BioOne COMPLETE

A Review of the Fossil Record of Spiders (Araneae) with Special Reference to Africa, and Description of a New Specimen from the Triassic Molteno Formation of South Africa

Authors: Selden, Paul A., Anderson, Heidi M., and Anderson, John M.

Source: African Invertebrates, 50(1) : 105-116

Published By: KwaZulu-Natal Museum

URL: https://doi.org/10.5733/afin.050.0103

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

African Invertebrates Vol. 50 (1) Pages 105–116 Pietermaritzburg June, 2009

A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from the Triassic Molteno Formation of South Africa

Paul A. Selden[1, 2*], Heidi M. Anderson[3] and **John M. Anderson[3]**

[1]Paleontological Institute and Department of Geology, University of Kansas, 1475 Jayhawk Boulevard, Lawrence, Kansas, 66045 USA; selden@ku.edu
[2]Department of Palaeontology, Natural History Museum, London SW7 5BD, UK
[3]South African National Biodiversity Institute, P. Bag X101, Pretoria, 0001 South Africa; preherb@nbipre.nbi.ac.za
*Author for correspondence

ABSTRACT

The fossil record of spiders as currently known is briefly reviewed, with special reference to Africa. The second specimen of *Triassaraneus andersonorum* Selden in Selden *et al*. 1999 is described from a different locality in the Triassic (Carnian, *c*. 225 Ma) Molteno Formation of South Africa.

KEY WORDS: Arachnida, Chelicerata, Palaeozoic, Mesozoic, Triassic, Carnian, fossils, palaeontology.

INTRODUCTION

Over 90 % of fossil spiders originate from ambers of Cainozoic age (less than 65 Ma old). Cainozoic ambers preserve representatives of the majority of the 109 spider families known today. Of greater interest for phylogeny, therefore, is the fossil record of Araneae from the Mesozoic and Palaeozoic eras, and what it can tell us about the origins and longevity of major clades. Fossil spiders have been known from the late Palaeozoic Coal Measures of Europe and North America for more than a century (although it must be mentioned that some of these specimens are certainly not spiders, Penney & Selden 2006), but the first genuine Mesozoic spider to be formally described was only in 1984 (Eskov 1984). Over the succeeding decades only a few new species have been reported. More recently, much new material is being discovered in, for example, lower Cretaceous deposits of north-east Brazil and China, which is being described at the moment.

It is because of their great rarity that almost every new specimen of spider from the Palaeozoic and Mesozoic eras is worthy of report, and each occurrence can drastically alter our perception of spider phylogeny. For example, the identification of a single record of a family earlier than previously known predicts the occurrence of its sister clade total group to the same date. Thus, Penney's (2002) description of Cretaceous Oonopidae predicted the occurrence of the family's sister group, Orsolobidae. As pointed out by Penney *et al*. (2003) and others, the true biodiversity at any time in the past is greater than estimated from raw fossil data because range extensions and ghost lineages need to be taken into account. Figure 1 illustrates the present state of knowledge of the fossil record of spiders.

For the last two decades, the oldest known spider in the fossil record was thought to be *Attercopus fimbriunguis* (Shear, Selden & Rolfe in Shear *et al*. 1987), from the Devonian of New York, USA. *Attercopus* was considered sister to all other spiders. Recently, however, *Attercopus* has been shown to belong to a new order of arachnids: the Uraraneida Selden & Shear in Selden *et al*. 2008, an order that also includes the Permian *Permarachne* Eskov & Selden, 2005, which was originally described as an unusual mesothele.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

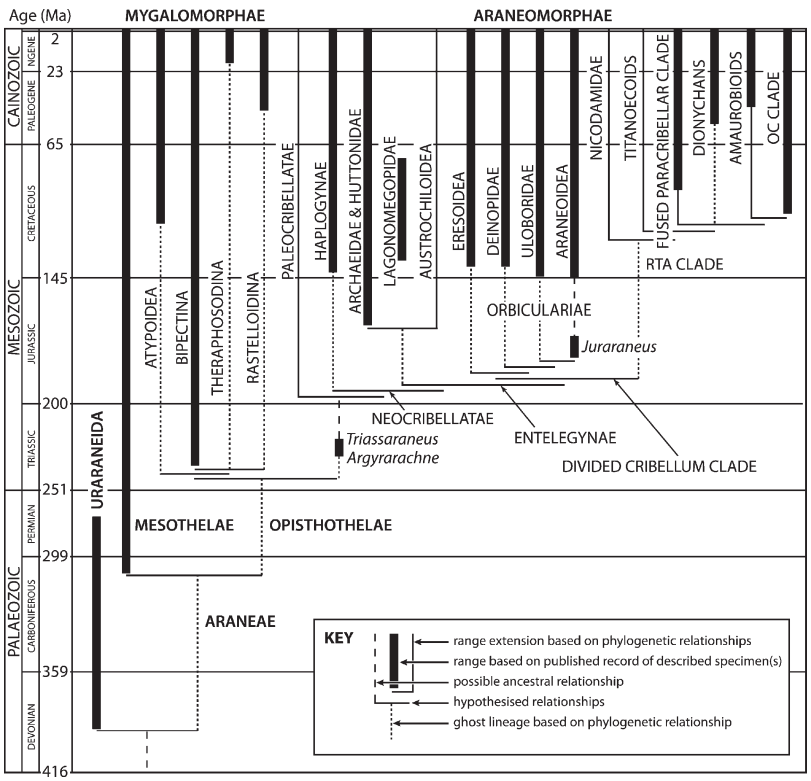


Fig. 1. Summary phylogenetic tree of Araneae, produced by combining the fossil record with the cladograms of Coddington and Levi (1991), Griswold (1993), Scharff and Coddington (1997), Griswold *et al*. (1998, 1999), and Ramírez (2000).

Mesotheles are known from upper Carboniferous and Permian strata (Selden 1996*a*, *b*, 2000; Eskov & Selden 2005), but no opisthotheles until Triassic time; putative Palaeozoic opisthotheles have been shown to be other arachnids or unrecognizable (Penney & Selden 2006). The oldest opisthothele known is the mygalomorph *Rosamygale grauvogeli* Selden & Gall, 1992, from the Lower Triassic (Anisian) of France, which was the first spider to be described from rocks of this period. Selden in Selden *et al*. (1999) described the oldest araneomorphs, *Triassaraneus andersonorum* (Fig. 3) and *Argyrarachne solitus*, from the Carnian Molteno Formation of KwaZulu-Natal, South Africa, and the Carnian Cow Branch Formation of Virginia, USA, respectively; their presence in the Triassic Period having been predicted by the occurrence of their sister group in 1992 (Selden & Gall 1992). Single, monotypic specimens were described from each of these localities; additional, but poorly preserved, specimens were noted, but not described. In this paper an additional specimen of *Triassaraneus*, now confirmed as an araneomorph spider, is described from the Molteno Formation locality of Telemachus Spruit in Eastern Cape, South Africa.

Few spiders have been described from the Jurassic Period. The first to be described was *Juraraneus* Eskov, 1984, an orb-weaver from Transbaikalia, and the second, *Jurarchaea*, Eskov, 1987, is an archaeid (*sensu lato*) from Kazakhstan. One, from the

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

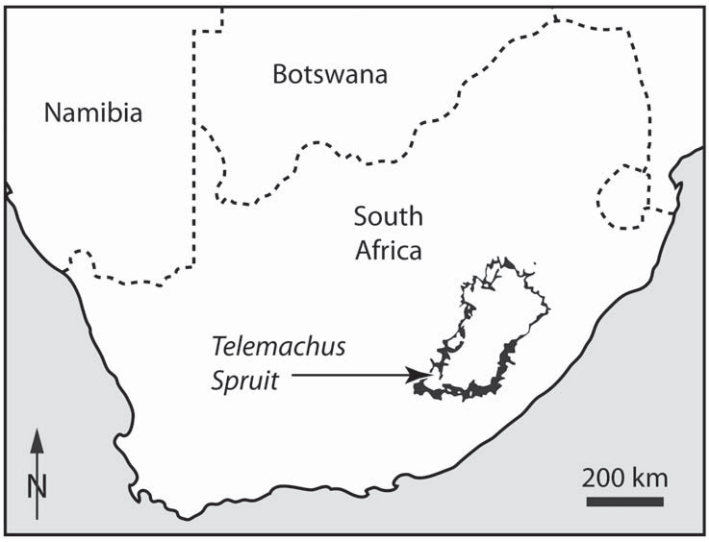


Fig. 2. Location map of the Telemachus Spruit locality (Eastern Cape, South Africa) in relation to the outcrop of the Late Triassic Molteno Formation (shown in black) (after Anderson *et al.* 1998).

Jurassic of Grimmen, Germany, has been figured but not yet formally described (Ansorge 2003; preliminary investigation by the senior author suggests this may be a palpimanoid), and additional specimens from Russian localities remain undescribed. More than 400 specimens recently become available for study from beds of Middle Jurassic age at Daohugou, Nincheng County, Inner Mongolia, China (Huang *et al*. 2006). Most belong to Uloboridae, and have yet to be studied, but some belonging to the superfamily Palpimanoidea (*sensu* Forster & Platnick 1984) were described recently (Selden *et al*. 2008).

Few Cretaceous spiders had been formally described and named until recently, but work is continuing apace to rectify this situation. Cretaceous records include: indeterminate Araneae from Koonwarra, South Australia (Jell & Duncan 1986); mygalomorphs from Transbaikalia and Mongolia (Eskov & Zonshtein 1990); orbicularian araneomorphs from the Sierra de Montsech and Las Hoyas localities, Spain (Selden 1989, 1990, 1991; Selden & Penney 2003); an unnamed lycosoid from Orapa, Botswana (Rayner & Dippenaar-Schoeman 1995); a poorly preserved specimen from Mexico (Feldmann *et al*. 1998); many new spider specimens reported from the Crato Formation of Brazil, of which just a few have been described so far (Mesquita 1996; Selden *et al*. 2002, 2006); and many also are now being collected from the Lower Cretaceous of China (Chang 2004; Cheng *et al*. 2008). Spiders are known from Cretaceous amber from Canada (McAlpine & Martin 1969; Penney & Selden 2006), the Caucasus and Siberia (Eskov & Wunderlich 1994; Zherikhin & Eskov 1999), France (Schlüter 1978; Saupe & Selden 2009), Lebanon (Penney 2003*a*; Penney & Selden 2002), Myanmar (Cockerell 1920; Rasnitsyn & Ross 2000; Zherikhin & Ross 2000; Penney 2003*b*; Wunderlich 2008), New Jersey (Grimaldi *et al*. 2000; Penney 2002), Álava, Spain (Alonso *et al.* 2000; Penney 2006), Asturias, Spain (Arbizu *et al*. 1999), Jordan (Kaddumi 2007; Wunderlich 2008) and the Isle of Wight, England (Selden 2002).

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

At the time of publication of Eskov and Zonshtein's (1990) paper on Cretaceous mygalomorphs, there were hardly any spiders known at all from the Mesozoic era. It appeared that mygalomorphs, perhaps already an archaic group, may have flourished at a time of biotic crisis, when araneomorphs became reduced in number (Eskov & Zonshtein 1990). Since then, however, many more Mesozoic spiders, and particularly araneomorphs, have been described. Figure 1 shows that by Cretaceous time, many of the modern families were in existence or predicted by sister-group relationships. By the time of formation of the mid-Cainozoic ambers, nearly all extant families have fossil representatives or are predicted to occur. Interestingly, there are very few families known only from fossils; some new families from Cretaceous ambers recently described by Wunderlich (2008) have yet to be critically assessed. Some families described initially from fossils were later found to be extant, e.g. Archaeidae were first described from Baltic amber and later found alive in Africa and Madagascar. The Cretaceous extinct family, Lagonomegopidae Eskov & Wunderlich, 1994, is interesting on account of (a) its enormous posterior median eyes, which suggest a possible relationship (homology or analogy) with Salticidae (the most speciose modern family, and unknown in pre-Cainozoic strata), and (b) the characteristic peg-teeth, which place it within the Palpimanoidea *sensu* Forster and Platnick (1984). Few arachnologists concur with the composition of this superfamily; in particular Schütt (2002) has provided evidence, mainly from spinneret morphology, that the palpimanoid families formerly allied with Araneoidea should be returned to that superfamily. These include Mimetidae and the archaeid families, which are araneophages characterised by elongated chelicerae bearing long peg-teeth. Of the described Jurassic spiders, several (*Jurarchaea*, *Patarchaea* Selden, Huang & Ren, 2008, *Metaxyostraca* Selden, Huang & Ren, 2008, and an undescribed specimen from Germany) belong in the Palpimanoidea, and the other (*Jurararaneus*) is an early orb-weaver. The earliest known araneomorphs, *Triassaraneus* and *Argyrarachne*, resemble araneoids more than any other group. Conversely, cursorial spiders such as the Dionycha, including such speciose families as Salticidae, Thomisidae, Gnaphosidae and the clubionoids, which represent some 35 % of genera and 37 % of species at the present day (data from Platnick 2009), are as yet unknown in pre-Cainozoic strata. The fossil record thus appears to support the hypothesis, well argued by Dippenaar-Schoeman and Jocqué (1997), that the more derived hunting spiders arose from ancestors which used webs for prey capture (Vollrath & Selden 2007).

A study by Penney *et al*. (2003) examined how spiders fared across well-known mass extinctions, specifically the mid-Cretaceous Cenomanian–Turonian (C/T, 93.5 Ma), and the better-known Cretaceous–Tertiary (K/T, 65 Ma) events. Using quantitative techniques combining taxonomic and numerical data on amber fossils only, these authors showed that spiders suffered no decline at the family level during these mass extinctions. On the contrary, they increased in relative numbers through the Cretaceous and beyond the K/T boundary. They suggested that this extinction resistance of spiders is due to the majority of them being generalist predators. Those feeding predominantly on plant-specific herbivores that became extinct could easily have switched to a new primary food source, such as many of the non-herbivorous insects or polyphagous herbivores, which appear to have been little affected by the K/T extinction (Labandeira & Sepkoski 1993; Labandeira *et al*. 2002). Thus, the mass extinction that killed off the dinosaurs seems to have had little effect on the Araneae, at least at family level.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

African fossil spiders

Spiders are common in African copal, which is a kind of sub-fossil amber; it chiefly occurs on the coasts of Kenya, Tanzania and Mozambique, and on the north-west coast of Madagascar. Softer and paler yellow than true amber, it dates from about Miocene and younger in age, and so its inclusions are generally of less interest for phylogenetic studies. It can be of great interest, however, for research on palaeogeography and palaeoclimatology of more recent geological times. For example, interesting work has been done comparing the fossil and extant spider species in Dominican amber and alive on the island of Hispaniola respectively (Penney 2008). In spite of specimens having been available in gem shops relatively cheaply throughout the world, few descriptions of African copal spiders appeared until recently. There can be a problem, however, in that some amber dealers will heat copal to make it appear to be true amber and thus gain higher prices. For example, Wunderlich (2004) suggested that the specimen of *Entomocephalus formicoides* Holl, 1829 from Baltic amber was really a fake in Madagascan copal. Holl's one-sentence description and figure (pl. 8, fig. 68a) suggests it almost certainly belongs to an ant-mimicing salticid genus such as *Myrmarachne* (which occurs in Madagascan copal), although the figure and description mentioned only six eyes (Penney 2003*b*). It was placed (erroneously) in Archaeidae by Petrunkevitch (1958); the location of the holotype is unknown.

Lourenço (2000) described *Archaea copalensis* (Archaeidae), which was thought to be the first record of this genus from Madagascan copal; the species was later synonymized with the extant *Archaea gracilicollis* Millot, 1948 by Wunderlich (2004). Previously, Wunderlich (1998) had described *Mysmena dominicana* (Mysmenidae) and *Grammonota deformans* (Linyphiidae, later placed in *Ceratinopsis* by Wunderlich (2004)) from supposed Dominican amber. He later realized that the amber was actually Madagascan copal treated to make it appear to be older and from a different provenance (Wunderlich 2004). Similarly, Wunderlich's (1999) report of the family Archaeidae from Dominican Republic amber also proved to be a mistake for Madagascan copal. Species from the following spider families are currently known as sub-fossils in Madagascan copal: Araneidae, Archaeidae, Clubionidae, Corinnidae, Deinopidae, Dictynidae, Hahniidae, Hersiliidae, Linyphiidae, ?Migidae, ?Miturgidae, Mysmenidae, Oonopidae, Philodromidae, Pholcidae, Salticidae, Scytodidae, Segestriidae, Selenopidae, Tetragnathidae, Theridiidae, Thomisidae and Uloboridae (Wunderlich 2004, 2008).

Only two specimens of fossil spider have been described from the continent of Africa: *Triassaraneus*, as mentioned above, and a supposed lycosoid spider from the Orapa diamond mine in Botswana (Rayner & Dippenaar-Schoeman 1995). The Orapa mine exploits a kimberlite pipe in which a crater lake developed during the Cretaceous period; the matrix bearing the spider and abundant insect remains has been dated to 93 Ma ago (Late Cretaceous: Turonian) by radiometry (Rayner *et al*. 1997). The relatively soft volcanic breccias of kimberlite pipes commonly accommodate circular crater lakes (see Gernon *et al*. 2009 for a review of the sedimentology of the Orapa kimberlite). The Orapa lake was shallow and the fine lamination of the sediment suggests little disturbance, so it was probably anoxic bottom waters which prevented decay of the biota. Because there has been little appreciable erosion since Cretaceous times, the lake sediments are still preserved. More than half of the insects at Orapa are Coleoptera, followed by Blattodea (about 20 %), and less than 10 % each of Diptera, Hymenoptera, Hemiptera,

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Orthoptera, Dermaptera and the rest (Rayner *et al*. 1997). A diverse flora of mainly angiosperms (about 90 %) that was washed into the lake has been described by Bamford (1990); ferns account for the remainder of the flora. The only spider to have been described from Orapa is an unnamed specimen with a body length of approximately 25 mm. It was referred to superfamily Lycosoidea on the basis of its habitus being that of a hunting spider. This was the first fossil spider to be described from Africa.

The second, and most important, fossil spider to be described from Africa comes from the Molteno Formation of the Karoo (Fig. 2), which was deposited in an extensive, intracontinental foreland basin bounded by rising fold mountains to the south and traversed by a system of braided rivers (Cairncross *et al*. 1995). The Molteno Formation reaches a maximum thickness of about 600 m and the erosional remnant extends over an area roughly 400 km north to south and 200 km west to east. The age of the formation is not tightly established, but on the basis of global biostratigraphic correlations (Anderson & Anderson 1983, 1989) is considered to be Carnian (Late Triassic), 222–229 Ma. No absolute radiometric ages are available. A 30-year collecting programme (Anderson 2001; Anderson & Anderson 1983, 1984, 1989; Anderson *et al.* 1998) has yielded 100 fossil plant assemblages from the Molteno Formation. The flora, the richest known globally from the Triassic, includes 56 genera with 204 vegetative species. It is particularly characterised by some 20 species of *Dicroidium* (Ginkgoopsida). There is a roughly equal diversity of gymnosperms, including conifers, cycads and ginkgos, along with several new orders, and 'pteridophytes,' primarily horsetails and ferns. Though rare, insects comprise by far the most frequently encountered element of the fauna. A remarkable diversity of 117 genera and 333 species in 18 orders is provisionally recognised in the over 2000 specimens from 43 of the 100 plant assemblages. Coleoptera, Blattodea and Hemiptera dominate. Conchostracan crustaceans, from 20 of the plant assemblages, are represented by some three genera and eight species. The remaining

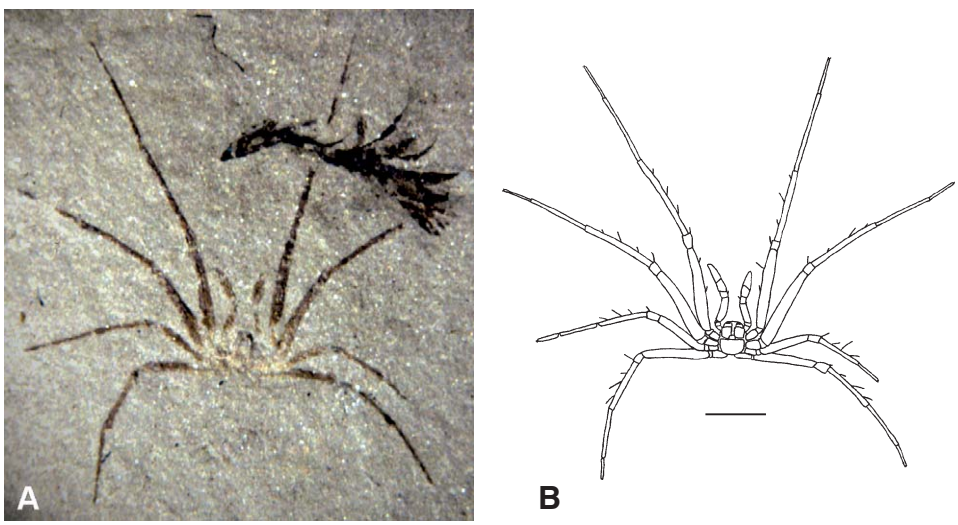


Fig. 3. Holotype of *Triassaraneus andersonorum* from the Triassic (Carnian) Molteno Formation, Upper Umkomaas 'Waterfall Locality' (UMK III), KwaZulu-Natal, South Africa: (A) photograph in incident light under ethanol, (B) *camera lucida* drawing. Scale bar = 1 mm.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

fauna is sparse: three species of fishes (impressions only) from three assemblages, two species of bivalve from one assemblage, and two spider specimens. Dinosaur trackways, but no skeletal remains, have been identified at a few (non-plant) sites. Anderson (2001) provided a review of the Molteno Formation flora and fauna.

At the Telemachus Spruit locality there is a 10 cm thick, buff mudstone that is interpreted as an abandoned channel-fill (Cairncross *et al*. 1995). The flora of 12 genera and 19 species is strongly dominated by the single coniferous species *Heidiphyllum elongatum* (Morris, 1845) Retallack, 1981. The assemblage most likely represents two distinct plant communities: a mono-dominant stand of reed-like conifers colonizing sand bars in the braided river and, from farther afield, a *Dicroidium*-dominated riparian forest occupying the river bank. The insect fauna at this site, is represented by only 17 fragmentary specimens, and is dominated, as at other Molteno localities, by Coleoptera, Blattodea and Hemiptera. Conchostracans have not been found. The rarity of the single spider specimen is emphasized by the fact that John and Heidi Anderson have spent 90 man-hours cleaving slabs at this site and that all 900 curated and catalogued slabs have been carefully scanned for insects or other faunal elements under the binocular microscope.

TAXONOMY

Infraorder Araneomorphae Smith, 1902
Superfamily ?Araneoidea Latreille, 1806
Triassaraneus Selden in Selden *et al*., 1999

Type and only species: *Triassaraneus andersonorum* Selden in Selden *et al*., 1999.

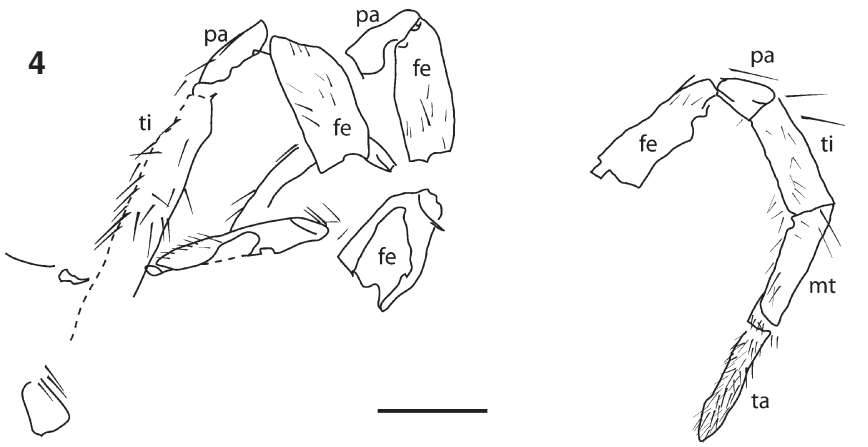
Triassaraneus andersonorum Selden in Selden *et al*., 1999

Figs 3–5

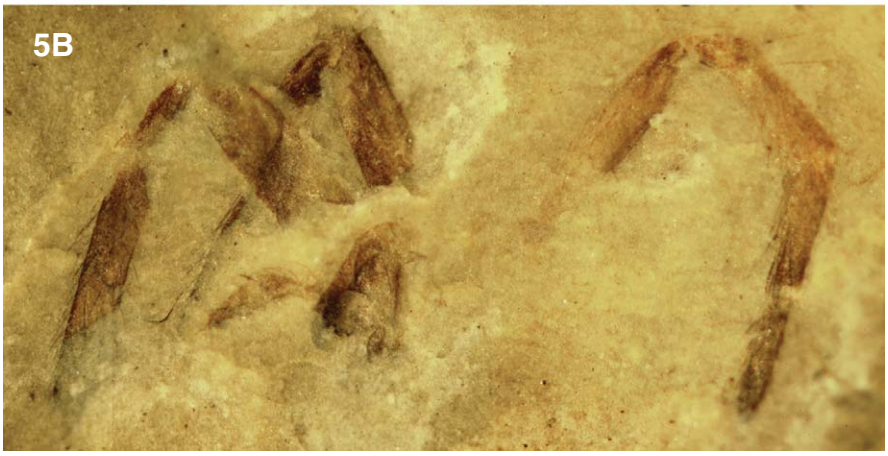
Material examined: SOUTH AFRICA: *KwaZulu-Natal*: Holotype PRE/F 18560a (part) and 18560b (counterpart), immature or mature female from Upper Umkomaas 'Waterfall Locality' (UMK III). *Eastern Cape*: PRE/F 17234 Tel 111, immature from Telemachus Spruit locality (Anderson & Anderson 1983, 1984). All material from from Member Z of the Late Triassic (Carnian) Molteno Formation and deposited in the palaeobotanical collection of the South African National Biodiversity Institute, Pretoria.

Description of new specimen: The specimen is preserved as brown, organic cuticle on a pale, grey-brown shale. The shale is splintery and pieces readily fall away. Scattered throughout the shale are abundant plant remains, including on the fossil slab a male cone of Ginkgoopsida. Parts of at least three legs are preserved, though it is not possible to determine which legs these are. No body parts are preserved. On the right in Figs 4, 5 is a nearly complete walking leg, showing most of the femur to the tarsus. On the left are some of the opposing walking legs, but less complete. Note that in Fig. 5A, there is a loose piece of matrix bearing parts of a leg; this became detached and is not present in Fig. 5B (under ethanol), which therefore reveals more of the tibia of on the left-hand walking legs. The walking legs bear setae on all podomeres, and larger, thin spines on all podomeres except the tarsus. These spines, for example on the right leg patella and tibia, are long, thin and erect. Although tarsal claws cannot be seen, it is certain from the shape of this podomere (only preserved on the right side) that its distal end is present, so the claws must be small. There is no evidence of tarsal scopulae or claw tufts. The legs appear to be rather short, although the only one which is nearly completely preserved, on the right, may be a third leg, which is commonly short in orbicularians (orb-web weavers).

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use







Figs 4, 5. *T. andersonorum* specimen PRE-F 17234 Tel 111 from Telemachus Spruit: (4) *camera lucida* illustration, (5) actual fossil dry (A) and under ethanol (B). Abbreviations: *fe* – femur, *mt* – metatarsus, *pa* – patella, *ta* – tarsus, *ti* – tibia. Scale bar = 0.5 mm.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

DISCUSSION

The small claws and lack of tarsal scopulae and claw tufts indicate that this was a web-living rather than a ground spider. Short legs suggest that this is a juvenile spider; however, if the right leg is indeed a third leg of an orbicularian, then this may not be the case. If a third leg, then it is not a great deal smaller than that of *T. andersonorum*, so it is unlikely to be a juvenile of that species. The leg spination of the right leg matches that of leg 3 in *T. andersonorum*, with one distally on the femur, one on the patella, two in the proximal half and one in the distal half of the tibia (compare Fig. 4 with fig. 2 in Selden *et al.* 1999). Therefore, this fossil is considered to be a second specimen of *T. andersonorum*. Triassic spiders are extremely rare, and this is only the second spider to come out of the Molteno Formation, after many years of painstaking search. It comes from a different locality from *T. andersonorum*, but is of the same age and possibly occupied the same habitat (*Dicroidium*-dominated riparian forest).

A general impression gained from studying fossil arachnids is that one spider fossil occurs for approximately every 1000 insects in the Mesozoic lacustrine or lagoonal fossil insect localities, e.g. the Cretaceous Crato Formation of Brazil (Mesquita 1996; Selden *et al*. 2002), the Cretaceous of Spain (Selden 1989, 1990; Selden & Penney 2003) and the Jurassic and Cretaceous of China (e.g. Selden *et al*. 2008). The ratio in the Lower Cretaceous locality of Baissa, Transbaikalia is 1:1623 (24,366 arthropod remains) and that in the Middle – Upper Jurassic locality of Karatau, Kazakhstan it is 1:904 (19,909 arthropod remains) (M. Mostovski pers. comm., 2009). With some 2000 insects collected from the Molteno Formation, and a new specimen described herein, this ratio of spider to insect fossils is in agreement, and a similar ratio seems to occur in the Cow Branch Formation of Virginia. However, when comparing other Triassic and Permian localities the ratios are rather different. For example, there are no spiders among over 22,000 insect remains in the Ladinian/Carnian locality of Madygen, Kyrgyzstan (Shcherbakov 2008), and, similarly, no arachnids have ever been found among the tens of thousands of insect specimens from the Artinskian Wellington Formation of Kansas and Oklahoma (Beckemeyer & Hall 2007). The ratio is 1:2129 in the Kazanian locality of Verkhnii Kaltan, Siberia (M. Mostovski pers. comm., 2009), and only one spider specimen, one trigonotarbid and one uraraneid are known out of more than 8000 insects in the Kungurian Koshelevka Formation (including the Chekarda locality) of the Urals (Eskov & Selden 2005). A quantitative study of the ratios of insect remains to those of spiders and other arachnids in localities with abundant insect fossils (Rasnitsyn & Zherikhin 2002) would be extremely interesting.

ACKNOWLEDGEMENTS

The senior author thanks David Penney (Manchester) for discussion on Mesozoic spiders in amber, Roger Smith (Iziko South African Museum, Cape Town) for hospitality and a field visit to the Molteno Formation, Mike Mostovski (Natal Museum, Pietermaritzburg) for help with insect and spider abundances, and Jason Dunlop and Kirill Eskov for constructive reviews.

REFERENCES

Alonso, J., Arillo, A., Barrón, E., Corral, J.C., Grimalt, J., López, J.F., López, R., Martínez-Delclòs, X., Ortuño, V., Peñalver, E. & Trincão, P.R. 2000. A new fossil resin with biological inclusions in lower Cretaceous deposits from Álava (northern Spain, Basque–Cantabrian Basin). *Journal of Paleontology* **74**: 158–178.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

ANDERSON, J.M., ed. 2001. *Towards Gondwana alive*. Vol. 1. Pretoria: Gondwana Alive Society.
ANDERSON, J.M. & ANDERSON, H.M. 1983. *Palaeoflora of southern Africa. Molteno Formation (Triassic) Volume 1*. Rotterdam: A.A. Balkema.
———1984. The fossil content of the Upper Triassic Molteno Formation, South Africa. *Palaeontologia Africana* **25**: 39–59.
———1989. *Palaeoflora of southern Africa. Molteno Formation (Triassic) Volume 2*. Rotterdam: A.A. Balkema.
ANDERSON, J.M., ANDERSON, H.M. & CRUICKSHANK, A.R.I. 1998. Late Triassic ecosystems of the Molteno/ Lower Elliot biome of southern Africa. *Palaeontology* **41**: 387–421.
ARBIZU, M., BERNÁRDEZ, E., PEÑALVER, E. & PRIETO, M.A. 1999. El ámbar de Asturias. *In*: Alonso, J., Corral, J.C. & López, R., eds, *Proceedings of the world congress on amber inclusions, Álava, Spain. Estudios de Museo de Ciencias Naturales de Álava* **14** (Núm. Espec. 2): 245–254.
ANSORGE, J. 2003. Insects from the Lower Toarcian of Middle Europe and England. *Acta Zoologica Cracoviensia* **46** (Suppl. – Fossil Insects): 291–310.
BAMFORD, M.K. 1990. *The angiosperm palaeoflora from the Orapa Pipe, Botswana*. Ph.D. dissertation. Johannesburg, South Africa: University of the Witwatersrand. (Unpubl.)
BECKEMEYER, R.J. & HALL, J.D. 2007. The entomofauna of the Lower Permian fossil insect beds of Kansas and Oklahoma, USA. *African Invertebrates* **48** (1): 23–39.
CAIRNCROSS, B., ANDERSON, J.M. & ANDERSON, H.M. 1995. Palaeoecology of the Triassic Molteno Formation, Karoo Basin, South Africa sedimentological and palaeontological evidence. *South African Journal of Geology* **98**: 452–478.
CHANG J.-P. 2004. Some new species of spider and Sacculinidae fossils in Jehol biota. *Global Geology* **23**: 313–320. (in Chinese with English summary)
CHENG X.-D., MENG Q.-J., WANG X.-R. & GAO C.-L. 2008. New discovery of Nephilidae in Jehol Biota (Araneae, Nephilidae). *Acta zootaxonomica sinica* **33**: 330–334. (in Chinese, with English summary)
COCKERELL, T.D.A. 1920. Fossil arthropods in the British Museum: IV. *Annals & Magazine of Natural History, Series 9* **6**: 211–214.
CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and the evolution of spiders (Araneae). *Annual Reviews of Ecology and Systematics* **22**: 265–292.
DIPPENAAR-SCHOEMAN, A.S. & JOCQUÉ, R. 1997. *African spiders. An identification manual*. Plant Protection Research Institute Handbook No. 9. Pretoria: Agricultural Research Council of South Africa.
ESKOV, K.Y. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1984**: 645–653.
———1987. A new archaeid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called "Gondwanan" ranges of recent taxa. *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen* **175**: 81–106.
ESKOV, K.Y. & SELDEN, P.A. 2005. First record of spiders from the Permian period (Araneae: Mesothelae). *Bulletin of the British Arachnological Society* **13**: 111–116.
ESKOV, K.Y. & WUNDERLICH, J. 1994. On the spiders from Taimyr ambers, Siberia, with the description of a new family and with general notes on the spiders from the Cretaceous resins. *Beiträge zur Araneologie* **4**: 95–107.
ESKOV, K.Y. & ZONSHTEIN, S.L. 1990. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the order Mygalomorphae (Chelicerata: Araneae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **178**: 325–368.
FELDMANN, R.M., VEGA, F.J., APPLEGATE, S.P. & BISHOP, G.A. 1998. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *Journal of Paleontology* **72**: 79–90.
FORSTER, R.R. & PLATNICK, N.I. 1984. A review of the archaeid spiders and their relatives, with notes on the superfamily Palpimanoidea (Arachnida, Araneae). *Bulletin of the American Museum of Natural History* **178**: 1–106.
GERNON, T.M., FIELD, M. & SPARKS, R.S.J. 2009. Depositional processes in a kimberlite crater: the Upper Cretaceous Orapa South Pipe (Botswana). *Sedimentology* **56**: 623–643.
GRIMALDI, D., SHEDRINSKY, A. & WAMPLER, T. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey, U.S.A. *In*: Grimaldi, D., ed., *Studies* in *fossil amber, with particular reference to the Cretaceous of New Jersey*. Leiden: Backhuys, pp. 1–76.
GRISWOLD, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). *Smithsonian Contributions to Zoology* **539**: 1–39.
GRISWOLD, C.E., CODDINGTON, J.A., HORMIGA, G. & SCHARFF, N. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society* **123**: 1–99.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

GRISWOLD, C.E., CODDINGTON, J.A., PLATNICK, N.I. & FORSTER, R.R. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). *Journal of Arachnology* **27**: 53–63.

HUANG D.-Y., NEL, A., SHEN, Y.-B., SELDEN, P.A. & LIN, Q.-B. 2006. Discussions on the age of Daohugou fauna — evidence from invertebrates. *Progress in Natural Science* **16** (Special issue): 308–312.

JELL, P.A. & DUNCAN, P.M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists* **3**: 311–205.

KADDUMI, H.F. 2007. *Amber of Jordan. The oldest prehistoric insects in fossilized resin*. 2nd edition. Amman: Eternal River Museum of Natural History.

LABANDEIRA, C.C. & SEPKOSKI, J.J., JR. 1993. Insect diversity in the fossil record. *Science* **261**: 310–315.

LABANDEIRA, C.C., JOHNSON, K.C. & WILF, P. 2002. Impact of the terminal Cretaceous event on plant insect associations. *Proceedings of the National Academy of Sciences of the USA* **99**: 2061–2066.

LATREILLE, P.-A. 1806. *Genera crustaceorum et insectorum. Vol. 1, Aranéides*. Paris: A. Koenig, pp. 82–127.

LOURENÇO, W.R. 2000. Premier cas d'un sub-fossile d'araignée appartenant au genre *Archaea* Koch & Berendt (Archaeidae) dans le copal de Madagascar. *Comptes Rendus de l'Académie des Sciences, Series IIA – Earth and Planetary Sciences* **330**: 509–512.

MCALPINE, J.F. & MARTIN, J.E. 1969. Canadian amber – a paleontological treasure-chest. *Canadian Entomologist* **101**: 819–838.

MESQUITA, M.V. 1996. *Cretaraneus martinsnetoi* n. sp. (Araneoidea) da Formação Santana, Cretáceo Inferior da Bacia do Araripe. *Revista Universidade Guarulhos, Série Geociências* **1**: 24–31.

MORRIS, J. 1845. Fossil flora. *In*: De Strzelecki, P.E., ed., *Physical description of New South Wales and Van Diemans Land*. London: Longman, Brown & Green, pp. 245–254.

PENNEY, D. 2002. Spiders in Upper Cretaceous amber from New Jersey (Arthropoda, Araneae). *Palaeontology* **45**: 709–724.

———2003*a*. A new deinopoid spider from Cretaceous Lebanese amber. *Acta Palaeontologica Polonica* **48**: 569–574.

———2003*b*. *Afrarchaea grimaldii,* a new species of Archaeidae (Araneae) in Cretaceous Burmese amber. *Journal of Arachnology* **31**: 122–130.

———2006. The oldest lagonomegopid spider, a new species in Lower Cretaceous amber from Álava, Spain. *Geologica Acta* **4**: 377–382.

———2008. *Dominican Amber Spiders: a comparative palaeontological–neontological approach to identification, faunistics, ecology and biogeography*. Manchester: Siri Scientific Press.

PENNEY, D. & SELDEN, P.A. 2002. The oldest linyphiid spider, in Lower Cretaceous Lebanese amber (Araneae, Linyphiidae, Linyphiinae). *Journal of Arachnology* **30**: 487–493.

———2006. Assembling the Tree of Life — Phylogeny of Spiders: a review of the strictly fossil spider families. *In*: Deltshev, C. & Stoev, P., eds, *European Arachnology 2005*. *Acta Zoologica Bulgarica Supplement* **1**: 25–39.

PENNEY, D., WHEATER, C.P. & SELDEN, P.A. 2003. Resistance of spiders to Cretaceous-Tertiary extinction events. *Evolution* **57**: 2599–2607.

PETRUNKEVITCH, A. 1958. Amber spiders in European collections. *Transactions of the Connecticut Academy of Arts and Sciences* **41**: 97–400.

PLATNICK, N.I. 2009. *The world spider catalog, version 9.5*. New York: American Museum of Natural History. (http://research.amnh.org/entomology/spiders/catalog/index.html; accessed April 3, 2009)

RAMÍREZ, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *Journal of Arachnology* **28**: 149–157.

RASNITSYN, A.P. & ROSS, A.J. 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London. *Bulletin of the Natural History Museum, London (Geology)* **56**: 21–24.

RASNITSYN, A.P. & ZHERIKHIN, V.V. 2002. Appendix: Alphabetic list of selected insect fossil sites. *In*: Rasnitsyn, A.P. & Quicke, D.L.J., eds, *History of Insects*. Dordrecht: Kluwer, pp. 437–444.

RAYNER, R.J., BAMFORD, M.K., BROTHERS, D.J., DIPPENAAR-SCHOEMAN, A.S., MCKAY, I.J., OBERPRIELER, R.G. & WATERS, S.B. 1997. Cretaceous fossils from the Orapa diamond mine. *Palaeontologia Africana* **33**: 55–65.

RAYNER, R.J. & DIPPENAAR-SCHOEMAN, A.S. 1995. A fossil spider (superfamily Lycosoidea) from the Cretaceous of Botswana. *South African Journal of Science* **91**: 98–100.

RETALLACK, G.J. 1981. Middle Triassic megafossil plants from Long Gully, near Otematata, North Otago, New Zealand. *Journal of the Royal Society of New Zealand* **11**: 167–200.

SAUPE, E.E. & SELDEN, P.A. 2009. First fossil Mecysmaucheniidae (Arthropoda: Chelicerata: Araneae), from Lower Cretaceous (Upper Albian) amber of Charente-Maritime, France. *In*: Perrichot, V. & Néraudeau, D., eds, *Cretaceous ambers from southwestern France: geology, taphonomy, and paleontology*. *Geodiversitas* **31**: 49–60.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

SCHARFF, N. & CODDINGTON, J.A. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society* **120**: 355–434.
SHCHERBAKOV, D.E. 2008. Madygen, Triassic Lagerstätte number one, before and after Sharov. *Alavesia* **2**: 113–124.
SCHLÜTER, T. 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. *Berliner Geowissenschaftliche Abhandlungen (Serie A)* **9**: 1–150.
SCHÜTT, K. 2002. The limits of the Araneoidea (Arachnida: Araneae). *Australian Journal of Zoology* **48**: 135–153.
SELDEN, P.A. 1989. Orb-web weaving spiders in the early Cretaceous. *Nature* **340**: 711–713.
———1990. Lower Cretaceous spiders from the Sierra de Montsech, northeast Spain. *Palaeontology* **33**: 257–285.
———1991. Aranyes del Cretaci inferior de la Serra del Montsec (Espanya). *In*: Martínez-Delclòs, X., ed., *Les calcàries litogràfiques del Cretaci inferior del Montsec. Deu anys de campanyes paleontològiques*. Lleida: Institut d'Estudis Ilerdencs, pp. 77–85.
———1996*a*. Fossil mesothele spiders. *Nature* **379**: 498–499.
———1996*b*. First fossil mesothele spider, from the Carboniferous of France. *Revue Suisse de Zoologie* Volume hors série **2**: 585–596.
———2000. *Palaeothele*, a replacement name for the fossil mesothele spider *Eothele* Selden *non* Rowell. *Bulletin of the British Arachnological Society* **11**: 292.
———2002. First British Mesozoic spider, from Cretaceous amber of the Isle of Wight, southern England. *Palaeontology* **45**: 973–983.
SELDEN, P.A., ANDERSON, J.M., ANDERSON, H.M. & FRASER, N.C. 1999. Fossil araneomorph spiders from the Triassic of South Africa and Virginia. *Journal of Arachnology* **27**: 401–414.
SELDEN, P.A., CASADO, F. DA C. & MESQUITA, M.V. 2002. Funnel-web spiders (Araneae: Dipluridae) from the Lower Cretaceous of Brazil. *Boletim do 6° Simpósio sobre o Cretácio do Brasil / 2do Simposio sobre el Cretácico de América del Sur (2002)*, pp. 89–91.
———2006. Mygalomorph spiders (Araneae: Dipluridae) from the Lower Cretaceous Crato Lagerstätte, Araripe Basin, north-east Brazil. *Palaeontology* **49**: 817–826.
SELDEN, P.A. & GALL, J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France. *Palaeontology* **35**: 211–235.
SELDEN, P.A., HUANG D.-Y. & REN, D. 2008. Palpimanoid spiders from the Jurassic of China. *Journal of Arachnology* **36**: 306–321.
SELDEN, P.A. & PENNEY, D. 2003. Lower Cretaceous spiders (Arthropoda: Arachnida: Araneae) from Spain. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **2003**: 175–192.
SELDEN, P.A., SHEAR, W.A. & SUTTON, M.A. 2008. Fossil evidence for the origin of spider spinnerets, and a proposed arachnid order. *Proceedings of the National Academy of Sciences of the USA* **105**: 20781–20785.
SHEAR, W.A., SELDEN, P.A., ROLFE, W.D.I., BONAMO, P.M. & GRIERSON, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida: Trigonotarbida). *American Museum Novitates* **2901**: 1–74.
SMITH, F.P. 1902. The spiders of Epping Forest. *Essex Naturalist* **12**: 181–201.
VOLLRATH, F. & SELDEN, P.A. 2007. The role of behavior in the evolution of spiders, silks, and webs. *Annual Review of Ecology, Evolution, and Systematics* **38**: 819–846.
WUNDERLICH, J. 1998. Beschreibung der ersten fossilen Spinnen der Unterfamilien Mysmeninae (Anapidae) und Erigoninae (Linyphiidae) im Dominikanischen Bernstein (Arachnida, Araneae). *Entomologische Zeitschrift* **108**: 363–367.
———1999. Two subfamilies of spiders (Araneae, Linyphiidae: Erigoninae and Anapidae: Mysmeninae) new to Dominican amber—or falsificated amber? *In*: Alonso, J., Corral, J. C. & López, R., eds, *Proceedings of the World congress on amber inclusions, Álava, Spain. Estudios de Museo de Ciencias Naturales de Álava* **14** (Núm. Espec. 2): 167–172.
WUNDERLICH, J., ed. 2004. Fossil spiders in amber and copal. *Beiträge zur Araneologie* **3**: 1–1908.
———2008. Fossil and extant spiders. *Beiträge zur Araneologie* **5**: 1–870.
ZHERIKHIN, V.V. & ESKOV, K.Y. 1999. Mesozoic and Lower Tertiary resins in former USSR. *In*: Alonso, J., Corral, J.C. & López, R., eds, *Proceedings of the World congress on amber inclusions, Álava, Spain. Estudios de Museo de Ciencias Naturales de Álava* **14** (Núm. Espec. 2): 119–131.
ZHERIKHIN, V.V. & ROSS, A.J. 2000. A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum, London (Geology)* **56**: 3–10.

Downloaded From: https://bioone.org/journals/African-Invertebrates on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use