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A new spider (Arachnida: Araneae) from the Middle Eocene Messel Maar, Germany

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The Fossil-Lagerstätte of Grube Messel, Germany, has produced some of the most spectacular fossils of the Paleogene (Schaal & Ziegler, 1992; Gruber & Micklich, 2007; Selden & Nudds, 2012; Schaal *et al.*, 2018). However, few arachnids have been discovered or described from this World Heritage Site. An araneid spider was reported by Wunderlich (1986). Wedmann (2018) reported that 160 spider specimens were known from Messel although, sadly, few are well preserved. She figured the araneid mentioned by Wunderlich (1986) and a nicely preserved hirsiliid (Wedmann, 2018: figs 7.8–7.9, respectively). Wedmann (2018) mentioned six opilionids yet to be described, and figured one (Wedmann, 2018: fig. 7.10). Here, we report a new, well preserved spider, *Lutetiana neli* **gen. et sp. nov.**, the first to be formally described from the locality, which is placed in the Marronoidea (the Marronoid Clade of Wheeler *et al.*, 2017), and possibly in the family Cybaeidae.

Apart from the abundance of fossil spiders described from Cenozoic ambers of Germany and the Baltic region, fossil spiders are also known from a number of sedimentary deposits in southern Germany (see Lutz *et al.* (2000) for helpful descriptions of maar lake Fossil-Lagerstätte). The Upper Oligocene lake deposits of Rott have produced members of the families Araneidae, Linyphiidae, Agelenidae and Thomisidae (von Heyden, 1859; Bertkau, 1878). The Upper Oligocene maar lake deposits of Enspel (Wedmann *et al.*, 2010; Wuttke *et al.*, 2010) have yielded a number of fossil spiders which have yet to be described. The Miocene brown coal deposits of Linz am Rhein have produced numerous specimens of spiders originally (and probably erroneously) referred to *Argyroneta* (Heyden, 1859), and the Miocene brown coals of Öhningen, on the Swiss-German border, have yielded numerous spiders which were referred to Theridiidae, Araneidae, *Argyroneta*, Thomisidae and Gnaphosidae (Heer, 1865; Dunlop *et al.*, 2019). All of the specimens from these deposits require description or redescription. The Miocene volcanic lake of Randecker Maar in the Swabian Alb has produced fossils of Lycosidae,

Thomisidae and Salticidae (Schawaller & Ono, 1979; Wunderlich, 1986). The Pliocene lake of Willershausen, produced by solution of evaporites and subsequent collapse, has produced some remarkably preserved arthropod fossils (Briggs *et al.*, 1998), including numerous spider families: Dysderidae, Lycosidae, Thomisidae and Salticidae (Straus, 1967; Schawaller, 1982). All of these localities are much younger than Messel.

Material and methods

Geological setting

Grube Messel is located on the eastern side of the Rhine Rift Valley, about 8 km northeast of Darmstadt, Germany. The lacustrine sediments of the Messel Formation were deposited within a maar volcanic crater which had a diameter of about 1.5 km and an initial depth of 300–400 m (Harms *et al.*, 2003; Felder & Harms, 2004). The sedimentary rocks have been dated as early middle Eocene (lower Geiseltalian), with a radiometric age (Ar40/39) determination of 47.8 ± 0.2 Ma from volcanoclastic sediments (Mertz & Renne, 2005) and $48.27\text{--}48.11$ Ma ± 0.22 Ma from high-resolution palynological analyses (Lenz *et al.*, 2015). The fossils represent a diverse biota of exceptionally preserved microorganisms, leaves, insects, fishes, amphibians, reptiles, birds, and mammals (Schaal & Ziegler, 1992; Wilde, 2004; Wedmann, 2005; Gruber & Micklich, 2007; Wappler *et al.*, 2015; Schaal *et al.*, 2018), inferred to represent a paratropical Eocene rainforest (Grein *et al.*, 2011). The stratigraphy of the Messel maar has been briefly summarized in Wappler & Engel (2003).

Preservation and interpretation

The specimen consists of a single slab and is housed in the Hessisches Landesmuseum Darmstadt (HLMD), Germany. The studied spider fossil is preserved in the collection by immersing the slab of oil shale in glycerine to prevent

damage by desiccation (Ackermann *et al.*, 1992). The legs of the spider are outstretched, indicating a likely death by drowning in fresh water (Downen *et al.*, 2015). The spider is preserved showing its ventral surface, so that the sternal region and ventral opisthosoma can clearly be interpreted. The dorsal side, *e.g.*, the carapace shape, is not accessible; however, at the anterior carapace margin, the clypeus and one pair of prominent eyes can be seen in front of the chelicerae. Some circular areas suggest smaller eyes may be present on the clypeus (Fig. 1A, B). The size of the spider and the unmodified pedipalps bearing a claw suggest that it is a female. A pair of triangular, light-coloured patches near the midline of the anterior ventral opisthosoma likely represent internal parts of the female genitalia; they are too close together to be related to the book lungs.

Methods

The described individual was observed and digitized using a Keyence VHX-1000 microscope, and all relevant structures were measured from the digitized images. All photographs were optimized using Adobe Lightroom CC. Drawings were made from the photographs using Affinity Designer (affinity.serif.com); measurements were made in Graphic (graphic.com). Final illustrations were manipulated and assembled using Affinity Photo and Publisher (affinity.serif.com). Abbreviations: I, II, III, IV walking legs, AME anterior median eye, car carapace, ch chelicera, cl clypeus, cx coxa, ep epigyne, fe femur, L length, lb labium, mt metatarsus, mx maxilla, op opisthosoma, pa patella, Pd pedipalp, PME posterior median eye, sp spinnerets, st sternum, ta tarsus, ti tibia, W width. All measurements are in mm. Leg formula longest to shortest. Tarsal length includes claws.

Systematic palaeontology

Order Araneae Latreille, 1802

Superfamily Marronoidea Wheeler *et al.*, 2017

?Family Cybaeidae, Banks, 1892

Remarks. See Discussion for the reasons for this suggested placement.

Lutetiana gen. nov.

Type species. *Lutetiana neli* sp. nov. by present designation.

Etymology. The new genus group name is derived from the name Lutetian, the age of the Eocene epoch from which the fossil originates (which, in turn, was derived from the Roman name for Paris). The gender of the name is feminine. The generic name is registered under ZooBank LSID urn:lsid:zoobank.org:pub:E7F92F14-A680-4D30-8CF5-2B27C5AED0AB.

Diagnosis. Spider with short, stout walking legs (leg IV L only slightly longer than body L); female pedipalp with pectinate claw; three tarsal claws (paired claws pectinate with ≥ 8 denticles), no claw tufts or scopulae; few, thin macrosetae on tibiae and metatarsi; trichobothria on at least tibiae and metatarsi; at least one pair of enlarged eyes.

Lutetiana neli sp. nov.

(Figs 1–3)

Material. Single specimen (part only), holotype: female, HLMD-Me-20335, a complete individual, dorsoventrally compressed. Deposited in the Hessisches Landesmuseum, Darmstadt, Germany.

Etymology. The specific epithet is a patronymic honoring André Nel for his extensive work on fossil arthropods. The specific epithet is registered under ZooBank LSID urn:lsid:zoobank.org:pub:E7F92F14-A680-4D30-8CF5-2B27C5AED0AB.

Diagnosis. As for the genus.

Type locality and horizon. Grube Messel near Darmstadt, Grabungsstelle Planquadrat I7, -22.0 – -61.5 cm under marker horizon beta, early middle Eocene (early Lutetian, ELMA Geiseltalian, MP11), Messel Formation.

Description. Medium-sized female spider, body L 6.43. Clypeus height ~ 0.12 . Pair of large median eyes (AME or PME), diameter 0.28 (Fig. 2A). Sternum scutiform, widest at $\frac{1}{3}$ length from anterior, L 0.92, W 0.69, L/W ratio 1.33. Chelicera L 0.71, W 0.43, L/W ratio 1.67. Maxilla slightly longer than wide, L 0.44, W 0.30, L/W ratio 1.42. Subtrapezoid labium between maxillae. Pedipalp with numerous curved macrosetae on tibia and tarsus, tarsus with pectinate claw (Fig. 2B). Leg formula I>IV>II>III. Trochanters with shallow, asymmetric notch. Femora rather stout (mean L/W ratio 2.27), bearing short, curved bristles infero-distally; tibiae slightly longer than metatarsi, wide tibia-metatarsal joint bearing row of short, curved bristles infero-distally (see Schaber & Barth, 2015: fig. 1); tarsi shorter than metatarsi, bearing pectinate paired claws each with ≥ 8 denticles, small median claw, straight setae but no claw tufts or scopula (Fig. 3). Few, thin macrosetae present on tibiae and metatarsi. Trichobothria: at least one of tibia III (Fig. 1) and row on distal tarsus IV (Fig. 3B). Lengths of podomeres: Pd pa 0.35, ti 0.41, ta 0.74; Leg I cx 0.60, tr 0.22, fe 1.68 (W 0.71, L/W ratio 2.37), pa 0.73, ti 1.40, mt 1.24, ta 0.89, total fe–ta 5.94; Leg II cx 0.69, tr 0.25, fe 1.62 (W 0.72, L/W ratio 2.26), pa 0.73, ti 1.37, mt 1.16, ta 0.87, total fe–ta 5.75; Leg III cx 0.59, tr 0.23, fe 1.47 (W 0.77, L/W ratio 1.90), pa 0.59, ti 1.14, mt 1.11, ta 0.79, total fe–ta 5.09; Leg IV cx 0.63, tr 0.23, fe 1.62 (W 0.63, L/W ratio 2.55), pa 0.68, ti 1.34, mt 1.27, ta 0.87, total fe–ta 6.74.

Opisthosoma suboval in outline, L 3.98, W 2.43, L/W ratio 1.64. Pair of light patches in anterior half of opisthosoma, separated by a median, elongate structure, represent parts of

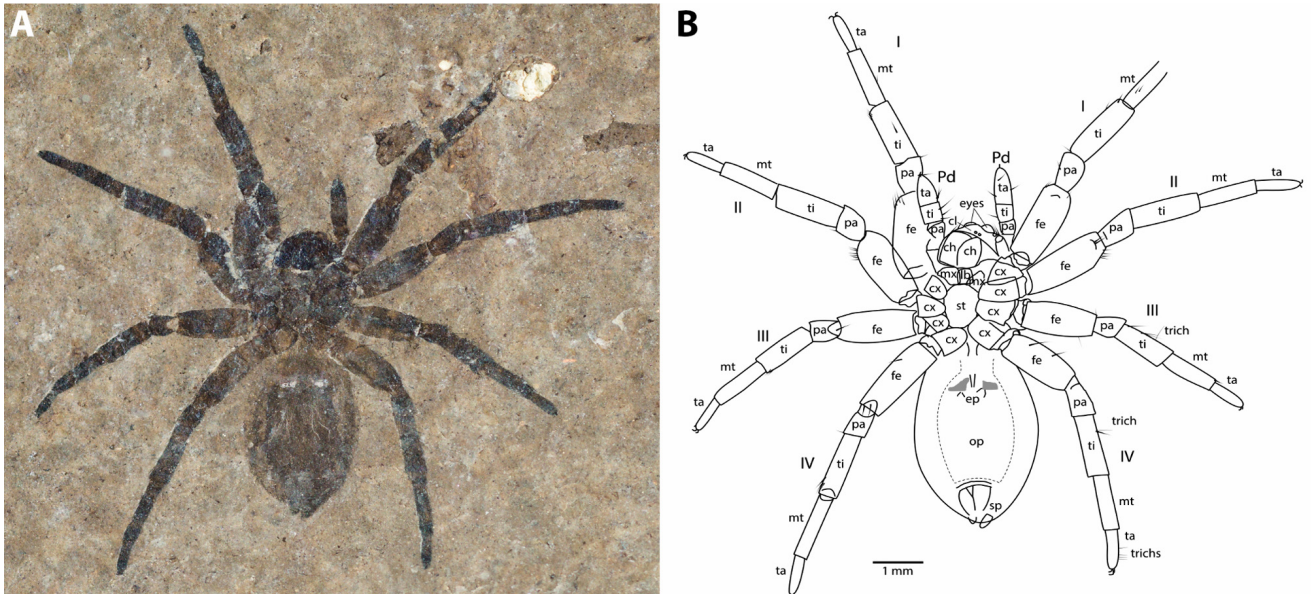


FIGURE 1. Holotype (HLMD-Me-20335) of *Lutetiana neli* gen. et sp. nov. from the Middle Eocene of Grube Messel, Germany. **A**, Photograph of only known specimen, ventral view. **B**, Explanatory drawing.

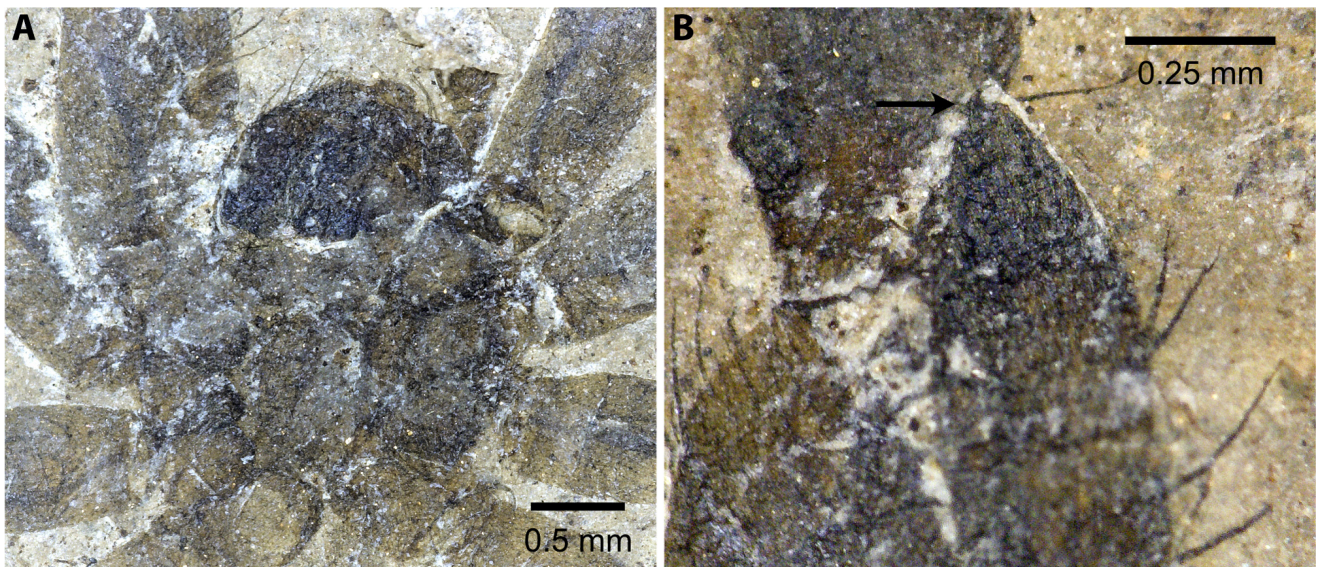


FIGURE 2. Holotype (HLMD-Me-20335) of *Lutetiana neli* gen. et sp. nov. from the Middle Eocene of Grube Messel, Germany. **A**, Detail of ventral prosoma, showing chelicerae, maxillae, sternum, coxae and trochanters; see Fig. 1B for explanation. **B**, Detail of left palpal tarsus, showing curved macrosetae (right) and claw (arrowed), and fringe of curved bristles on distal femur I (left).

the female epigyne. Spinnerets positioned subapically on opisthosoma, anterior laterals fairly robust, L 0.56 either side of elongate triangular colulus; posterior laterals short, L ~0.32, slightly protruding beyond apex (Fig. 1).

Discussion

It is difficult to identify the spider to a family because of its lack of unique characters. The general habitus suggests a free-living spider (ground spider), rather than an inhabitant of an aerial web. Legs subequal in length support this.

Possession of three tarsal claws and lack of tarsal scopulae or claw tufts narrows the possibilities yet further. The lack of a calamistrum on the fourth leg metatarsus confirms that this is an ecribellate spider, although many families contain both cribellate and ecribellate genera. Recent work on living spider families using molecular methods has revealed a distinct clade of essentially ground and foliage hunting spiders that show three tarsal claws for which Wheeler *et al.* (2017) coined the term marronoid clade (herein superfamily Marronoidea). It consists of the families Agelenidae, Amaurobiidae, Amphinectidae, Cybaeidae, Cycloctenidae, Desidae, Dictynidae, Hahniidae, Stiphidiidae, and Toxopidae. Within the marronoid clade, some families are distinctly

austral (e.g., Amphinectidae, Cycloctenidae, Desidae, Stiphidiidae, Toxopidae), while others are mainly cribellate (e.g., Amaurobiidae, Dictynidae). Among the remainder, most Agelenidae have elongate posterior lateral spinnerets (there are exceptions, e.g., *Coelotes*), while the spinnerets of most hahniids are both elongated and arranged in a transverse row. The Mediterranean *Desis* bears large, porrect chelicerae and lives in the intertidal zone. So, among marronoids, the fossil spider shows most similarity to members of the Cybaeidae, some Hahniidae and Agelenidae, and cribellate Dictynidae. The group of genera in this assemblage (e.g., *Argyroneta*, *Cicurina*, *Coelotes*, *Cryphoea*, *Cybaeus*) have been moved around among these families several times (see Wheeler *et al.*, 2017).

The water spider *Argyroneta* shows distinct features such as large chelicerae and distinctive long hairs on legs III and IV, which the fossil spider does not possess. *Cicurina* and *Cryphoea* have moved between Agelenidae, Cybaeidae, and Hahniidae (World Spider Catalog, 2019). *Cicurina* is presently in Hahniidae, despite its spinnerets not being in a transverse row, while *Cryphoea* is in Cybaeidae, along with *Cybaeus*. *Coelotes* differs from other agelenids by its short posterior lateral spinnerets. Murphy & Roberts (2015) placed *Cicurina*, *Cryphoea*, and a number of related genera, into their new family Cicurinidae Murphy & Roberts, 2015, though this family was not recognized in the World Spider Catalog (2019). Features of the fossil species which place it among these genera are: medium sized spiders, cribellate, legs not dissimilar in length, three tarsal claws with teeth, lacking claw tufts or scopulae, a row of trichobothria on the tarsus, and short spinnerets not in a transverse row.

An alternative placement, suggested by the presence of what appears to be a pair of large eyes in the specimen (Figs 1, 2A), might be the Lycosidae, a family distant from the marronoids within the Oval Calamistrum clade of Wheeler *et al.* (2017). The spiders in this family bear three tarsal claws and, whilst many also bear scopulae, not all do. Large, forward-facing eyes and notched trochanters are also characteristic of many lycosids. However, these spiders have longer legs than those seen in the fossil, and generally run freely across open grassland habitats (Jocqué & Alderweireldt, 2006), whereas the paleoecology of Messel was most likely rainforest-like. Jocqué & Alderweireldt (2006) formulated the hypothesis that, in families whose species normally show claw tufts and scopulae, more primitive members do not and are web-dwellers. They postulated that modern lycosids, which are predominantly grassland dwellers, evolved when steppes, prairies and savannas appeared in the Miocene. This view was corroborated by the analysis of Lycosidae by Piacentini & Ramírez (2019), except that their analysis suggested that the earliest lycosids were vagrant, and later lineages developed web building. Piacentini & Ramírez (2019) explained the lack of lycosid fossils in Cenozoic ambers as

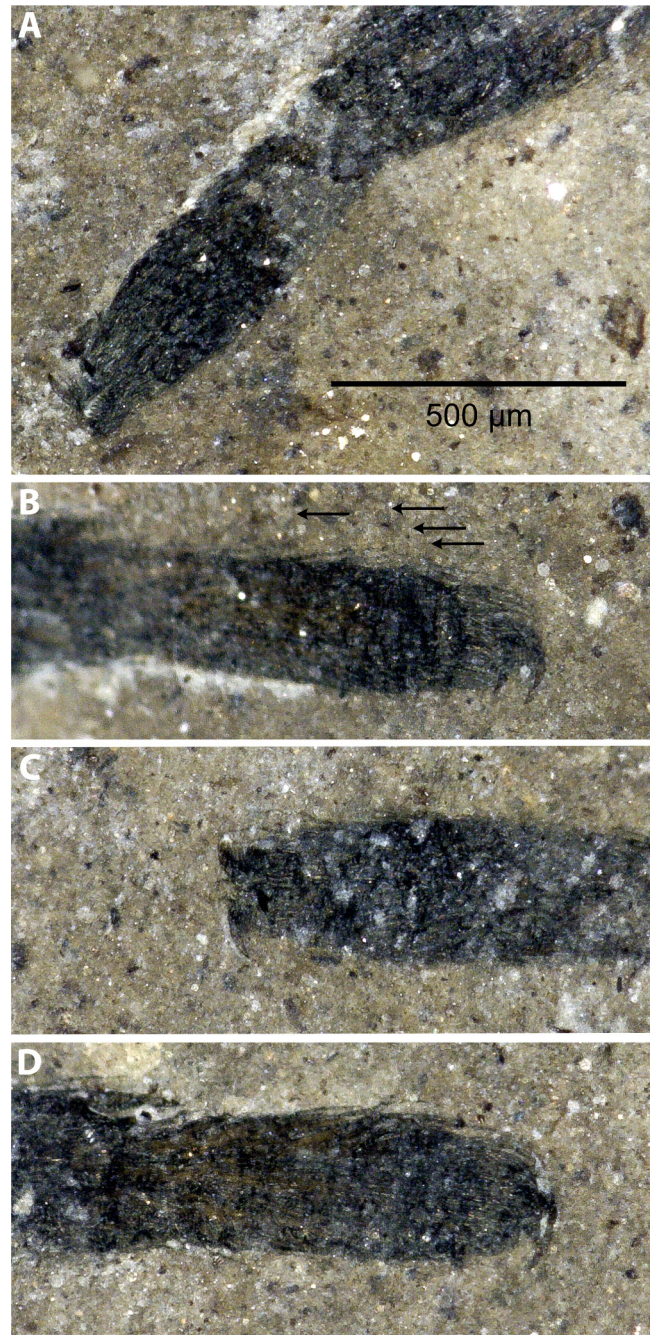


FIGURE 3. Holotype (HLMD-Me-20335) of *Lutetiana neli* gen. et sp. nov. from the Middle Eocene of Grube Messel, Germany. **A**, Detail of tarsus and claws of left leg III. **B**, Detail of tarsus and claws of right leg IV, arrows indicate trichobothria; scale as in **A**. **C**, Detail of tarsal claws of left leg I; scale as in **A**. **D**, Detail of tarsus and claws of right leg III; scale as in **A**.

a result of their grassland habitat, and the same may well be true of Messel. The few short-legged lycosids which lack scopulae, e.g., *Pterartoria*, are web builders.

The relatively short, stout legs, three tarsal claws and lack of claw tufts and scopulae, shallowly notched trochanters, row of tarsal trichobothria, general habitus, and habitat, does point towards the Cybaeidae, as presently constituted. Previously a poorly defined family, the analysis

of Wheeler *et al.* (2017) provided strong support and these authors redelimited the group. Few spiders show legs almost sub-equal in size and leg IV only slightly longer than the body. Examples include the cybaeid *Cryphoea*; this spider is rather small, but does inhabit mainly forests. *Coelotes*, presently in Agelenidae (but see note under Agelenidae in World Spider Catalog 2019), is larger and is also silvicolous. North American cybaeids such as *Blabomma*, *Dirksia* and *Ethobuella* also have relatively short legs. Some cybaeids have relatively large eyes, *e.g.*, the six-eyed *Blabomma* and *Cybaeus* (Roth, 1993: figs 16 and 20, respectively). The eyes of *Cybaeozyga heterops* somewhat resemble the arrangement in lycosids (Roth, 1993: fig. 19).

Spiders with relatively short, subequal in size legs belong to cursorial guilds, as opposed to those which live suspended from webs and which benefit from longer and more differentiated leg lengths (Moya-Laraño *et al.*, 2008). Members of the Marronoidea, and those lycosids which lack scopulae, live mainly on the ground or low on trees and bushes, generally on permanent sheet webs. Considering the evidence presented by the morphology of the fossil spider, together with considerations of the likely paleoecology of Messel, we consider that the fossil spider most likely is a member of the Cybaeidae.

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