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Oldest true orb-weaving spider (Araneae: Araneidae)

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The aerial orb web woven by spiders of the family Araneidae typifies these organisms to laypersons and scientists alike. Here we describe the oldest fossil species of this family, which is preserved in amber from Álava, Spain and represents the first record of Araneidae from the Lower Cretaceous. The fossils provide direct evidence that all three major orb web weaving families: Araneidae, Tetragnathidae and Uloboridae had evolved by this time, confirming the antiquity of the use of this remarkable structure as a prey capture strategy by spiders. Given the complex and stereotyped movements that all orb weavers use to construct their webs, there is little question regarding their common origin, which must have occurred in the Jurassic or earlier. Thus, various forms of this formidable prey capture mechanism were already in place by the time of the explosive Cretaceous co-radiation of angiosperms and their flying insect pollinators. This permitted a similar co-radiation of spider predators with their flying insect prey, presumably without the need for a 'catch-up lag phase' for the spiders.

Keywords: amber; fossil; palaeontology; Spain

1. INTRODUCTION

Two-dimensional orb webs are spun by numerous spider families, for example, Tetragnathidae, Theridiosomatidae and Uloboridae. However, it is the web of the true orb-weavers (family Araneidae) that typifies spiders to laypersons and scientists alike. The status of this family as an icon of all spiders is reflected in their name, which is based on the type genus *Araneus* Clerck, 1757 and is the basionym of both the family and the order (Araneae; Scharff & Coddington 1997). The evolutionary significance of the ability to spin orb webs is reflected in the high diversity of araneid spiders which currently consist of 2847 extant species described from 167 genera and ranks third (out of 110) in terms of number of described spider species (Platnick 2006). However, total global species richness for this family is predicted to be considerably higher (Coddington & Levi 1991).

The antiquity of the use of orb webs in prey capture by spiders was proposed by Selden (1989) who described deinopoid and araneoid spiders preserved in Lower Cretaceous lithographic limestone from Sierra de Montsech, northeast Spain. The extinct species, formally described by Selden (1990), were assigned subsequently to the families Tetragnathidae and Uloboridae by Selden & Penney (2003), and the oldest Theridiosomatidae are preserved in Eocene amber from the Baltic region (Wunderlich 2004). Fossils of the true orb-weaving spider family Araneidae are common as Tertiary amber inclusions and also occur occasionally in sediments, but the oldest specimen described to date is an unnamed juvenile preserved in upper Cretaceous (Turonian) amber from New Jersey (Penney 2004*a*). The tiny (1.5 mm body length) spiderling reported as Araneidae in Lebanese amber (upper Neocomian–basal Lower Aptian) by Wunderlich (2004) can hardly be considered a reliable identification, nor can the spiders reported, but not described, as Araneidae? from Canadian amber (middle Campanian) by McAlpine & Martin (1969) and Araneidae juv. from Siberian amber (upper Cretaceous) by Eskov & Wunderlich (1995).

The Cretaceous araneoids described to date possess three tarsal claws with characteristic accessory setae, which are considered adaptations for efficient manoeuvrability in aerial webs, despite their occurrence in some non-web spinning spider families such as Hersiliidae (e.g. Griswold *et al*. 2005), where their function is unclear. Such claws are not visible in the monotypic Jurassic araneoid spider family Juraraneidae described by Eskov (1984), so whether or not this was an orb web weaver remains unclear (Selden 1989). In addition to the aforementioned spider fossils, the use of aerial webs by spiders in the Mesozoic is evident through the presence of sticky, viscid spider silk preserved in Lower Cretaceous Lebanese amber (Zschokke 2003).

Here we describe the oldest fossil species of Araneidae, which is preserved in amber from Álava, Spain. It represents the first record of the family from the Lower Cretaceous and only the second spider species to be described from this important fossil locality, the other being a member of the extinct family Lagonomegopidae (Penney In press).

2. MATERIAL AND METHODS

The specimens upon which this paper is based are preserved in Lower Cretaceous amber from Álava and held in the collections of the Museo de Ciencias Naturales de Álava, Vitoria, Spain (MCNA). A thorough review of the chemistry, geology and fossil inclusions of the Álava amber deposit was provided by Alonso *et al*. (2000), although few fossil species have been described to date (see Penney (In press) for a synopsis). The amber is of araucariacean origin and was previously dated as upper Aptian–middle Albian, but more recently this dating has been refined to 115–121 Myr (ago) (Aptian) by Larrasoaña *et al*. (2003) based on magnetostratigraphic data and the qualitative and quantitative palynological data of Barrón *et al*. (2001). Therefore, this is one of the oldest inclusion-bearing ambers so is of extreme importance to palaeoarthropodologists. The amber pieces containing the spiders were polished and embedded in clear, synthetic resin by museum staff, following the method of Corral *et al*. (1999) and were studied using incident and transmitted light microscopy. All measurements are in mm.

3. SYSTEMATIC PALAEONTOLOGY

Higher taxon names: Araneae Clerck, 1757; Opisthothelae Pocock, 1892; Araneomorphae Smith, 1902; Araneidae Simon, 1895

Mesozygiella gen. nov.

(a) *Type species*

Mesozygiella dunlopi sp. nov., by monotypy.

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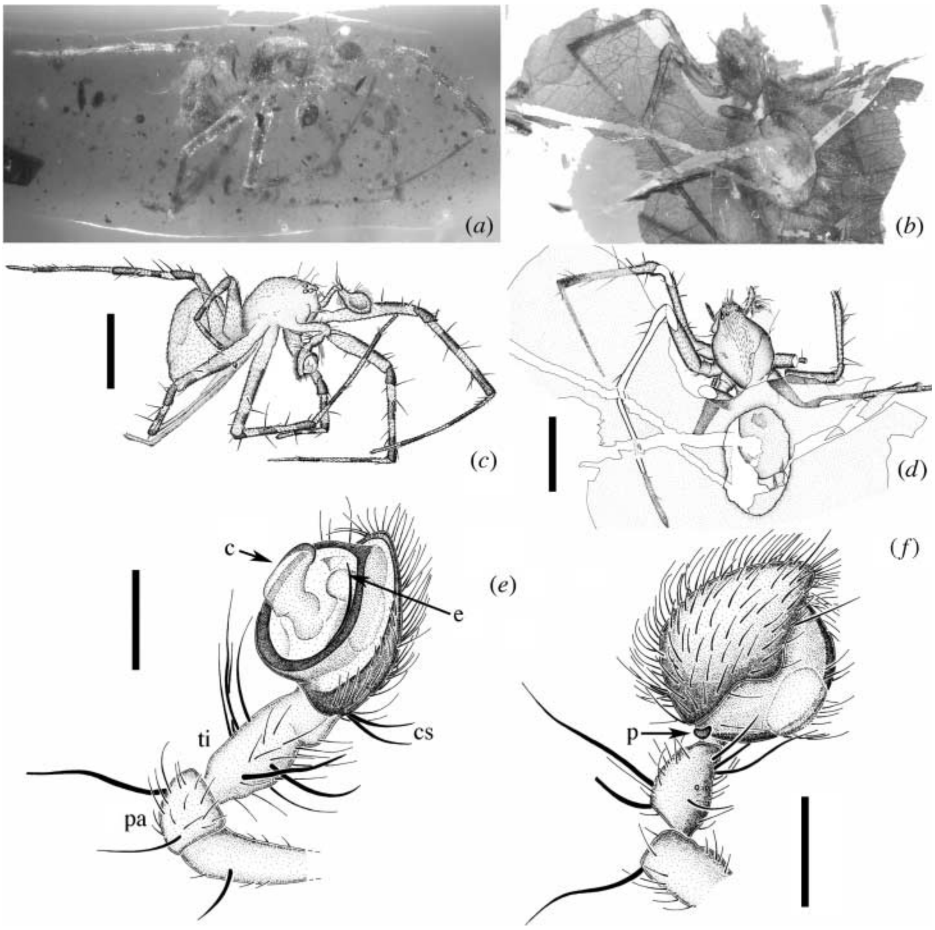

Figure 1. *Mesozygiella dunlopi* new species. (*a*) Photograph of holotype; (*b*) photograph of paratype; (*c*) drawing of holotype; (*d*) drawing of paratype; (*e*) right pedipalp of holotype, subventral view; (*f*) left pedipalp of paratype medial view. Abbreviations: c, conductor; cs, cymbial spines; e, embolus; p, paracymbium; pa, patella; ti, tibia. Scale bars: (*c*), (*d*) 1.0 mm; (*e*), (*f*) 0.2 mm.

(b) *Diagnosis*

As for the extant genus *Zygiella* F. O. Pickard-Cambridge, 1902, but with the embolus originating medially rather than distally (see also diagnosis of the type species).

(c) *Etymology*

'*Meso*' after Mesozoic, the geological era from which the type species originates and '*zygiella*' after the extant genus *Zygiella*, to which the fossil genus is closely related.

Mesozygiella dunlopi sp. nov.

(d) *Diagnosis*

Palpal tibia distinctly longer than wide, cymbium basally with paired dorsal spines, membranous conductor large and with a dark rim, filiform embolus originating medially, paracymbium a tiny, highly sclerotized, free sclerite.

(e) *Description*

Male. Body length: holotype 2.06, paratype 2.73. Eight eyes in two rows, body without unusual modifications. Leg formula 1,2,4,3, anterior legs no more robust than posterior. Holotype: leg 1 femur 1.12, patella 0.25, tibia 1.12, metatarsus 1.41, tarsus 0.41, total 4.40; leg 2 femur 1.13, patella 0.24, tibia 1.01, metatarsus 1.17, tarsus 0.39, total 3.94; leg 3 femur 0.72, patella 0.22, tibia 0.50, metatarsus 0.62, tarsus 0.35, total 2.41; leg 4 femur 1.12, patella 0.26, tibia 0.87, metatarsus 0.92, tarsus 0.41, total 3.58. All legs distinctly annulated, with numerous spines (figure 1) and with three tarsal claws and accessory setae. Pedipalp structure as in diagnosis and figure 1; additional sclerites representing terminal and median apopheses may be present but these are unclear in these specimens. The left pedipalp of the paratype is visible only in medial view and the right pedipalp is badly distorted. Female unknown. Apart from the embolus originating medially, rather than distally, the fossil specimens are highly similar to extant *Zygiella* species (see Levi 1974).

(f) *Types, locality and distribution*

Holotype: MCNA 8938a; male in Cretaceous Álava amber, Peñacerrada II amber site (*sensu* Alonso *et al.* 2000), held in the Museo de Ciencias Naturales de Álava, Vitoria, Spain. Paratype: MCNA 9579; male, same data as holotype. Known only from the type locality.

(g) *Etymology*

The specific epithet is a patronym in honour of Dr Jason A. Dunlop (Humboldt Museum, Berlin) for his contributions to palaeoarachnology.

4. DISCUSSION

The new species extends the known geological range of the extant spider family Araneidae back to the Lower Cretaceous and demonstrates a high degree of morphological conservatism in this family, since it can be distinguished from extant genera only by details of the male pedipalp. It also provides direct evidence of all three major orb web weaving spider families in the Lower Cretaceous. Given the complex and stereotyped movements that all orb weavers use to construct their webs, there is little question regarding their common origin (Griswold *et al.* 2005), which must have occurred in the Jurassic or earlier as suggested by Selden (1989). Thus, various forms of this formidable prey capture mechanism (cribellate, ecribellate, vertical, horizontal) were already in place by the time of the explosive Cretaceous co-radiation of angiosperms and their flying insect pollinators (Grimaldi 1999), permitting a similar co-radiation of spider predators with their insect prey (e.g. Penney 2004*b*), presumably without the need for a 'catch-up lag phase' for the spiders.

Detailed examinations of spider spinneret and spigot morphology (not visible in fossils) provides rich support for the inclusion of non-orb weaving spider families in the orb web weaving superfamily Araneoidea and it seems clear that the orb web has been lost or modified several times over the course of their evolution, for example in linyphioids, theridiioids, cyatholipoids and symphytognathoids *sensu lato* (Griswold *et al.* 2005). Identifying the phylogenetic intermediates between these web types is the holy grail in understanding the evolution of spider webs (Griswold *et al.* 2005). In addition, knowledge of when such events occurred is also of great interest for calibrating the spider tree of life.

The oldest representative of the family Linyphiidae is from Lebanese amber, which is of a similar age to these orb-weaving spider fossils, but the cyatholipoids, theridioids and symphytognathoids do not appear until the Tertiary (Penney & Selden 2002). These authors suggested that this observation might have been the result of a sampling artefact based on the limited number of Cretaceous fossils studied up until that time and predicted that they would be discovered subsequently in the Mesozoic fossil record. However, over the past five years the former author has studied more than 100 Cretaceous amber spiders, and the latter has examined approximately 200 Mesozoic spiders preserved in various rock matrices and these families are still absent from the pre-Tertiary fossil record. Thus, it may well be that these families derive from radiations that occurred following the end-Cretaceous extinction event, which appears not to have had deleterious effects on spiders in terms of extinction at family level (Penney *et al.* 2003). Unfortunately, most of these higher araneoid families, other than Theridiidae, have a poor fossil record. However, based on an assessment of Theridiidae subfamilies preserved in Baltic and Dominican ambers, Marusik & Penney (2004) proposed that the major radiations of the higher theridiid subfamilies were relatively recent, occurring between the Mid-Eocene and Early Miocene, some 20–40 Myr (ago), an idea recently supported by Agnarsson (2006) in an analysis of extant Theridiidae.

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