

A new spider (Araneae: Haplogynae: Plectreuridae) from the Cretaceous Fossil-Lagerstätte of El Montsec, Spain

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Abstract. Two specimens of a new spider from the Cretaceous (ca. 129 Ma) El Montsec Fossil-Lagerstätte, northeastern Spain, are described as *Montsecarachne amicus* gen. et sp. nov. and referred to the extant haplogyne family Plectreuridae. Plectreurids are found today in only in the southwestern USA, Mexico, Central America and Cuba, but fossils show a more widespread distribution in Eurasia. The new species adds an additional stratigraphic and biogeographical record. The paleobiogeographical history of plectreurids is discussed, and it is concluded that the most likely scenario is that the family was more widespread in the past, and has suffered extinction over much of its range, resulting in the present distribution. Possibly, extant plectreurids represent a living remnant of a more diverse group of haplogynes that were widespread in the Mesozoic.

Keywords: Mesozoic, paleobiogeography, Pholcoidea

Spiders from the Cretaceous Fossil-Lagerstätte (locality of exceptional fossil preservation) of El Montsec, Spain, were among the earliest Mesozoic Araneae to be described (Selden 1989, 1990). In these works, both araneoid and deinopoid orbweavers were recognized, superfamilies that belong to the Entelegynae Simon 1893 of the infraorder Araneomorphae Smith 1902. Within this infraorder, the Haplogynae Simon 1893 are considered more primitive spiders, and the new species described here belongs to that group. The two specimens, conspecific adult males, come from the lithographic limestones of earliest Barremian age (ca. 129 Ma), from the locality of La Cabrua in the Sierra de Montsec, northeast Spain (Selden & Nudds 2012).

The fossils show distinctive characters, which allow them to be placed in the modern haplogyne superfamily Pholcoidea Koch 1850. This superfamily includes three families with the sister-group relationship: Pholcidae Koch 1850 (Diguettidae Pickard-Cambridge 1899, Plectreuridae Simon 1893) (Dunlop & Penney 2011). Among these, the fossil species most closely resembles the relatively plesiomorphic haplogyne family Plectreuridae. The fossils are placed in a new genus and species, *Montsecarachne amicus* gen. et sp. nov., in Plectreuridae.

Today, plectreurids are restricted in their distribution to southwestern North America, Central America and the Caribbean, but fossils show a more widespread distribution in Eurasia. The new species described here, from the Cretaceous of Spain, adds an additional biogeographical record. It is possible that extant Plectreuridae represent a living remnant of a group of haplogynes which were widespread in the Mesozoic.

STRATIGRAPHY AND PALAEOECOLOGY

The specimens come from the outcrop known as La Cabrua, which is an old quarry on the track between Rúbies and Santa Maria de Meià, just above the Sant Sebastia hermitage, in the Sierra de Montsec mountain range (Bataller et al. 1953). They were collected during an expedition from the Institut d'Estudis Ilerdencs, Lleida, Spain.

The lithographic limestones of El Montsec were mapped as a subunit of the Calcaires à Charophytes du Montsec (Peybernès & Oertli 1972). Marine fossils such as rudist bivalves and foraminiferans occur beneath and above the Calcaires à Charophytes du Montsec. Studies on regional stratigraphy, charophytes, and fossil assemblages have shown that the age of the El Montsec lithographic limestones is earliest Barremian (Gomez et al. 2002). The lithographic limestones are rhythmically laminated carbonate mudstones without any sign of currents or emersion features such as raindrop marks or mud cracks. The exceptional preservation of soft tissues, skeletons undisturbed by scavengers or decomposers and random orientation of fossils, all point to deep water, probably an anoxic lake bottom. The rhythmic laminations are typical of lacustrine conditions and reflect seasonal changes in the lake environment. Although the lake was close to the sea, there is no evidence of a permanent connection; e.g., in the form of marine fossils (De Gibert et al. 2000).

METHODS

The fossils are preserved on thin slabs of pale buff-grey limestone. Grains are not visible in the rock, and the hackly fracture and vitreous appearance under high-power microscopy suggest crystallization from a lime mud. Calcite-filled cracks cross the specimens. The spiders are preserved as pieces of cuticle on, and slightly within, the bedding surface. The cuticle is brittle and brown: thicker parts are deep brown and the thinnest cuticle pale buff. The cuticle is presumed to be preserved as kerogen (Gupta et al. 2008). The best-preserved parts are visible through a thin layer of translucent limestone, but their morphological details are hazy due to the presence of the overlying matrix. In such instances, 2–4% hydrochloric acid was used, sparingly and with care, to remove the matrix and thus to reveal fine structural details. The specimens are fairly complete, with part and counterpart available for both.

The specimens were studied and photographed under 70% ethanol (to enhance contrast) using a Leica MZ16 stereomicroscope, and photographed using a Canon EOS 5D MkIII

digital camera attached to the microscope and DSLR Assistant software (www.kaasoft.com) on an Apple MacBook Pro computer. Photographs were manipulated using Adobe Photoshop software, and final drawings were made from the photographs using Adobe Illustrator. All measurements are in millimeters and were made from the drawings using Photoshop's analysis tools. Measurements of paired organs are means of left and right of part and counterpart; i.e., maximally four measurements if all are preserved.

Leg formula (e.g., 1423) indicates the length of each leg relative to the others, from longest to shortest. Abbreviations: car carapace, ch chelicera, cx coxa, fe femur, L length, lb labium, mt metatarsus, mx maxilla, op opisthosoma, pa patella, Pd pedipalp, sp spinnerets, st sternum, ta tarsus, ti tibia, W width.

MORPHOLOGICAL INTERPRETATION

The two specimens are both adult males with identical pedipalp morphology; they differ slightly in size (the holotype is slightly larger), but otherwise any other morphological differences can be explained by preservation, so they are considered to be conspecific. Like other spider specimens from this locality, and others from similar Mesozoic lacustrine deposits (e.g., the Daohugou Lagerstätte of China (Selden & Huang 2010), only cuticular structures are preserved, dorsal and ventral superimposed. After splitting the rock, part and counterpart may bear mainly dorsal or ventral structures, but may show structures from both surfaces superimposed, or some structures split between part and counterpart. For example, LC-2936 B and LC-3780 B show mostly dorsal features of the body (Figs. 1C, 3C), while their counterparts, LC-2936 A and LC-3780 A (Figs. 1A, 3A), show predominantly ventral body features. Nevertheless, chelicerae, pedipalps, and legs occur on all specimens, in some cases ventral, others dorsal, and in places both sides superimposed. As with most matrix-preserved fossil spiders, eyes are very difficult to discern on the carapace. Commonly in fossil spiders, the chelicerae splay apart during compression (e.g., in the palpimanoids from Daohugou: Selden et al. 2008). This phenomenon is not seen in the Montsec specimens, however, which show a distinct overlap in the basal half; this suggests cheliceral fusion, which is common in haplogyne spiders.

A peculiar feature of LC-2936 is an elongate piece of setose cuticle running along the length of the tibia of leg 4 (on the right in the part, LC-2936 A). The cuticle is identical in pattern to that of the podomere and most likely belongs to the animal. Since it is an adult male, which would not undergo post-adult molting, the fossil represents a carcass, and so this feature can best be explained as part of the podomere disrupted post mortem, possibly by decay or scavenging.

SYSTEMATIC PALEONTOLOGY

Order Araneae Clerck 1757
Suborder Opisthothelae Pocock 1892
Infraorder Araneomorphae Smith 1902
Haplogynae Simon 1893

Remarks.—A number of features identify this species as a member of the Haplogynae (see Table 1), including the distinctive, pyriform pedipalpal bulb and embolus; swollen male pedipalpal tibia; basally fused chelicerae and convergent

pedipalpal endites (maxillae). Also, the general habitus, with legs of subequal length and low carapace, is haplogyne in appearance.

Superfamily Pholcoidea Koch 1850
Family Plectreuridae Simon 1893

Remarks.—The characters of swollen male pedipalpal tibia, chelicerae fused basally, and convergent (parallel) maxillae are indicative of the pholcoid-scytodoid branch of the Haplogynae (Platnick et al. 1991; Griswold et al. 2012; table 1). Plectreurid characters are unfused labium and sternum (also shared with Periegopidae), and legs bearing macrosetae. The distinctive tarsal bristles (Figs. 3E,F) are not unique to plectreurids among haplogynes (e.g., figures in Labarque & Ramírez 2012), but very similar bristles were described and figured by Gertsch (1958, fig. 9). The new fossils show particular resemblance to the extant *Plectreurys castanea* Group, in having a short embolus, and the Jurassic *Eoplectreurys gertschi* Selden & Huang 2010 in lacking onychium, subsegmented tarsus and cheliceral stridulatory ridges.

Genus *Montsecarachne* new genus

Diagnosis.—Distinguished from all other plectreurids, except those belonging to the *Plectreurys castanea* Group (Gertsch 1958), by its short embolus; all except *Kibramoa* Chamberlin 1924 and *Palaeoplectreurys* Wunderlich 2004 by its lack of a spur on the tibia of leg 1 of the male; from *Kibramoa* by the robust femur, as long as the carapace; and from *Palaeoplectreurys* by the pedipalp and the presence of additional spines.

Etymology.—After the type locality, El Montsec, and the Greek ἀράχνη (L. *arachne*), a spider.

Type species.—*Montsecarachne amicorum* n. sp. (monotypic).

Montsecarachne amicorum new species
Figs. 1–3

Etymology.—Latin *amicus*, a friend, in honor of the Amics de la Paleontologia (Friends of Paleontology), who began the series of organized excavations at the quarry of La Cabrua in the 1970s and discovered so many of the exciting fossils from the Fossil-Lagerstätte of El Montsec (Selden & Nudds 2012).

Type series.—Holotype adult male, LC-3780 IEI A,B (part and counterpart); paratype LC-2936 IEI A,B (part and counterpart) adult male; from lithographic limestones within the Calcaires à Charophytes du Montsec, of Cretaceous (earliest Barremian) age, in the quarry of La Cabrua, Sierra de Montsec, northeast Spain; deposited in the Institut d'Estudis Ilerdencs, Lleida, Spain.

Diagnosis.—As for the genus.

Description.—Holotype and paratype, adult males. Body thickly clothed in fine setae. Macrosetae on legs, especially distally. Carapace subcircular, very slightly longer than wide, narrowed somewhat anteriorly; opisthosoma suboval, ca. 1.25× longer than wide (Figs. 1, 3). Sternum suboval, ca. 1.15× longer than wide, gently scalloped around coxae; labium approximately pyriform, slightly longer than wide, separate from sternum; maxillae longer than wide, convergent and meeting in front of labium (Fig. 3A,B). Chelicerae parallel, elongate, porrect, apparently conjoined in basal half; fang short, curved; small tooth on paturon adjacent to fang tip

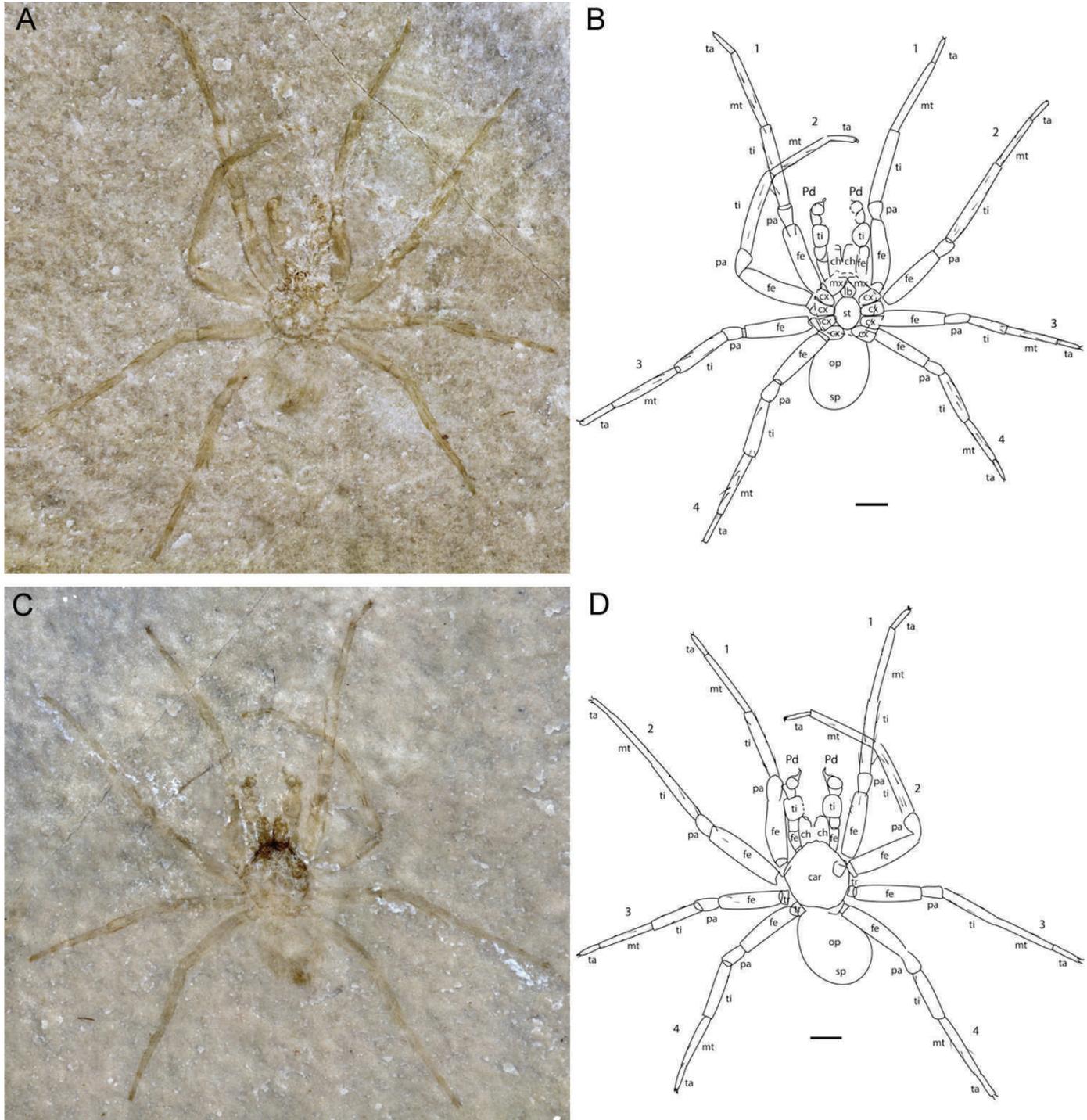


Figure 1.—*Montsecarachne amicorum* gen. et sp. nov.: A. photograph of holotype part LC-3780 IEI A; B. explanatory drawing of A; C. photograph of holotype counterpart LC-3780 IEI B; D. explanatory drawing of C. Scale bars = 1 mm.

(Fig. 2A). Pedipalp approximately equal in length to leg 1 femur + patella; tibia swollen, bulb subspherical, embolus narrows rapidly, from wide base, in short spiral to sharp pointed apex. Leg formula 2134; legs subequal in length. Long podomeres (femora, tibiae and metatarsi) approximately equal in length (Figs. 1, 3). Leg 1 femur slightly curved, approximately equal in length to carapace length. Few, thin

macrosetae on femora; distal femur of leg 1 with two strong, curved macrosetae mesiodistally, another in midline, adjacent to swollen pedipalp tibia (Fig. 1C,D). No macrosetae on patellae; tibiae and metatarsi with numerous, stronger macrosetae along their lengths; macrosetae at distal joints of metatarsi. Tarsi without macrosetae but with strong bristles distally, especially two or three large ones dorsally at distal

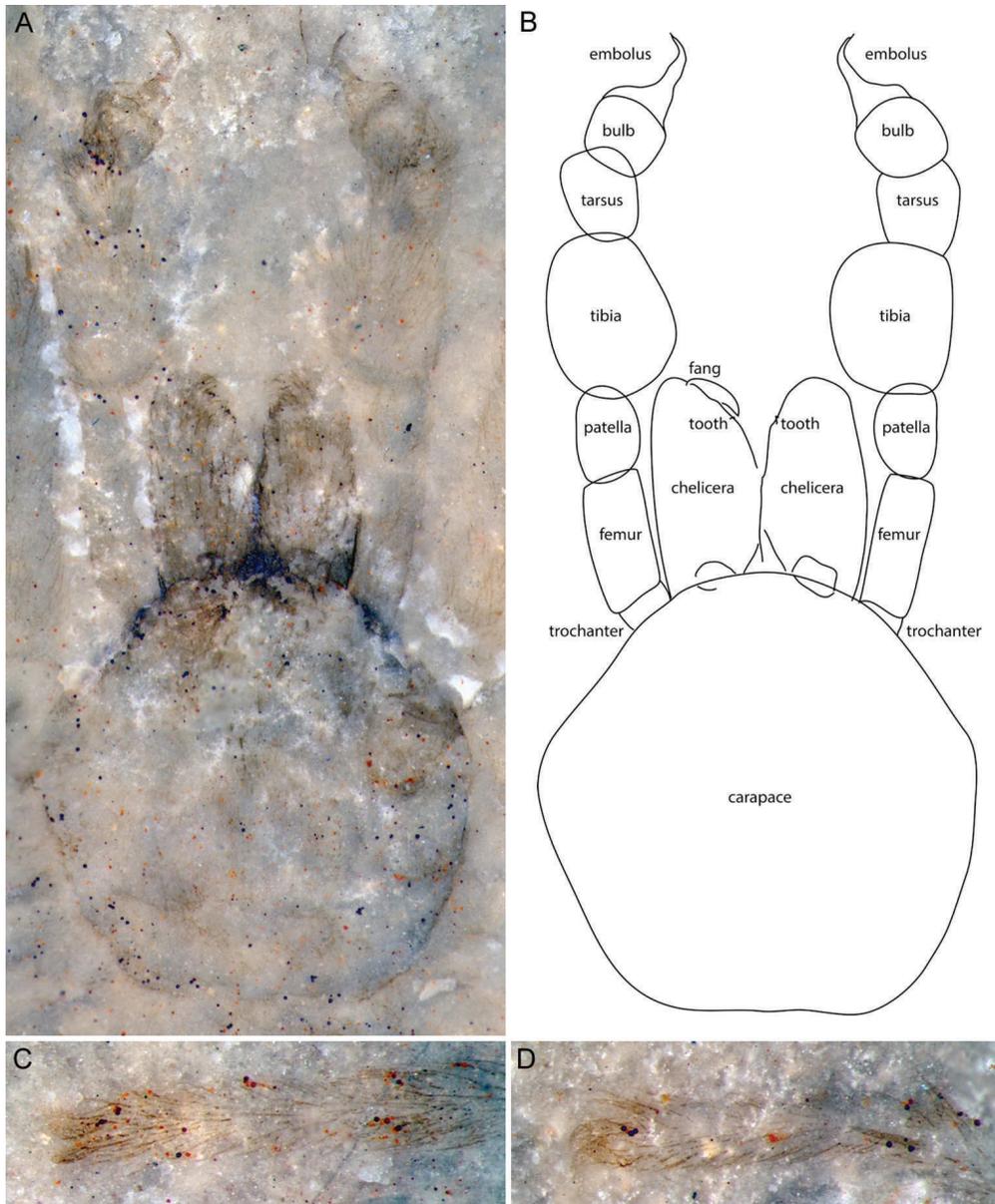


Figure 2.—*Montsecarachne amicorum* gen. et sp. nov. holotype counterpart LC-3780 IEI B: A. detail of carapace, chelicerae, and pedipalps; B. explanatory drawing of A; C. tarsus of left leg 3, note pectinate paired claws; D. tarsus of right leg 2, note strong bristles dorsal to paired claws and distal macroseta on metatarsus. Scale bars = 0.5 mm.

functionally by the strong, curved macrosetae at the distal end of femur 1 in *Montsecarachne* (Figs. 1C, 3C). The femur of leg 1 of *Montsecarachne* is slightly curved and robust, and approximately equal in length to the length of the carapace; this character state resembles that in most plectreurids except *Kibramoa* (femur 1 slender, much longer than carapace length: Gertsch 1958). Interestingly, both of the Mesozoic plectreurids have rather short carapaces in comparison with all other plectreurid species. No phylogenetic analysis has been performed on the Plectreuridae, so it is impossible to know the relationships between any of the genera and species, fossil and extant, of the family.

Biogeography.—Plectreurids are distributed today only in the southwestern USA, Mexico, Central America and Cuba

(Alayón & Viquez 2011), but fossils are known from Miocene Dominican Republic amber (Penney 2009), from Eocene Baltic amber (Wunderlich 2004) and from the Jurassic of China (Selden & Huang 2010). The presence of a plectreurid in Dominican amber is unsurprising, given their present-day distribution; indeed, it might be expected that a living specimen will turn up in the Recent fauna of Hispaniola (Penney 2009). The presence of a plectreurid in middle Eocene Baltic amber, however, suggests that the family either migrated from Eurasia to its present area of endemism, or that it was once more widespread and its range has contracted. The existence of plectreurids in the early Cretaceous of Spain and the mid-Jurassic of the North China Block (Selden & Huang 2010) suggests that the family had a more widespread

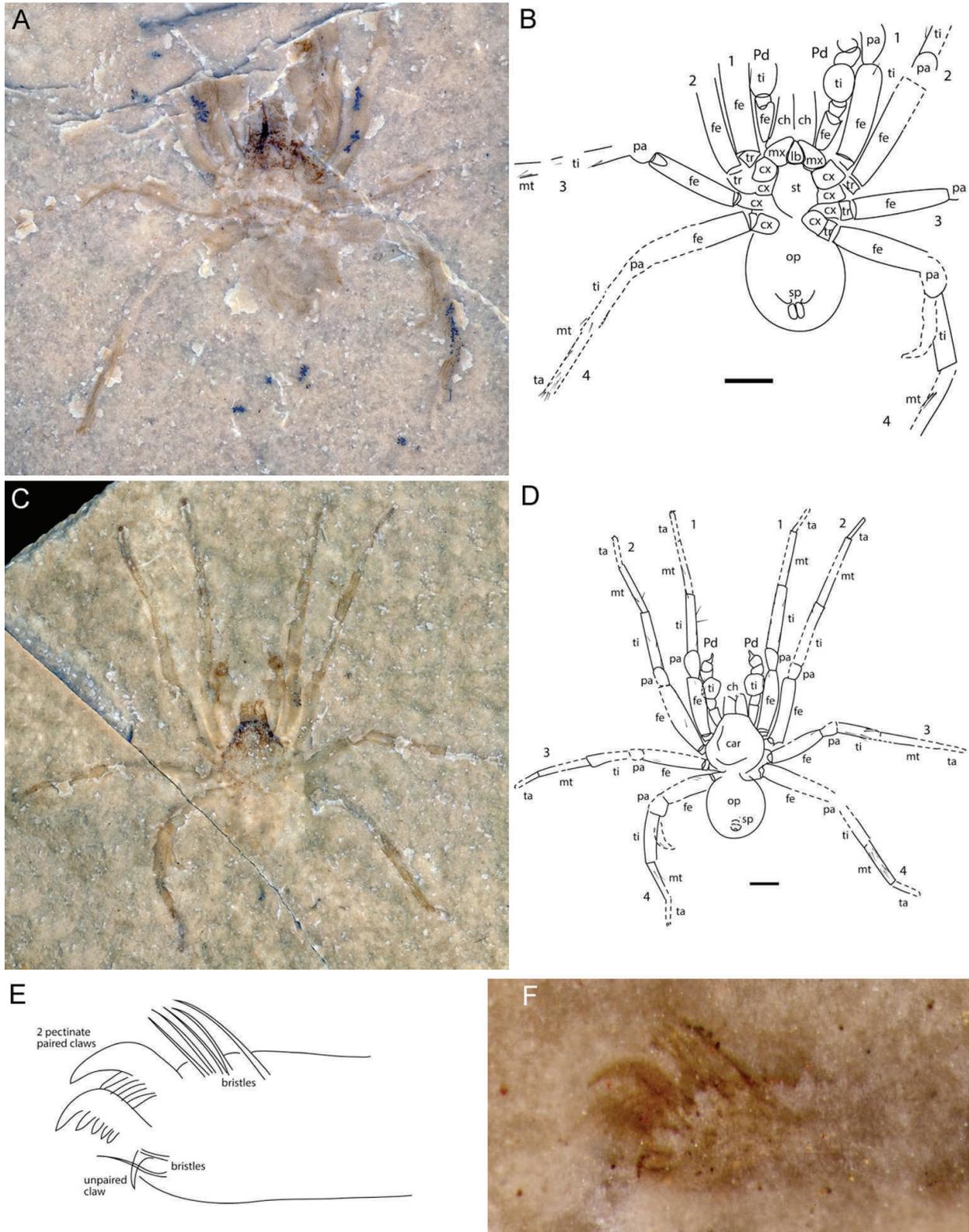


Figure 3.—*Montsecarachne amicomum* gen. et sp. nov.: A. photograph of paratype part LC-2936 IEI A; B. explanatory drawing of A; C. photograph of paratype counterpart LC-2936 IEI B; D. explanatory drawing of C; E. explanatory drawing of F; F. detail of tarsal claws of left leg 4. Scale bars = 1 mm.

distribution in the past; alternatively, its distribution could have migrated from the Eastern Palearctic region to the Western Palearctic, and then to the Western Nearctic, though this scenario seems less likely.

Sanmartín et al. (2001) provided a concise description of the reconstructions of the history of the Holarctic region from the Mesozoic to the present day. By mid-Jurassic times (ca. 165 Ma), the North China Block, on which the oldest known plectreuid, *Eoplectreurys*, was living by a volcanic lake (Selden & Huang 2010), was close enough to eastern Asia for biota to exchange between these continents (Metcalf 2009). The climate at the locality at this time was warm temperate (Ren et al. 2010). However, America and Asia were widely separated by a polar ocean in the mid-Jurassic, though some dispersal may have been possible from Eurasia to North America either directly, or by island-hopping via the British Isles block (Sanmartín et al. 2001). By early Cretaceous times, *Montsecarachne* was living near a lake in what is now northern Spain, which was also part of Eurasia. This locality was in the same warm temperate zone as occupied by *Eoplectreurys* (Boucot & Scotese 2012). Dispersal of plectreurids had been possible from eastern to western Eurasia through this period, though interrupted much of the time by the presence of the central Asian Turgai Sea (Cox & Moore 2010). Also at this time, dispersal was possible from western Eurasia to North America, via the same route through the British Isles across the incipient Atlantic Ocean but, by the later Cretaceous, this route became impassable. In the later Cretaceous, a seaway developed dividing western North America (at that time linked to Asia by the Beringian land bridge) from eastern North America, which was becoming more isolated from Europe as the Atlantic Ocean continued to open northwards. By the end of the Cretaceous, the mid-continental seaway dividing North America had regressed and the continent became one again.

After the opening of the North Atlantic in late Cretaceous times, terrestrial connections between Europe and North America persisted across possible North Atlantic land bridges until at least the early Eocene (ca. 50 Ma). The Thulean Bridge is supposed to have connected southern Europe to Greenland via Scotland, Iceland, and the Faeroes; Greenland was then connected with eastern North America through the Queen Elizabeth Islands. As the climate improved after the end-Cretaceous extinction event and subsequent nuclear winter, the climate warmed through the early Cenozoic, allowing an exchange of temperate biota until the breaking of the Thulean Bridge in the early Eocene (ca. 50 Ma). It was during the earliest Eocene, when the combination of the availability of the Thulean Bridge and the short-lived Paleocene–Eocene Thermal Maximum climatic event, which saw temperatures rise sharply, that mammals were able to interchange between Eurasia and North America (Jones 2011), and also likely caused a turnover in mammal faunas (Gingerich 2006). This was also a time when plectreurids could have migrated to North America. Another possible North Atlantic land bridge is the so-called de Geer Land Bridge, connecting Greenland to Eurasia via Svalbard, though this is likely never to have been a complete bridge, rather a stepping-stone, and may have been too northerly and cold for thermophilic biota to have utilized (Jones 2011).

Another available land bridge between Eurasia and North America was Beringia. Eastern Asia and western North America became connected by land across the Bering Sea in the mid-Cretaceous (ca. 100 Ma), and they remained joined until the Pliocene. However, dispersal by this route appears to have been less common than via the North Atlantic land bridges for many plants and animals, with some exceptions (Condamine et al. 2012). In the early Cenozoic, as the temperature rose, boreal and, later, boreotropical forest developed across Beringia, facilitating biotic interchange until the Eocene–Oligocene transition event (EOT) (Hren et al. 2013), when temperatures decreased rapidly, rarely to return to their previous levels. At the end of the Eocene, shortly after *Palaeoplectreurys* was living in the Baltic amber forest (Wunderlich 2004), the North Atlantic land bridges were no longer available and the EOT had created a cold climate in Beringia; so, if plectreurids had not spread to North America before this time, then later opportunities became fewer and less likely.

Selden & Huang (2010) discussed the possible center of origin of the plectreurids, which was most likely on Eurasia. Dispersal to the North American continent could have occurred in the Jurassic, or later in the early Eocene. The present distribution of plectreurids is most likely the result of extinction across the large part of their range. Moreover, they appear to have changed their habitat preference somewhat, in that now they occur principally in arid environments. However, although the records from Cuba (Alayón García 2003) and Central America (Alayón & Viquez 2011) are not from obvious arid habitats, the specimens were found in arid habitats within otherwise humid environments. The Cenozoic amber plectreurids come from humid forest environments, though it is possible that they, too, were living in arid situations within these environments. The Mesozoic plectreurids come from perilacustrine environments, which could include xeric habitats.

CONCLUSION

The new genus *Montsecarachne* can be accommodated within the modern family Plectreuridae; it adds to the diversity within that family and adds an additional stratigraphic and biogeographical record. Plectreurids are restricted today to arid habitats in the southwestern USA, Mexico, Central America and Cuba, but Mesozoic and Cenozoic fossils show a more widespread distribution in Eurasia. The most likely paleobiogeographic history of the family is that it was more widespread in the past and has suffered extinction over much of its range, resulting in the present distribution. It is possible that the extant plectreurids represent a living remnant of a greater diversity of haplogynes, which were widespread during the Mesozoic.

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LITERATURE CITED

Agnarsson, I., J. Coddington & M. Kuntner. 2013. Systematics: progress in the study of spider diversity and evolution. Pp. 58–111.

- In Spider Research in the 21st Century: Trends and Perspectives.* (D. Penney, ed.). Siri Scientific Press, Manchester, UK.
- Alayón García, G. 2003. Nueva especie de *Plectreureys* Simon (Araneae: Plectreuridae) de Cuba. *Revista Ibérica de Aracnología* 7:85–88.
- Alayón, G. & C. Viquez. 2011. Nueva especie de *Plectreureys* (Araneae: Plectreuridae) de América Central. *Boletín de la Sociedad Entomológica Aragonesa* 48:227–232.
- Ausserer, A. 1867. Die Arachniden Tirols nach ihrer horizontalen und verticalen Verbreitung. I. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 17:137–170.
- Bataller, R.J., V. Masachs & A. de Galvez-Cañero. 1953. Mapa Geológico de España. Hoja 290 ISONA, 1:50,000. Instituto Geológico y Minero de España y Diputación de Provincia Lérida, Madrid.
- Boucot, A.J. & C.R. Scotese. 2012. Pangaeon aggregation and disaggregation with evidence from global climate belts. *Journal of Palaeogeography* 1:5–13.
- Chamberlin, R.V. 1924. The spider fauna of the shores and islands of the Gulf of California. *Proceedings of the California Academy of Sciences* 12:561–694.
- Clerck, C. 1757. *Aranei Svecici, Descriptionibus et Figuris Aeneis Illustrati, ad Genera Subalterna Redacti, Speciebus ultra LX Determinati.* Laur. Salvii, Stockholm.
- Condamine, F.L., F.A.H. Sperling & G.J. Kergoat. 2012. Global biogeographical pattern of swallowtail diversification demonstrates alternative colonization routes in the Northern and Southern hemispheres. *Journal of Biogeography* 40:9–23.
- Cox, C.B. & P.D. Moore. 2010. *Biogeography: an Ecological and Evolutionary Approach*, Eighth Edition. Wiley, London.
- De Gibert, J.M., M.A. Fregenal-Martínez, L.A. Buatois & M.G. Mángano. 2000. Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 156:89–101.
- Dunlop, J.A. & D. Penney. 2011. Order Araneae Clerck, 1757. *In Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness.* (Z.-Q. Zhang, ed.). *Zootaxa* 3148:149–153.
- Gertsch, W.J. 1958. The spider family Plectreuridae. *American Museum Novitates* 1920:1–53.
- Gingerich, P.D. 2006. Environment and evolution through the Paleocene–Eocene thermal maximum. *Trends in Ecology and Evolution* 21:246–253.
- Gomez, B., C. Martín-Closas, G. Barale, F. Thévenard & G. Guignard. 2002. *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera from the Lower Cretaceous of Spain. *Palaeontology* 45:997–1036.
- Griswold, C.E., T. Audisio & J. Ledford. 2012. An extraordinary new family of spiders from caves in the Pacific Northwest (Araneae, Trogloraptoridae, new family). *ZooKeys* 215:77–102.
- Gupta, N.S., O. Cambra-Moo, D.E.G. Briggs, G.D. Love, M.A. Fregenal-Martínez & R.E. Summons. 2008. Molecular taphonomy of macrofossils from the Cretaceous Las Hoyas Formation, Spain. *Cretaceous Research* 29:1–8.
- Hren, M.T., N.D. Sheldon, S.T. Grimes, M.E. Collinson, J.J. Hooker & M. Bugler et al. 2013. Terrestrial cooling in Northern Europe during the Eocene–Oligocene transition. *Proceedings of the National Academy of Sciences of the USA* 110:7562–7567.
- Jones, R.W. 2011. *Applications of Palaeontology.* Cambridge University Press, Cambridge, UK.
- Koch, C.L. 1850. *Übersicht des Arachnidensystems.* C. H. Zeh, Nürnberg.
- Král, J., J. Musilová, F. Štáhlavský, M. Řezáč, Z. Akan & R.L. Edwards et al. 2006. Evolution of the karyotype and sex chromosome systems in basal clades of araneomorph spiders (Araneae: Araneomorphae). *Chromosome Research* 14:859–880.
- Labarque, F.M. & M.J. Ramírez. 2012. The placement of the spider genus *Periegops* and the phylogeny of Scytodoidea (Araneae: Araneomorpha). *Zootaxa* 3312:1–44.
- Marx, G. 1888. On a new and interesting spider. *Entomologica Americana* 4:160–162.
- Metcalf, I. 2009. Late Palaeozoic and Mesozoic tectonic and palaeogeographical evolution of SE Asia. *Geological Society, London, Special Publications* 315:7–23.
- Penney, D. 2009. A new spider family record for Hispaniola—a new species of *Plectreureys* (Araneae: Plectreuridae) in Miocene Dominican amber. *Zootaxa* 2144:65–68.
- Peybernès, B. & H. Oertli. 1972. Le série du passage du Jurassique au Crétacé dans le bassin sud-pyrénéen (Espagne). *Comptes Rendus de l'Académie des Sciences Paris, Série D* 274:3348–3351.
- Pickard-Cambridge, F.O. 1899. *Arachnida – Araneidea and Opiliones.* *In Biologia Centrali-Americana, Zoology.* (F. du Cane Godman & O. Salvin, eds.). R.H. Porter and Dulau & Co., London.
- Platnick, N.I., J.A. Coddington, R.R. Forster & C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *American Museum Novitates* 3016:1–73.
- Pocock, R.I. 1892. XXXVIII.—*Liphistius* and its bearing upon the classification of spiders. *Annals and Magazine of Natural History, Series (6)* 10:306–314.
- Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *Journal of Arachnology* 28:149–157.
- Ren, D., C. Shih, G. Taiping, Y. Yunzhi & Z. Yunyun. 2010. *Silent Stories.* Science Press, Beijing.
- Sanmartín, I., H. Enghoff & F. Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society* 73:345–390.
- Selden, P.A. 1989. Orb-web weaving spiders in the early Cretaceous. *Nature* 340:711–713.
- Selden, P.A. 1990. Lower Cretaceous spiders from the Sierra de Montsec, north-east Spain. *Palaeontology* 33:257–285.
- Selden, P.A. & D. Huang. 2010. The oldest haplogyne spider (Araneae: Plectreuridae), from the Middle Jurassic of China. *Naturwissenschaften* 97:449–459.
- Selden, P.A. & J. Nudds. 2012. *Evolution of Fossil Ecosystems*, Second Edition. Manson, London.
- Selden, P.A., D. Huang & R. Dong. 2008. Palpimanoid spiders from the Jurassic of China. *Journal of Arachnology* 36:306–321.
- Simon, E. 1893. *Histoire Naturelle des Araignées*, Second Edition. Roret, Paris.
- Smith, F.P. 1902. *The Spiders of Epping Forest.* *Essex Naturalist* 12:181–201.
- Ubick, D. 2005. Plectreuridae. Pp. 201–202. *In Spiders of North America: an Identification Manual.* (Ubick, D., P. Paquin, P.E. Cushing & V.D. Roth, eds.). American Arachnological Society, College Park, Maryland.
- Wunderlich, J. 2004. Fossil spiders (Araneae) of the superfamily Dysderoidea in Baltic and Dominican amber, with revised family diagnoses. *Beiträge zur Araneologie* 3:633–746.
- Wunderlich, J. 2008. Descriptions of fossil spider (Araneae) taxa mainly in Baltic amber, as well as certain related extant taxa. *Beiträge zur Araneologie* 5:44–139.
- Wunderlich, J. 2012. On the fossil spider (Araneae) fauna in Cretaceous ambers, with descriptions of new taxa from Myanmar (Burma) and Jordan, and on the relationships of the superfamily Leptonetoidea. *Beiträge zur Araneologie* 7:157–232.