ORIGINAL PAPER

Computed tomography recovers data from historical amber: an example from huntsman spiders

**Jason A. Dunlop · David Penney · Natalie Dalüge ·
Peter Jäger · Andrew McNeil · Robert S. Bradley ·
Philip J. Withers · Richard F. Preziosi**

Abstract Computed tomography (CT) methods were applied to a problematic fossil spider (Arachnida: Araneae) from the historical Berendt collection of Eocene (ca. 44–49 Ma) Baltic amber. The original specimens of *Ocypete crassipes* Koch and Berendt 1854 are in dark, oxidised amber and the published descriptions lack detail. Despite this, they were subsequently assigned to the living Pantropical genus *Heteropoda* Latreille, 1804 and are ostensibly the oldest records of huntsman spiders (Sparassidae) in general. Given their normally large size, and presumptive ability to free themselves more easily from resin, it would be surprising to find a sparassid in amber and traditional (optical) methods of study would likely have left *O. crassipes* as an equivocal record—probably a *nomen dubium*. However, phase contrast enhanced X-ray CT revealed exquisite morphological detail and thus 'saved' this historical name by revealing characters which confirm that it's a bona fide member both of Sparassidae and the subfamily Eusparassinae. We demonstrate here that CT studies facilitate taxonomic equivalence even between recent spiders and unpromising fossils described in older monographs. In our case, fine structural details such as eye arrangement, cheliceral dentition, and leg characters like a trilobate membrane, spination and claws, allow a precise referral of this fossil to an extant genus as *Eusparassus crassipes* (Koch and Berendt 1854) comb. nov.

Keywords Fossil · Eocene · Baltic amber · Araneae · Sparassidae

Communicated by: Sven Thatje

J. A. Dunlop (✉)
Museum für Naturkunde,
Leibniz Institute for Research on Evolution
and Biodiversity at the Humboldt University Berlin,
10115 Berlin, Germany
e-mail: jason.dunlop@mfn-berlin.de

D. Penney · R. F. Preziosi
Faculty of Life Sciences, University of Manchester,
Manchester M13 9PT, UK

N. Dalüge
Zoologisches Institut und Museum,
Martin-Luther-King-Platz 3,
20146 Hamburg, Germany

P. Jäger
Senckenberg Research Institute,
Senckenberganlage 25,
60325 Frankfurt am Main, Germany

A. McNeil · R. S. Bradley · P. J. Withers
Henry Moseley X-ray Imaging Facility, School of Materials,
University of Manchester,
Manchester M1 7HS, UK

Introduction

Tomographic methods (e.g., Pohl et al. 2010) are becoming increasingly important in the description of amber inclusions. For arachnid examples, see Henderickx et al. (2006); Penney et al. (2007, 2011) and Heethoff et al. (2009). Under ideal circumstances, they yield images and character sets which are hard to achieve using traditional optical techniques and permit a degree of equivalence between fossil and living species in terms of the morphological data recovered; see also Bosselaers et al. (2010) for a recent example using copal, a subfossil type of resin. Indeed, the overview of Saupe and Selden (2011) referred to a contemporary 'renaissance' in the description of fossil spiders. Thus far, most of these approaches have been applied to freshly

collected, usually optically translucent material. Yet Baltic (or 'Prussian') amber fossils have been described for over 150 years (e.g., Koch and Berendt 1854). The historically older—often name-bearing type specimens—used by these authors are sometimes in a poor condition (Fig. 1), the amber darkening through oxidation and/or cracked at the surface. Furthermore, descriptions and illustrations in the 19th century literature can leave much to be desired and do not always focus on the apomorphies required to place the fossil in modern classifications. In the worst-case scenario (amber dark, original description inadequate), the name may have to be treated as a *nomen dubium*, and potentially useful information, such as the oldest example of a clade or historical patterns of biogeography, is lost.

Here, we aimed to examine whether oxidised amber material could be 'saved' through computed tomography. As an example, we chose the enigmatic spider *Ocypete crassipes* Koch and Berendt 1854 (Arachnida: Araneae) from the historically famous Berendt collection of Eocene (ca. 44–49 Ma) Baltic amber in the Museum für Naturkunde Berlin. More than a thousand valid species of fossil spider are presently documented in the literature (Dunlop et al. 2011), with regular updates as an appendix to the *World Spider Catalog*. While assembling this raw data has proved a useful step towards understanding the spider fossil record (reviewed by Selden and Penney 2010); the potential value of this dataset has not always been appreciated—see Penney (2010a) for a recent discussion relating to jumping spiders (Salticidae). Fossil taxa assigned to extant families or genera are not only interesting in themselves, but can potentially help to date periods of radiation and/or cladogenesis by documenting oldest records (and thus

minimum ages) or by offering calibration points for analyses based on molecular clocks. The latter is particularly important for contextualising molecular clock data because most origination dates proposed using this technique often tend to extend back much further than the fossil record would predict (see Penney and Selden 2011 for a discussion of spiders). Recent examples of this from other groups of arachnids would include (Giribet et al. (2009), Fig. 10) for harvestmen and (Dabert et al. (2010), Fig. 11) for acariform mites.

The devil is often in the detail, and a caveat to these techniques are their reliance upon accurate assignments of fossils to taxa. Selden and Penney (2010) argued that most referrals of fossil spiders to families are likely to be correct. However, doubts could be expressed about some Mesozoic fossils described in, e.g., the Chinese and Korean literature, as critiqued by Saupe and Selden (2011). Generic referrals can additionally be problematic, especially where the full suite of diagnostic apomorphies seen in living representatives is not preserved. A future focus of palaeoarachnology should be the careful assessment of the oldest records of families and genera in particular to gauge their suitability as anchor points for (molecular) calibrations. A survey of Dunlop et al. (2011) revealed a number of records which appear, on the face of it, to be unexpected or out of place. *O. crassipes* is a case in point. The original genus is preoccupied (see Systematics) and the fossil was subsequently listed either under *Olios* Walckenaer, 1837 or *Heteropoda* Latreille, 1804. The problem here is that both these genera belong to Sparassidae (huntsman spiders) which are typically rather large, active, nocturnal spiders today. They are intuitively less likely to become trapped in

Fig. 1 *Eusparassus crassipes* (Koch and Berendt 1854) comb. nov. **a** Original museum labels; 'fig. 79' number refers to the Koch and Berendt monograph, 7313 and 7235 are the original numbers from the Berendt collection. **b** Facsimile copy of the original reconstruction of Koch and Berendt (1854, fig. 79). **c** Dorsal view of MB.A. 149 [=7313]; note that this is an exuvium revealing the internal side of the coxo-sternal region. **d** Camera lucida drawing of the same. **e** MB.A. 1604 [=7235]; now in very dark amber and primarily visible only in outline. **f** Camera lucida drawing of the same. Scale bars 5 mm
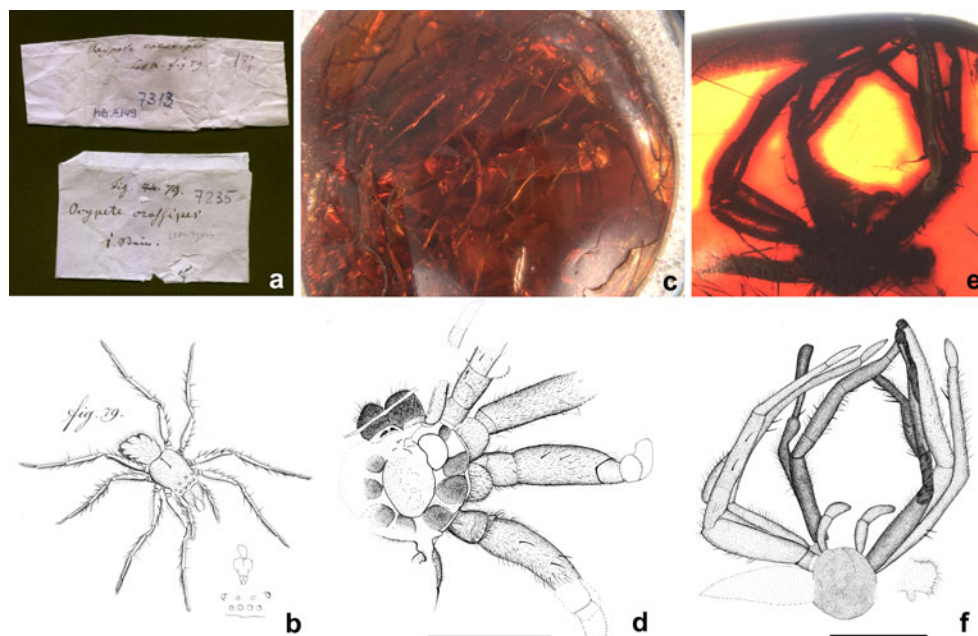
resin; see also comments in Wunderlich (2008). While there are convincing records (Wunderlich 1988) of Sparassidae in Miocene (ca. 16 Ma) Dominican Republic amber, Wunderlich (2004) suggested that there were no fossil sparassids in Baltic amber and that previous records were probably misidentifications. Subsequently, Wunderlich (2008: 477–478) himself described two potential records of the family from Baltic amber, albeit only from juveniles placed as "Sparassidae indet. sp. 1–2". In this context, we felt that the oldest putative record of *Heteropoda* merited further investigation, specifically as a test case for the efficacy of tomographic methods applied to historical inclusions in Baltic amber.

Materials and methods

Two specimens labelled "*crassipes*" were located in the Berendt amber collection, bearing the inventory numbers MB.A. 149 and MB.A. 1604 (for Museum Berlin Arthropoda), plus the original Berendt numbers 7313 and 7235, respectively. Both consist of darkened, oxidised pieces of amber wrapped in grey-brown paper envelopes (Fig. 1a, c, e), whose annotations refer to the original figure 79 in the monograph of Koch and Berendt (1854) (reproduced here as Fig. 1b). It is noteworthy that the two labels were written by different people (perhaps at different times?) and that MB.A. 149 bears a misspelling of the genus name as "*Oxypete*", while MB.A. 1604 has the correct spelling "*Ocypete*"—and a pencil addition stating "non typus". Fixing the type status of these specimens proved challenging (see "Discussion"), but current museum policy is to permit tomographic study of putative non-types only. Based on this pencil annotation, MB.A. 1604 was thus made available for scanning as detailed below.

Both inclusions were photographed using a Leica stereomicroscope running the software package *Leica Application Suite* to generate a stack of images at different focal planes. These were combined into a single final image using *Auto Montage*. Specimens were drawn using a Leica stereomicroscope with a *camera lucida* attachment. In general, MB.A. 149 was drawn and photographed under incident light, while MB.A. 1604—in a darker piece of amber—could only be adequately illuminated from below using transmitted light. Under light microscopy, this largely revealed the animal in outline only (Fig. 1e, f). Extant spider material from the zoological collections of the Senckenberg Research Institute and the Museum für Naturkunde was examined for comparative purposes, together with literature focussing on subfamily and genus groups within Sparassidae (e.g., Jäger 1998, 2001, 2002, 2008; Jäger and Kunz 2005; Jäger and Ono 2000; Jäger and Otto 2007; Jäger et al. 2009).

Amber

Fossil spiders are common in amber deposits from around the world (Dunlop et al. 2011; Penney 2010b; Selden and Penney 2010; Penney and Selden 2011), but Baltic amber is by far the most famous and richly endowed fossiliferous amber deposit, with more than 3,000 described arthropod species; see Weitschat and Wichard (2010) for the most recent review. This amber is dated as mid-Eocene (i.e., Lutetian) or ca. 44–49 Ma (Ritzkowski 1997) and is thought to have been produced by an umbrella pine (*Sciadopitys* sp.) (Wolfe et al. 2009); although the identity of the Baltic amber tree is still somewhat of an enigma— see discussion in Weitschat and Wichard (2010). The fossil assemblage is indicative of a tropical–subtropical forest with lightly wooded areas and plenty of freshwater habitats (Weitschat and Wichard 2010). The spider fauna in Baltic amber is generally well understood and, with more than 500 named species described to date (Wunderlich 2004; Dunlop et al. 2008, 2011; Selden and Penney 2010), represents the most diverse fossil spider assemblage.

Tomography

Three scans of the specimen were carried out using the Xradia MicroXCT system at the University of Manchester's 'Henry Moseley X-ray Imaging Facility'. In each case, a total of 1,200 projections were acquired over 180° using a 10-W tungsten target microfocus X-ray source and 2,000×2,000 pixel detector. It has been shown that in many cases, traditional attenuation-based X-ray CT is unable to accurately resolve fine anatomical features (McNeil et al. 2010), thus additional phase contrast was used. This was achieved using the propagation-based technique where the detector is placed at a large distance from the sample, thereby allowing interference fringes to form at material boundaries, enhancing edge contrast. In this case, a propagation distance of around 200 mm was used. The low magnification scan was acquired at 100 kV using the ×1 optical magnification setting, giving a pixel size of 11.4 μm. The two higher magnification scans of the chelicerae and leg were acquired at 40 kV using ×4 optical magnification, resulting in a pixel size of 3.8 μm. The combined scan time for all three datasets was 120 h, demonstrating that amber is stable to prolonged X-ray exposure and may therefore be scanned without risk of damaging the fossilised specimen. Tomographic reconstruction was carried out using the TXMReconstructor software by Xradia (Xradia, Inc., 4385 Hopyard Road, Pleasanton, CA 94588, USA), with each slice exported as a 16-bit TIFF image and imported into Avizo 6.3 for visualisation (see also movie clip under Supplementary Material). Segmentation was performed through simple thresholding of the phase fringes, with the inherent phase artefacts removed manually.

Systematic palaeontology

Family Sparassidae Bertkau, 1872

  Subfamily Eusparassinae Järvi, 1912

  Genus *Eusparassus* Simon, 1903

  Eusparassus crassipes (Koch and Berendt 1854) comb. nov. (Figs. 1, 2 and 3)

  Ocypete crassipes Berendt 1845: 872 (*nomen nudum*).

  O. crassipes Koch and Berendt 1854: 84–85, pl. IX, fig. 79; Giebel 1856: 465; Scudder 1891: 276; Petrunkevitch 1942: 361–362; Petrunkevitch 1958: 376 (as being of questionable affinity); Keilbach 1982: 183.

  Olios crassipes: Bonnet 1958: 3128, 3167.

  Heteropoda crassipes: Dunlop et al. 2011: 167.

  Material, locality and horizon MB.A. 1604 (*ex* Berendt nr. 7235), subsequently labelled in pencil as "non typus"; here designated the lectotype (see "Discussion"). MB.A. 149 (*ex* Berendt nr. 7313) genus given as *Oxypete* [sic], subsequently labelled in pencil as "Exuvie"; here designated the paralectotype (see "Discussion"). Baltic amber, Palaeogene: Eocene: Lutetian. Exact locality not recorded.

Diagnosis. Fossil *Eusparassus* with subdistally swollen pedipalps.

Description MB.A. 1604. Prosoma and limbs preserved largely in outline in an oxidised piece of amber (Fig. 1e–f). Prosoma rounded, length ca. 3.6 mm, width ca. 3.0 mm. Details of carapace equivocal under light microscopy, but tomography reveals anterior eye row to be slightly recurved, posterior eye row slightly procurved; eyes within rows about the same size (Fig. 2a–b). Coxo-sternal region and opisthosoma also equivocal. Chelicerae robust with slight frontal bulge (Fig. 2a), with two anterior (promarginal) and five posterior (retromarginal) teeth (Fig. 2d); cheliceral furrow with four to five denticles (Fig. 2e–f). Pedipalps at least 3.0 mm long, apparently subdistally swollen (Fig. 2c), i.e., tibiae and (in part) patellae; patellar spination (following Jäger 2008): femur 131, patella 101(?), tibia 2121, tarsus 1014; palpal claws broken off. Legs robust, densely setose; length (legs I and II?) up to ca. 17 mm. Metatarsus distally with dorsal trilobate membrane (Fig. 3a), in which median hook is slightly longer than lateral projections; tip of hook curled inwards (Fig. 3b). Leg

Fig. 2 *Eusparassus crassipes* (Koch and Berendt 1854) comb. nov. Phase contrast enhanced X-ray CT images of MB.A. 1604; here designated the lectotype. Compare these results with Fig. 1e–f. **a** Overview of the prosoma in frontal view, showing eye arrangement and slightly bulging chelicerae. **b** The same in dorsal view, again principally showing eye arrangement; right posterior lateral eye not scanned. **c** Ventro–lateral view indicating unusual swelling of the pedipalp (*arrowed*); present in both left and right palps thus unlikely to be an artefact. **d** Ventral aspect of chelicerae showing the fangs and cheliceral dentition; note especially the presence of only two anterior teeth (*arrowed*). **e–f** Details of, respectively, the left and right cheliceral furrow; each with a patch of minute denticles (*arrowed*) close to the anterior teeth (at)
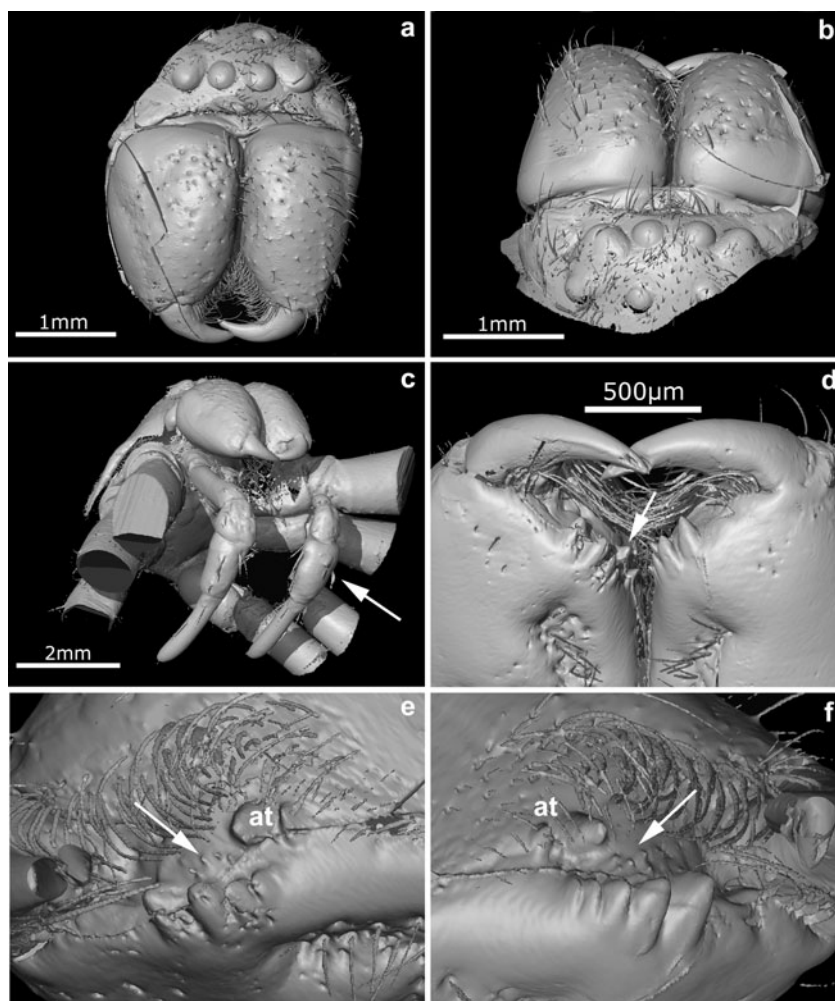
Fig. 3 Details of the legs from MB.A. 1604. **a** Dorsal view of the metatarsus-tarsus joint revealing the 'W'-shaped trilobate membrane (*arrowed*); a key synapomorphy of Sparassidae. **b** The same in lateral view showing inward curving median hook. **c** Distal end of the leg in ventrolateral view, showing in particular the sparse setae and tarsal claws (*arrowed*)—each with a primary tooth and a series of (at least) four distinctly smaller secondary teeth
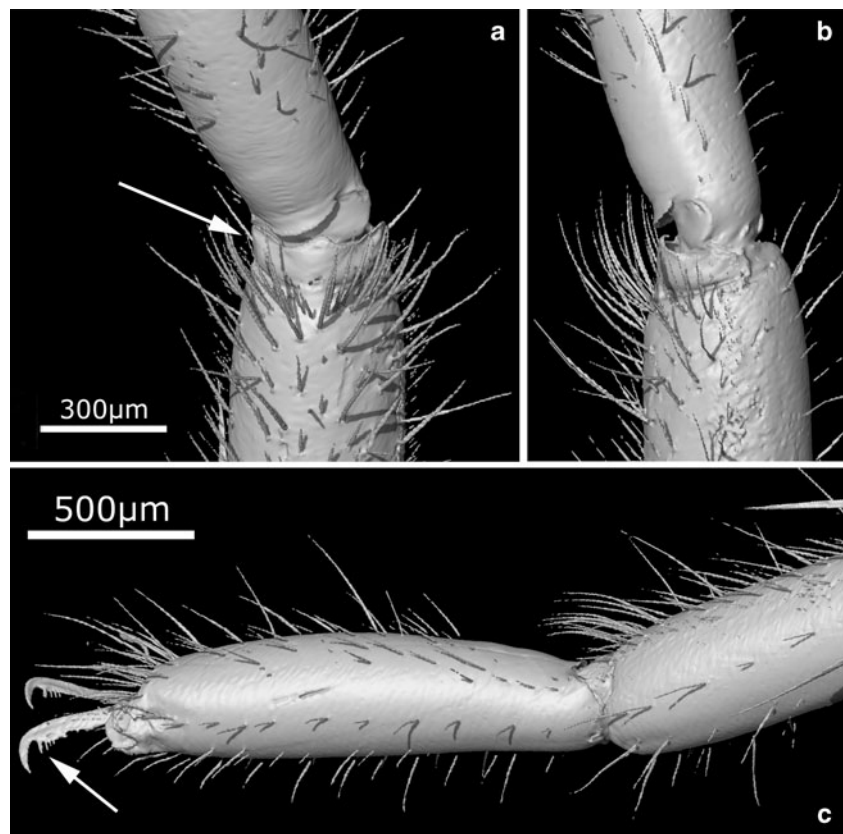
claws (Fig. 3c) bear prominent primary tooth and distinctly smaller secondary teeth (terminology according to Jäger 2004); ventral tarsus and metatarsus with scopula, clearly visible under light microscopy but not resolved in the scans.

MB.A. 149 is an exuvium of a relatively large amber spider (Fig. 1c–d). Prosoma rounded, probably slightly wider than long: length 4.6 mm, width ca. 5.4 mm. Carapace, eyes, etc. equivocal. Chelicerae robust, length ca. 1.2 mm, setose but details lacking. Pedipalps more slender than legs, but details again lacking. Sternum large, oval, length 3.2 mm, width 2.1 mm, with a lightly punctuate ornament. Opisthosoma preserved as small fragment of setose cuticle only (Fig. 1d). Legs robust, densely setose; length up to ca. 18 mm (Leg III); all legs fairly homogenous in form. Legs folded under body, but femora at least 5 mm long. At least femur, tibia and metatarsus with robust spines.

Discussion

Historical context

O. crassipes was first mentioned by Berendt (1845), but since this simply included a list of names from a forthcoming monograph, the 1845 version is a *nomen nudum*. The name was first used formally by Koch and Berendt (1854) in their major study of amber spiders. These authors offered a fairly detailed description, including aspects of the carapace, with eyes in two rows, the chelicerae and pedipalps, and the large and spiny legs which were supposedly bent back over the dorsal side of the body. The opisthosoma was described as small and pressed together. In general, it should be noted that the drawings in the monograph of Koch and Berendt (1854) (Fig. 1b) are idealised reconstructions rather than accurate drawings of the appearance of the fossil in the matrix. They also noted (our translation): "This handsome spider is a female and lies in a pale stone, however, in a position such that the back of the breast [carapace] cannot be clearly seen from above; the breast [sternum] can be more clearly seen through the depth of the stone. Eyes, mouthparts and legs can be very clearly observed." Additionally, a prosomal length of 2 and 1/2''' was given, but since a German line had regional variations in the 19th century from 1/12 of an inch up to 3 mm, this roughly translates into a length of between 5 and 7.5 mm; quite large for an amber spider. Koch and Berendt's monograph was compiled posthumously by Anton Menge who also offered comments (as footnotes) about their species (Menge 1854). To try and fix which specimen(s) belong to the type series, Menge's footnote is quoted here in full (again our translation).

"Note. This spider species belongs to the largest which I have encountered in amber. Although it matches the genera

Micrommata Walk. or *Sparassus* K. in the body shape, setation and long diverging tarsal claws, it differs in the eyes from that which Koch gave for *Ocypete*. In my collection, there are two female examples of this species. Since Berendt's collection appears only to have the cast-off exuvium of a moulted animal, whereby the feet are pressed against the breast [sternum] and the abdomen consists only of a folded clump of skin, it would have been better, to avoid confusion, to show this in figure 79 only through dots. The abdomen is elongate, a little thinner than the breast [sternum], wide at the front, rounded at the sides and pointed towards the back; densely, almost velvety, haired. The front and back spinnerets are almost the same length and similarly robust, projecting beyond the tip of the abdomen. On the metatarsus ["Fussschenkeln"] one sees one or two spines, not as many as shown in the drawing, the lower tibial spines should be longer and the so-called upper knee and tibial spines should be shown at all. In the Berendt collection, there is another exuvium of a moulted animal, which Koch did not see. M."

O. crassipes was subsequently listed in this combination by Giebel (1856); Scudder (1891); Petrunkevitch (1942, 1958) and Keilbach (1982). As was normal for sparassids at that time, Scudder assigned this species to the crab spiders as "Thomisides", while both Petrunkevitch and Keilbach listed it under Eusparassidae—see Jäger (1999) for details of why Sparassidae should be the correct family name. Petrunkevitch (1942) expressed doubts about the exact affinities of *O. crassipes* and subsequently (Petrunkevitch 1958) placed a question mark by it in his summary list of amber spiders. However, he did not discuss the species in the main text of the latter work. *Ocypete* Koch, 1836—the name is derived from one of the three harpies in Greek mythology—originally included material which is now found under a range of sparassid genera (see Platnick 2011 for details) including *Heteropoda* and *Olios*; whereby the type species, *Ocypete setulosa* Koch, 1836 is a junior synonym of the ubiquitous *Heteropoda venatoria* (Linnaeus, 1767). In any case, Bonnet (1958) recognised that *Ocypete* is preoccupied as a spider genus and formally referred *O. crassipes* to *Olios*; albeit without comment. Bonnet's transfer was overlooked by Keilbach (1982) and to an extent by Dunlop et al. (2011) in their online catalogue of fossil arachnids. Dunlop et al. (2011) mistakenly assumed that *Ocypete* was a junior synonym of *Heteropoda* only. Thus, the fossil was listed online as *H. crassipes* (Koch and Berendt 1854), making it ostensibly the only record of *Heteropoda* in amber and potentially the oldest record of the genus.

Fixing the type

Koch and Berendt (1854) did not explicitly designate type specimens, nor did they give repository numbers, but the initial impression from the annotated specimen labels (see "Materials and methods") is that MB.A. 149 is the original (holo)type. This, however, is evidently a moulted exuvium (Fig. 1c–d) and in his footnote to the original description Menge described an exuvium in the Berendt collection very similar to MB.A. 149. Specifically, Menge noted legs bent under the body towards the sternum and an opisthosoma represented by only a fragment of skin (cf. Fig. 2d). Curiously, he mentioned another exuvium among the Berendt material "…which Koch did not see." The scanned specimen (MB.A. 1604), does not appear to be an exuvium— the carapace is still attached to the rest of the body (Fig. 2a–b)—and is thus unlikely to be the 'other' Berendt specimen. Furthermore, in their original description, Koch and Berendt asserted that the eyes and mouthparts were clearly visible (see above): as per the scans of MB.A. 1604. We saw no evidence for a displaced carapace (and eyes) in MB.A. 149 (Fig. 1c–d) and doubt whether this fossil, in isolation, could have provided all the characters in Koch and Berendt's description. In the absence of better evidence, we feel forced to treat both MB.A. 149 and MB. A. 1604 as potentially part of the type series. Even though MB.A. 1604 was annotated as "non typus", it is unclear who made this designation and/or whether this was ever published. Keilbach (1982) listed both specimens as Berlin types, here under their original Berendt numbers 7313 and 7235. Menge's specimens were originally in the 'West-preussisches Provinzial Museum, Danzig' [=Gdansk] and are widely assumed to be lost. Elements of this collection may, however, be present in other museums (e.g., Hoffeins 2008), but spiders from Menge explicitly associated with the 1854 monograph have yet to be formally identified and would not have been part of the Koch and Berendt type series anyway. They may, however, have contributed to the description of the abdomen and spinnerets, which is more detailed in Menge's footnote than in Koch and Berendt's original text. We have, of course, no way of independently checking that Menge's material really was conspecific with Koch and Berendt's. In summary, given the wealth and quality of the data retrieved from MB.A. 1604, we choose to designate this the lectotype; with MB. A. 149 the paralectotype.

Affinities

Phase contrast enhanced computed tomography resolved an unequivocal 'W'-shaped trilobate membrane (Fig. 3a–b) between the tarsus and metatarsus of MB.A. 1604—a vital feature which was not clearly visible under light microscopy. This trilobate membrane is an autapomorphy of Sparassidae. It is thought to aid tarsal mobility, and its presence in the fossil proves beyond doubt that Koch and Berendt were correct; this is a huntsman spider and the group was present

in a recognisable form in the Baltic amber forest. With respect to the sparassid genera suggested for the fossil in the published literature, Jäger (2001, 2002) argued that *Heteropoda* can only be diagnosed on genital characters, e.g., a sheath-like conductor and a filiform embolus in the male pedipalp, and not by somatic characters as proposed in some older schemes. *Olios* is also problematic. As discussed by Jäger and Ono (2000) and Jäger and Otto (2007), this is the most species-rich sparassid genus. However, it has not been recently revised and contains many (probably misplaced) records of spiders known only from their original description, or later transferred to this genus; for which a robust, modern generic diagnosis is lacking.

An important systematic character for sparassid ingroups is cheliceral dentition (Fig. 2d). Some genera also express additional, minute denticles *within* the cheliceral furrow. Our CT scans of the fossil reveal two anterior cheliceral teeth and a small group of denticles (Fig. 2e–f). It is worth remembering that these denticles lie deep in the mouthparts, and would have been almost impossible to resolve using traditional methods of amber study. Unlike our fossils, all Heteropodinae (from Asia: *Heteropoda*, *Pseudopoda*, *Sinopoda*, *Bhutaniella*, *Yiinthi*, *Martensopoda*, *Barylestis* and *Spariolenus*, from Africa: *Barylestis*, cf. Jäger 2002) and related genera from South America (*Sparianthina*, *Anaptomecus*, *Sadala*, etc; cf. Jäger et al. 2009) have three anterior cheliceral teeth. Moreover, their cheliceral denticles are more numerous than in the fossil and are usually located in a dense patch, close to the anterior teeth. In *Sparianthina selenopoides*, however, a single line of denticles was observed (Jäger et al. 2009), but in this species, the trilobate membrane has distinctly longer lateral projections compared to the amber fossil. Moreover, it has more than two anterior teeth. *Gnathopalystes* and *Prychia*, known from South East Asia, possess even more denticles than Heteropodinae and also exhibit a completely different eye position relative to the amber specimen.

Instead, the amber fossil is referred here to *Eusparassus* based on the unique combination of the two anterior cheliceral teeth, the presence of a relatively small number of denticles (never present in *Olios* or any other Sparassinae species) as well as by its eye arrangement. In extant *Eusparassus*—currently being revised by M. Moradmand in a PhD thesis under PJ's supervision—cheliceral denticles can occur. They are currently known from two unidentified species from Saudi Arabia and Tanzania and the number of denticles may vary between 5 and 20 (Jäger 2001: fig. 13c; Jäger and Kunz 2005: fig. 211; PJ pers. obs.). *Eusparassus* was first revised, albeit tentatively, by Jäger (1998). In subsequent years, the genus was recognised as being closely related to

Pseudomicrommata and *Arandisa* from southern Africa; all three belonging to the subfamily Eusparassinae.

The modern distribution of *Eusparassus* is Africa, southern Europe, the Near and Middle East, Central Asia and parts of South Asia. Interestingly, these spiders today prefer arid environments, mostly under stones, where they hide during the day and build a silken retreat as a shelter. Adults tend to be large spiders, with a prosoma length of 5.6–13.3 mm and a total length of 12.8–31.0 mm in adults. Thus, the amber specimen is most likely immature. Given that a few sparassids change their lifestyle during ontogeny, it is conceivable that young *Eusparassus* spiders in the Baltic amber forest lived on trees. The fact that extant species live mostly under stones may simply be due to the absence of trees in these environments. Furthermore, the amber forest is widely perceived as being tropical–subtropical (see above), and this would be an unusual habitat for extant *Eusparassus* representatives. However, Baltic amber yields other records of arachnid species usually known today from arid habitats; e.g., a camel spider and a genus of opilioacarid mite known today from Central Asia. This may indicate that the fauna from additional, dryer areas— perhaps from higher elevations?—also contributed to the fossil assemblage found as amber inclusions.

Another fossil *Heteropoda*?

For completeness, it should be noted that there is a younger fossil spider, this time in a diatom shale, from the Neogene of Shanwang in China, originally described as *Retina robusta* Hong 1985; i.e., in a new, extinct genus. It was subsequently redescribed by Lin et al. (1989), who interpreted *Retina* Hong 1985 as a junior synonym of *Heteropoda* and thus transferred the fossil species to *Heteropoda robusta* (Hong 1985). This nomenclatural act is problematic for two reasons. First, it creates a homonym with an extant Indian sparassid, *H. robusta* Fage, 1924. Second, the justification of Lin et al. (1989) for the transfer is unconvincing, being based on "powerful chelicerae and walking legs" and a superficial resemblance to living Japanese examples of *H. venatoria*. We concede that the Shanwang spider could be a sparassid based on its overall appearance. However, we have not seen the original material (Natural Museum of Shandong Province and the Museum of Linqu County, Nr. 79104) and no characters are elaborated or illustrated either by Hong or Lin et al. which would support the unequivocal referral of the fossil to *Heteropoda*—or any other modern genus. The illustrations hint at expanded pedipalps which implies a male, but there is no indication of details of the palpal organ. For this reason we question the wisdom of introducing a replacement name for the preoccupied *H. robusta* (Hong 1985) at

this stage, as it seems unlikely that it can really be placed in this genus using diagnostic characters applicable to recent spiders. Tomography would, unfortunately, be unhelpful for a shale fossil. Overall, it reiterates the dangers of fixing a fossil record for a (living) genus on an uncritical reading of the literature and/or on fossil descriptions which are not apomorphy-based and do not meet similar standards to those used in peer-reviewed papers on neontological material; see again Saupe and Selden (2011) for discussion.

Conclusions

Phase contrast enhanced computed tomography can be successfully applied to opaque, oxidised pieces of (historical) amber. It yields high-resolution images of remarkable fidelity (hairs, membranes, denticles, etc.) which greatly enhance the original descriptions produced over 150 years ago; see also the film clip under Supplementary Material. Specifically, we could demonstrate that *O. crassipes* is indeed a huntsman spider and can be unequivocally treated as the oldest record of both Sparassidae and Eusparassinae; *Eusparassus* can now be provisionally dated back to at least ca. 44–49 Ma. Through resolving these fine apomorphic details, we could integrate an ostensibly rather poor (but historically still significant) fossil quite successfully into modern spider systematics. While there have been reservations about allowing scans of historical (type) specimens, we observed no additional ill-effects on the amber piece using our methodology. We hope to have demonstrated here—compare especially Figs. 2, 3 with 1e–f based on traditional photography and camera lucida work—that the risks are vastly outweighed by the obtainable benefits.

References

Berendt GC (1845) Die im Bernstein befindlichen organischen Reste der Vorwelt, gesammelt, in Verbindung mit Mehren bearbeitet und herausgegeben. N Jb Min Geog Geol Petrefaktknd 1845:864–879

Bonnet P (1958) Bibliographia Araneorum. Tome II (4me partie N–S). Douladoure, Toulouse, pp 3027–4230

Bosselaers J, Dierick M, Cnudde V, Masschaele B, Vlassenbroeck J, van Hoorebeke L, Jacobs P (2010) High-resolution X ray computed tomography of an extant new *Donuea* (Araneae: Liocranidae) species in Madagascan copal. Zootaxa 2427:25–35

Dabert M, Witalinski W, Kazmierski A, Olszanowski Z, Dabert J (2010) Molecular phylogeny of acariform mites (Acari, Arachnida): strong conflict between phylogenetic signal and long-branch attraction artifacts. Mol Phylogenet Evol 56:222–241

Dunlop JA, Penney D, Tetlie OE, Anderson LI (2008) How many species of fossil arachnids are there? J Arachnol 36:267–272

Dunlop JA, Penney D, Jekel D (2011) A summary list of fossil spiders and their relatives. In: Platnick, NI (ed) The world spider catalog, version 11.5. American Museum of Natural History. Available at http://research.amnh.org/iz/spiders/catalog. doi:10.5531/db.iz.0001

Giebel CG (1856) Die Insekten und Spinnen der Vorwelt mit steter Berücksichtigung der lebenden Insekten und Spinnen; monographisch dargestellt. Leipzig, p 511

Giribet G, Vogt L, Pérez González A, Sharma P, Kury AB (2009) A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. Cladistics 25:1–30

Heethoff M, Helfen L, Norton RA (2009) Description of *Neoliodes dominicus* n. sp. (Acari, Oribatida) from Dominican amber, aided by synchrotron X-ray microtomography. J Paleontol 83:153–159

Henderickx H, Cnudde V, Masschaele B, Dierick M, Vlassenbroeck J, van Hoorebeke L (2006) Description of a new fossil *Pseudogarypus* (Pseudoscorpiones: Pseudogarypidae) with the use of X-ray micro CT to penetrate opaque amber. Zootaxa 1623:47–53

Hoffeins C (2008) Animal and plant inclusions in the collection of Otto Helm (1826–1902), Gdańsk. Bursztyinsko 31:36–43

Hong Y-c (1985) Fossil insects, scorpionids and araneids in the diatoms of Shanwang. Geological Publishing House, Beijing, p 80

Jäger P (1998) First results of a taxonomic revision of the SE Asian Sparassidae (Araneae). pp 53–59. In: Selden PA (ed) Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997. p 350. British Arach. Soc., Burnham Beeches, Bucks

Jäger P (1999) Sparassidae—the valid scientific name for the huntsman spider (Arachnida: Araneae). Arachnol Mitt 17:1–10

Jäger P (2001) Diversität der Riesenkrabbenspinnen im Himalaya – die Radiation zweier Gattungen in den Schneetropen (Araneae: Sparassidae: Heteropodinae). Cour Forsch-Inst Senckenberg 232:1–136

Jäger P (2002) Heteropodinae: transfers and synonymies (Arachnida: Araneae: Sparassidae). Acta Arachnol 51:33–61

Jäger P (2004) A study of the character 'palpal claw' in the spider subfamily Heteropodinae (Araneae: Sparassidae). pp 107–125.In: Logunov DV, Penney D (eds) Proceedings of the 21st European Colloquium of Arachnology, St.-Petersburg, 4–9 August 2003. p 374. KMK Scientific Press, Moscow

Jäger P (2008) Revision of the huntsman spider genus *Heteropoda* Latreille 1804: species with exceptional male palpal conformations (Araneae: Sparassidae: Heteropodinae). Senckenberg biol 88:239–310

Jäger P, Kunz D (2005) An illustrated key to genera of African huntsman spiders (Araneae: Sparassidae). Senckenberg biol 85:163–213

Jäger P, Ono H (2000) Sparassidae of Japan. I. New species of *Olios*, *Heteropoda* and *Sinopoda* with remarks on known species (Arachnida: Araneae). Acta Arachnol 49:41–60

Jäger P, Otto S (2007) New records of *Olios sericeus* (Kroneberg 1875) with notes on its taxonomy and biogeography (Araneae: Sparassidae: Sparassinae). Rev Ibér Arachnol 14:19–24

Jäger P, Rheims CA, Labarque FM (2009) On the genera *Sparianthina* Banks 1929 and *Anaptomecus* Simon 1903 from South and Central America (Araneae: Sparassidae). Zookeys 16:115–147

Keilbach R (1982) Bibliographie und Liste der Arten tierische Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. Teil 1 Dt Ent Z (NF) 29:129–286

Koch CL, Berendt GC (1854) Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. In: Berendt GC (ed) Die im Bernstein befindlichen organischen Reste der Vorwelt, vol 1, part II. Nicholai, Berlin, p i–iv + 1–124

Lin Q-b, Zhang Z-f, Wang B-z (1989) New evidences for Miocene climatic optimum event—review on the Miocene spider fossils from Shanwang collection. Proceedings of International Symposium on Pacific Neogene and Marine Events. Nanjing University Press, pp 137–147

McNeil A, Bradley RS, Withers PJ, Penney D (2010) Developments in X-ray tomography VII In: Stock SR (ed) Proc. SPIE, San Diego, vol 7804, pp 78041Q-1

Menge A (1854) Footnotes. In: Koch CL, Berendt GC Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. In: Berendt GC (ed) Die im Bernstein befindlichen organischen Reste der Vorwelt. Vol. 1, part II. Nicholai, Berlin, p i–iv + 1–124

Penney D (2010a) The evolution of jumping spiders (Araneae: Salticidae): the palaeontological evidence. Peckhamia 81(1):1–3

Penney D (ed) (2010b) Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester, p 304

Penney D, Selden PA (2011) Fossil spiders: the evolutionary history of a mega-diverse order. Monograph Series, vol 1. Siri Scientific Press, Manchester, p 128

Penney D, Dierick M, Cnudde V, Masschaele B, Vlassenbroeck J, van Hoorebeke L, Jacobs P (2007) First fossil Micropholcommatidae (Araneae), imaged in Eocene Paris amber using X-Ray computed tomography. Zootaxa 1623:47–53

Penney D, Green DI, McNeil A, Bradley R, Marusik YM, Withers PJ, Preziosi RF (2011) A new species of anapid spider (Arthropoda: Araneae, Anapidae) in Eocene Baltic amber, imaged using X-ray computed tomography. Zootaxa 2742:61–68

Petrunkevitch AI (1942) A study of amber spiders. Trans Conn Acad Arts Sci 34:119–464

Petrunkevitch AI (1958) Amber spiders in European collections. Trans Conn Acad Arts Sci 41:97–400

Platnick NI (2011) The world spider catalog, version 11.5. American Museum of Natural History. Available at http://research.amnh.org/iz/spiders/catalog. doi:10.5531/db.iz.0001

Pohl H, Wipfler B, Grimaldi D, Beckmann F, Beutel RG (2010) Reconstructing the anatomy of the 42 million-year-old fossil †*Mengea tertiara* (Insecta, Strepsiptera). Naturwiss 97:855–859

Ritzkowski S (1997) K-Ar-Altersbestimmungen der bernsteinfuehrenden Sedimente des Samlandes (Palaeogen), Bezirk Kaliningrad. Metalla Sond 66:19–23

Saupe EE, Selden PA (2011) The study of fossil spider species. C R Palevol 10:181–188

Scudder SH (1891) Index to the known fossil insects of the world including myriapods and arachnids. Bull US Geol Surv 71:1–744

Selden P, Penney D (2010) Fossil spiders. Biol Rev 85:171–206

Weitschat W, Wichard W (2010) Baltic amber. In: Penney D (ed) Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester, pp 80–115

Wolfe AP, Tappert R, Muehlenbachs K, Boudreau M, McKellar RC, Basinger JF, Garret A (2009) A new proposal concerning the botanical origin of Baltic amber. Proc R Soc B 276:3403–3412

Wunderlich J (1988) Die fossilen Spinnen im dominikanischen Bernstein. Beitr Araneol 2:1–378

Wunderlich J (2004) Fossil spiders (Araneae) of the family Sparassidae in Baltic and Dominican amber. Beitr Araneol 3:1694–1698

Wunderlich J (2008) On extant and fossil members of the RTA-clade in Eocene European ambers of the families Borboropactidae, Corinnidae, Selenopidae, Sparassidae, Trochanteriidae, Zoridae s. l., and of the superfamily Lycosoidea. Beitr Araneol 5:470–523