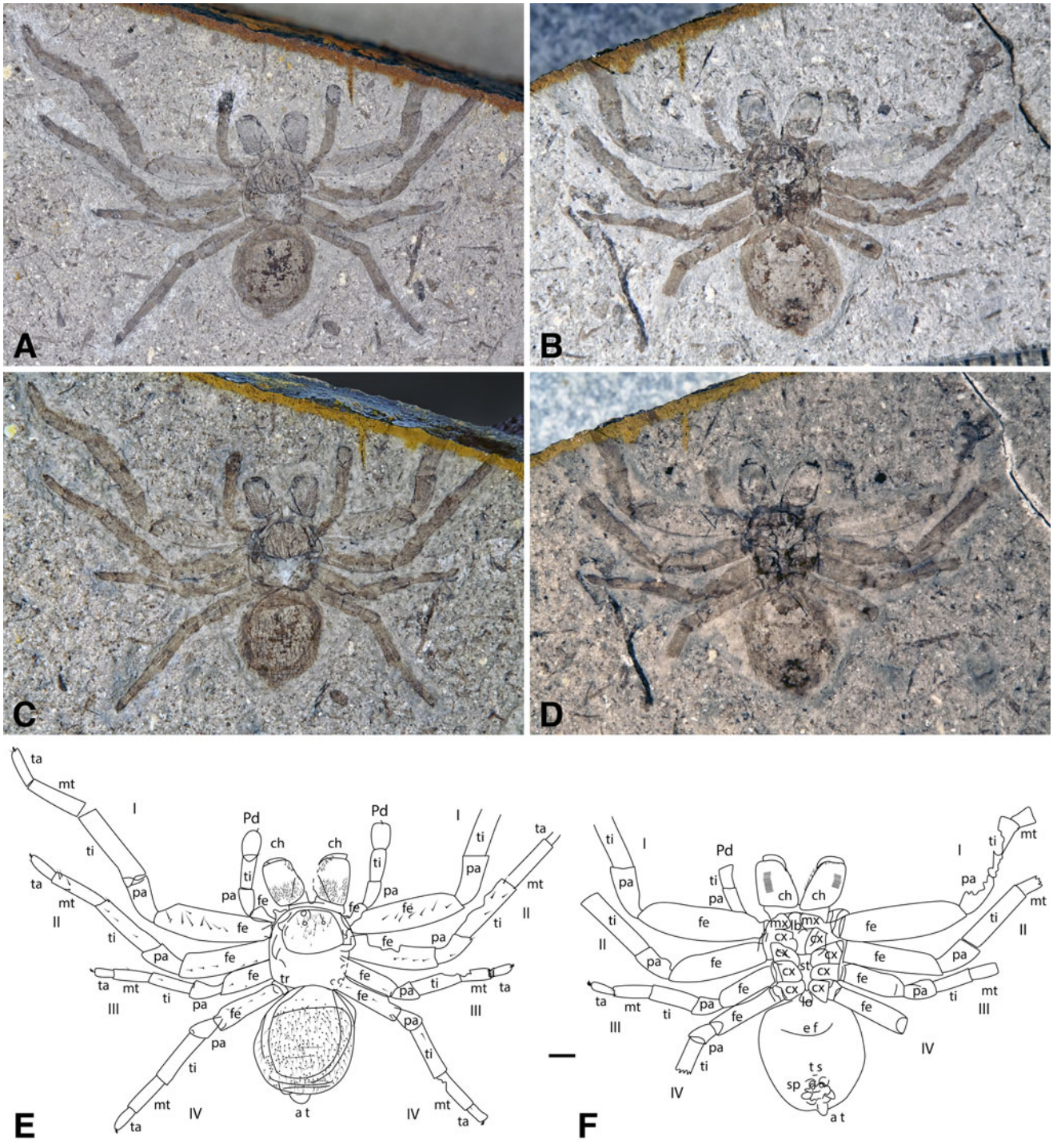


Figure 15. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, habitus. **A,** part, dry. **B,** counterpart, dry. **C,** part, under ethanol. **D,** counterpart, under ethanol. **E,** explanatory drawing of part. **F,** explanatory drawing of counterpart. Scale bar = 1 mm.

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

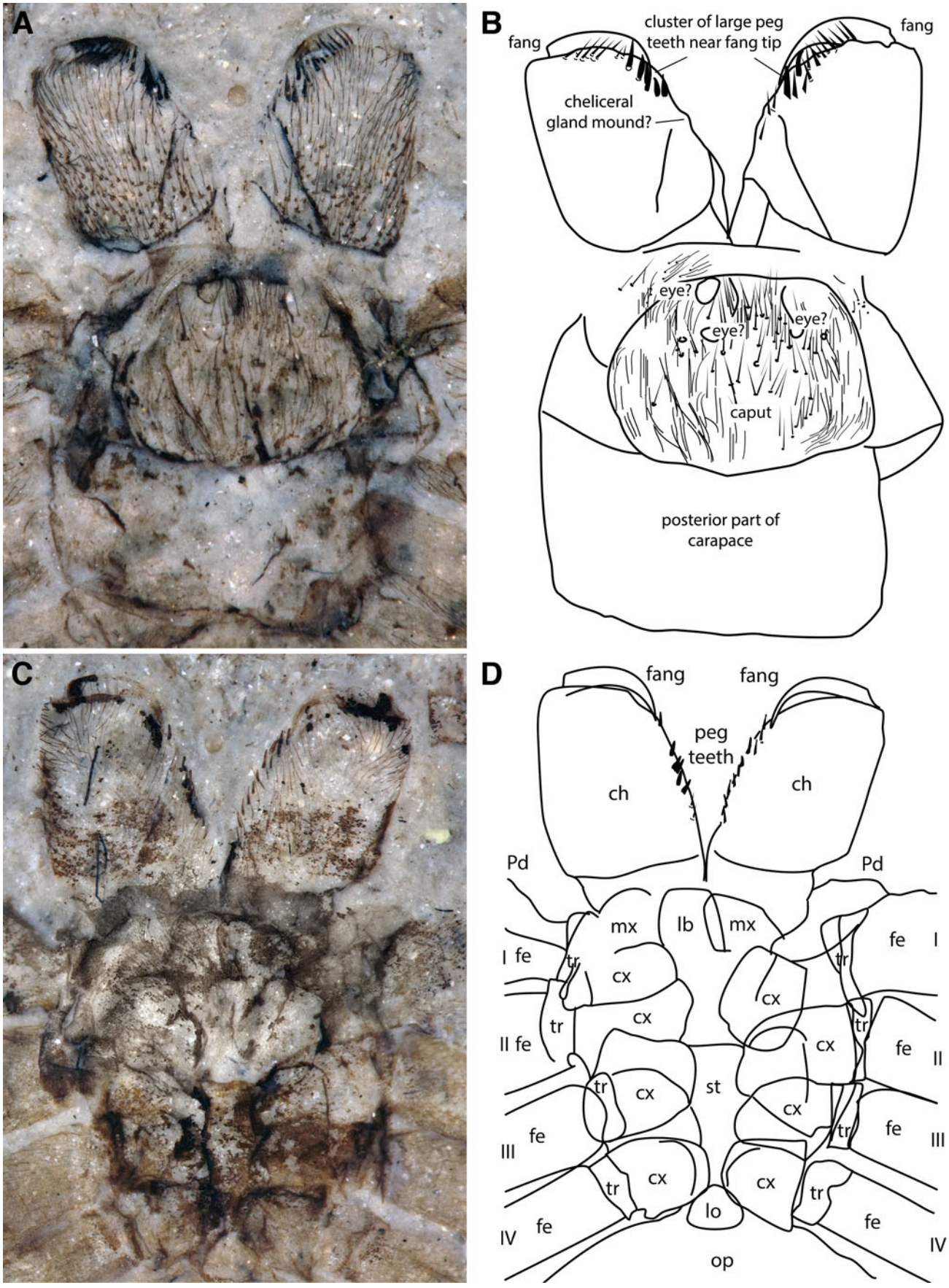


Figure 16. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, anterior prosoma, under ethanol. **A,** part, carapace and chelicerae. **B,** explanatory drawing of A. **C,** counterpart, chelicerae showing peg teeth clustered near the tip of the fang and extending the length of the paturon edge. **D,** explanatory drawing of C.

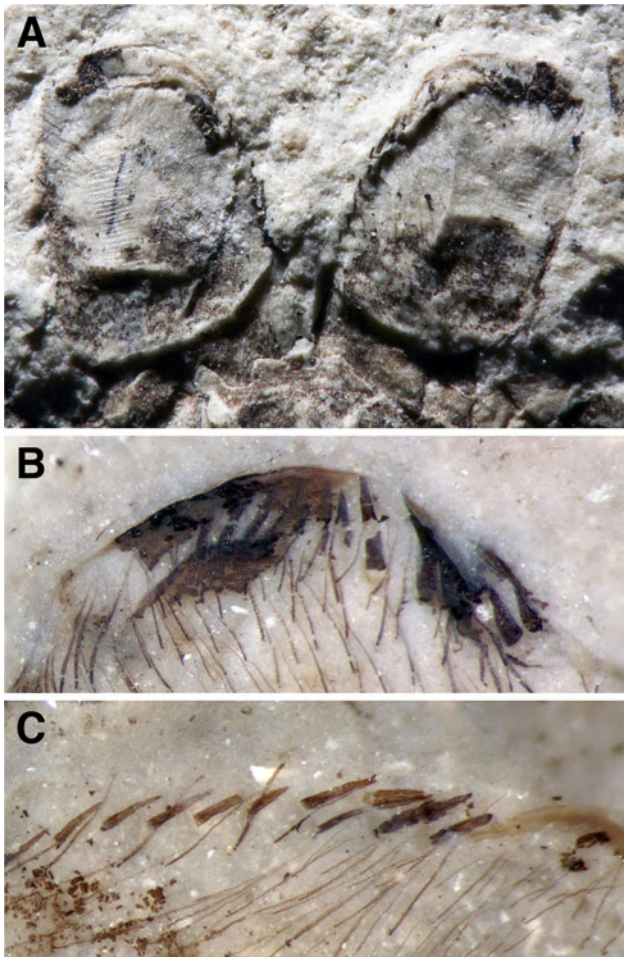


Figure 17. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, chelicerae. **A,** counterpart, chelicerae, dry; note the stridulatory ridges. **B,** part, detail of cheliceral fang and peg teeth on left side, under ethanol. **C,** counterpart, detail of peg teeth along edge of paturon of chelicera on right side (i.e. counterpart of B), tip of fang at right, under ethanol.

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 may have been present in these animals (Wood *et al*. 2016).

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.

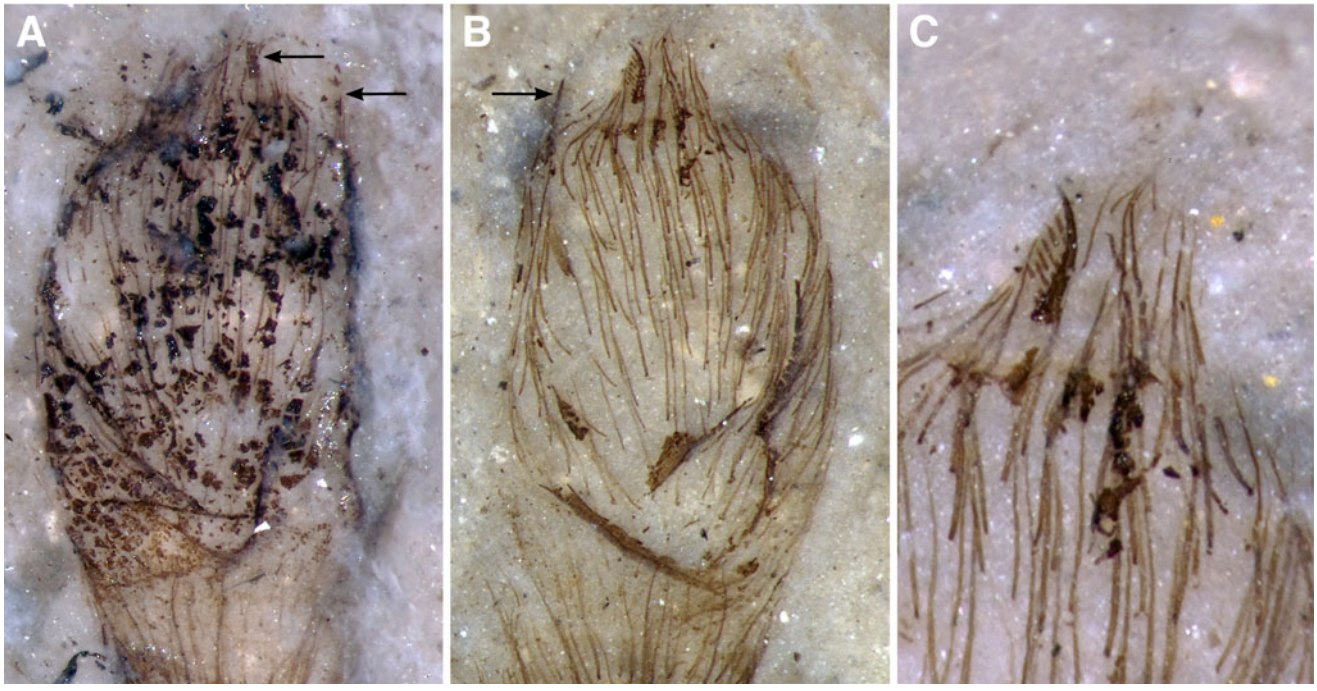


Figure 18. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, pedipalps, under ethanol. **A,** part, pedipalp tarsus of left side, left arrow points to part of claw, right arrow to large spine. **B,** part, pedipalp tarsus of right side, spine arrowed. **C,** detail of claw and setae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

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; allotype 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 measurements 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, scutiform, 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 (fe–ta) 1.75–2.19. Leg formula 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 pectinate 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 outline, 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

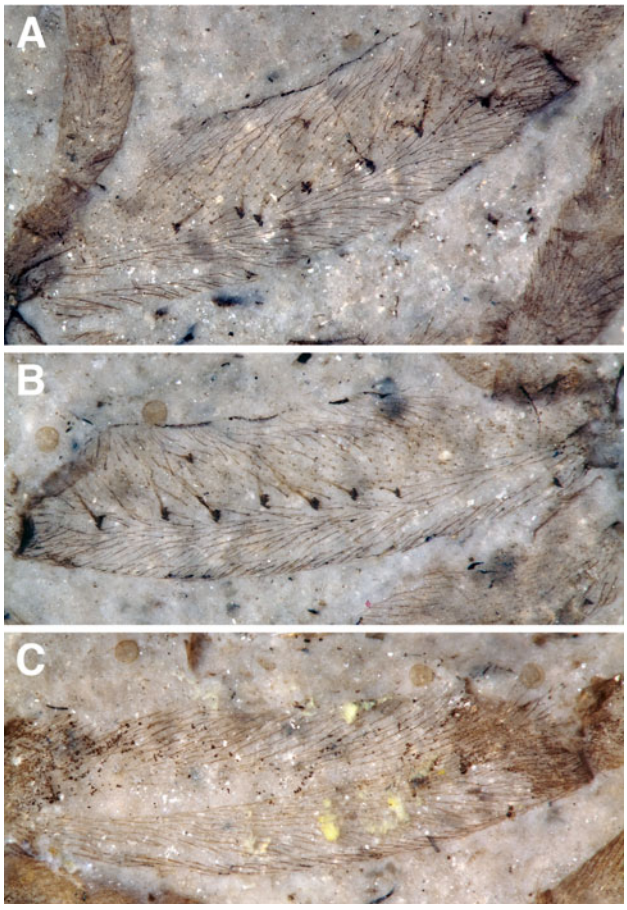


Figure 19. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, femora, under ethanol. **A,** part, femur of leg I on right side, dorsal view showing row of macrosetae. **B,** part, femur of leg I on left side, dorsal view with row of macrosetae. **C,** counterpart, femur of leg I on right side (i.e. counterpart of B), ventral view showing glabrous area.

NIGP148238 (Fig. 9) and NIGP148239a,b (Fig. 10). For specimen measurements see Table 1. Body L 5.04–5.23. Carapace sub-oval, L 2.07–2.50, W 1.59–1.96, L/W ratio 1.19–1.36; caput clearly demarcated, L 0.71, W 1.24, L/W ratio 0.57. Sternum longer than wide, with gently scalloped border, L 0.87–0.95, W 0.48–0.59, L/W ratio 1.61–1.81 (Fig. 3). Bilobed pedicel (Fig. 4). Chelicera L 1.20–1.44, W 0.82–0.89, L/W ratio 1.46–1.62, large, robust, with peg teeth extending from distal edge down length of mesial edge, dense cluster of peg teeth on paturon near fang tip, dense peg teeth along promargin of cheliceral furrow, row of curved teeth on retromargin, medially directed setae (trigger hairs) present at proximal end of peg tooth row (Fig. 11C); fang (L 0.55–0.65) 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; spinnerets *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.

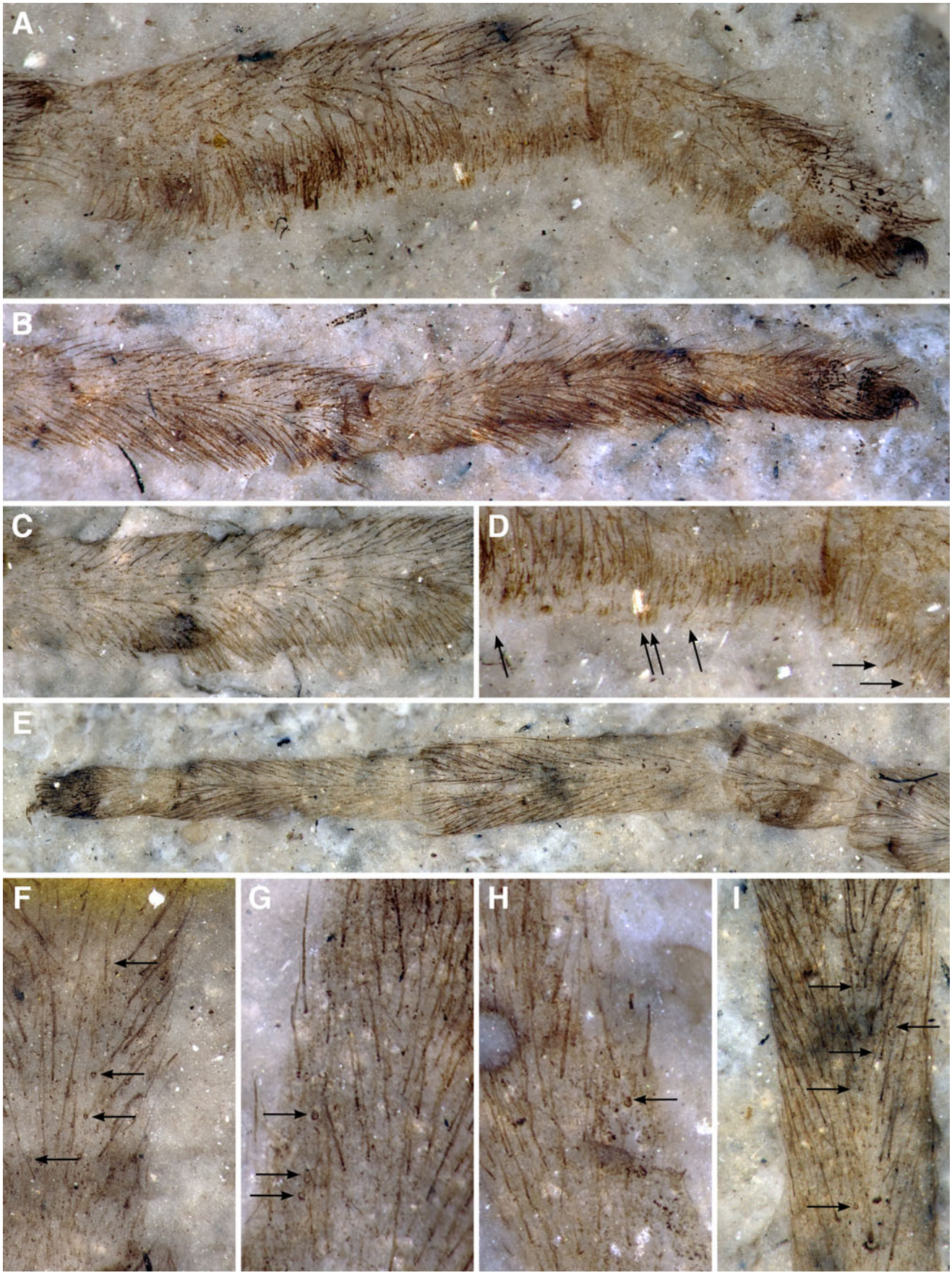
Type species. *Onychopalpus thomisoides* sp. nov.

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 *ονυξ*, 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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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 mesotheles, and occurs in elongate spiders, e.g. *Deinopis* MacLeay, 1839, *Miagrammopes* Pickard-Cambridge, 1870, some segestriids and salticids. It is rare in thomisids (except the elongate *Monaeses* Thorell, 1869), but the palpimanoid *Eriauchenius* Pickard-Cambridge, 1881 (Archaeidae) 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 trailli* (Pickard-Cambridge, 1873) (Almquist 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 *Dusmadiores* Jocqué, 1987, *Heradida* 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. Almquist (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

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).

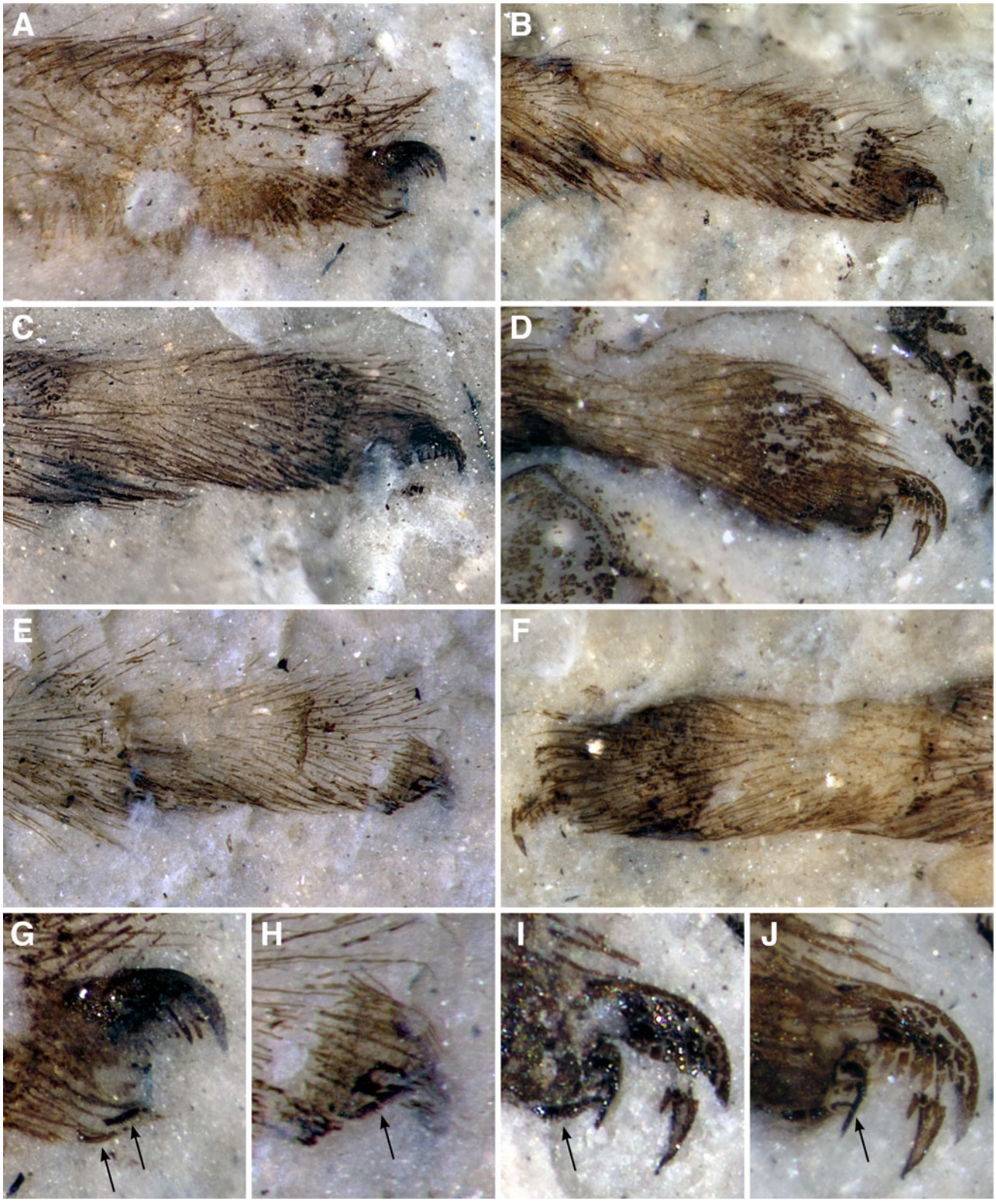


Figure 21. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, tarsi, under ethanol (except I). **A,** part, tip of tarsus of leg I on left side; circular pale patches are artifacts of preparation. **B,** part, tarsus of leg II on left side. **C,** part, tarsus of leg III on left side. **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.

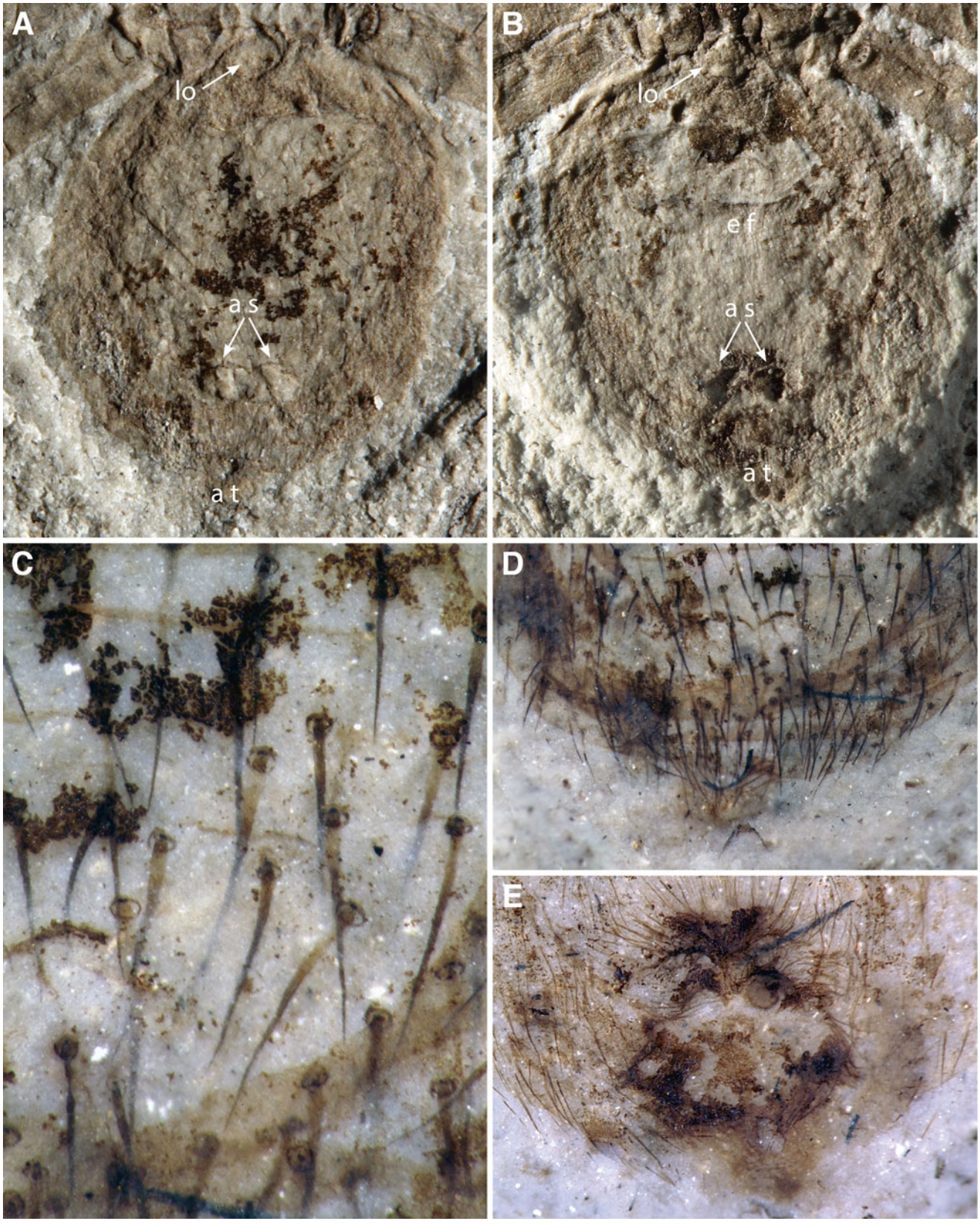
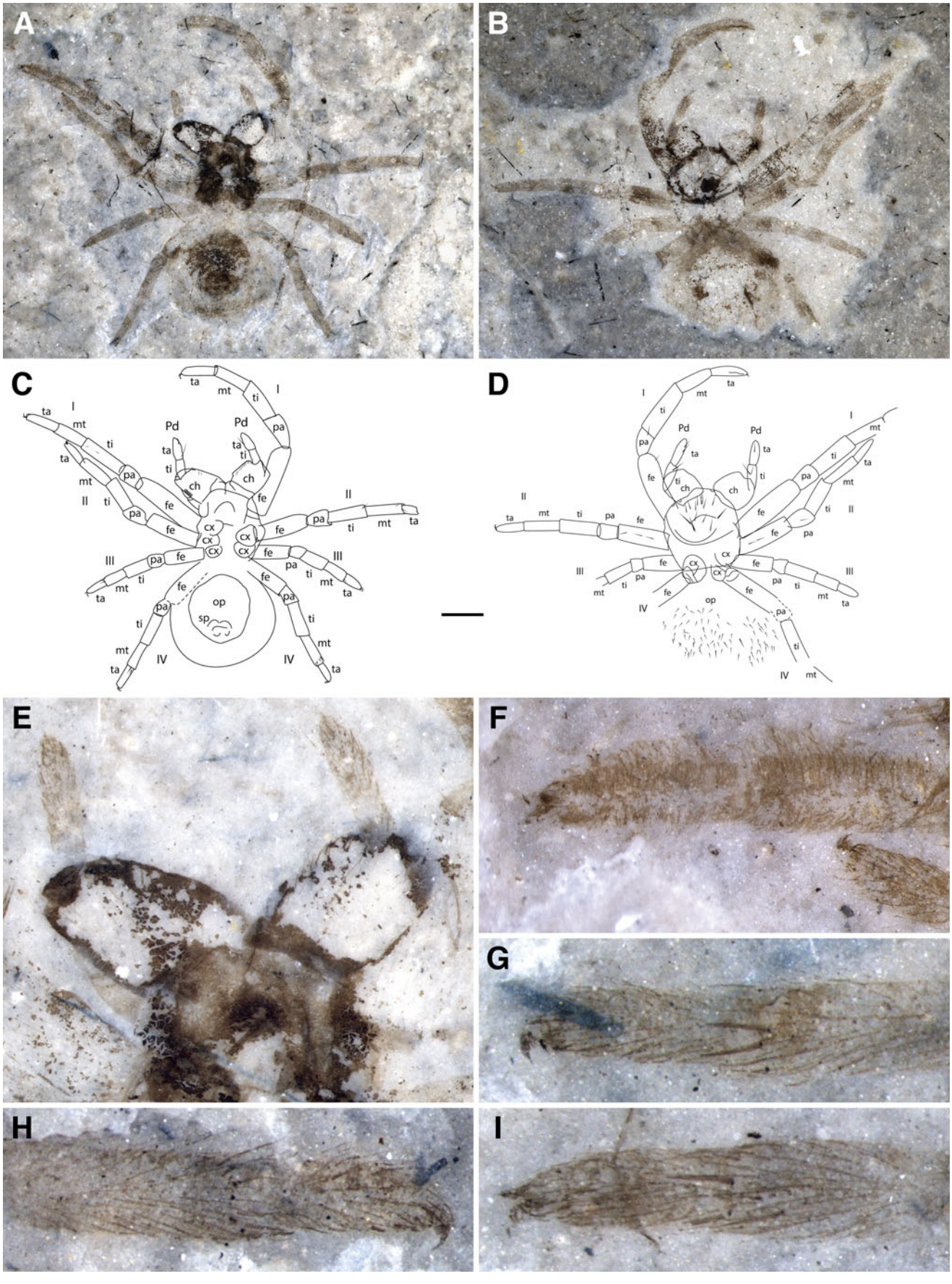


Figure 22. *Onychopalpus thomisoides* gen. et sp. nov., holotype NIGP168488a,b, opisthosoma. **A,** part, showing lorum, more rigid central dorsal area, anterior spinnerets and anal tubercle, dry. **B,** counterpart, showing lorum, anterior spinnerets and anal tubercle, dry. **C,** part, opisthosomal bristles, under ethanol. **D,** part, anal tubercle, under ethanol. **E,** counterpart, spinnerets, under ethanol.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ratio 0.95); anterior caput clearly delimited (likely raised in life), broader than long (L 1.68, W 2.34, L/W ratio 0.72), occupying anterior half of carapace. Caput with numerous, forward-pointing macrosetae; posterior part of carapace lacking strong setae. Four eyes forming rectangle (L 0.38, W 0.72) at anterior of caput (more eyes presumably present). Sternum long, narrow (L 2.00, W 0.60, L/W ratio 3.33); labium longer than wide (L/W ratio *c*. 1.5), maxillae (pedipalp coxae) equant, not meeting in front of labium (Fig. 16C, D). Chelicera large, sub-rectangular in outline, protrusive, L 2.08, W 1.38 (L/W ratio 1.51); curved fang at anterior border, L (measured along curvature) 1.21; 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 $\geq$ 7 blade-like teeth and stout spine distally on mesial side (Fig. 18), total L (fe–ta) $\geq$ 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 laterigrade, 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 $\geq$ 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 ($\geq$ 7) and II ($\geq$ 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.

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, fine setae over paturon surfaces; stridulating ridges on lateral part of paturon, fang L 0.38–0.56 (Figs 26A, 29D). Pedipalp simple, bearing macrosetae especially distally on tarsus, total L (fe–ta) 2.06–2.68. Leg formula I > II > III > IV; leg I bearing scopula of spatulate setae extending along entire ventral surface of tibia, metatarsus and tarsus (Figs 23A, E, 24D), distal tarsus with elongate patch of denser scopulae setae (Fig. 26B–E); row of large macrosetae on dorsal surface of tibia I (Fig. 29C); patella I longer (L 0.67–1.33) than patellae II–IV (L 0.53–0.93, 0.37–0.62, 0.42–0.69, respectively); metatarsi II–IV bearing pair of macrosetae ventrodistally (Figs 23G–I, 25); tarsi shorter than metatarsi (mean ta/mt ratio 0.65–0.95), bearing three claws: paired claws pectinate with $\geq$ 7 blade-like teeth, median

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.

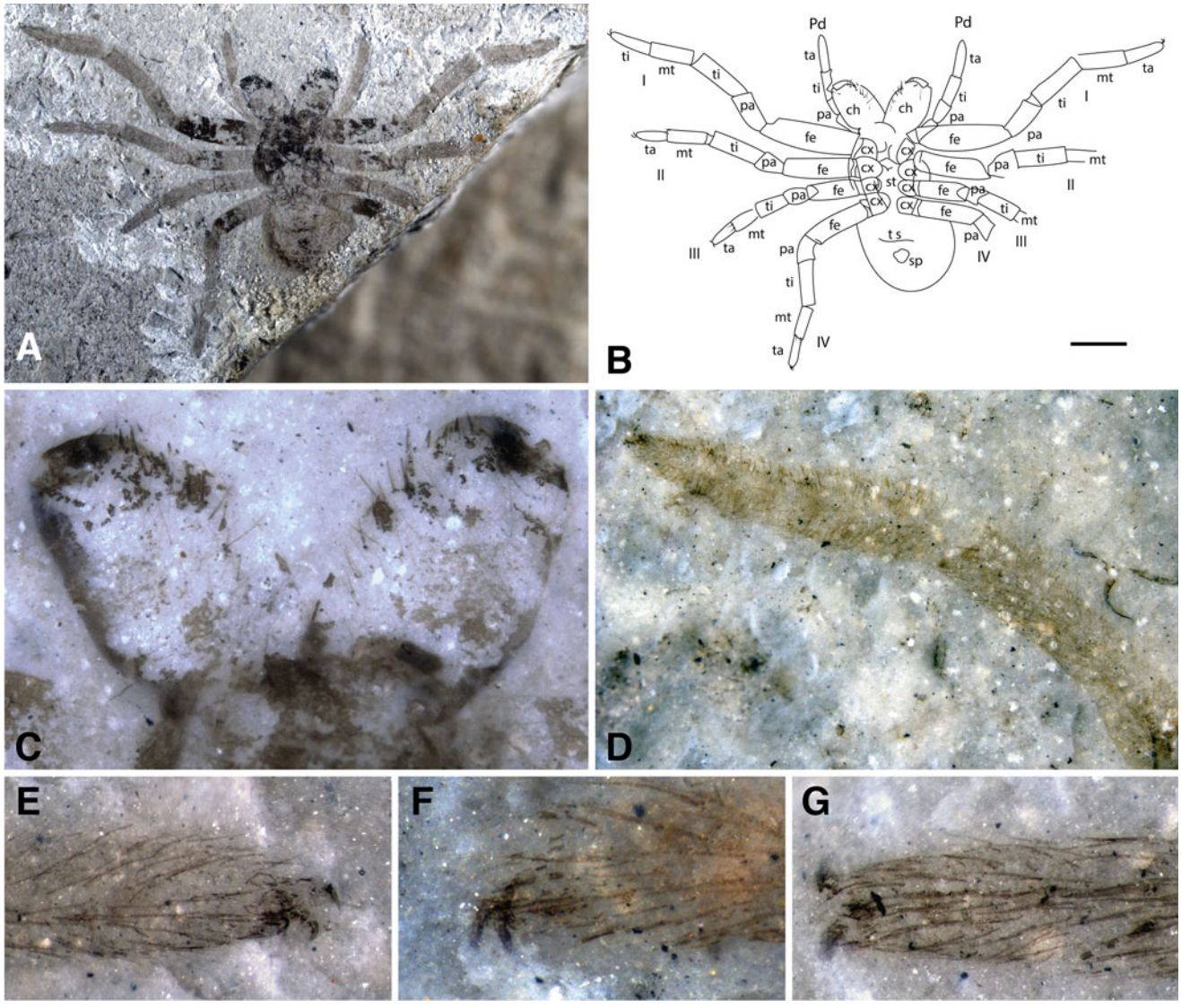

Figure 24. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168489, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. **C,** chelicerae. **D,** left leg I tibia to tarsus, showing scopulae. **E,** left tarsus II showing claws. **F,** left tarsus IV showing claws. **G,** left leg III distal metatarsus showing ventrodistal macrosetae and tarsus showing claws. Scale bar = 1 mm.

claw small, hooked, lacking teeth, with fimbriate accessory claws (Figs 23E–H, 24E–G). Leg lengths: leg I 4.97–6.89, leg II 3.96–5.56, leg III 2.82–5.68 and leg IV 3.51–5.14. Opisthosoma sub-circular in outline, L 1.74–2.65, W 1.59–2.57, L/W ratio 1.03–1.09, dorsal median area sub-circular L 1.67, W 1.48, L/W ratio 1.13. Spinnerets subterminal, *c*. one-third of opisthosomal length from posterior (Figs 23A, C, 24, 27, 29A, B).

Sinaranea Selden, Huang & Ren, 2008

Type species. *Sinaranea 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. *Sinaranea 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

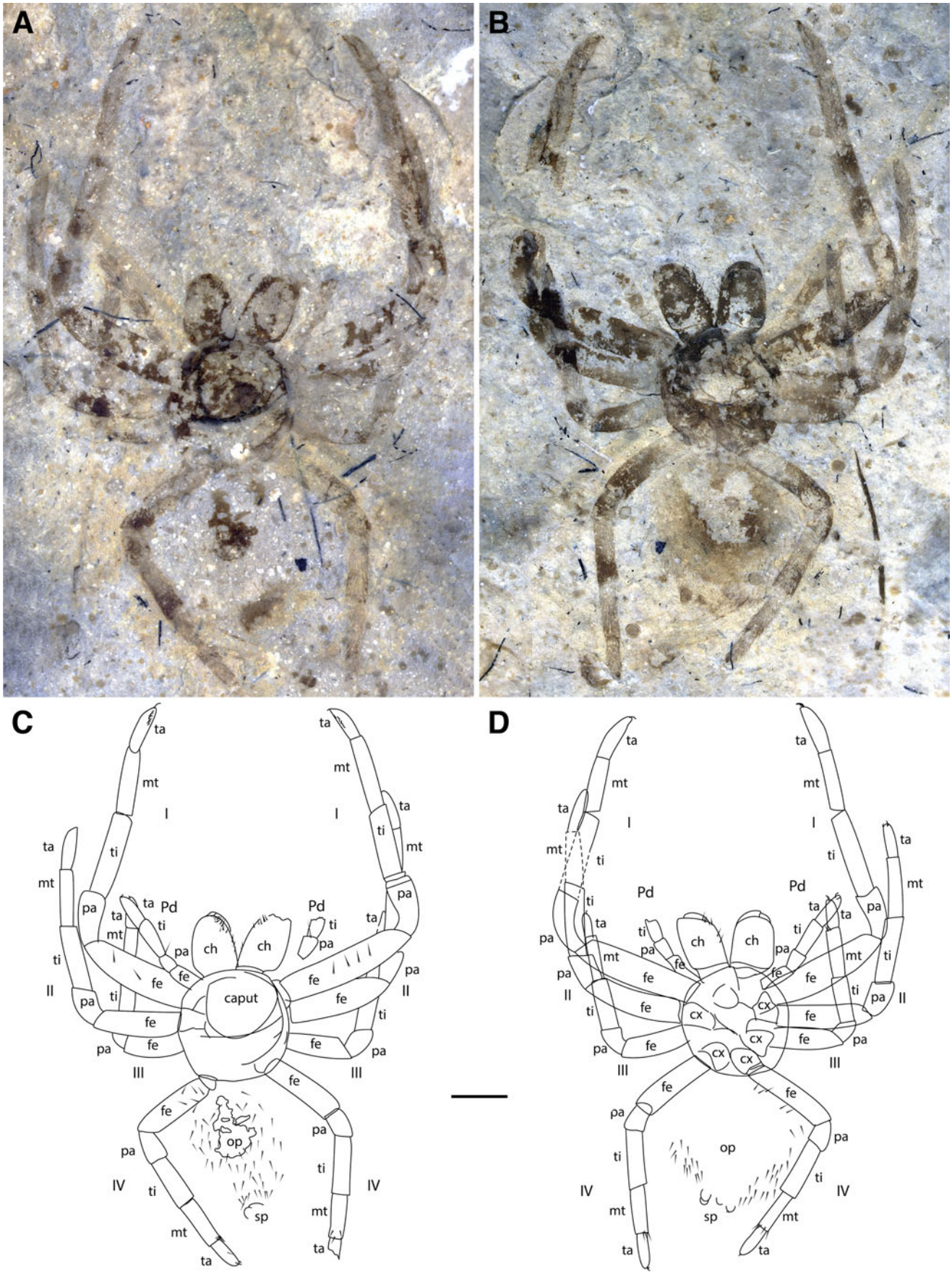

Figure 25. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168490a,b, under ethanol. **A,** whole specimen, part. **B,** whole specimen, counterpart. **C,** explanatory drawing of A. **D,** explanatory drawing of B. Scale bar = 1 mm.

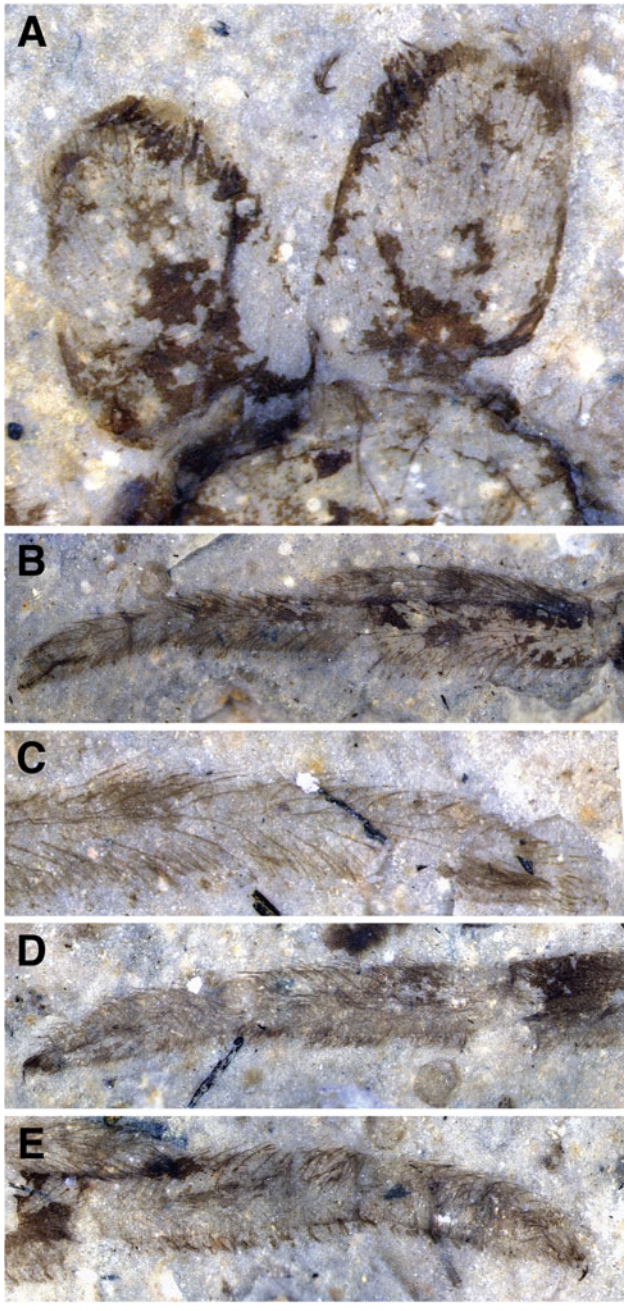

Figure 26. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168490a,b, under ethanol. **A,** part, chelicerae. **B,** part, right pedipalp tibia and tarsus, and leg I tibia to tarsus, showing scopulae. **C,** part, left leg I distal metatarsus and tarsus showing scopulae. **D,** counterpart, right leg I metatarsus and tarsus showing scopulae and tarsal claws. **E,** counterpart, right pedipalp tarsus, and leg I metatarsus and tarsus, showing scopulae and tarsal claws.

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 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" (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 I/car L > 1.7; fe I/body L > 0.5; fe I/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.

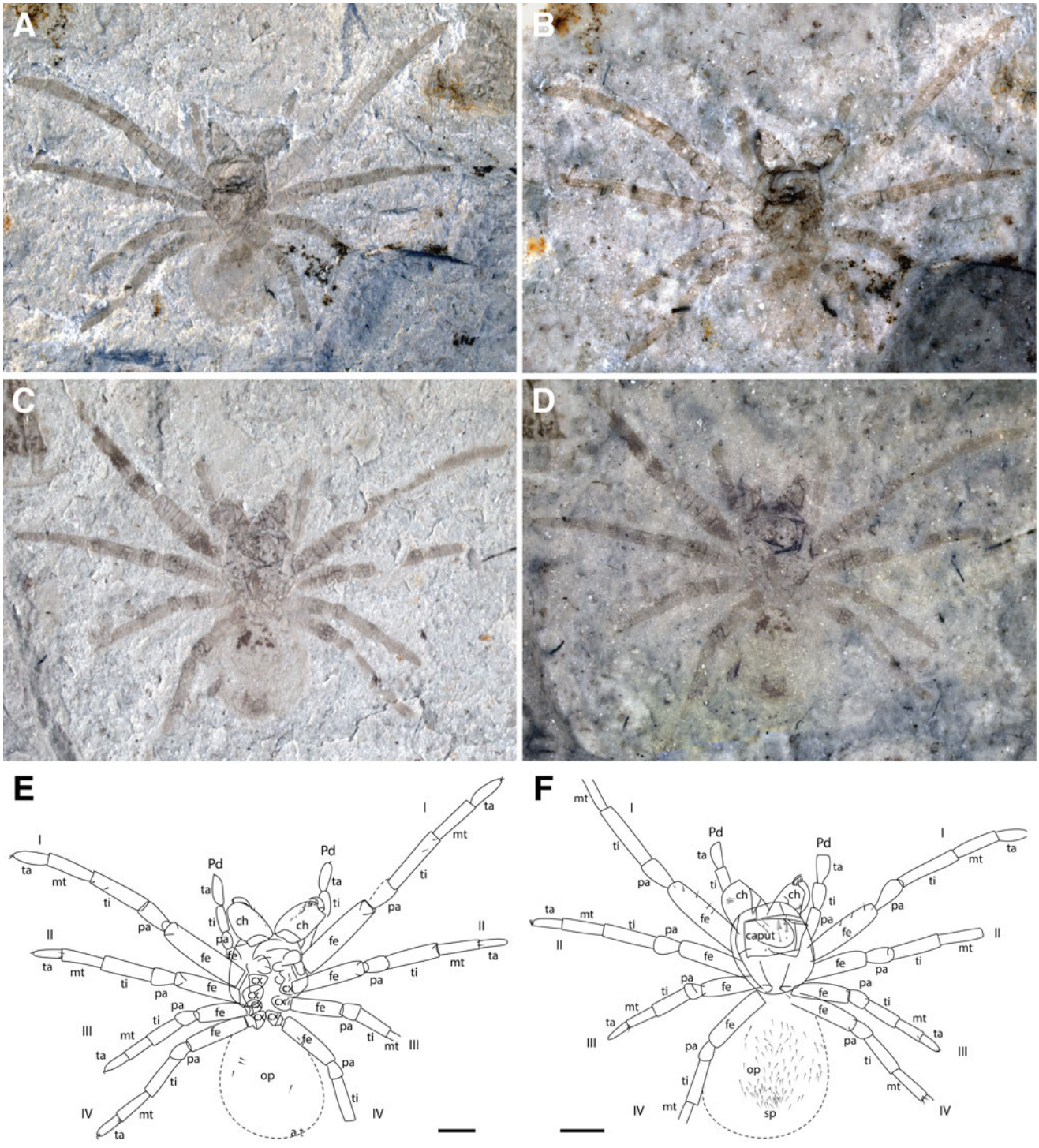

Figure 27. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168491a,b. **A,** part, dry. **B,** part, under ethanol. **C,** counterpart, dry. **D,** counterpart, under ethanol. **E,** explanatory drawing of A, B. **F,** explanatory drawing of C, D. Scale bars = 1 mm.

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

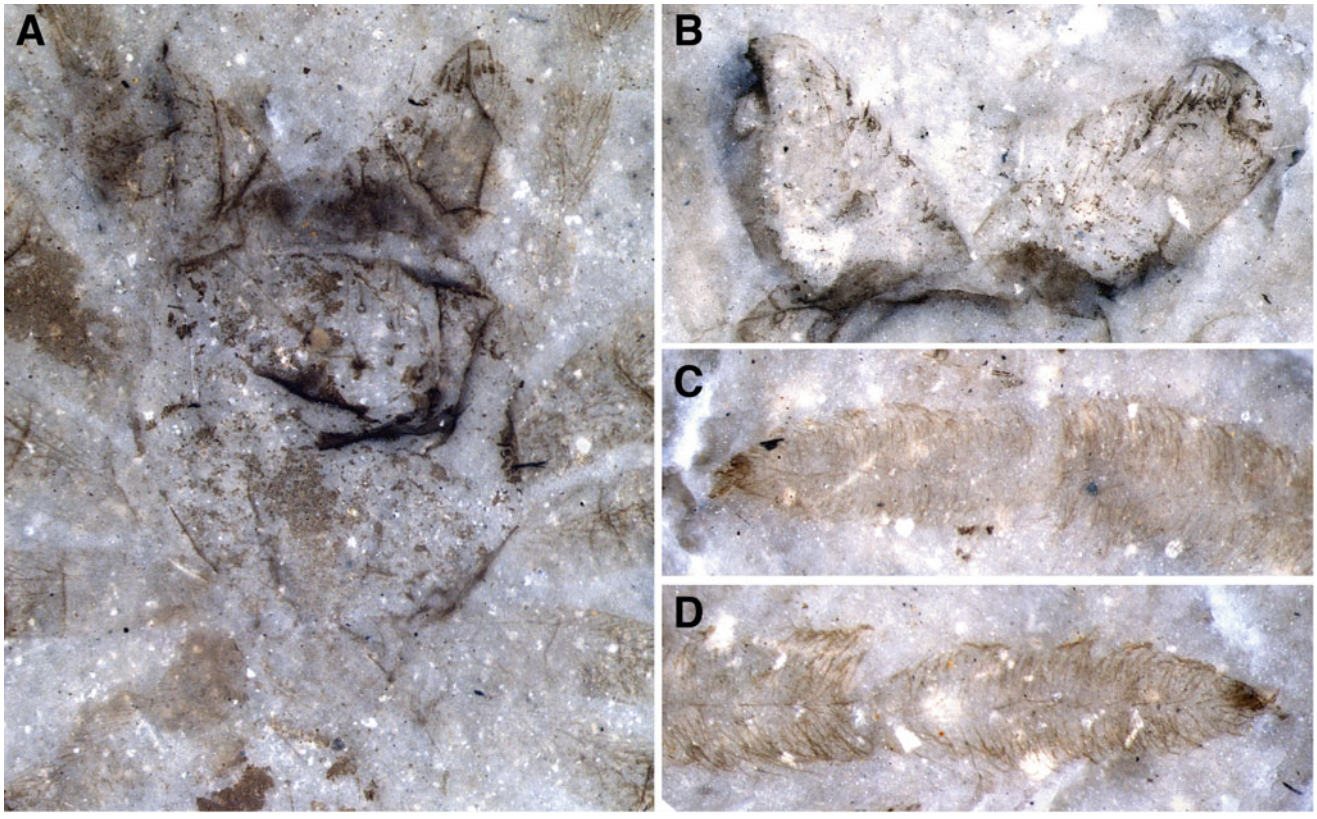

Figure 28. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168491a,b, under ethanol. **A,** counterpart, carapace showing caput region bearing large macrosetae and chelicerae showing peg teeth. **B,** part, chelicerae. **C,** part, left leg I distal metatarsus and tarsus showing scopulae and tarsal claws. **D,** part, right leg I distal metatarsus and tarsus showing scopulae and tarsal claws.

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 pro- 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 I/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).

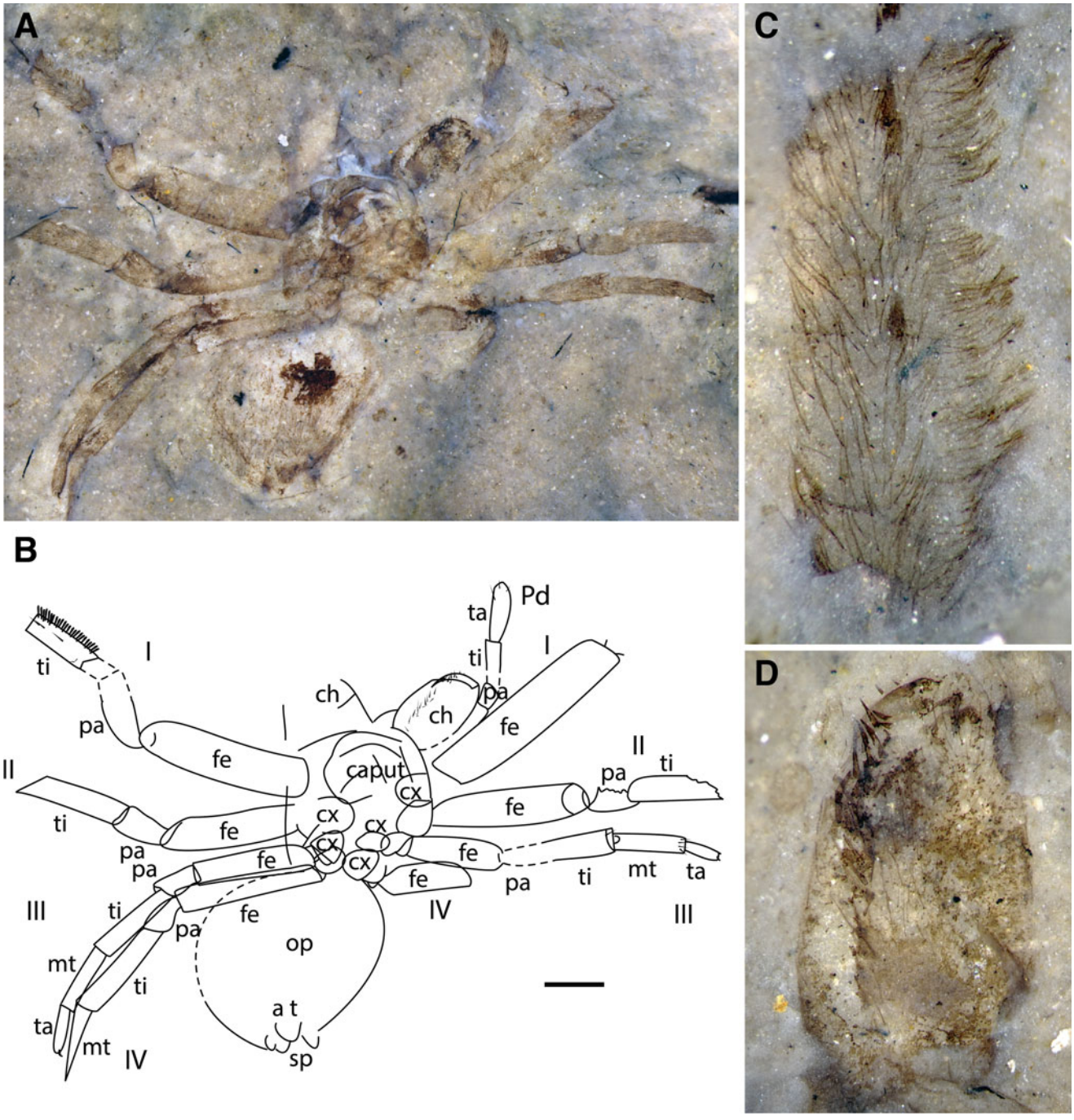

Figure 29. *Onychopalpus thomisoides* gen. et sp. nov., specimen NIGP168492, under ethanol. **A,** whole specimen, part. **B,** explanatory drawing of A. **C,** left leg I tibia showing scopulae and tarsal claws. **D,** chelicera. Scale bar = 1 mm.

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*; fe I/ch L ratio < 2.0 cf. > 2.6 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.

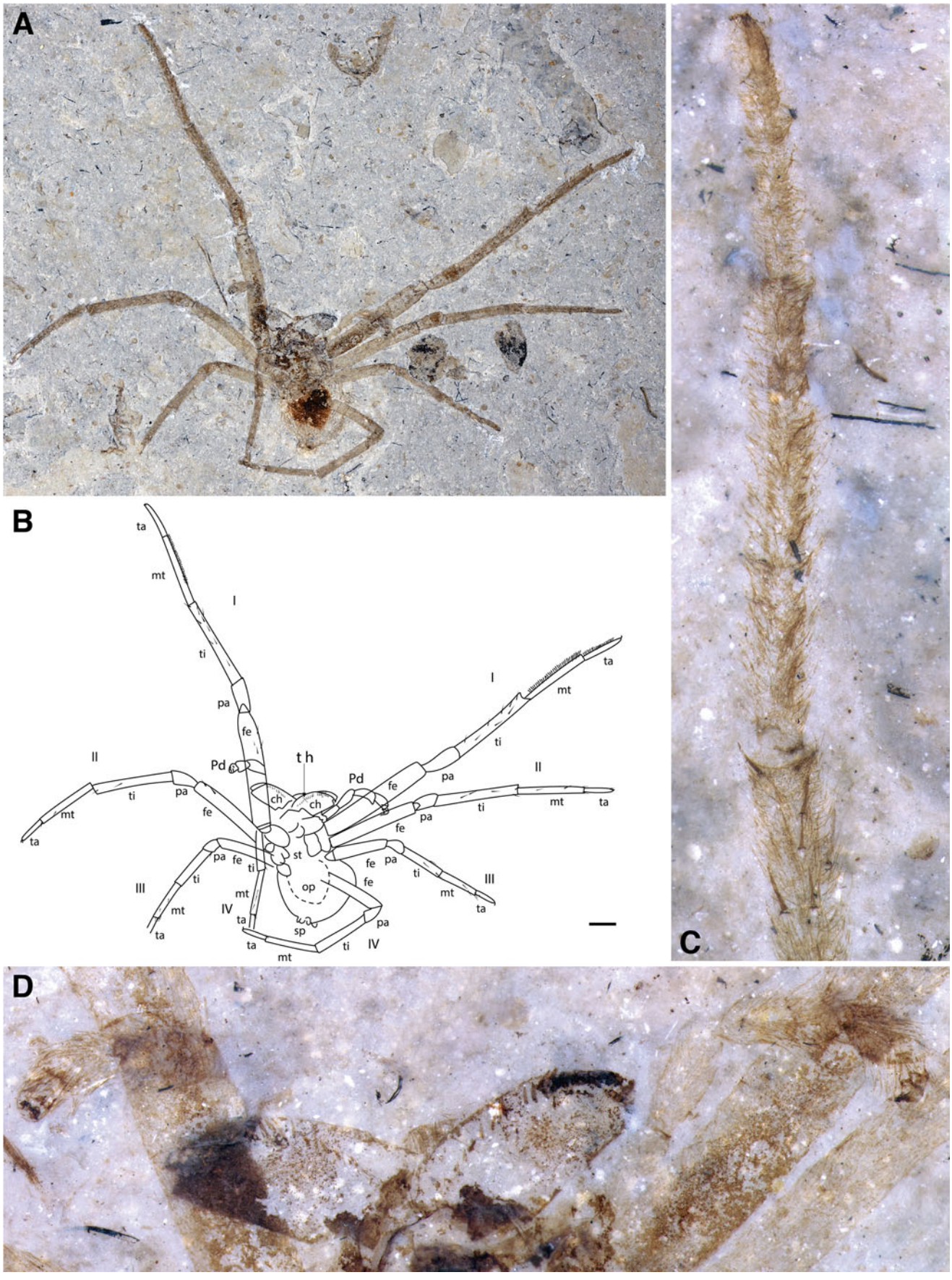

Figure 30. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168492a,b, part. **A,** whole, dry. **B,** explanatory drawing of A. **C,** left leg I tibia-tarsus, showing macrosetae, scopulae and tarsal claws, under ethanol. **D,** chelicerae and palps, under ethanol. Scale bar = 1 mm.

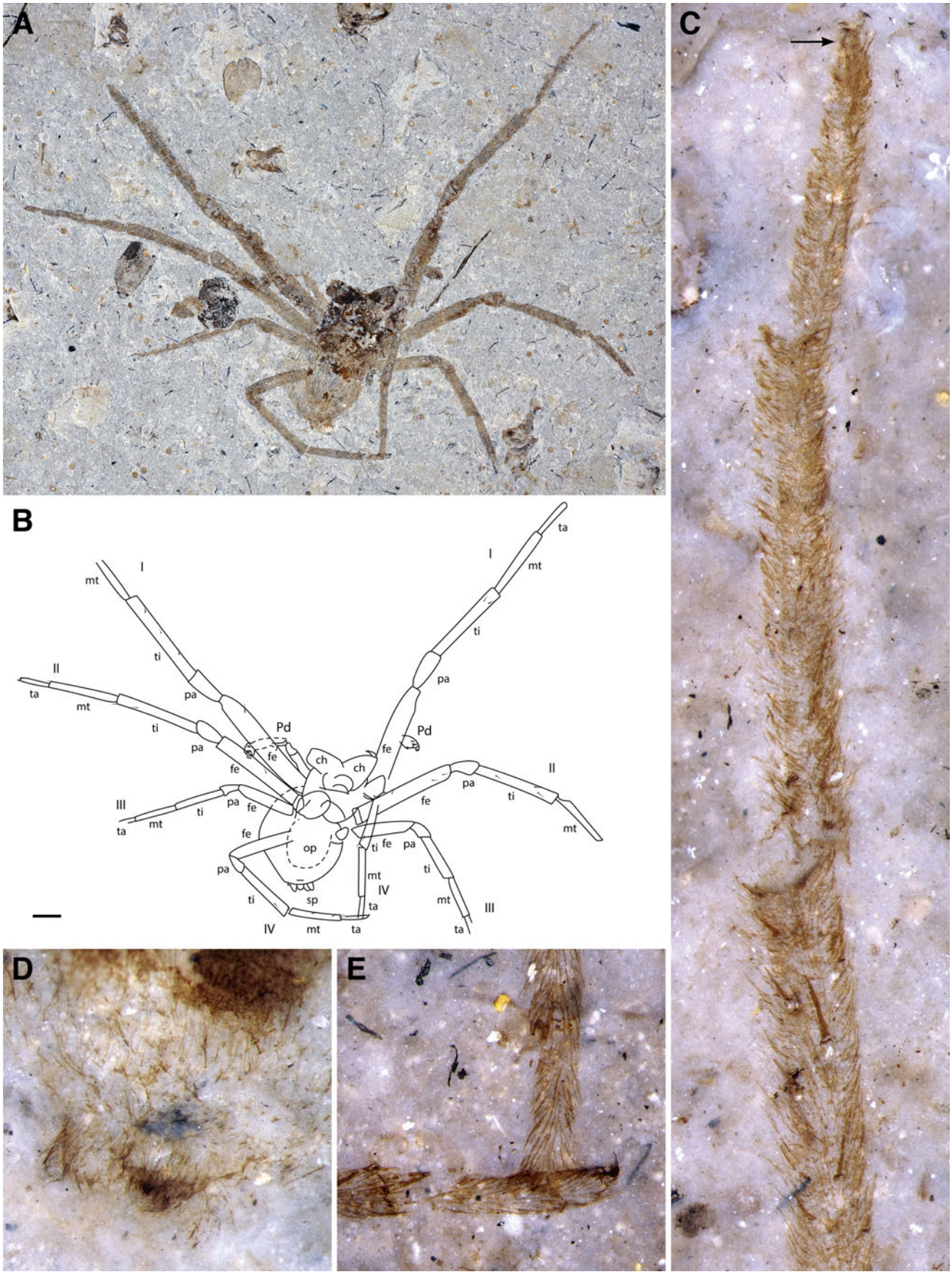

Figure 31. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168492a,b. **A,** counterpart, whole, dry. **B,** explanatory drawing of A. **C,** part, right leg I tibia-tarsus, showing macrosetae, scopulae, tarsal claws and fimbriate accessory claws (arrow), under ethanol. **D,** part, spinnerets and anal tubercle, under ethanol. **E,** counterpart, distal metatarsi and tarsi of legs IV, showing macrosetae and tarsal claws. Scale bar = 1 mm.

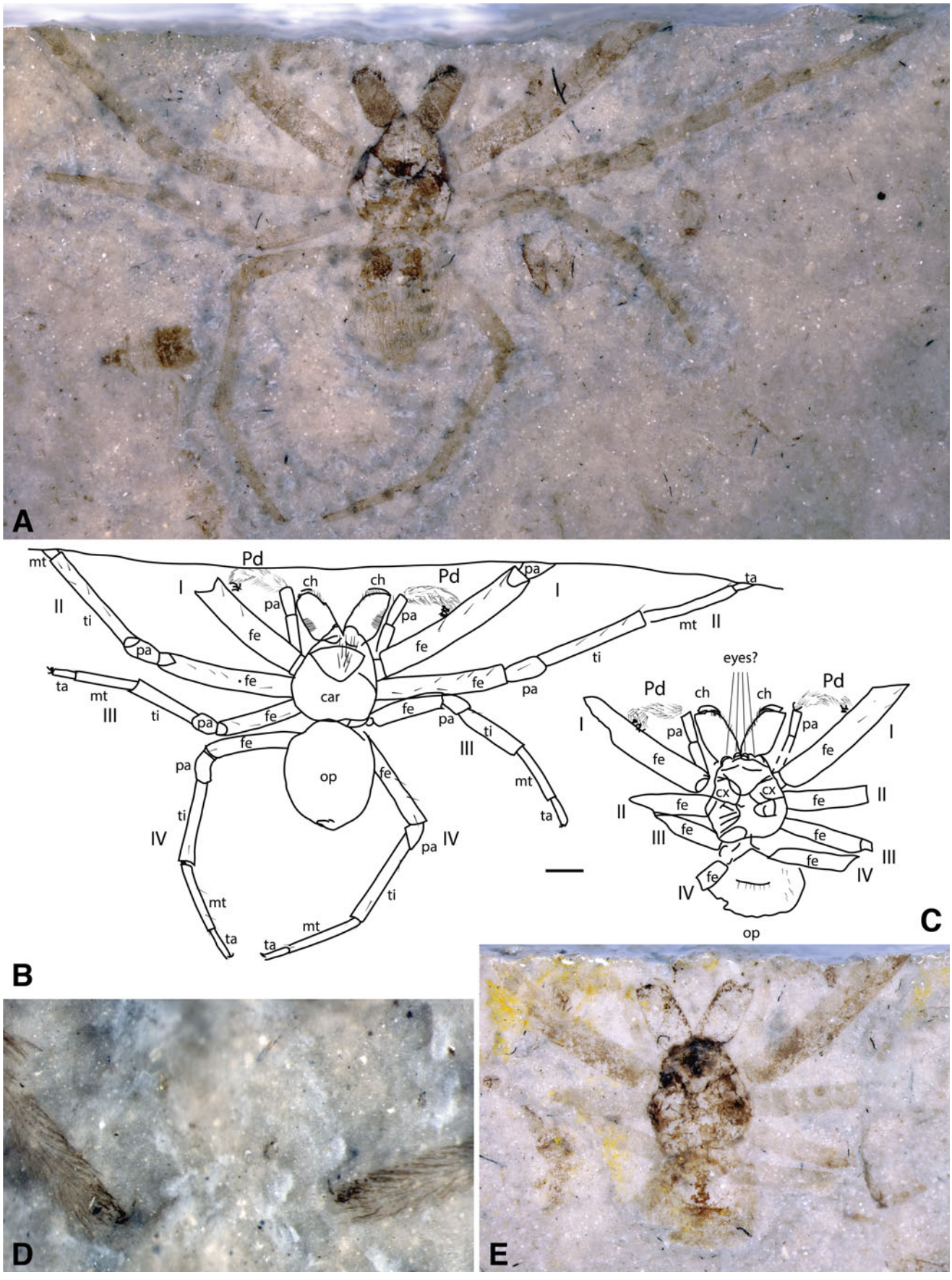

Figure 32. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168493a,b, under ethanol. **A,** part, whole. **B,** explanatory drawing of A. **C,** explanatory drawing of E. **D,** part, leg IV tarsi showing claws. **E,** counterpart, whole. Scale bar = 1 mm.

Figure 33. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168493a,b, part, under ethanol. **A,** chelicerae showing peg teeth, fangs and stridulatory ridges, and pedipalps showing spiral emboli. **B,** left leg III distal metatarsus and tarsus, showing claws. **C,** right leg III distal metatarsus and tarsus, showing claws.

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 $\geq$ 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 $\geq$ 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 $\geq$ 2.0, W $\geq$ 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.

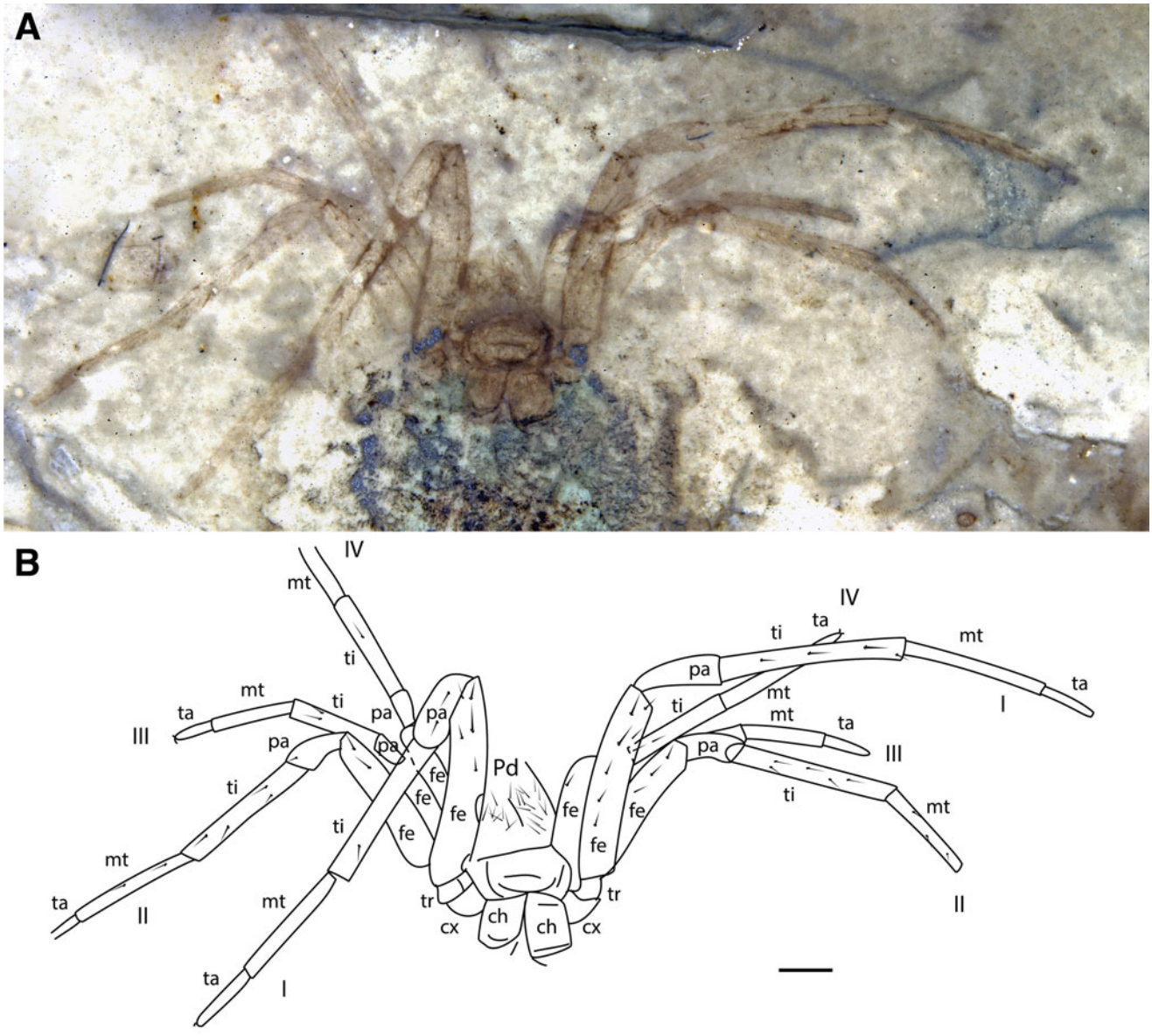

Figure 34. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, specimen NIGP168494, under ethanol. **A,** whole. **B,** explanatory drawing of A. Scale bar = 1 mm.

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

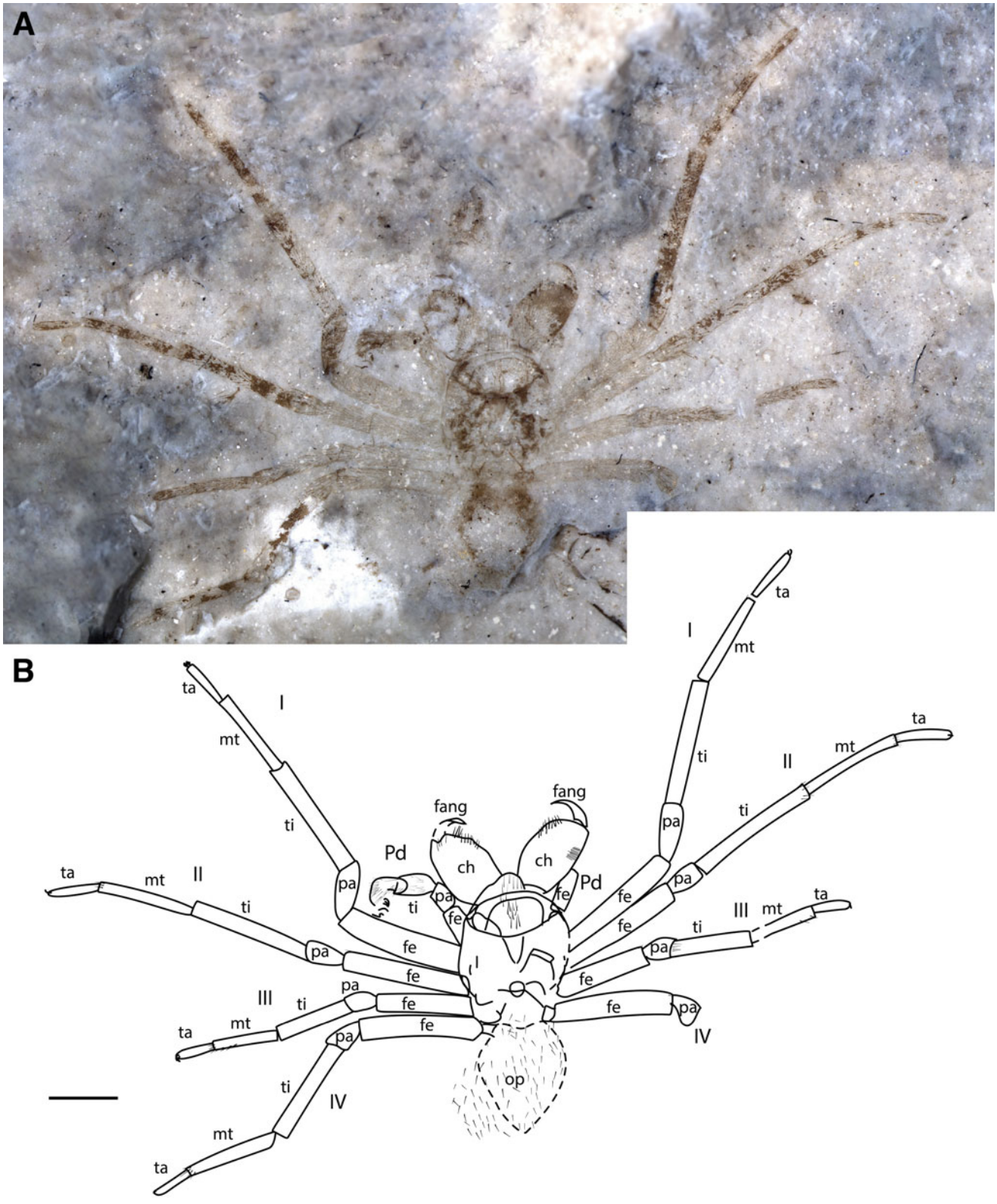

Figure 35. *Sinaranea brevicrus* sp. nov., holotype male NIGP168495, part, under ethanol. **A,** whole specimen. **B,** explanatory drawing of A. Scale bar = 1 mm.

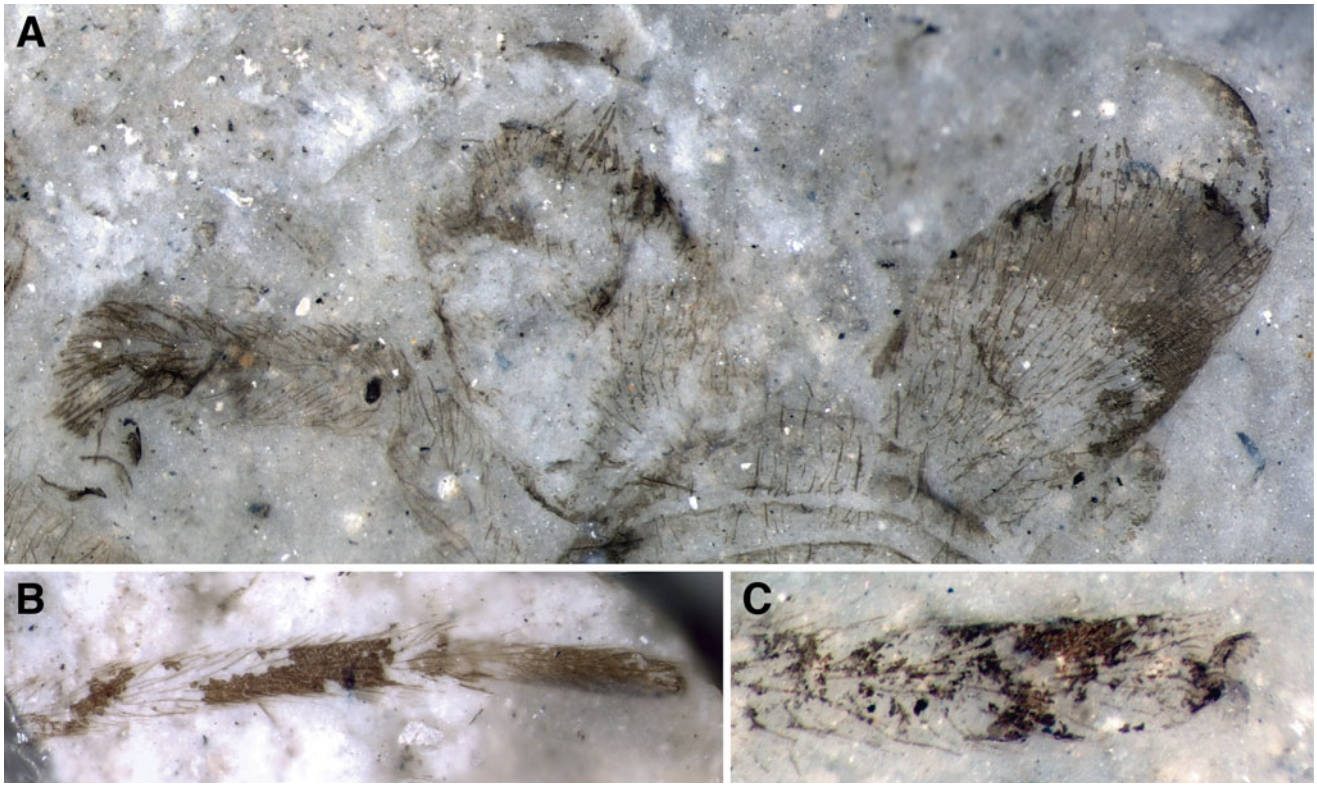

Figure 36. *Sinaranea brevicrus* sp. nov., holotype male NIGP168495, under ethanol. **A,** part, chelicerae showing peg teeth, fang and stridulatory ridges on right chelicera, and left male pedipalp with remnants of spiral structure. **B,** counterpart, metatarsus and tarsus of left leg IV, with metatarsal macrosetae and tarsal claws. **C,** part, left leg I tarsus showing pectinate paired tarsal claws.

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: absent (0), present (1); all of the taxa described here show scopulae on the anterior legs, so are scored 1. Character 36, scopula 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 length of 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,

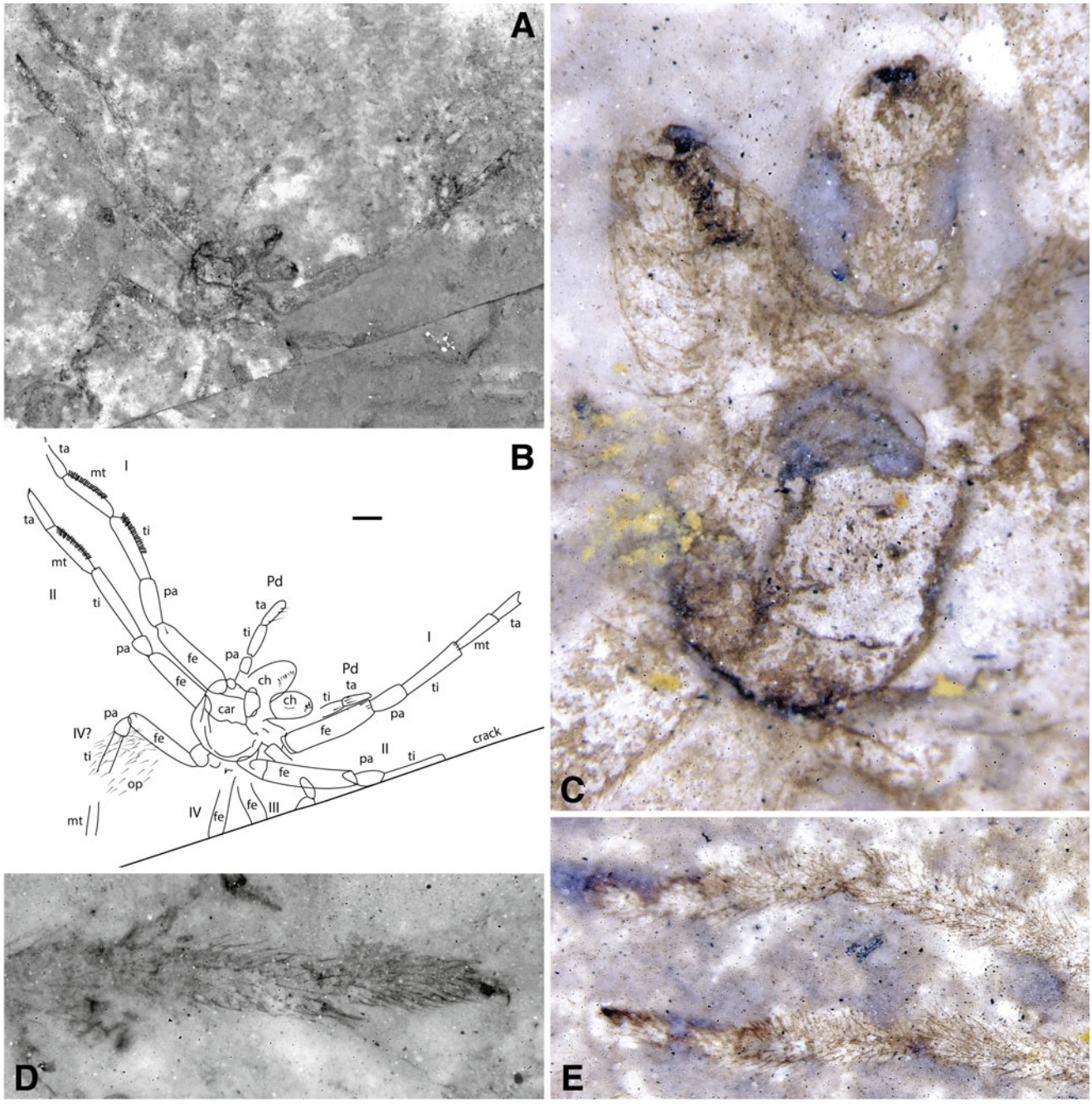

Figure 37. *Sinaranea brevicrus* sp. nov., allotype NIGP168496a,b, under ethanol. **A,** whole specimen, part. **B,** explanatory drawing of A. **C,** carapace and chelicerae of part. **D,** counterpart, right leg IV metatarsus and tarsus with distal metatarsal macrosetae and tarsal claws. **E,** part, left legs I and II showing scopulae. Scale bar = 1 mm.

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.

Specimen	Holotype 168480a,b	Paratype 168482	Paratype 168483	Paratype 168484a,b	Allotype 168481a,b	148238	148239a,b	168485	168486a,b	168487	148236
Sex	♂	♂	♂	♂	♀	♀	♀	♀	juv.♀	juv.♂	juv.
Body L excl. ch	3.86	4.25	4.02	3.74	5.13	5.05	5.23	*5.04*	*4.49*	3.10	3.28
Carapace L	1.87	2.08	1.81	1.64	2.17	*2.07*	2.13	*2.50*	*1.82*	1.36	1.26
Carapace W	1.46	1.67	1.59	1.25	1.59	1.74	*1.70*	*1.96*		1.01	*0.83*
Carapace L/W ratio	1.28	1.25	1.14	1.31	1.36	*1.19*	*1.25*	*1.28*		1.35	*1.52*
Caput L					0.71					0.48	
Caput W					1.24					0.77	
Caput L/W ratio					0.57					0.62	
Opisthosoma L	*2.20*	*2.41*	*2.37*	*2.24*	*2.72*	*3.00*	*3.01*		2.72	*1.73*	*1.73*
Opisthosoma W	*2.20*	*2.25*	*2.14*	*1.87*	*2.42*	*2.73*	*2.27*		1.88	*1.38*	*1.20*
Opisthosoma L/W ratio	*1.00*	*1.07*	*1.11*	*1.20*	*1.12*	*1.10*	*1.33*		1.45	*1.25*	*1.44*
Opisthosoma central L		0.88	1.14	1.13			*1.21*				
Opisthosoma central W		0.76	1.04	0.84			*0.94*				
Opisthosoma central L/W ratio		1.16	1.10	1.35			*1.29*				
Sternum L	0.69			0.56	0.95		0.87				
Sternum W	0.40			0.42	0.59		0.48				
Sternum L/W ratio	1.73			1.33	1.61		1.81				
Chelicera L incl. fang	1.09	1.27	0.96	0.92	1.20	1.38	1.44	1.44	1.23	0.75	0.74
Chelicera W	0.67	0.70	0.57	0.59	0.82	0.85	0.89	0.89	0.76	0.51	0.39
Chelicera L/W ratio	1.63	1.81	1.68	1.56	1.46	1.62	1.62	1.62	1.62	1.47	1.90
Chelicera fang L	0.55	0.49	0.42	0.38		0.55	0.65	0.65	0.52	0.35	0.30
Pedipalp fe L				0.55				*0.83*	*0.49*		
Pedipalp pa L	0.35	0.33		0.22	0.27		0.20	0.31	0.19	0.15	
Pedipalp ti L	0.51	0.58		0.43	0.58		0.57	0.69	0.54	0.30	0.31
Pedipalp ta L	0.71	0.55		0.62	0.59	0.75	0.61	0.75	0.59	0.44	0.36
Pedipalp L									1.81		
Leg I fe L	1.63	1.48	1.38	1.34	1.73	1.65	1.42	1.87	1.51	1.07	1.81
Leg I pa L	0.60	0.58	0.54	0.48	0.66	0.75	0.59	0.72	0.57	0.47	0.48
Leg I ti L	1.20	1.13	1.09	1.03	1.11	1.54	1.13	1.44	1.08	0.77	0.80
Leg I mt L	0.98	0.84	0.85	0.85	0.97		0.75	1.24	0.85	0.75	0.65
Leg I ta L	0.72	0.70	0.62	0.60	0.61		0.53	0.69	0.58	0.49	0.57
Leg I Total fe–ta	5.13	4.73	4.48	4.30	5.08		4.42	5.96	4.59	3.55	4.31
Leg I ta/mt	0.73	0.83	0.73	0.71	0.63		0.71	0.56	0.68	0.65	0.88
Leg II fe L	1.45	1.21	1.32	1.24	1.44	1.51	1.10	1.71	1.27	0.81	
Leg II pa L	0.47	0.46	0.39	0.40	0.47	0.53	0.41	0.55	0.46	0.31	
Leg II ti L	1.26	1.11	1.01	0.97	1.14	1.32	0.96	1.56	1.14	0.68	
Leg II mt L	1.05	0.93	0.94	0.84	0.96		0.61		0.83	0.53	
Leg II ta L	0.57	**0.56**	0.67	0.53	0.66		0.64		0.56	0.38	
Leg II Total fe–ta	4.80	**4.27**	4.33	3.98	4.67		3.72		4.26	2.71	0.00
Leg II ta/mt	0.54	**0.60**	0.71	0.63	0.69		1.05		0.67	0.72	
Leg III fe L	1.07	0.98	0.91	0.90	1.12	0.95	1.02	1.26	1.10	0.72	0.63
Leg III pa L	0.40	0.37	0.32	0.26	0.34	0.39	0.31	0.43	0.39	0.20	0.22
Leg III ti L	0.78	0.73	0.75	0.65	0.83	0.91	0.84	1.00	0.83	0.51	0.46
Leg III mt L	0.78	0.66	0.56	0.56	0.70	0.75	0.60		0.70	0.48	0.41

(*Continued*)

(*Continued*).

Leg III ta L	0.45	0.50	0.49	0.24	0.46	0.51	0.52		0.56	0.42	0.32
Leg III Total fe–ta	3.48	3.24	3.03	2.61	3.45	3.51	3.29		3.58	2.33	2.04
Leg III ta/mt	0.58	0.76	0.88	0.43	0.66	0.68	0.87		0.80	0.88	0.78
Leg IV fe L	1.34	1.36	1.30	1.15	1.45	1.32	1.59	1.61	1.59	0.97	0.84
Leg IV pa L	0.42	0.42	0.34	0.36	0.39		0.38	0.51	0.42	0.29	0.30
Leg IV ti L	1.12	0.96	0.99	0.88	1.25	1.30	1.29		1.09	0.71	0.67
Leg IV mt L	1.00	0.85	0.81	0.89	1.11	1.06	0.95		0.90	0.68	0.51
Leg IV ta L	0.65	0.63	0.64	0.30	*0.60*	0.63	0.70		0.58	0.47	0.47
Leg IV Total fe–ta	4.53	4.22	4.08	3.58	*4.80*		4.91		4.58	3.12	2.79
Leg IV ta/mt	0.65	0.74	0.79	0.34	*0.54*	0.59	0.74		0.64	0.69	0.92
mean ratio ta/mt	0.63	0.73	0.78	0.53	0.63	0.64	0.84	0.56	0.70	0.73	0.86

promargin: all taxa described here were scored as for most other palpimanoids (1 and 0, respectively). Characters 81, 84 and 86, namely heavy sclerotization around anterior part of abdomen, abdominal cuticle wrinkle pattern, and abdominal cuticle wrinkle pattern: all taxa described here were scored for absence (0).

The resulting Bayesian topology is presented in Figure 38. The analysis recovered the new fossils as palpimanoids. *Onychopalpus* resolves as the sister group to other palpimanoids, including the other fossils described herein. The next node comprises a polytomy of the *Sinaranea* species, as sister group to a (*Caestaranea* + all remaining Palpimanoidea) clade. The support for this topology is weak, most notably that with the *Sinaranea* polytomy. The new taxa unequivocally belong in Palpimanoidea, as evidenced by the well-supported branch (posterior probability 1.00), reflecting the palpimanoid characters of these taxa mentioned in the Systematic palaeontology section, above. Of course, some characters, such as the male pedipalps of the new taxa, were not included in the analysis because 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. Pékar *et al*. 2012; Pékar & 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

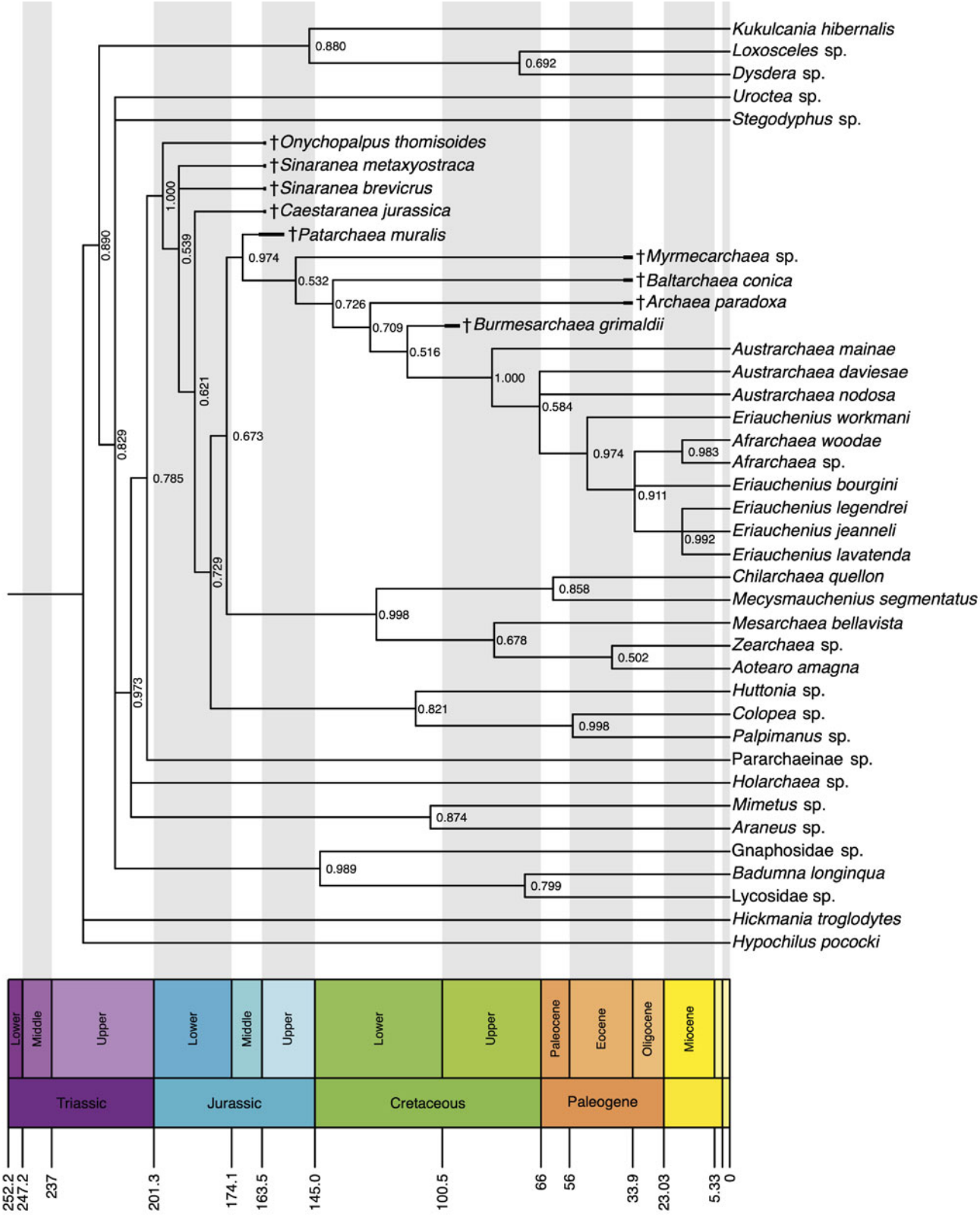

Figure 38. Phylogeny of palpimanoid spiders and their outgroups from Bayesian analysis of morphological data, plotted against geological time using fossil dates and equal branch lengths (see methods). Numbers at nodes represent posterior probabilities. Based on the matrix of Wood *et al.* (2012, appendix 2) with the addition of the fossil taxa described here. † denotes fossil taxa. Compare with Wood *et al.* (2012, fig. 4).

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

Specimen	Holotype 168488a,b	148237a,b	168489	168490a,b	168491a,b	168492
Sex	sub.♂	juv.	juv.	juv.	juv.	juv.
Body L exc. ch	7.90	4.44	3.10	4.64	5.50	6.00
Carapace L	3.11	1.87	1.62	2.00	2.18	2.77
Carapace W	3.27	1.69	1.38	1.98	2.01	2.43
Carapace L/W ratio	0.95	1.11	1.17	1.01	1.08	1.14
Caput L	1.68	1.27		1.12	0.89	
Caput W	2.34	1.57		1.62	1.47	
Caput L/W ratio	0.72	0.81		0.69	0.61	
Opisthosoma L	2.65	2.65	1.74			
Opisthosoma W	2.57	2.57	1.59			
Opisthosoma L/W ratio	1.03	1.03	1.09			
Chelicera L incl. fang	2.08	0.99	0.96	1.19	1.29	1.62
Chelicera W	1.38	0.77	0.67	0.78	0.83	0.98
Chelicera L/W ratio	1.51	1.29	1.43	1.53	1.55	1.65
Chelicera fang L	1.21	0.53	0.38	0.56		
Pedipalp fe L	*1.05*	0.45	0.51	0.59	0.77	
Pedipalp pa L	1.15	0.52	0.37	0.32	0.48	0.44
Pedipalp ti L	1.26	0.53	0.49	0.67	0.65	0.80
Pedipalp ta L	1.06	0.58	0.69	0.65	0.78	0.99
Pedipalp L	*4.52*	2.08	2.06	2.23	2.68	
Leg I fe L	4.63	1.71	1.67	2.28	2.28	3.18
Leg I pa L	1.84	0.67	0.77	1.01	0.88	1.33
Leg I ti L	2.78	1.08	0.95	1.48	1.64	
Leg I mt L	2.13	0.84	0.80	1.18	1.18	
Leg I ta L	1.56	0.90	0.78	0.90	0.91	
Leg I Total fe–ta	12.94	5.20	4.97	6.85	6.89	
Leg I ta/mt	0.73	1.07	0.98	0.76	0.77	
Leg II fe L	3.64	1.27	1.24	1.73	1.79	2.49
Leg II pa L	1.47	0.57	0.53	0.64	0.63	0.93
Leg II ti L	2.78	0.89	0.90	1.26	1.29	1.78
Leg II mt L	2.12	0.87	0.70	1.00	1.04	
Leg II ta L	1.27	**0.65**	0.59	0.75	0.81	
Leg II Total fe–ta	11.28	**4.25**	3.96	5.38	5.56	
Leg II ta/mt	0.60	**0.75**	0.84	0.75	0.78	
Leg III fe L	2.29	0.96	0.87	1.18	1.37	1.76
Leg III pa L	1.14	0.41	0.37	0.55	0.49	0.62
Leg III ti L	1.65	0.59	0.59	0.91	0.90	1.39
Leg III mt L	1.40	0.56	0.50	0.75	0.73	1.16
Leg III ta L	0.99	0.54	0.49	0.55	0.67	0.75
Leg III Total fe–ta	7.47	3.06	2.82	3.94	4.16	5.68
Leg III ta/mt	0.71	0.96	0.98	0.73	0.92	0.65
Leg IV fe L	2.75	1.19	1.12	1.47	1.65	2.38
Leg IV pa L	0.99	0.43	0.42	0.56	0.55	0.69
Leg IV ti L	2.07	0.80	0.80	1.02	1.13	1.74
Leg IV mt L	1.66	0.73	0.58	0.81	0.99	
Leg IV ta L	0.98	0.57	0.59	0.66	0.82	
Leg IV Total fe–ta	8.45	3.72	3.51	4.52	5.14	
Leg IV ta/mt	0.59	0.78	1.02	0.81	0.83	
mean ratio ta/mt	0.66	0.89	0.95	0.77	0.82	0.65

show such exaggerated features – but neither do some modern palpimanoid families, e.g. Palpimanidae, yet they are also araneophagous predators (Pékar *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 (Pékar *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 3. *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008 and *S. brevicrus* sp. nov., specimen measurements. Italics denote uncertain measurements.

Specimen	*S. metaxyostraca* 168492a,b	*S. metaxyostraca* 168493a,b	*S. metaxyostraca* 168494	*S. brevicrus* Holotype 168495	*S. brevicrus* Allotype 168496a,b
Sex	♂	♂	?	♂	♀
Body L excl. ch	4.96	5.42		*4.18*	
Carapace L	*2.31*	2.45		2.11	2.67
Carapace W		2.19		1.65	2.53
Carapace L/W ratio		1.12		1.28	1.06
Opisthosoma L	*2.90*	2.96		*2.00*	
Opisthosoma W	2.90	2.37		*1.67*	
Opisthosoma L/W ratio	1.00	1.25		*1.20*	
Chelicera L incl. fang	1.47	1.45	*1.32*	1.37	1.88
Chelicera W	0.85	0.82	0.75	0.75	1.07
Chelicera L/W ratio	1.73	1.77	1.76	1.83	1.76
Chelicera fang L		0.59		0.59	
Pedipalp fe L	0.81	1.01		0.58	
Pedipalp pa L	0.72	0.80		0.35	0.56
Pedipalp ti L	0.82	0.86		0.54	1.21
Pedipalp ta L	0.79	0.84		0.65	1.03
Pedipalp L	3.14	3.51		2.12	
Leg I fe L	4.27	4.46	3.85	1.85	3.12
Leg I pa L	1.35		1.57	0.85	1.44
Leg I ti L	2.32		3.19	1.81	2.31
Leg I mt L	2.57		2.52	1.33	1.85
Leg I ta L	1.51		1.21	0.79	1.54
Leg I Total fe–ta	12.02		12.34	6.63	10.26
Leg I ta/mt	0.59		0.48	0.59	0.83
Leg II fe L	3.48	3.53	2.81	1.84	2.78
Leg II pa L	1.02	1.03	1.19	0.52	0.92
Leg II ti L	2.98	2.93	2.75	1.87	2.43
Leg II mt L	2.37	2.54	2.31	1.43	2.05
Leg II ta L	1.10		0.90	0.79	1.53
Leg II Total fe–ta	10.95		9.96	6.45	9.71
Leg II ta/mt	0.46		0.39	0.55	0.75
Leg III fe L	2.13	2.20	1.68	1.36	
Leg III pa L	0.70	0.72	0.62	0.44	
Leg III ti L	1.68	1.70	1.64	1.10	
Leg III mt L	1.47	1.61	1.49	0.96	
Leg III ta L	0.85	0.81	0.81	0.56	
Leg III Total fe–ta	6.83	7.04	6.24	4.42	
Leg III ta/mt	0.58	0.50	0.54	0.58	
Leg IV fe L	2.53	2.60	2.40	1.71	2.71
Leg IV pa L	0.76	0.78	0.67	0.48	0.73
Leg IV ti L	2.10	2.35	1.98	1.48	
Leg IV mt L	1.82	1.94	1.50	1.40	
Leg IV ta L	0.92	0.85	0.50	0.58	
Leg IV Total fe–ta	8.13	8.52	7.05	5.65	
Leg IV ta/mt	0.51	0.44	0.33	0.41	
Mean ratio ta/mt	0.53	0.47	0.44	0.54	0.79

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

similar. Also, thomisids generally have small chelicerae. The overall impression of *Onychopalpus* is that of a palpimanoid 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 chelicerae arising from a raised, strongly demarcated caput region of the carapace, and bearing peg teeth in the standard arrangement. *Sinaranea* 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 *Sinaranea* are slender and either quite long (*S. metaxyostraca*) or shorter (*S. brevicrus*). They also show typical palpimanoid characters. In Mecysmaucheniidae 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 *Lacunauchenius* Wunderlich, 2008b, and can be seen in *Caestaranea* and *Sinaranea 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

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