

A new deinopoid spider from Cretaceous Lebanese amber

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Palaeomicromenneus lebanensis gen. et sp. nov. (Araneae: Deinopidae) is described from Upper Neocomian–basal Lower Aptian (ca. 125–135 Ma) Cretaceous amber from the Hammana/Mdeyrij outcrop, Lebanon. This is the oldest known, and possibly the first true fossil, deinopid. The lack of ocular modifications in the new fossil genus does not exclude it from having exhibited the same net-casting prey capture behaviour as extant deinopids. Alternatively, this prey-capture behaviour may be highly derived and whether it had evolved by the Early Cretaceous cannot be determined for sure; early deinopids (as diagnosed by pedipalp morphology rather than behaviour) may have been orb-web weavers as is their sister taxon the Uloboridae.

Key words: Araneae, Deinopidae, Cretaceous, Lebanon, spiders.

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Introduction

Lebanese amber deposits date from the Early Cretaceous (upper Neocomian–basal Lower Aptian, c. 125–135 Ma) and contain the oldest known arthropod inclusions of any fossil resin. The amber was produced by the coniferous tree *Agathis levantensis* (Araucariaceae) in a tropical–subtropical forest (Lambert et al. 1996; Poinar and Milki 2001). Poinar and Milki (2001) cited Wunderlich and Milki (in press) as having described the first spider (Oonopidae) in Lebanese amber; however, at the time of proof reading of this manuscript, their description had not been published and is not due until 2004 (Lörg Wunderlich personal communication 2003). The only spider described from Lebanese amber is a female Linyphiidae: Linyphiinae by Penney and Selden (2002). Cretaceous amber spiders have previously been described from the Santonian of Siberia (Eskov and Wunderlich 1994: Lagonomegopidae), the Turonian of New Jersey (Penney 2002a: Segestriidae, Oonopidae, Oecobiidae, Dictynidae, Linyphiidae, Lagonomegopidae; in press: Segestriidae, Oonopidae, Araneidae), the Barremian of the Isle of Wight (Selden 2002: Nemesiidae), and the Albian of Burma (Penney 2003: Archaeidae). For a general review of spiders in amber see Penney (2002b).

The monophyly of the Orbicularia (Araneoidea—cribellate + Deinopoidea—cribellate) has been extensively tested (Griswold et al. 1998). The Araneoidea is the largest and best known superfamily of spiders; Deinopoidea is considerably smaller and consists only of two families (Uloboridae and Deinopidae). The spider family Uloboridae contains 243 extant species in 19 genera and the Deinopidae 56 extant species in 4 genera (Platnick 2003). Deinopidae are nocturnal and commonly known as net-casting, or ogre-faced spiders. The former because of their unique mode of prey cap-

ture, which consists of holding a small, rectangular miniature orb-web in their long anterior legs and swinging this at their prey, and the latter because of their enlarged posterior median eyes (Fig. 1) which facilitate this predatory behaviour in low light conditions. Uloboridae, commonly called feather-legged spiders, construct complete orb webs (subfamily Uloborinae) or reduced orb webs ranging from a triangular section (subfamily Hyptiotinae) to a single line (subfamily Miagrammopinae). The detailed motor patterns used to construct the deinopid web shows that they are derived phylogenetically from the classic orb web, an architecture found in their sister taxon, the Uloboridae (Coddington and Sobrevila 1987). Deinopidae are more derived in many ways than uloborids and mature males have a distinctive pedipalp (Coddington 1990). It has one central, distal, tegular apophysis, which probably acts as a conductor to the embolus, which is usually elongate and strongly coiled from one to six times around it. The tegulum is reduced to a band of sclerotized tissue that covers the reservoir of the sperm duct (Coddington 1990) (Fig. 1). The mature male pedipalp of uloborids is dissimilar to that of deinopids, being quite variable and more complicated in structure (e.g., Opell 1979).

Fossil Uloboridae from the extant genus *Miagrammopes* have been described from Miocene Dominican Republic amber (Schawaller 1982; Wunderlich 1988; Penney 2001). *Palaeouloborus lacasae* Selden, 1990 from Lower Cretaceous lithographic limestone of Sierra de Montsech, Lérida Province, Spain, was placed in Uloboridae by Selden and Penney (2003). Only one possible fossil deinopid has been described, from a single Baltic amber specimen as *Linoptes oculus* by Menge (1854). The specimens described by Menge (1854) are currently considered lost. His collection was originally donated to the Westpreussische Provinzialmuseum, Gdańsk (formerly Danzig), which was established

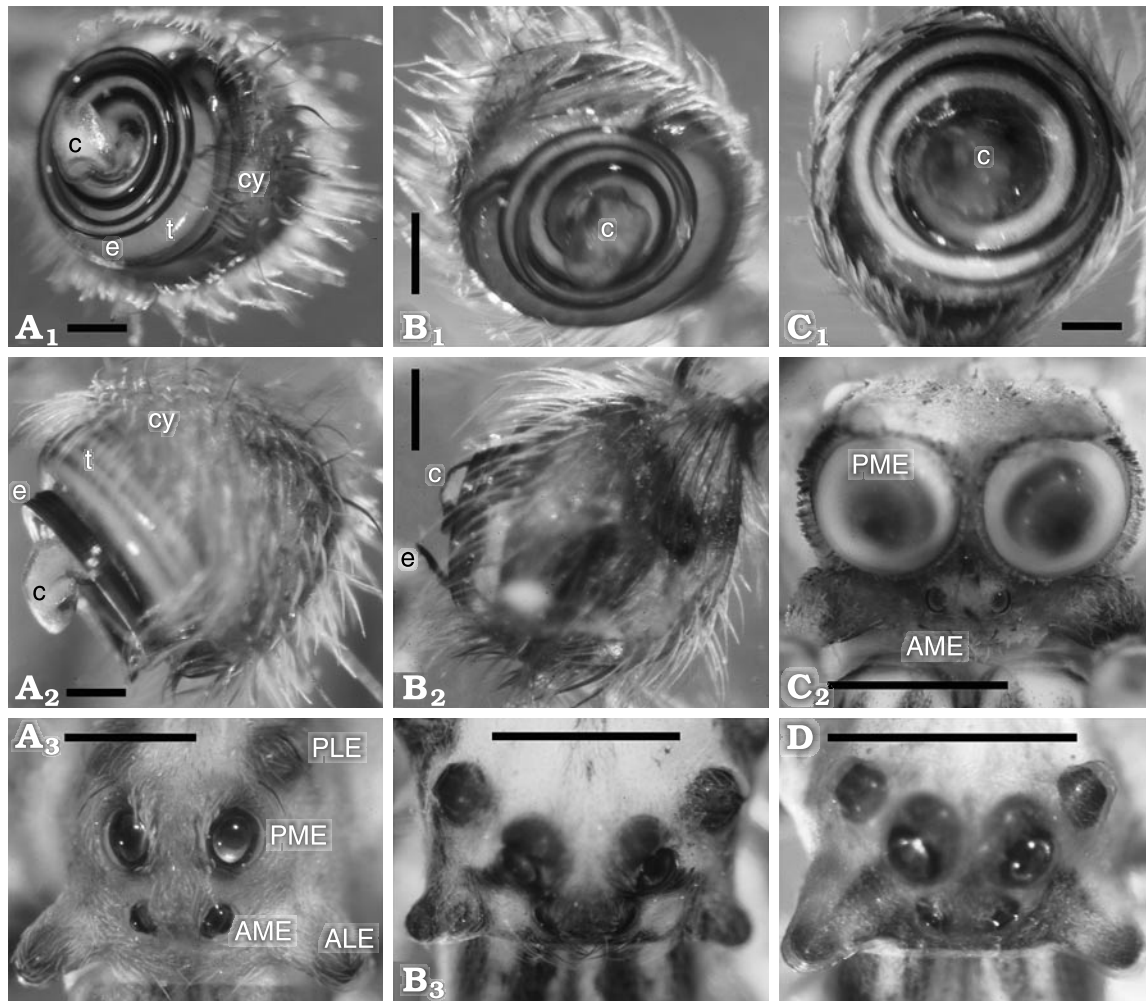


Fig. 1. Anatomy of extant deinopid spiders. **A.** *Avella* sp. male (WAM 97/2350). Pedipalp, ventral (A_1) and lateral (A_2) views; eyes, anterior view (A_3). **B.** *Menneus camelus* male (NCP 95/241). Pedipalp, ventral (B_1) and lateral (B_2) views; eyes, anterior view (B_3). **C.** *Deinopis* sp. male (NCP 2000/480). Pedipalp, ventral view (C_1); eyes, anterior view (C_2). **D.** *Avellopsis capensis* juvenile male (MRAC 207.457), eyes, anterior view. For the structure of the mature male pedipalp of *A. capensis* see Lehtinen (1967: fig. 37). Scale bars: A_1 , A_2 , B_1 , B_2 , C_1 , 0.2 mm; A_3 , B_3 , C_2 , D, 1.0 mm. Abbreviations: ALE, anterior lateral eye; AME, anterior median eye; c, conductor; cy, cymbium; e, embolus; PLE, posterior lateral eye; PME, posterior median eye; t, tegulum.

in 1880. In 1945 the collection was moved to a number of villages in northern Poland and has not been seen since. Although single samples of his collection have been found in Germany and Poland, there seems little hope that further items will be found (Kosmowska-Ceranowicz 2001). *Linoptes* was synonymized with *Deinopis* by Wunderlich (1986) but the fossil species may actually belong in the family Pisauridae (Jörg Wunderlich personal communication 2003). In this paper I describe the first Mesozoic and oldest known deinopid, from Lower Cretaceous Lebanese amber.

Material and methods

The specimen upon which this paper is based is deposited in the Laboratoire d'Entomologie, Muséum National d'Histoire naturelle, Paris. Prior to receiving the specimen, it was embedded in clear synthetic resin for protection and to facilitate han-

dling, then ground and polished by MHNP staff to reveal the inclusion. The specimen is beautifully preserved in clear amber. There are some flaws, air bubbles and inorganic debris but these obscure very few details of the spider's morphology. The only biological syninclusions are an insect wing, two partial legs and a single antenna, which due to their proximity come from a single individual. All measurements are in mm and were made using an ocular graticule. Drawing was done under incident light with a camera lucida attached to an Olympus SZH stereomicroscope, and photographs were taken with a Nikon DIX digital camera attached to a Leica Wild M8 stereomicroscope. In the leg formula (e.g., 1243), the legs are ranked in order of length (longest first). Recent spiders of the genera *Avella*, *Avellopsis*, *Deinopis*, *Hyptiotes*, and *Uloborus* housed in the collections of MRAC, NCP, NHM, and WAM were examined for comparative purposes.

Institutional abbreviations.—MHNP, Muséum National d'Histoire Naturelle, Paris; MRAC, Musée Royal de l'Afrique

Centrale, Tervuren; NCP, National Collection, Pretoria; NHM, Natural History Museum, London; WAM, Western Australian Museum, Perth.

Description

Order Araneae Clerck, 1757

Suborder Araneomorphae Smith, 1902

Superfamily Deinopoidea Koch, 1850

Family Deinopidae Koch, 1850

Genus *Palaeomicromenneus* gen. nov.

Type species: Palaeomicromenneus lebanensis sp. nov. by monotypy.

Derivation of the name: Greek, *palaios*, old; Greek, *mikros*, small; and the extant genus *Menneus*, which the fossil genus resembles.

Diagnosis.—As for the type species, see below.

Palaeomicromenneus lebanensis sp. nov.

Figs. 2, 3.

Holotype and only known specimen: Male, specimen MHNP 723A preserved in Cretaceous Lebanese amber.

Type horizon: Upper Neocomian–basal Lower Aptian (ca. 125–135 Ma) Cretaceous amber from the Hammana/Mdeyrij outcrop, Lebanon.

Type locality: The outcrop is in Caza Baabda, Mouhafazit Jabal Loubnan (central Lebanon), approximately 45 km WSW of Beirut.

Derivation of the name: The specific epithet is after Lebanon, the provenance of the fossil.

Diagnosis.—The new genus and species is diagnosed by the structure of the male pedipalp: cymbium cup-shaped and without spines, tegulum shallow, appearing as a band of sclerotized tissue between the embolus and cymbium in lateral view. Embolus elongate, tightly coiled three times around the conductor; final coil diameter slightly exceeds that of the cymbium. Distal region of embolus distinctly removed from the main coil and with a slightly constricted bend sub-terminally. Conductor curved and tongue-shaped, extending outwards. Primarily, it differs from extant deinopid genera by having the distal region of the embolus distinctly removed from the main coil and the conductor protruding outwards further than in other genera, to a distance approximately equal to the diameter of the embolic coil.

Description.—Measurements: body length 2.86; carapace 1.29 long, 1.21 at its widest point, narrowed to 0.57 in the ocular region. Carapace with rounded sides and a concave posterior margin. There is a medio-lateral band of pale, feathery setae, which lie flat and run longitudinally (visible on the right side of the carapace when viewed dorsally) (Fig. 2). The band has a slightly “furry” appearance; a corresponding band is not clear on the left side due to flaws in the amber, but is presumed present. The carapace has been damaged during preservation and flaws also obscure the foveal region. Eight eyes: posterior median eyes separated by 0.14, directed forwards and subequal to the posterior lateral eyes, which are slightly wider apart; posterior eye row distinctly recurved

(Fig. 3). Posterior median eyes slightly larger than anterior lateral eyes which are on small but distinct cuticular projections (Fig. 2). The left anterior median eye which appears subequal to the anterior lateral eye is just visible between the anterior lateral eye and posterior median eye when the specimen is viewed from above. Detailed structure of chelicerae and mouthparts not visible. Sternum length not measurable but does not extend between fourth coxae, width 0.43, with slight concave invaginations along the sides and covered with feathery setae. Opisthosoma 1.57 long, 1.36 wide, with both normal and feathery setae; the latter more prevalent on the sides of the abdomen. There is no evidence of humps, however, part of the dorsum is missing and in extant species the humps can be reduced in mature males. Cribellum undivided, spinneret region 0.64 wide, as in Fig. 2.

Leg formula 1243 (Figs. 2, 3). Leg 1 coxa 0.50, femur 2.26, patella 0.54, tibia 1.93, metatarsus 2.21, tarsus 1.07, total 8.51; leg 2 coxa 0.41, femur 1.59, patella 0.50, tibia 1.10, metatarsus 1.21, tarsus 0.64, total 5.54; leg 3 coxa 0.21, femur 0.79, patella 0.29, tibia 0.60, metatarsus 0.66, tarsus 0.39, total 2.94; leg 4 coxa 0.29, femur 1.29, patella 0.36, tibia 0.83, metatarsus 1.24, tarsus 0.43, total 4.44. Several long, distinctive spines present on all leg segments except patella 4, which has only one distal spine, and all coxae and tarsi which are spineless (Fig. 3). All segments setose; tibiae, metatarsi and tarsi of all legs with numerous short, thin, erect setae dorsally, retrolaterally, prolaterally and ventrally; feathery setae present on all legs. Femora lack the trichobothria typical of Uloboridae. Femora 2, 3, and 4 ventrally with many long, fine, erect setae that resemble trichobothria but they are not situated in shallow alveoli. Uniseriate calamistrum occupies proximal half of metatarsus 4 (Fig. 2) and in part, lies in a slight cuticular depression. Tarsi with three claws, superior pair with at least six teeth. Tarsus 4 has ventral spines, the tips of these are visible on the right leg; left tarsus 4 is not preserved.

Pedipalp (Fig. 2): femur not elongate, and lacking ventral lobes or other modifications; with one distal, long, curved spine retrolaterally. Cymbium cup-shaped, 0.31 deep and without spines, but covered with long setae. Tegulum shallow, appearing as a band of sclerotized tissue between the embolus and cymbium in lateral view. Embolus elongate, tightly coiled three times around the conductor; final coil 0.64 in diameter, which slightly exceeds that of the cymbium. Distal region of embolus distinctly removed from the main coil and with a slightly constricted bend sub-terminally. Conductor curved and tongue-shaped, extending outwards 0.64.

Discussion

Based on the structure of the pedipalp of the fossil there is no doubt that this species is correctly placed within the Deinopoidea. For differentiation from the extant genera see the diagnosis. In addition, the new fossil genus is smaller than extant genera. In general appearance the habitus of *Palaeo-*

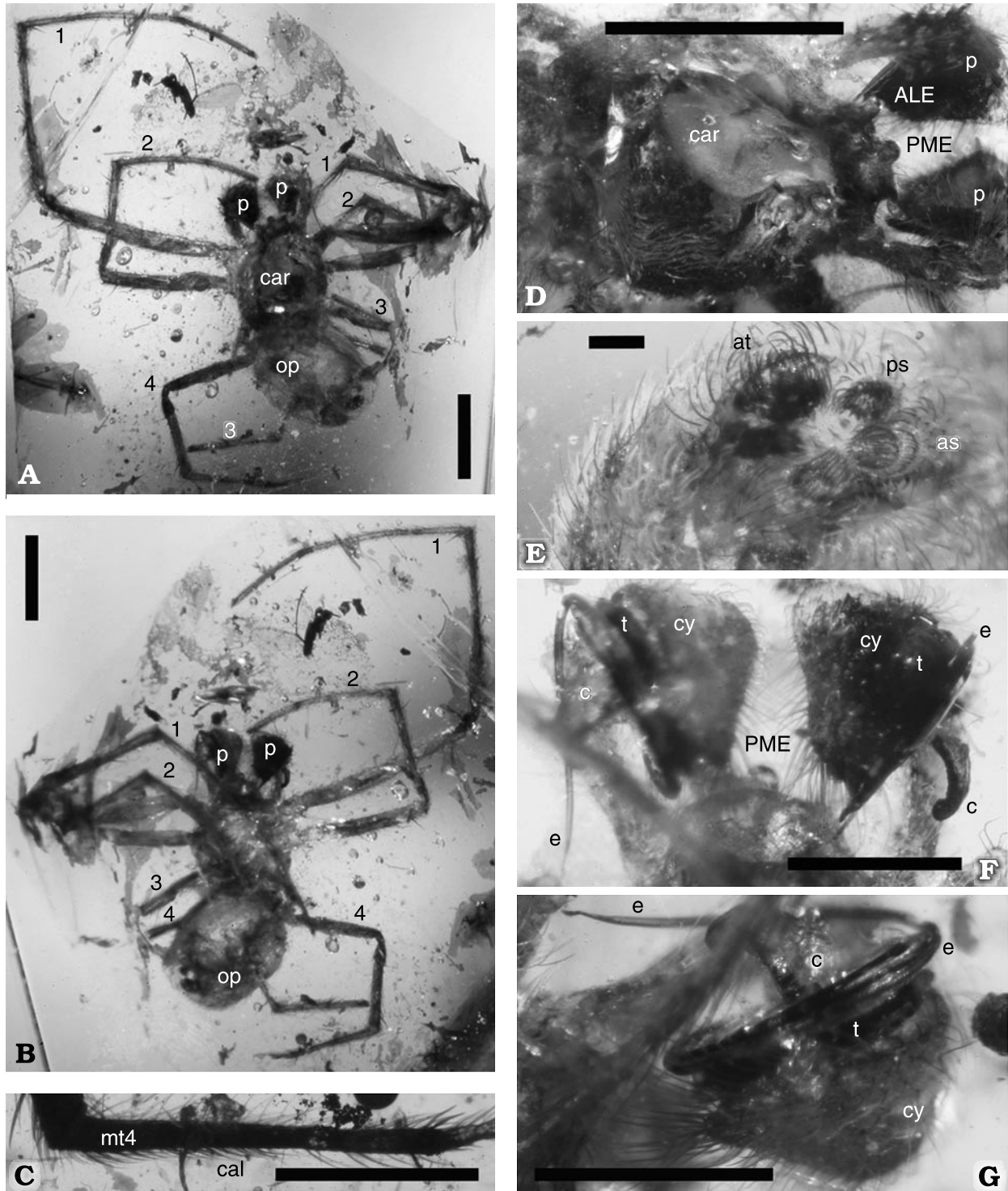


Fig. 2. *Palaeomicromenneus lebanensis* gen. et sp. nov. Holotype male. Cretaceous Lebanese amber, MHNP 723A. **A.** Dorsal view. **B.** Ventral view. **C.** Calamistrum on metatarsus 4. **D.** Carapace, dorsal view. **E.** Spinneret region. **F.** Pedipalps in lateral view as seen from below. **G.** Left pedipalp in lateral view showing diagnostic features. Scale bars: A, B, D, 1.0 mm; C, F, G, 0.5 mm; E, 0.1 mm. Abbreviations: ALE, anterior lateral eye; as, anterior spinneret; at, anal tubercle; c, conductor; cal, calamistrum; car, carapace; cy, cymbium; e, embolus; mt4, metatarsus 4; op, opisthosoma; p, pedipalp; PME, posterior median eye; ps, posterior spinneret; t, tegulum.

micromenneus lebanensis (Figs. 2, 3) most closely resembles that of the extant genus *Menneus* than any of the remaining deinopid genera. Among extant taxa, only *Menneus* bears the ventral, long, fine, erect femoral setae that resemble tricho-

bothria. However, in the extant species studied these were only present on femur 3, whereas in *P. lebanensis* they occur on femora 2, 3, and 4. Also, the leg spines and setae are numerous, long and distinct in both the fossil and *Menneus*. Al-

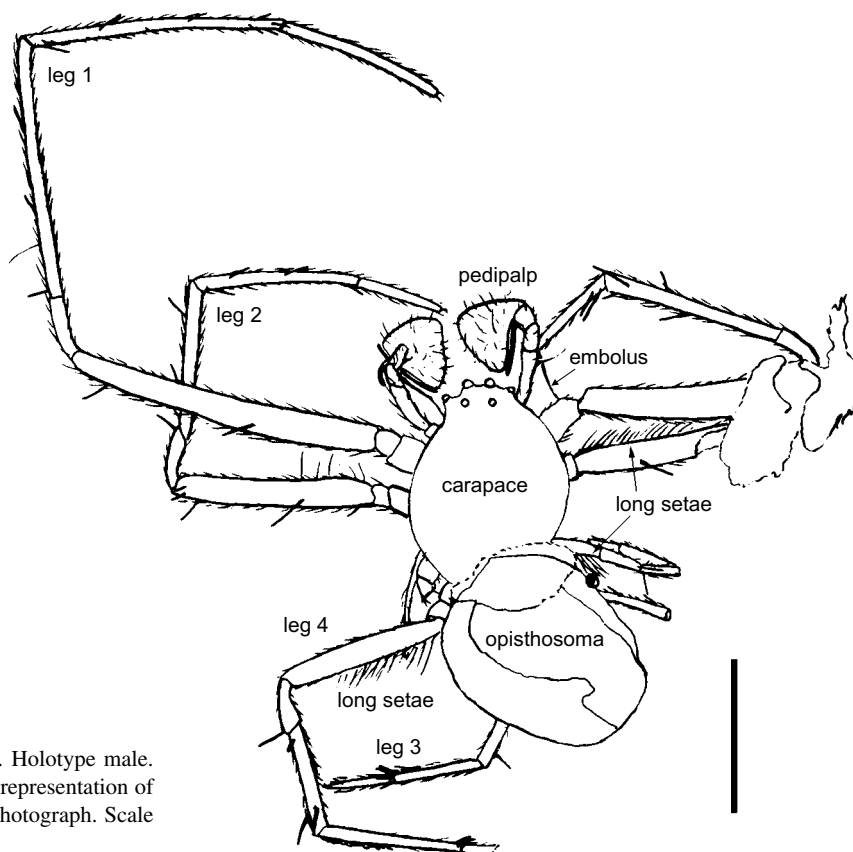


Fig. 3. *Palaeomicromenueus lebanensis* gen. et sp. nov. Holotype male. Cretaceous Lebanese amber, MHNP 723A. Diagrammatic representation of Fig. 2A illustrating additional details not visible in the photograph. Scale bar 1.0 mm.

though *Deinopis* has numerous leg spines and setae, these are much reduced in length. In *Avella* both leg spines and setae are numerous; the spines are relatively long and distinct but the setae are very faint. In *Avellopsis* both the leg spines and setae are extremely reduced.

Opell (1979) considered the presence of tarsal and metatarsal macrosetae synapomorphic for the Uloboridae. However, shortly after his publication, Opell (1982) identified these macrosetae in Deinopidae. They consist of a poorly developed row of spines that can be difficult to see because they often blend into the general hirsuteness of the tarsus (Selden 1990). Their presence in Deinopidae is confirmed here from the extant comparative material studied; they also occur in the fossil. Selden (1990) mentioned that the Deinopidae lacked feathery leg setae, however, they were observed in all extant deinopids studied here and the fossil specimen.

Although *Palaeomicromenueus lebanensis* is placed in the family Deinopidae the web structure and net-casting behaviour which are considered synapomorphies for the family (e.g., Coddington 1986) cannot be confirmed. One of the most distinctive features of the extant genus *Deinopis* is the extremely large posterior median eyes which are 3,000 times more sensitive to light than the anterior median eyes of *Portia* (Salticidae), but their resolution is relatively poor (Land 1985). In some spiders visual acuity is excellent and rivalled amongst invertebrates only by cephalopods (Land 1985). However, the majority of spiders build webs and

their principal senses are mechanoreceptive. Resolution and sensitivity to light are in competition in the design of eyes. Resolution improves as the ratio of receptor diameter to focal length decreases, but sensitivity improves as the same ratio increases. If greater resolution is required without sacrificing sensitivity, then the eye must increase in size to accommodate more receptors, and if increased sensitivity is required without loss of resolution, then the eye must become larger because each receptor must be wider (Land 1985). We see the former in the anterior median eyes of diurnal Salticidae and the latter in the posterior median eyes of *Deinopis* (Land 1985; Blest and Land 1977). *Deinopis* is a nocturnal hunter and thus requires highly developed eyes (Fig. 1) to make the most of extremely low light levels, however, *Menneus* is a crepuscular hunter and does not require such extreme modifications (Land 1985) (Fig. 1). It should also be noted that the remaining deinopid genera *Avella* and *Avellopsis* do not have such highly developed eyes (Fig. 1). Therefore the lack of ocular modifications in the new fossil genus does not exclude it from having exhibited the same prey capture behaviour as extant deinopids; maybe it too was a net-casting, crepuscular hunter. However, this prey-capture behaviour may be highly derived and whether it had evolved by the Early Cretaceous cannot be determined for sure; maybe the early deinopids (as diagnosed by pedipalp morphology rather than behaviour) were orb-web weavers as is their sister taxon, the Uloboridae.

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