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A fossil tarantula (Araneae: Theraphosidae) from Miocene Chiapas amber, Mexico

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ARTÍCULO:

A fossil tarantula (Araneae: Theraphosidae) from Miocene Chiapas amber, Mexico

Jason A. Dunlop, Danilo Harms & David Penney

Abstract:
A fossil tarantula (Araneae: Mygalomorphae: Theraphosidae) is described from an exuvium in Tertiary (Miocene) Chiapas amber, Simojovel region, Chiapas State, Mexico. It is difficult to assign it further taxonomically, but it is the first mygalomorph recorded from Chiapas amber and only the second unequivocal record of a fossil theraphosid. With a carapace length of *ca*. 0.9 cm and an estimated leg span of at least 5 cm it also represents the largest spider ever recorded from amber. Of the fifteen currently recognised mygalomorph families, eleven have a fossil record (summarised here), namely: Atypidae, Antrodiaetidae, Mecicobothriidae, Hexathelidae, Dipluridae, Ctenizidae, Nemesiidae, Microstigmatidae, Barychelidae, Cyrtaucheniidae and Theraphosidae.
Key words: Araneae, Theraphosidae, Palaeontology, Miocene, amber, Chiapas, Mexico.

Un fósil de tarántula (Araneae: Theraphosidae) en ambar del mioceno de Chiapas, México.

Resumen:
Se describe una tarántula fósil a partir de una exuvia en ámbar del terciario (mioceno) de Chiapas, región de Simojovel, estado de Chiapas, Mexico. Es difícil de clasificar taxonómicamente, pero es el primer registro de migalomorfo en ámbar para chiapas y el segundo inequívoco fósil de terafósido. Con una longitud del prosoma de cerca de 0.9 cm y una envargadura de la pata estimada como mínimo en 5 cm, representa la araña más grande que se ha registrado nunca en ámbar. De las 15 familias reconocidas actualmente de migalomorfos, once tienen un registro fósil (resumidas aquí) y son las siguientes: Atypidae, Antrodiaetidae, Mecicobothriidae, Hexathelidae, Dipluridae, Ctenizidae, Nemesiidae, Microstigmatidae, Barychelidae, Cyrtaucheniidae and Theraphosidae.
Palabras clave: Araneae, Theraphosidae, Palaeontología, Mioceno, ambar, Chiapas, Mexico.

Introduction

Fossil mygalomorphs (Araneae: Opisthothelae: Mygalomorphae) go back at least 240 million years (Selden & Gall, 1992), but are generally rarer than fossils of other – mostly araneomorph – spiders. Platnick's (2008) *World Spider Catalog* recognizes fifteen families of mygalomorph spiders, eleven of which have been recorded thus far as fossils (Table 1, Fig. 1) [see also Dunlop (1993) Selden (1997, 2002) and Wunderlich (2004) for further summaries]. Some of these familial referrals were only made tentatively due to the equivocal nature of some characters, but the general impression is of a group of spiders which had radiated into its major lineages during the early part of, or perhaps even prior to, the Mesozoic. Indeed, noting an apparent preponderance of mygalomorphs compared to araneomorphs in the late Mesozoic, Eskov & Zonshtein (1990) proposed an "age of mygalomorphs" during the Cretaceous; part of a trend between a Palaeozoic mesothele-dominated fauna and a Cenozoic, araneomorph-dominated fauna which persists to this day. However, many new records of araneomorph spiders in various Cretaceous ambers and non-amber fossil deposits, largely undermine this hypothesis (see e.g. Selden, 2002; Penney *et al.*, 2003, fig. 2; Penney, 2006a and references therein). On current data, at least the late Mesozoic boasted a diversity of both mygalomorph and araneomorph lineages. Note that the putative giant Carboniferous mygalomorph *Megarachne* has now been shown to be a eurypterid (an extinct, aquatic sea scorpion) (Selden *et al*., 2005).

The largest and perhaps the most familiar of the modern mygalomorphs are the so-called tarantulas (Theraphosidae). Despite over 900 extant species (Platnick, 2008), only one fossil has been formally named and convincingly assigned to this family: *Ischnocolinopsis acutus* Wunderlich, 1988 (Ischnocolinae), from Dominican amber. An additional, large, theraphosid-like spider in Dominican amber was figured by Grimaldi *et al.* (1994). However, the authenticity of this fossil was questioned at the time and to date the owner has not permitted any physical or chemical tests to be performed on the sample. Among non-amber spiders, *Mygale ambigua* Gourret, 1887 from the Tertiary of Aix en Provence, France was compared by Gourret to Recent theraphosids. Note the title page of the whole volume bears the date 1888, but part three (including Gourret's paper) is listed in the contents as 1887. '*Mygale*' is no longer a valid generic name. The original material held in Marseille (S. Pichard, pers. comm.) clearly requires restudy. It cannot be placed in any modern family based on Gourret's description and figure, which shows a segmented abdomen (a mesothele character) and unusual features for a spider such as subdivided leg articles. Another species, *Eodiplurina cockerelli* Petrunkevitch, 1922 was originally described as a putative theraphosid (as 'Avicullariidae') from the Oligocene of Florissant, Colorado, USA, but was later transferred to Nemesiidae by Eskov & Zonshtein (1990). Here we describe the exuvium of a spider (Figs. 2–9) from the Miocene Chiapas amber of southern Mexico, which represents the second formally documented example of Theraphosidae in the fossil record. It is also the largest ever spider to be formally described from amber.

Materials and methods

The specimen described here originates from Chiapas amber from the Simojovel region of Chiapas State, Mexico. It was purchased from a private collector by the National Museum of Scotland (NMS), Edinburgh, UK, where it is held under the repository number NMS G.2004.6.1. The specimen was photographed using a Canon Power Shot G6 digital camera, with images assembled using Adobe Photoshop 6, and was drawn under a steromicroscope with the aid of a *camera lucida* attachment. Variable lighting arrangements proved helpful during study in order to reveal all the details of setae, including fine trichobothria. The fossil was compared to extant spider material in the collections of the Museum für Naturkunde, Berlin, and the literature.

Chiapas amber

The history, geological setting and locality details of Chiapas – sometimes just referred to as Mexican – amber were detailed by Poinar (1992), Poinar & Poinar (1994) and Poinar & Brown (2002, 2004) and further references can be found in García-Villafuerte & Penney (2003). In brief, this amber is mostly recovered from the state of Chiapas in southern Mexico, typically from the northern mountain ranges of the state (the Chiapas highlands) in the Simojovel area between Rapilula, Yajalón and Los Cruces. Our new fossil, and all previous records of Chiapas amber spiders, are reported as coming from the Simojovel area; where amber is actively mined locally. The exact provenance of the new specimen is unfortunately unknown, but it was purchased from this general region before being sold on to its present repository. Chiapas amber, which is typically very transparent and shares much in common in its appearance and formation history with Dominican amber, originated from the extinct Leguminoseae tree *Hymenaea mexicana* Poinar & Brown, 2002. Langenheim (1995) suggested deposition in mangrove vegetation in a shallow marine environment; i.e. a near-shore context such as a coastal lagoon. The putative amber-forming period was originally thought to span the Palaeogene–Neogene boundary, thus Poinar (1992) gave age estimates of late Oligocene (26 Ma) to early Miocene (22.5 Ma). However, recent work suggests a slightly younger, mid- Miocene, date (Rust & Solórzano-Kraemer, in prep., cited in Solórzano-Kraemer, 2006); perhaps *ca*. 16 Ma.

Spiders in Chiapas amber were initially described, in part posthumously, by Petrunkevitch (1963, 1971) who recorded eleven families, from which he recognised around twenty species. As was his habit, Petrunkevitch largely assigned species to new, extinct genera; some of which were later synonymised – albeit based only on the original drawings – with recent genera by Wunderlich (1986, 1988). Two spiders were described, but not na-

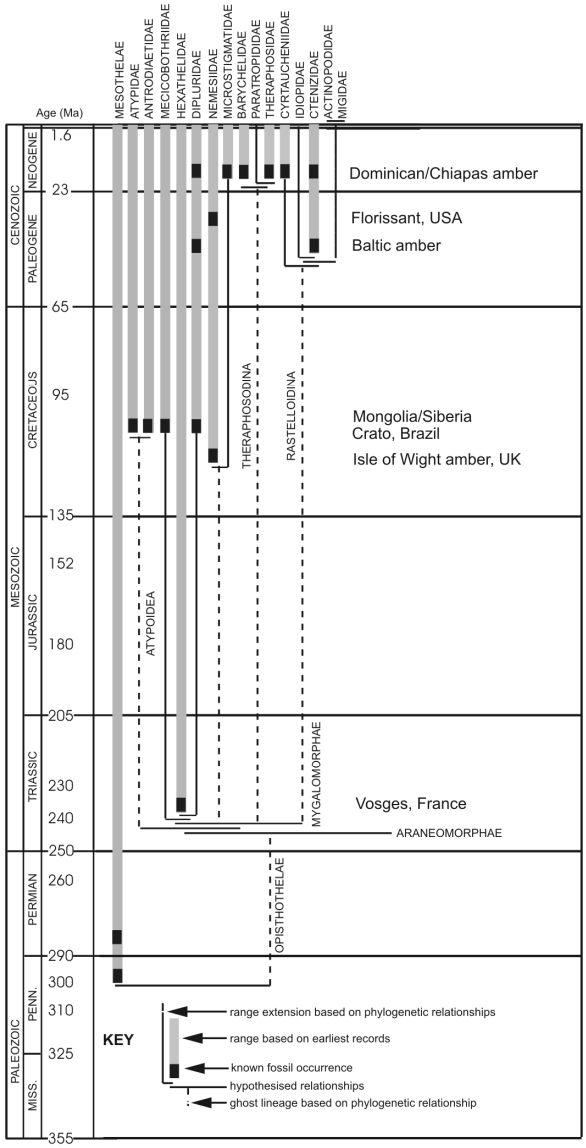


Fig. 1. Evolutionary tree of the mygalomorph families (Araneae: Mygalomorphae). Cladogram superimposed on the known fossil record. Emended and updated from Penney *et al*. (2003, fig. 1) who detail the sources and methods used in its construction. The approximate stratigraphical position and age of the localities mentioned in Table 1 is indicated, with the exception of Aix-en-Provence and the Palaeogene of the Isle of Wight, whose fossils cannot be placed with confidence in any family.

med, by García-Villafuerte & Vera (2002), who attributed them to the families Salticidae and Theridiidae. A further salticid, assigned to *Lyssomanes* sp., was added by Garciá-Villafuerte & Penney (2003). New combinations for the hersiliids were proposed by Penney (2006b), who recognised some Chiapas genera in this family as *nomina dubia* and García-Villafuerte (2006) described a new species of *Episinus* (Theridiidae). Thus no mygalomorph spiders have hitherto been described from Chiapas amber. Other arachnid inclusions reported from Chiapas amber include two whip spiders (Amblypygi) (Petrunkevitch, 1971; Poinar & Brown (2004), various mites (Acari) (Türk, 1963; Hirschmann, 1971; Woolley, 1971), pseudoscorpions (Pseudoscorpiones) (Schawaller, 1982a) and scorpions (Scorpiones) (Santiago-Blay & Poinar, 1993). A complete list of fossil arthropod inclusions in Mexican Chiapas amber was provided by Engel (2004).

Morphological interpretation

The specimen (Figs. 2–9) is preserved in a large, hourglass-shaped piece of polished amber, with maximum dimensions of about 7.5 x 4.5 x 3.0 cm. The amber has a blue-green tinge to it, which is typical for Chiapas material, and helps to confirm the authenticity of the specimen. There are various organic syninclusions such as flies (Diptera). These syninclusions show a certain degree of stratification, possibly relating to different phases of amber flow, and partly obscure the specimen; which can be taken as further evidence of its authenticity. We could detect no cracks or joins in the amber piece which would suggest a forgery.

The specimen itself is clearly an exuvium. The carapace is disarticulated from the rest of the body (Figs. 2–3, 9) and the opisthosomal cuticle is largely shrivelled and is twisted into an amorphous, setose band between the leg-bearing region and the carapace (Fig. 9). The pedipalps and most of the legs extend forwards – more or less at right angles to the orientation of the carapace – in a manner characteristic for the exoskeleton of modern mygalomorph spiders after ecdysis (cf. Kraus, 1961). Two legs deviate from this position and are more or less parallel to the orientation of the carapace. One lies partly across the opisthosomal cuticle and carapace (Fig. 9); the other is diametrically opposite it (Figs. 5, 9). The fossil represents an animal with a leg span in life of at least 5 cm and is thus unusually large for an amber spider inclusion and about twice as large as the Dominican amber theraphosid described by Wunderlich (1988), from whose measurements a leg span of around 2.5 cm in life can be estimated. Wunderlich (pers. comm., 2006) mentioned other very large – but as yet undescribed – amber spider inclusions, but this present specimen is the largest to be formally described in the literature. The carapace of the theraphosid includes typical details seen in modern examples such as the eye tubercle close to the anterior margin of the carapace (i.e. no large clypeus) (Figs. 3, 9), diverging furrows (or striae) radiating from a fovea, the shape of which is not so easy to resolve, and marginal fringes of hairs. A single setose spinneret can be recognised close to the abdominal cuticle (Figs. 8–9). Three articles can be recognised, the distal one quite long. The pedipalps and legs are preserved most completely. Relatively long and slender, they include details such as probable leg spines, the dense hair (or scopulae) on the palpal tarsus and the metatarsus and tarsus of the legs, as well as various fine hairs and/or trichobothria emerging amongst the scopulae (Figs. 6–7). The tarsus exhibits two pairs of slender, smooth-looking (i.e. non-dentate) claws on at least some legs (Fig. 9). The pedipalp lacks a modified tarsus so this was either a female and/or juvenile animal.

Family Theraphosidae Thorell, 1870
Gen. et sp. indet.
(Figs. 2–9)

MATERIAL: NMS G.2004.6.1. From the Simojovel area (precise locality not recorded), Chiapas State, Mexico. Neogene: Miocene.

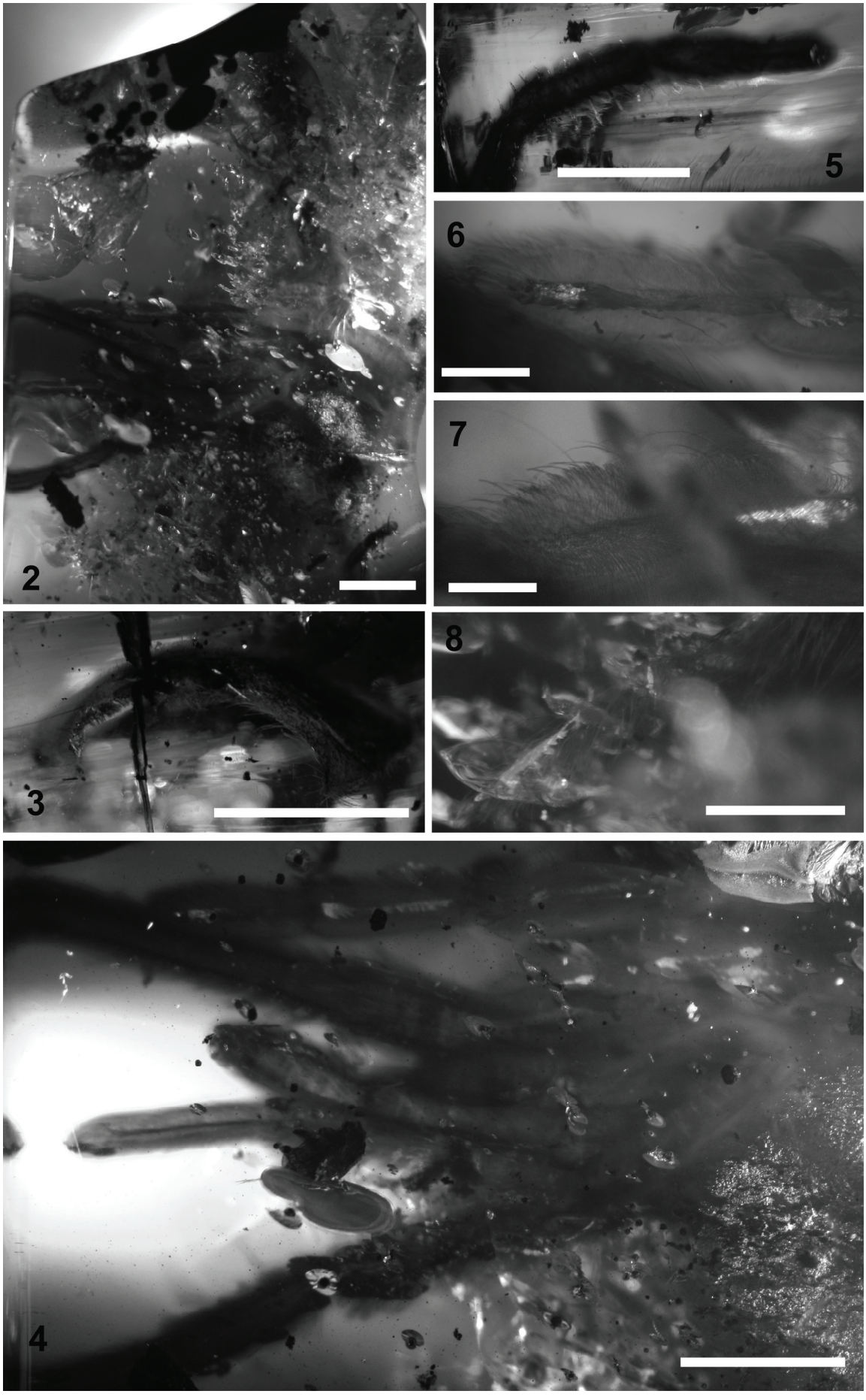
DESCRIPTION: Complete, but partly disarticulated exuvium. Carapace oval, length *ca*. 9 mm, maximum width 7.2 mm. Fovea with oblique striae, cephalic region slightly raised and differentiated from thoracic region by two shallow furrows. Carapace with tufts of marginal setae as well as a pubescence of short setae across its general surface. Ocular tubercle oval; clypeus between tubercle and anterior margin of carapace short. Chelicerae – and coxo-sternal region generally – indistinct. Distal articles of pedipalps present, scopulate, length of tarsus 3.5 mm. Legs highly setose, largely overlying one another, making it hard to assign legs unequivocally to their sequence on the body. Best preserved example at least 23 mm long with article lengths (in mm) as follows: tibia, 5.2, metatarsus, 4.4 and tarsus, 4.1. Distal ends of legs scopulate. Long axis strongly hirsute with at least one row of four or five trichobothria, identifiable by emerging perpendicular to the cuticle. Paired claws of legs, where preserved, smooth and at least one limb with apparent claw tufts. Leg IV? possibly with stouter, upstanding spines on the tibia and metatarsus. Opisthosomal cuticle still attached to carapace, twisted and folded into an indistinct mass, but highly setose with quite long (nearly 1.5 mm) hairs. One setose spinneret preserved, length 3.0 mm, with distal article longest.

REMARKS: The tarsal scopulae in this fossil (Figs. 6–7) are characteristic for the Theraphosoidina clade *sensu* Raven (1985), which comprises three mygalomorph families: Theraphosidae, Paratropididae and Barychelidae. Both theraphosids and barychelids are known from Dominican amber (Table 1) although in a geographical context it is worth mentioning that there is only a single known (Recent) Mexican barychelid, and no paratropidids. Indeed there are only eight living South American paratropidids world-wide – compared to a diverse Central American theraphosid fauna (cf. Smith, 1994; Schmidt, 2003; Platnick, 2008) which includes for example 66 recent species in eight genera from Mexico alone. Although we lack data for the important characters of maxillary lobes and the presence or absence of a third tarsal claw, the isolated spinneret (Figs. 8–9) has a long apical article which is diagnostic for Theraphosidae – as compared to the shorter, stubbier spinnerets of Barychelidae. Barychelids also tend to be smaller, more compact spiders, and we can further exclude Paratropididae which are not so setose and have a characteristic scaly cuticle ornament, absent in our specimen. Raven (1994) also mentioned that in Barychelidae the legs are relatively stout in comparison to Theraphosidae and that the patella is enlarged or, in the case of leg III, larger than the tibia. The legs in our fossil are not noticeably stout.

The subfamilial position of our fossil is less straightforward to resolve, but of the groups currently recognised (see e.g. Raven 1985; Peréz-Miles & Locht 2003), only four occur today in or around Central America: Aviculariinae, Ischnocolinae, Theraphosinae and Selenocosminae; although the later may turn out to be endemic to Southeast Asia. The fossil lacks the particularly broad scopulae on the tarsi of the pedipalps and the tarsi and metatarsi of the legs which is characteristic for the arboreal aviculariines *sensu* Schmidt (2003). It is worth noting that in Mexico today there are no bone-fide aviculariines (F. Perez-Miles, D. O. Martinez, pers. comm.). Tarsus shape, and perhaps geography, thus tends to imply a member of Ischnocholinae or Theraphosinae. Both would be expected to show tarsal scopulae divided by a row of longer hairs or spines (e.g. Gerschman de Pikelin & Schiapelli, 1973), but we were unable to test this character adequately here. The presence and/or form of the urticating hairs are also of taxonomic value in theraphosids (Cooke et al. 1972; Bertani 2001), but this character cannot be tested in this fossil. Thus, a combination of morphology and its Neotropical origins – although we accept that past distributions do not necessarily reflect those of today – tends to favour affinities with Theraphosinae. In the absence of further characters, such as those available to Wunderlich (1988) when describing his Dominican amber theraphosid, we prefer not to name the fossil or place it further. We also feel uncomfortable about treating an exuvium as type material, although this unfortunate practice is occasionally used in the taxonomy of Recent theraphosids (e.g. Schmidt & Peters 2005: p. 4) and was also used for Mexican amber Hersiliidae by Petrunkevitch (cf. Penney 2006b, p. 1, figs 1–3).

Wunderlich (2004) suggested that mygalomorphs are probably quite rare in amber, i.e. compared to araneomorphs, in part because of their large size and strength which presumably meant they could struggle free of the sticky resin more easily. Amber tends preferentially to trap active, trunk-dwelling spiders (e.g. Penney 2002, 2005) and the fact that our new fossil looks more like a fossorial rather than an arboreal spider is interesting in this context. We speculate that this could be an exuvium thrown out of a burrow at the base of a tree, such that the cuticle was trapped in a mass of sticky resin.

Figs. 2–8. Fossil tarantula (Araneae: Theraphosidae) in amber collected in the Simojovel district of Chiapas State, Mexico; repository NMS G.2004.6.1. 2. Overview. 3. Specimen tilted to show disarticulated carapace in anterior view. 4. Close-up of limbs. 5. Detail of putative fourth leg with possible spination. 6–7. Detail of two tarsi showing scopulae and trichobothria. 8. Detail of isolated, setose spinneret with long distal article. Scale bars equal 5 mm (Figs. 2–5) and 1 mm (Figs. 6–8).


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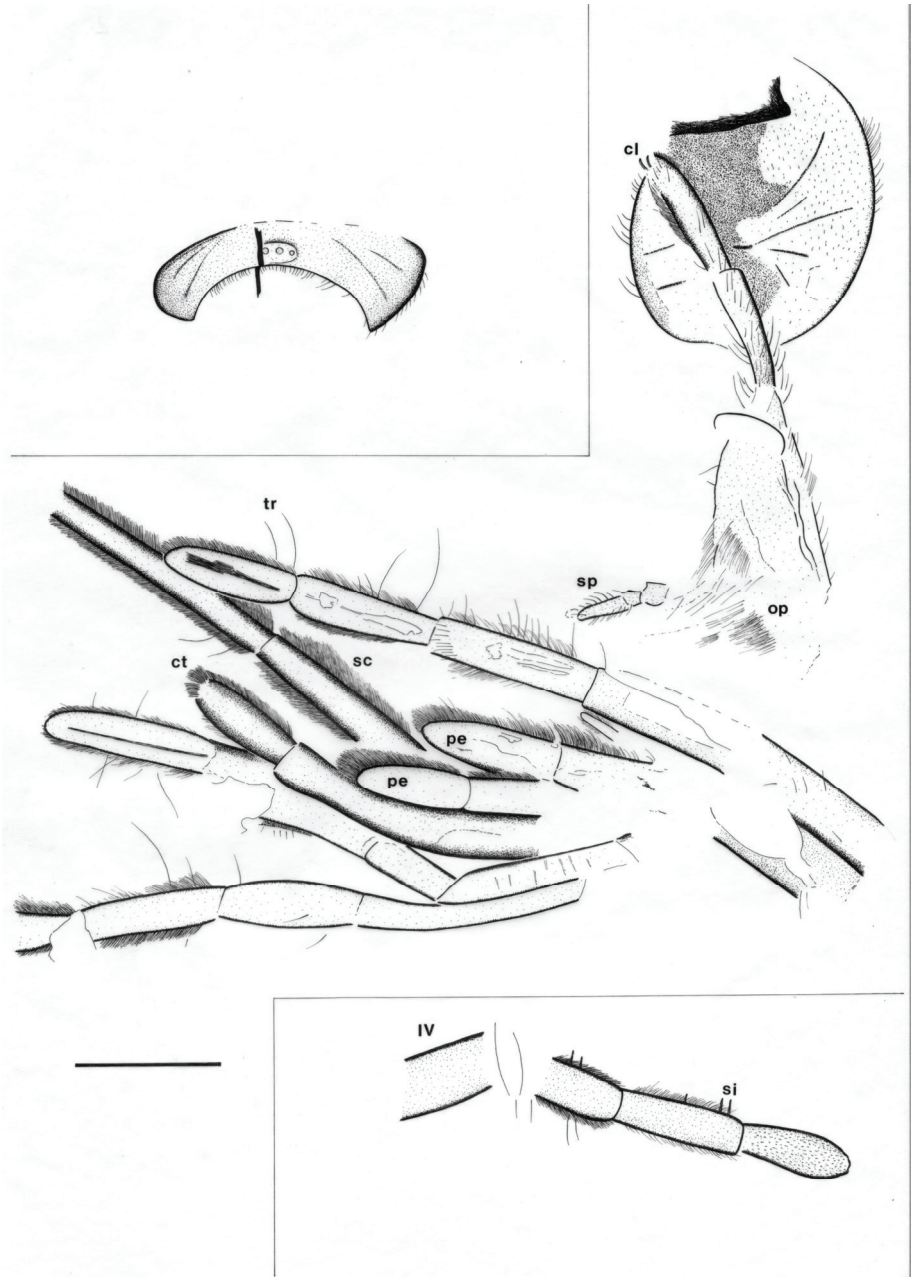


Fig. 9. *Camera lucida* drawing of the specimen shown in Figs 2–8. Insets show carapace and probable fourth leg. Abbreviations: IV = probable fourth leg; cl = tarsal claws; ct = claw tuft; op = opisthosomal cuticle; pe = pedipalp; sc = scopulae; si = possible spines on leg; sp = spinneret; tr = trichobothria. Scale bar equals 5 mm.

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Table 1. Overview of the fossil mygalomorph families described to date. Order of families follows (Platnick 2007).

Family	Locality	Age	References
Opisthothelae *incertae sedis* (described as a mygalomorph)	Isle of Wight, UK	Palaeogene (Eocene)	McCook (1888); see Selden (2001) for discussion of its affinities
Family *incertae sedis*	Aix-en-Provence, France	Tertiary	Gourret (1887); may not be a mygalomorph
Atypidae	Bayan-Kongar Amiak, Mongolia	Early Cretaceous (?Albian)	Eskov & Zonshtein (1990)
Antrodiaetidae	Bayan-Kongar Amiak, Mongolia	Early Cretaceous (?Albian)	Eskov & Zonshtein (1990)
Mecicobothriidae	Transbaikalia, Siberia, Russia	Early Cretaceous (?Albian)	Eskov & Zonshtein (1990)
Hexathelidae	Vosges, France	Triassic (Anisian)	Selden & Gall (1992); tentative referral
Dipluridae	a. Crato Formation, Brazil	Early Cretaceous (Aptian)	Selden *et al*. (2006)
Dipluridae	b. Baltic amber	Palaeogene (Eocene)	Menge (1869); Wunderlich (2004)
Dipluridae	c. Dominican Republic amber	Neogene (Miocene)	Schawaller (1982b); Wunderlich (1988)
Cyrtaucheniidae	Dominican Republic amber	Neogene (Miocene)	Wunderlich (1988)
Ctenizidae	a. Baltic amber	Palaeogene (Eocene)	Eskov & Zonshtein (1990); Wunderlich (2000, 2004); Eskov & Zonstein (2000)
Ctenizidae	b. Dominican Republic amber	Neogene (Miocene)	Wunderlich (1988); but see comments in Wunderlich (2004)
Idiopidae	no fossil record		
Actinopodidae	no fossil record		
Migidae	no fossil record		
Nemesiidae	a. Isle of Wight amber, UK	Early Cretaceous (Barremian)	Selden (2002); tentative referral
Nemesiidae	b. Florissant, Colorado, USA [as Theraphosidae]	Palaeogene (Oligocene)	Petrunkevitch (1922); transferred by Eskov & Zonshtein (1990)
Microstigmatidae	Dominican Republic amber	Neogene (Miocene)	Wunderlich (2004)
Barychelidae	Dominican Republic amber	Neogene (Miocene)	Wunderlich (1988)
Theraphosidae	a. Dominican Republic amber	Neogene (Miocene)	Wunderlich (1988)
Theraphosidae	b. Chiapas (Mexican) amber	Neogene (Miocene)	this study
Paratropididae	no fossil record		