

The first fossil spider (Araneae: Palpimanoidea) from the Lower Jurassic (Grimmen, Germany)

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Abstract

The first Lower Jurassic (Lias) spider is described as *Seppo koponeni* n. gen. & n. sp. from a single female specimen from Grimmen, Germany. It most likely belongs to the Palpimanoidea, on account of the presence of cheliceral peg teeth and other features consistent with palpimanoid families, though its familial placement is uncertain. Its presence in the region at that time concurs with ideas about the more widespread presence of palpimanoids across the world in the early Mesozoic, before the break-up of Pangaea.

Key words: Fossil-Lagerstätte, Lias, Mesozoic, *Seppo koponeni*, new genus, new species

Introduction

Spiders are generally rather rare components of Mesozoic terrestrial fossil assemblages, and especially so in strata older than the earliest common occurrences of organic inclusions in amber of Cretaceous age. Few localities containing Jurassic spiders are known, and these include the famous Fossil-Lagerstätte of Daohugou, Inner Mongolia, China (Hong 1984; Selden & Huang 2008, 2010; Selden *et al.* 2011, 2013), localities renowned for their fossil insect fauna in Russia (Eskov 1984) and Kazakhstan (Eskov 1987), and the Talbragar Fish Bed of New South Wales, Australia (Selden & Beattie 2013). All of these are Middle or Upper Jurassic, so the specimen described here, from the Lower Toarcian, is the first Lower Jurassic (=Liassic) spider to be described.

Here, we report on a single specimen of a new spider species from another locality known for its fossil insects: Grimmen, near Greifswald, Germany. The specimen was figured in a preliminary report on the entomofauna of the Lower Toarcian (Lower Jurassic) of Europe by Ansorge (2003), but identified only as a spider. The specimen is fairly complete but presents only a ventral view, and is a mixture of internal and external moulds, with some organic material (e.g. setae) preserved in adjacent matrix. Enough information is preserved to describe it as a new genus and species, *Seppo koponeni* n. sp., and suggest its identity as a palpimanoid (*sensu* Wood *et al.* 2012a), but its familial placement is uncertain.

Material and Methods

The single specimen (part only) is preserved in a sliver of calcareous nodule from the grey-green claystone, which comes from the now-closed opencast clay pit of Klein Lehmhagen, near Grimmen, Western Pomerania, Germany (Ansorge 1996, 2007). The preservation is curious, being one of only a few examples of spiders preserved in calcium carbonate (another is the Late Eocene Insect Limestone of the Isle of Wight, England: Selden 2001, 2014). Some parts are preserved as external moulds, and these show setation and spination (e.g. Fig. 3C). Most of the specimen, however, is an internal mould of calcium carbonate. This presents the animal nicely in three dimensions,

but lacks external cuticular features except at the edges where setae and similar structures, preserved as organic material, can be seen protruding into the adjacent matrix (Fig. 3B). The contrast can be seen most clearly in the comparison of right (internal mould) and left (external mould) chelicerae (Figs 1–2).

The spider had been skilfully developed from the rock matrix by its discoverer, Jörg Ansorge, before receipt for study. The specimen was studied and drawn using Leica MZ16 and MZ12.5 stereomicroscopes equipped with camera lucida drawing attachments. Photographs were taken on the stereomicroscopes using polarized incident light, with the specimen both dry and under 70% alcohol, with Canon EOS 5D MkII and MkIII cameras, and also using a Leica DM2500 M microscope, using reflected light, for higher magnification of structural details (Figs 3A–C). Drawings were finalized using iDraw software (www.indeeo.com). The holotype, MB.A 2966, is housed in the palaeontological collections at the Museum für Naturkunde, Berlin.

All measurements are in mm. Note that, because the fossil is preserved in three dimensions, and podomeres are therefore not necessarily lying flat on the matrix, some podomere measurements are less accurate than under usual, flattened, matrix preservation. Leg formula (e.g. 1234) expresses legs I–IV as longest to shortest. All paired structures are handed according to the symmetry of the spider; i.e. because the specimen is ventral-side up, legs seen on the left are actually right legs, and labelled thus.

Abbreviations: **car** carapace, **ch** chelicera, **cx** coxa, **fe** femur, **ms** macroseta, **mt** metatarsus, **op** opisthosoma, **pa** patella, **Pd** pedipalp, **st** sternum, **ta** tarsus, **ti** tibia, **tr** trochanter.

Morphological Interpretation

The single specimen is presented ventral side up on the rock matrix, so most of the carapace and dorsal features cannot be seen. As preserved, the chelicerae are large and porrect. The three-dimensional preservation of the specimen, lacking compaction, suggests that this orientation would have been so in life. Behind the chelicerae there is a rectangular sclerotized area. How the chelicerae relate to this piece is not clear, and we interpret it as the clypeus, in which case, the chelicerae are not located in a foramen. The cheliceral furrow bears no true teeth, but a row of stiff, socketed bristles, apparently on the promargin. Because they would perform the function of true teeth, these are interpreted as peg teeth, although they are not so strong and lack the boss-like bases commonly seen in archaeids, for example. About six peg teeth are visible (Fig. 3A) and the bases of another six or so can also be seen; a few fine hairs also occur more proximally along the furrow; the external mould of the left chelicera shows scattered setae. The sternum is visible; it has a straight anterior border where it abuts the labium (there is a sharp demarcation where the labium is oriented upwards), slightly bowed, posteriorly converging sides, and a strongly curved posterior margin in front of coxae IV. It is not possible to discern whether the lateral edges have projections between the coxae, but none can be seen. The straight, posterior margin of the labium can be seen, but its overall length and shape cannot be determined. The area anterior to the sternum was excavated prior to study, but mouthparts were not revealed; hence, only the more distal parts of the pedipalps (patella–tarsus) are preserved. The leg coxae surrounding the lateral sides of, and meeting behind, the sternum ascend towards the viewer before the trochanters and more distal leg parts extend laterally across the rock surface. Coxa I is particularly large and protrudes forwards.

Leg I is particularly robust, turned forwards, and well-armed with rows of thin macrosetae, especially on the ventral surfaces of the tibia and metatarsus (the tarsus cannot be seen). The other legs are weak in comparison. Leg II (left) is preserved only on the right side of the specimen, and trails backwards. All other legs are preserved at least to metatarsus, but only legs II and III (left, seen on the right), preserve the tarsus, albeit poorly. So, in order to determine leg formula, length of proximal parts needs to be used as a proxy for the whole leg. Legs II–IV are either strongly bent or broken between the patella and tibia, suggesting a natural break at this joint, possibly a site of autospasy (although this phenomenon is not known from palpimanoids). However, left leg III also has the metatarsus separate from the tibia, so this effect might be just an artefact of preservation. A short piece of podomere lying between the tibia and femur of left leg I might be a piece of metatarsus (? on Fig. 2), indicating strong flexure of this leg too. An alternative possibility is that this fragment belongs to the tarsus of right leg I, by extrapolation making the leg an altogether much longer appendage, but this seems less likely. Bristles (thin macrosetae) and setae are numerous, where preserved, on the podomeres. In particular, there are rows on femora to tarsi, seen best on right leg I tibia and metatarsus (Fig. 3B), left leg II femur and tibia, and right leg IV metatarsus

(Fig. 3C). A trichobothrium can be seen distally on right leg I metatarsus (Fig. 3B). Legs IV show a slight, but distinct, mesial curvature (Figs 1, 2) The opisthosoma is preserved as a subcircular patch of dark organic matter, lacking relief, and with a scattering of bristles within and extending beyond the dark area. The dark area is presumed to be ventral, on account of the preservation of the rest of the spider with ventral side uppermost, and the coloration suggests it is sclerotized. Two subparallel lines are the only structures seen on this dark area. It is possibly related to the epigyne.

Systematic Palaeontology

Class Arachnida Lamarck, 1801

Order Araneae Clerck, 1757

Superfamily Palpimanoidea *sensu* Wood et al. (2012) (but see comment in Wunderlich (2008))

Family uncertain

Genus *Seppo* n. gen.

Type species. *Seppo kaponeni* n. sp.

Diagnosis. Palpimanoid without a cheliceral foramen; enlarged, forwardly directed leg I; short leg III; curvature of femur IV.

Etymology. After Seppo Koponen, to celebrate his 70th birthday.

Remarks. The new genus is accommodated in Palpimanoidea (Palpimanidae, Stenochilidae, Huttoniidae, Mecysmaucheniidae, Archaeidae, †Lagonomegopidae, †Spatiatoridae, †Micropalpimanidae) on account of a variety of characters which are commonly found in, but not exclusive to, this superfamily: enlarged chelicerae with peg teeth, and a lack of true teeth, along the cheliceral furrow, the presence of a distal trichobothrium on metatarsus I, paucity of large macrosetae on the legs, curved femur of leg IV, ventral anterior sclerotization and scattered bristles on the opisthosoma. Some Palpimanoidea have large chelicerae, and peg teeth are a characteristic of the superfamily (although these are also found in other spiders, e.g. Mimetidae). A distal metatarsal trichobothrium is characteristic of mecysmaucheniids and archaeids (Lehtinen 1980), although we cannot be sure if others were present on this podomere, A claw on the female pedipalp tarsus occurs in many spiders; in palpimanoids, for example, it is found in *Eriauchenius* O. Pickard-Cambridge, 1881, *Afrarchaea* Forster & Platnick, 1984 and *Austrarchaea* Forster & Platnick, 1984 (Wood *et al.* 2012a). The lack of macrosetae on the legs is an unusual feature of some spider families. In the new genus, numerous bristles (thin macrosetae) are present. Reduced leg spination occurs throughout Palpimanoidea and only a few other families (Wood *et al.* 2012a). A curved femur IV is characteristic of all living Archaeidae (Wood *et al.* 2012a). Sclerotization on the opisthosoma occurs in a variety of spider families, often in the form of a dorsal scutum; however, ventral sclerotization occurs in the epigynal area in *Eriauchenius* and *Afrarchaea*, and a reduced palpal claw is present in *Colopea* Simon, 1893 and in several mecysmaucheniid genera (Wood 2008; Wood *et al.* 2012a). Sparse bristles on the opisthosoma is also a feature of Archaeidae (Jocqué & Dippenaar-Schoeman 2006).

Arguing against Palpimanoidea is the possibility of patella–tibia autospasy, which is best known from Linyphiidae, Pimoidae, Filistatidae, Leptonetidae and Hersiliidae, and some genera in the Clubionidae and Philodromidae also show a tendency for the legs to separate at this joint (Roth & Roth 1984).

The genus differs from all palpimanoid families except Huttoniidae and the extinct families in the lack of a cheliceral foramen. A bent fourth femur is found in Archaeidae, but the femora of the fossil lack the hump seen in this family (Wood *et al.* 2012a). While the combination of characters suggest Palpimanoidea, there are some characters of the superfamily which cannot be seen in the fossil, e.g. cheliceral gland mound, and sclerotization around the spinnerets. Nor it is not clear to which existing family, if any, the new genus belongs.

***Seppo kaponeni* n. sp.**

Figs 1–3

Diagnosis. As for the genus.



FIGURE 1. *Seppo koponeni* n. gen. & n. sp. Holotype and only known specimen MB.A 2966. A, photograph of dry specimen in low-angle light, ventral. B, photograph under 70% ethanol and cross-polarized light. Scale bars = 1 mm.

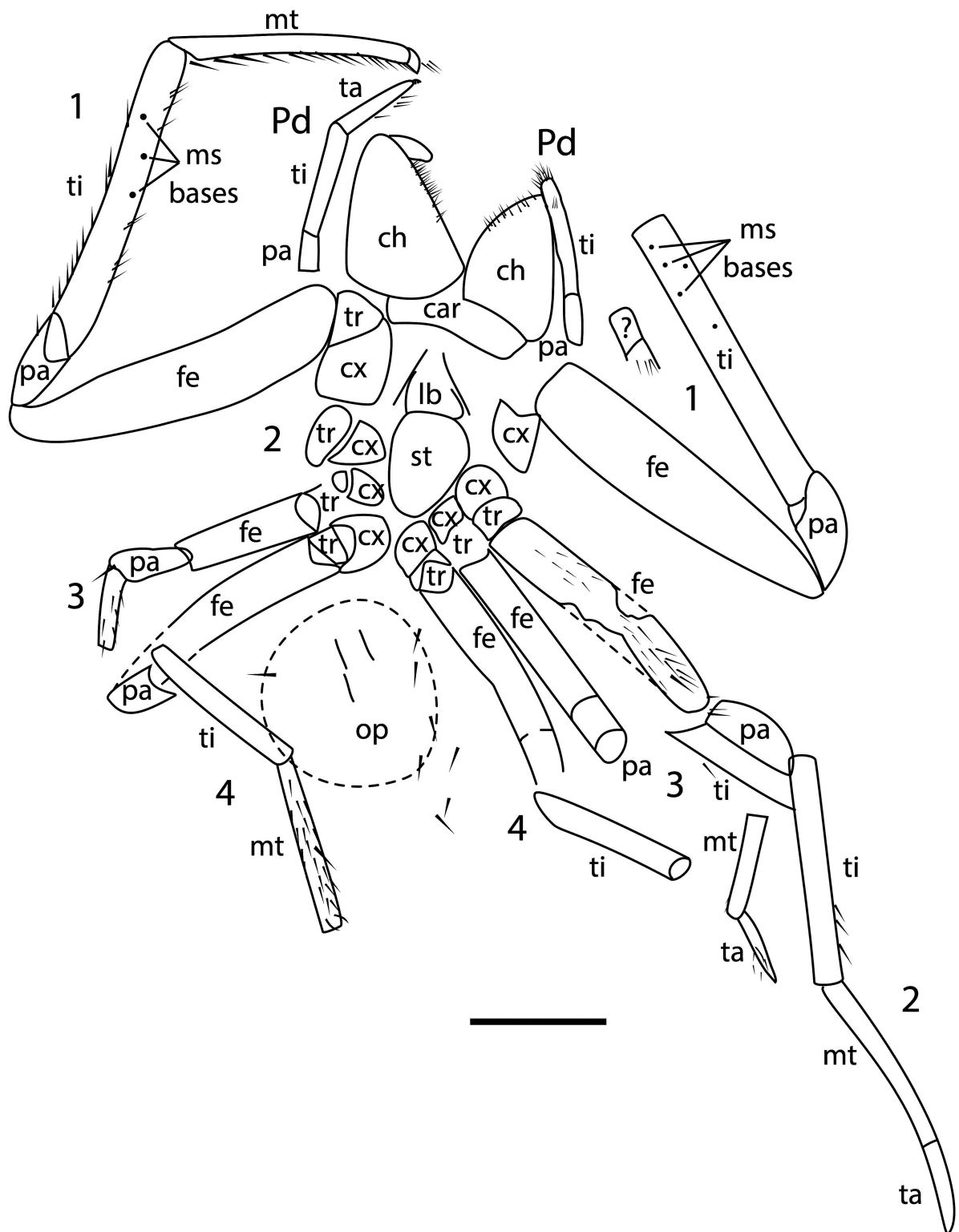


FIGURE 2. *Seppo koponeni* n. gen. & n. sp. Holotype and only known specimen MB.A 2966. Explanatory drawing to accompany Figure 1. Scale bar = 1 mm.

Description. Adult? female. Carapace unknown; st L 0.76, W 0.58, ratio 1.30, straight anterior border, slightly bowed posteriorly converging sides, strongly curved posterior margin; lb with straight posterior border, not fused to st; ch large, subtriangular, with row of at least 12 peg teeth along cheliceral furrow, no true teeth, scattered setae on anterior surface, L 1.26. Pedipalp slender, setose, bearing serrate claw. Leg formula 1243; legs I, II much longer than III, IV; leg I particularly longer than others (ratios fe-mt: 1:2, 1:3, 1:4). Legs well clothed in setae and bristles,

especially tibiae and metatarsi of leg I. Leg I with rows of thin macrosetae along length of tibia and metatarsus, metatarsus with distal trichobothrium. Leg IV metatarsus with at least 3 rows of bristles along length, pair of thin, curved macrosetae at distal joint. Podomere lengths: all tr ~0.2; Pd pa 0.36, ti 0.84, ta L 0.65, total pa–ta 1.85; leg I fe 2.58, pa 0.77, ti 2.40, mt 1.75, total fe–mt 7.49; leg II fe 2.00, pa 0.74, ti 1.72, mt 1.40, ta 0.68, total fe–mt 5.86; leg III fe 1.16, pa 0.53, ti 1.04, mt ≥ 0.80 , ta ≥ 0.59 ; total fe–mt 3.53; leg IV fe 1.82, pa ≥ 0.43 , ti 1.28, mt 1.32, total fe–mt 4.85. Opisthosoma with subcircular antero-ventral sclerotized region and scattered bristles.

Material. Single specimen (part only), number MB.A 2966, deposited in the Museum für Naturkunde, Berlin.

Type locality and horizon. Klein Lehmhagen clay pit, Grimmen, Vorpommern, Germany; Lower Jurassic: Lower Toarcian: falciferum zone (exaratum subzone), c. 180 Ma.

Etymology. After Seppo Koponen, to celebrate his 70th birthday.

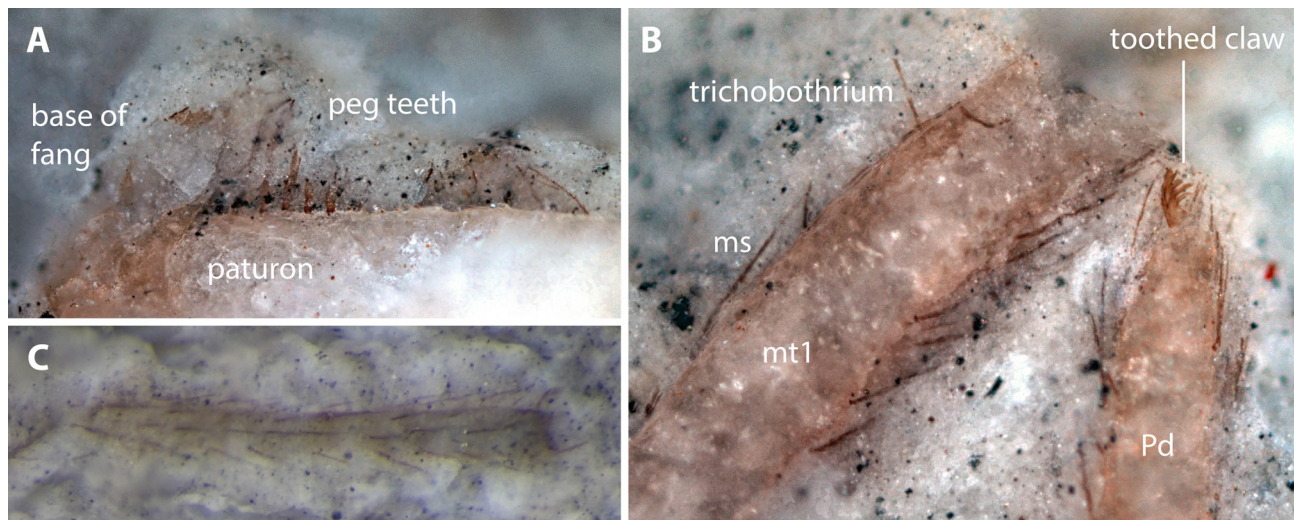


FIGURE 3. *Seppo koponeni* n. gen. & n. sp. Holotype and only known specimen MB.A 2966. A, cheliceral furrow showing base of fang and row of ?promarginal peg teeth. B, distal end of metatarsus I, retrolateral, showing bristle-like macrosetae and trichobothrium, and pedipalp tarsus showing toothed terminal claw. C, metatarsus of right leg IV, prolateral, showing rows of bristles and distal pair of curved bristles. All photographs taken under 70% ethanol and in cross-polarized light.

Discussion

Spider fossils are rare in rocks older than the Cretaceous because of the scarcity of amber with biotic inclusions before that time, so every occurrence of a Jurassic spider needs to be documented. The single specimen described here shows an unusual preservation style, even for rock-matrix preserved spiders, in calcium carbonate. Nevertheless, it shows glimpses of an interesting morphology, allowing us to understand a little more about Jurassic araneofaunas. The spider fauna of the Jurassic known to date includes a plectreuid (Haplogynae) (Selden & Huang 2010), palpimanoids (including Archaeidae) (Selden *et al.* 2008b), and basal, cribellate orbicularians (Selden *et al.* 2013) from China; an archaeid (Eskov 1987) and a basal orbicularian (Eskov 1984; Selden 2012) from Russia; and a possible uloborid from Australia (Selden & Beattie 2013). Earlier Mesozoic (Triassic) opisthotheles are two mygalomorphs (Selden & Gall 1992; Dalla Vecchia & Selden 2013) and two araneomorphs (Selden *et al.* 1999). The present find adds a further palpimanoid to this fauna, albeit from much older times.

Together with a scorpion from Braunschweig (Bode 1951; Dunlop *et al.* 2007), the Grimmen spider is one of only two arachnids ever to have been found in the Liassic rocks of north Germany. These two arachnid fossils are outnumbered by several thousand insect specimens at several localities (the most important being Grimmen, Braunschweig, and Dobbartin: Ansorge 2003), and the Grimmen spider occurs among nearly 3000 insect specimens now known from that locality (Ansorge 2007). This highly skewed ratio of insects to spiders was discussed by Selden *et al.* (2009) although, as yet, no quantitative studies have been done on this phenomenon, nor explanations forthcoming, except the general observation that insects fly over, and fall into, water far more easily than spiders do. How the spider came to be preserved in marine clay, far from land, is somewhat mysterious. However, given the abundance of flying insects in these beds, ballooning is a possibility as a method of transport

(though this has not been observed in palpimanoids), as are severe storms, hurricanes, and tornadoes. Moreover, occasionally terrestrial biota is carried far out to sea, on floating vegetation for example. A terrestrial mite was discovered in the Lower Jurassic marine Oxford Clay (Selden *et al.* 2008a), in which much driftwood and even dinosaur bones have been found. Similarly, dinosaurs are known from the German Lias sites (Ansorge 2007).

Seppo n. gen. shows a rather unusual morphology, with large (but not elongated), porrect chelicerae, especially long, robust legs I, and short legs III. The robust, well-armed legs I, directed forwards, suggest they were prey-capture appendages. Such a morphology is typical of a sit-and-wait predator. Short legs III is typical of web spiders, especially orbweavers although also found in some palpimanoids, but not in substrate dwellers, whose legs are more equal in length. This suggests the spider was not a habitual ground dweller, and the armoured front legs could be related to capturing dangerous prey. Many palpimanoids today are araneophages, for example.

The combination of characters shown by *Seppo* n. gen. suggest Palpimanoidea, although the discovery of further material would be most helpful to confirm this determination. A recent study by Wood *et al.* (2012b), incorporating fossil and extant palpimanoids, came to the conclusion that Palpimanoidea is an ancient group, with diversification of major lineages occurring before the break-up of Pangaea; i.e. in the Permo-Trias. During the Toarcian, the geography of present-day central Europe was dominated by an epicontinental sea with scattered islands, on the western edge of the opening Tethys ocean, created by rifting caused by the break-up of Pangaea (Scotese 2004). At this time there was a widespread marine extinction event (the Toarcian oceanic anoxic event) recorded, for example, in the coeval Posidonia shales found in southern Germany. This event was connected to a global warming episode, resulting in a warm temperate climate in the region at the time (Brański 2012), and hence ideal conditions for palpimanoids, assuming they had similar ecological preferences then as today. The presence of *Seppo* n. gen. in this region at that time reflects the likely widespread occurrence of the superfamily as suggested by Wood *et al.* (2012b). Given the mosaic distribution of characters exhibited by extant and extinct palpimanoids, as well as those genera (*Seppo* n. gen., *Sinaranea* Selden, Huang & Ren, 2008) not assigned to family, it is possible that we see today remnant lineages of a former larger, more diverse, and widespread group of Mesozoic spiders.

Acknowledgments

We are extremely grateful to Jörg Ansorge (Greifswald) for presenting the specimen for study and providing information on the locality and biostratigraphy. We thank Yuri Marusik, Hannah Wood, Jörg Wunderlich and Sergei Zonstein for their helpful comments. A research visit to Berlin by PAS was courtesy of an Alexander von Humboldt Foundation Research Award.

References

- Ansorge, J. (1996) Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paläontologische Abhandlungen*, 2, 1–132.
- Ansorge, J. (2003) Insects from the Lower Toarcian of Middle Europe and England. *Acta Zoologica Cracoviensia*, 46 (suppl. - Fossil Insects), 291–310.
- Ansorge, J. (2007) Liastongrube Grimmen. *Biuletyn Państwowego Instytutu Geologicznego*, 424, 37–41.
- Bode, A. (1951) Ein liassischer Scorpionide. *Paläontologische Zeitschrift*, 24, 58–65.
<http://dx.doi.org/10.1007/BF03044552>
- Brański, P. (2012) The mineralogical record of the Early Toarcian stepwise climate changes and other environmental variations (Ciechocinek Formation, Polish Basin). *Volumina Jurassica*, 10, 1–24.
- Dalla Vecchia, F. & Selden, P.A. (2013) A Triassic spider from Italy. *Acta Palaeontologica Polonica*, 58, 325–330.
- Dunlop, J.A., Kamenz, C. & Scholtz, G. (2007) Reinterpreting the morphology of the Jurassic scorpion *Liassoscorpionides*. *Arthropod Structure & Development*, 36, 245–252.
<http://dx.doi.org/10.1016/j.asd.2006.09.003>
- Eskov, K.Y. (1984) A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1984, 645–653.
- Eskov, K.Y. (1987) A new archaetid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called «Gondwanan» ranges of recent taxa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 175, 81–106.
- Hong, Y. (1984) Arachnida. In: *Palaeontological Atlas of North China II. Mesozoic Volume*, Beijing, pp. 185–187. [In Chinese]
- Jocqué, R. & Dippenaar-Schoeman, A.S. (2006) *Spider families of the world*. Royal Museum for Central Africa, Tervuren,

Belgium, 336 pp.

- Lehtinen, P.T. (1980) Trichobothrial patterns in high level taxonomy of spiders. *Proceedings of the VIIIth International Arachnological Congress, Vienna*, 1980, 493–498.
- Roth, V.D. & Roth, B.M. (1984) A review of appendotomy in spiders and other arachnids. *Bulletin of the British Arachnological Society*, 6, 137–146.
- Scotese, C.R. (2004) Cenozoic and Mesozoic paleogeography: changing terrestrial biogeographic pathways. In: Lomolino, M.V. & Heaney, L.R. (Eds.), *Frontiers of biogeography: new directions in the geography of nature*, Sinauer, Sunderland, Massachusetts, pp. 9–26.
- Selden, P.A. (2001) Eocene spiders from the Isle of Wight with preserved respiratory structures. *Palaeontology*, 44, 695–729.
<http://dx.doi.org/10.1111/1475-4983.00199>
- Selden, P.A. (2012) A redescription of *Juraraneus rasnitsyni* Eskov, 1984 (Araneae: Juraraneidae), from the Jurassic of Russia. *Bulletin of the British Arachnological Society*, 15, 315–321.
<http://dx.doi.org/10.13156/ arac.2012.15.9.315>
- Selden, P.A. (2014) Spiders (Arachnida: Araneae) from the Insect Limestone (Bembridge Marls, Late Eocene) of the Isle of Wight, southern England. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 104, 1–8.
- Selden, P.A., Anderson, H.M. & Anderson, J.M. (2009) A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from the Triassic Molteno Formation of South. *African Invertebrates*, 50, 105–116.
<http://dx.doi.org/10.5733/afin.050.0103>
- Selden, P.A. & Beattie, R.G. (2013) A spider fossil from the Jurassic Talbragar Fossil Fish Bed of New South Wales. *Alcheringa*, 37, 203–208.
<http://dx.doi.org/10.1080/03115518.2013.735072>
- Selden, P.A. & Gall, J.C. (1992) A Triassic mygalomorph spider from the northern Vosges, France. *Palaeontology*, 35, 211–235.
- Selden, P.A. & Huang, D. (2008) Palpimanoid spiders from the Jurassic of China. *Journal of Arachnology*, 36, 306–321.
<http://dx.doi.org/10.1636/CA07-106.1>
- Selden, P.A. & Huang, D. (2010) The oldest haplogyne spider (Araneae: Plectreuridae), from the Middle Jurassic of China. *Naturwissenschaften*, 97, 449–459.
<http://dx.doi.org/10.1007/s00114-010-0649-z>
- Selden, P.A., Anderson, J.M., Anderson, H.M. & Fraser, N.C. (1999) Fossil araneomorph spiders from the Triassic of South Africa and Virginia. *Journal of Arachnology*, 27, 401–414.
- Selden, P.A., Baker, A.S. & Phipps, K.J. (2008a) An oribatid mite (Arachnida: Acari) from the Oxford Clay (Jurassic: Upper Callovian) of South Cave Station Quarry, Yorkshire, UK. *Palaeontology*, 51, 623–633.
<http://dx.doi.org/10.1111/j.1475-4983.2008.00769.x>
- Selden, P.A., Shih, C. & Ren, D. (2011) A golden orb-weaver spider (Araneae: Nephilidae: *Nephila*) from the Middle Jurassic of China. *Biology letters*, 7, 775–778.
<http://dx.doi.org/10.1098/rsbl.2011.0228>
- Selden, P.A., Shih, C. & Ren, D. (2013) A giant spider from the Jurassic of China reveals greater diversity of the orbicularian stem group. *Naturwissenschaften*, 100, 1171–1181.
<http://dx.doi.org/10.1007/s00114-013-1121-7>
- Wood, H.M. (2008) A revision of the assassin spiders of the *Eriauchenius gracilicollis* group, a clade of spiders endemic to Madagascar (Araneae: Archaeidae). *Zoological Journal of the Linnean Society*, 152 (2), 255–296.
<http://dx.doi.org/10.1111/j.1096-3642.2007.00359.x>
- Wood, H.M., Griswold, C.E. & Gillespie, R.G. (2012a) Phylogenetic placement of pelican spiders (Archaeidae, Araneae), with insight into evolution of the ‘neck’ and predatory behaviours of the superfamily Palpimanoidea. *Cladistics*, 28, 598–626.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00411.x>
- Wood, H.M., Matzke, N.J., Gillespie, R.G. & Griswold, C.E. (2012b) Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpimanoid spiders. *Systematic Biology*, 62, 264–284.
<http://dx.doi.org/10.1093/sysbio/sys092>
- Wunderlich, J. (2008) On extant and fossil spiders (Araneae) of the RTA-clade in Eocene European ambers of the families Borboropactidae, Corinnidae, Selenopidae, Sparassidae, Trochanteriidae, Zoridae s.l., and of the superfamily Lycosoidea. *Beiträge zur Araneologie*, 5, 470–523.