GOVERNO DO ESTADO DO CEARÁ

UNIVERSIDADE REGIONAL DO CARIRI – URCA

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE – CCBS

PROGRAMA DE PÓS-GRADUAÇÃO EM DIVERSIDADE BIOLÓGICA E RECURSOS NATURAIS - PPGDR

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Aspectos taxonômicos e tafonômicos das aranhas fósseis da Formação Crato, Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil

CRATO/CE

2024

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Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Recursos Naturais da Universidade Regional do Cariri-URCA, como parte dos requisitos para obtenção do título de Mestre em Diversidade Biológica e Recursos Naturais.

Orientador: Prof. Dr. Antônio Álamo Feitosa Saraiva
Coorientador: Dr. Ivan Luiz Fiorini de Magalhães

CRATO-CEARÁ

2024

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S232aa Aspectos taxonômicos e tafonômicos das aranhas fósseis da Formação Crato, Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil / Elis Maria Gomes Santana. Crato - CE, 2024.

90p. il.

Dissertação. Programa de Pós-Graduação em Diversidade Biológica e Recursos Naturais da Universidade Regional do Cariri - URCA.

Orientador(a): Prof. Dr. Antônio Álamo Feitosa Saraiva

Coorientador(a): Prof. Dr. Ivan Luiz Fiorini de Magalhaes

1.Lagerstätten, 2.Araneae, 3.Mesozoic; I.Título.

CDD: 577

ELIS MARIA GOMES SANTANA

ASPECTOS TAXONÔMICOS E TAFONÔMICOS DAS ARANHAS FÓSSEIS DA FORMAÇÃO CRATO, CRETÁCEO INFERIOR DA BACIA DO ARARIPE, NORDESTE DO BRASIL

Dissertação de Mestrado em Diversidade Biológica e Recursos Naturais apresentada à Universidade Regional do Cariri – URCA, como parte dos requisitos para obtenção do título de Mestre em Diversidade Biológica e Recursos Naturais.

APROVADO EM: 22/07/2024

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AGRADECIMENTOS

Primeiramente, agradeço a todos da minha família, que sempre foram meu pilar em todos os momentos. Em especial, agradeço à minha mãe, Lucinete Santana, por todo o sacrifício e por ter dado o seu melhor para me proporcionar uma educação de qualidade, mesmo diante dos desafios. Às minhas irmãs, Roberta Heloyse, a quem sempre admirei sua inteligência e me inspirei a vida inteira, e Celina Luz, nossa caçula, sempre esperta e curiosa, que futuramente será uma cientista brilhante! Obrigada por acreditarem em mim e por sempre estarem ao meu lado.

Ao meu orientador, Álamo Saraiva, por acreditar em mim durante estes quase seis anos de colaboração. Agradeço por todo o incentivo, orientação, puxões de orelha e conselhos que me ajudaram a crescer tanto academicamente quanto pessoalmente. Muito obrigada por ir além da responsabilidade de um orientador e me apoiar sempre em todas as questões da minha vida. Você foi fundamental para que eu não desistisse no meio do caminho, e me motivou a sempre buscar as melhores oportunidades. Serei eternamente grata por isso!

Ao meu coorientador, Ivan Magalhães, por toda a paciência, compreensão e amizade. Houve várias vezes em que me senti perdida durante o desenvolvimento do trabalho, mas após nossas conversas, tudo ficava mais claro e fazia mais sentido. Muito obrigada por esse direcionamento e pelo apoio de sempre. Eu certamente não teria conseguido sem sua ajuda. Aprendi muito com você e espero que nossa parceria continue em futuros trabalhos.

A Rodrigo T. Figueroa, a pessoa que se tornou fundamental na minha vida no último ano. Obrigada por ficar ao meu lado e ver o melhor em mim, mesmo no meu pior momento. Você tem sido meu suporte diário e sou muito grata por isso. Eu tenho muito orgulho e me inspiro muito em você, pessoalmente e profissionalmente, e espero que possamos crescer ainda mais juntos!

Aos meus queridos amigos do Laboratório de Paleontologia da URCA (e agregados): Ednalva Santos, Artur Fernandes, Eugênio Moura, Gustavo Pinho, Fernanda Sampaio, Thatiany Alencar, Edilson Santos, Renan Bantim, Naiara Cipriano, Flaviana Lima, Alita Neves, Elane Soares, Aline Dino, Francielma Amparo, David Renato, e tantos outros. Aprendi muito com cada um de vocês e admiro todos imensamente. Sou muito grata por todos os momentos vividos no LPU, tanto academicamente como também os momentos de descontração; essa rotina da pós-graduação certamente seria muito mais difícil sem esse ambiente acolhedor. Eu não poderia ter escolhido um laboratório melhor para essa fase tão

importante da minha vida, e sei que, independente de onde esteja, o LPU sempre será minha casa. Vocês se tornaram uma verdadeira segunda família para mim e estarei sempre torcendo pelo sucesso de cada um!

À nossa querida Francy Brito (Cy), secretária do Programa de Pós-Graduação em Diversidade Biológica e Recursos Naturais – PPGDR, que nunca mediu esforços para auxiliar todos os discentes com muito zelo e paciência.

Ao Museu de Paleontologia Plácido Cidade Nuvens (MPPCN/URCA) e ao Laboratório de Paleontologia e Sistemática da Universidade Federal Rural de Pernambuco (LAPASI/UFRPE) pelo empréstimo dos espécimes do trabalho.

Ao Programa de Pós-Graduação em Diversidade Biológica e Recursos Naturais e à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão de bolsa de mestrado ao longo de todo o curso.

RESUMO

Aranhas fósseis são consideradas raras devido ao seu exoesqueleto não-mineralizado, condição que não favorece a preservação na maioria dos depósitos. Neste trabalho, é fornecida uma visão geral dos *Lagerstatten* Mesozoicos que preservam aranhas, revisando classificações taxonômicas de espécies conhecidas, padrões de preservação e distribuição temporal. Destaca-se que a maioria das espécies conhecidas foi atribuída a famílias modernas, embora muitas careçam de caracteres suficientes para garantir essas colocações. Há uma predominância de Mygalomorphae no Triássico e Araneomorphae no Jurássico, com um aumento na diversidade e distribuição geográfica de ambas infraordens no Cretáceo, evidenciado por registros na Formação Yixian, na China, e na Formação Crato, no Brasil. Neste contexto, foram também analisadas dezenas de aranhas fósseis da Formação Crato, descrevendo 7 espécimes adicionais de *Cretaraneus martinsnetoi* Mesquita, 1996, fornecendo novas informações acerca de sua morfologia. Além disso, duas espécies distintas foram identificadas, mas apesar de terem uma forma corporal geral similar aos representantes modernos da superfamília Araneoidea, não puderam ser atribuídos seguramente a nenhum grupo dentro de Araneomorphae. Também é destacada a preservação de microestruturas cuticulares em aranhas fósseis, ressaltando as excepcionais condições tafonômicas da Formação Crato. Essa pesquisa enfatiza a importância de revisitar espécimes já conhecidos para elucidar sua classificação taxonômica e destaca a relevância da Formação Crato como um importante sítio paleontológico para o estudo da diversidade de aranhas do passado.

Palavras-chave: Lagerstätten; Araneae; Mesozoico.

ABSTRACT

Fossil spiders are considered rare due to their non-mineralized exoskeleton, a condition that does not favor preservation in most deposits. This work provides an overview of Mesozoic *Lagerstätten* that preserve spiders, reviewing the taxonomic classifications of known species, patterns of preservation, and temporal distribution. It is highlighted that most known species are attributed to modern families, although many lack sufficient characters to ensure these placements. There is a predominance of Mygalomorphae in the Triassic and Araneomorphae in the Jurassic, with an increase in diversity and geographic distribution of both infraorders in the Cretaceous, evidenced by records in the Yixian Formation in China and the Crato Formation in Brazil. In this context, dozens of fossil spiders from the Crato Formation were also analyzed, describing 7 additional specimens of *Cretaraneus martinsnetoi* Mesquita, 1996, providing new information about its morphology. Furthermore, two distinct species were identified; however, despite their overall body shape resembling modern representatives of the superfamily Araneoidea, they could not be securely assigned to any group within Araneomorphae. The preservation of cuticular microstructures in fossil spiders is also emphasized, highlighting the exceptional taphonomic conditions of the Crato Formation. This research underscores the importance of revisiting previously known specimens to clarify their taxonomic classification and highlights the relevance of the Crato Formation as a significant paleontological site for studying the diversity of spiders from the past.

Key words: Lagerstätten; Araneae; Mesozoic.

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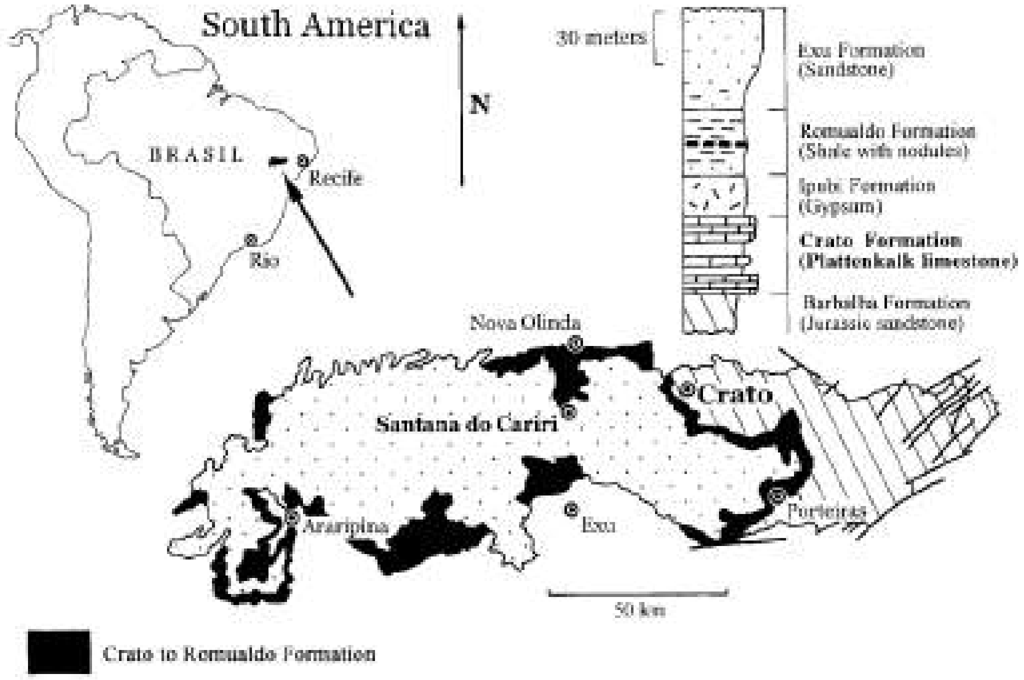
GENERAL INTRODUCTION

The Araripe Basin spans through the southern portion of the state of Ceará, northwest of Pernambuco, and eastern Piauí, covering approximately 12,000 km², making it the largest geological basin in the interior of Northeastern Brazil (BANTIM; LIMA; SARAIVA, 2021). Among its geological units, the Crato Formation (Figure 1) stands out for its extremely abundant fossils with preserved soft tissues, often compressed or in impression form (SARAIVA et al., 2007). It mainly consists of laminated micritic limestones, ranging from gray to cream colors, with halite pseudomorphs, indicating increasing aridity in this paleoenvironment (MARTILL; LOVERIDGE; HEIMHOFER, 2007; HEIMHOFER et al., 2010). The depositional environment represented is that of a restricted lacustrine or lagoon setting with a stratified water column. The upper water column was likely brackish and well-oxygenated, while the lower column and lake bottom were hypersaline and anoxic (HEIMHOFER et al., 2010).

Figure 1. Crato Formation locality and its distribution within the Araripe Basin. Modified from MAISEY (1991).



The Crato Formation is one of the most significant localities for the study of fossil arachnids. This geological formation yields specimens often better preserved than other Mesozoic shale records and, in some cases, even easier to study than amber inclusions (DUNLOP; MENON; SELDEN, 2007). Additionally, it constitutes one of the few paleontological sites in the Southern Hemisphere with preserved spiders in its strata. These deposits date approximately from the Gondwana supercontinent breakup, during the time of separation of South America and Africa (ASSINE et al., 2014). Thus, they hold considerable interest in understanding the biogeographical history of this group throughout the Mesozoic.

Spiders (order Araneae) are abundant animals, ranking as the seventh most diverse group after the five largest orders of insects and mites in modern terrestrial ecosystems (SELDEN; PENNEY, 2010), with more than 50.000 species up to date (WSC, 2024). These organisms are rarely preserved in the fossil record due to their fragility and lack of mineralization (SELDEN; PENNEY, 2010). Thus, spider fossils define the occurrence of a *Konservat-Lagerstatte,* signifying the exceptional preservation of a fossil biota (SEILACHER, 1970).

Fossil-Lagerstätten are important sources of information about the paleobiology of various groups, facilitating the visualization of life's development over geological time (SEILACHER et al., 1985). Other examples of *Lagerstätten* with preserved spiders as organic matter in fluvial, lagoonal, or lacustrine environments include the Miocene of Germany (HEYDEN, 1859), Switzerland (HEER, 1865), and Shanwang, China (ZHANG; SUN; ZHANG, 1994), the Oligocene of Florissant, Colorado, United States (PETRUNKEVITCH, 1922), and Aix-en-Provence, France (THORELL, 1870), the Lower Cretaceous of Montsec and Las Hoyas, Spain (SELDEN; PENNEY, 2003), Mongolia (ESKOV; ZONSTEIN, 1990), and Mexico (FELDMANN et al., 1998), the Jurassic and Cretaceous of Northeast China (SELDEN; HUANG; REN, 2008; SELDEN; HUANG, 2010; CHENG ET AL., 2019), the Cretaceous and Jurassic of Transbaikalia and Kazakhstan (ESKOV, 1984, 1987, SELDEN, 2010), the Triassic of the Voltzia Sandstone Formation, France (SELDEN; GALL, 1992), the Permian of the Ural Mountains, Russia (ESKOV; SELDEN, 2005), and the Triassic of the Molteno Formation, South Africa (SELDEN, 2009).

At present, five spider species formally described are known from the Crato Formation (MESQUITA, 1996; SELDEN, 2006; RAVEN; JELL; KNEZOUR, 2015; DOWNEN; SELDEN, 2021). Many of the known spider specimens have not yet been described (DUNLOP; MENON; SELDEN, 2007), and their study is currently primarily focused on taxonomy, with few studies investigating the mechanisms and processes involved in the preservation of such organisms (e.g., DOWNEN; SELDEN; HASIOTIS, 2016).

Taxonomy of fossil spiders remains a complex field, with limited species described compared to extant spiders (PENNEY, 2012). The study of fossil spider families is pivotal, often revealing a mix of valid taxa and those needing revision (PENNEY, 2006). Imaging techniques, particularly X-ray CT scanning, have revolutionized fossil spider research, facilitating detailed morphological analysis and taxonomic classification (SELDEN, 2017). However, other challenges exist, including difficulties in species diagnosis due to incomplete preservation of copulatory organs (SAUPE, 2011), although advancements in imaging techniques have improved the capture of fine morphological details (SELDEN, 2017).

The study of preservation pathways of arthropods from the Crato Formation is mainly limited to insects (BARLING et al., 2015, OSÉS et al., 2016, VAREJÃO et al., 2019, BEZERRA et al., 2020, DIAS; CARVALHO, 2020). Arachnids, although relatively common, have not been the primary focus of taphonomic studies for this unit, and little is known about the preservational means of spiders in lacustrine sedimentary environments (OLCOTT et al., 2022).

The fossil record of spiders, in comparison to other taxa, is generally sparse. However, with exceptionally preserved and abundant specimens, the Araripe Basin holds significant importance in the study of these organisms, being one of the few locations in the Southern Hemisphere to preserve them. The aim of this study is to enhance understanding of fossil spiders preserved in lacustrine environments of the Gondwana during the Cretaceous period, aiming for a better comprehension of the diversity within this order and the conditions related to their preservation in the fossil record.

Specifically, we aim to describe new spider specimens from the Crato Formation, based on fossils deposited in the collections of Laboratório de Paleontologia da URCA (LPU), Museu de Paleontologia Plácido Cidade Nuvens (MPPCN) and Universidade Federal Rural de Pernambuco (UFRPE). Additionally, the study seeks to employ advanced electron microscopy techniques (SEM) to examine the specimens and obtain diagnostic morphological characteristics. We also intend to compare the taxonomic diversity and taphonomic processes of the fossil spiders from the Crato Formation with other *Lagerstätten*. This will allow us to contextualize the findings of the Crato Formation in relation to other known fossil-bearing areas, providing a broader view of the evolution and preservation of spiders throughout their geological history.

This dissertation is divided into two chapters: "**An Overview of Mesozoic Spider Diversity in Non-Amber Deposits**," which presents a literature review on the diversity of Mesozoic fossil spiders, excluding amber, providing an analysis of fossil deposits and suggesting taxonomic revisions of the species found, and "**Araneoid Spiders from the Crato Formation, Lower Cretaceous of the Araripe Basin, Brazil**," in which new specimens of Araneoidea from the Crato Formation are described and interpreted taxonomically and taphonomically, offering a specific analysis of spiders found in this geological context.

CHAPTER ONE: AN OVERVIEW OF MESOZOIC SPIDER DIVERSITY IN NON-AMBER DEPOSITS

ABSTRACT

Spiders are a major component of modern terrestrial ecosystems, but their fossil record is sparse due to their soft-bodied nature. Most of this record is found in amber, but this type of preservation offers limited data, as the age range of fossils extends to the Cretaceous at its oldest. Here, we synthesized the fossil record of spiders on rock-matrices, including a review of their taxonomic classifications, preservational patterns and distribution along geologic time. Many of the known fossil species have been classified into recent families, but without sufficient characters to ensure these placements. Triassic spiders are dominated by Mygalomorphae, while Jurassic shows a prevalence of Araneomorphae. The Cretaceous had an increase in geographical distribution and diversity, with several records in diverse localities such as the Crato Formation in Brazil and the Yixian Formation in China. Rock-matrices fossil spiders strictly occur in *Konservat-Lagerstätte* deposits and are often preserved in fine-grained lacustrine sediments through processes like phosphatization and pyritization. This review highlights the importance of revisiting previously known specimens that have no certain taxonomic placements.

Key words: Araneae; *Lagerstätten;* Taxonomy; Taphonomy.

INTRODUCTION

Throughout the Mesozoic, the diversity, abundance and distribution of terrestrial fauna experienced a series of transformations led by ecological, zoogeographic, and evolutionary factors, resulting in a broad biotic reorganization (PONOMARENKO, 2006). Following the Permo-Triassic mass extinction, there was a notable increase in provincialism and diversification of lineages. Terrestrial arthropods, in particular, experienced substantial increase in diversity, with many groups diversifying mainly during the Lower Jurassic and Lower Cretaceous (JARZEMBOWSKI; ROSS, 1996). This increase seems to be influenced by the proliferation of angiosperms (BENTON; WILF; SAUQUET, 2022), related to climatic fluctuations driven by tectonics, especially the fragmentation of Pangea. This led to an expansion of temperate zones and the emergence of new humid bioclimatic continents, providing new habitats (CHABOUREAU et al., 2014).

The oldest fossil record of a true spider is from the Late Carboniferous (330.9–323.2 Ma) (SELDEN et al., 2014), but their increase in diversity was during the Cretaceous (DUNLOP et al., 2023). Today, spiders can be found globally and in most terrestrial ecosystems, making them one of the most diverse groups on the planet with about 52,000 species spread across 136 families (WSC, 2024). So far, 1,427 species of fossil spiders are known (DUNLOP et al., 2023). Despite being the majority among arachnids (73.6%), this number is still low compared to other groups of arthropods. This is mainly due to the difficulty of spider fossilization, as they are soft-bodied organisms without mineralized tissues (BRIGGS, 2003). Thus, fossil spiders only occur in *Konservat-Lagerstätte* deposits (SEILACHER, 1970; SELDEN & PENNEY, 2010).

Most fossil spiders are found in amber inclusions, primarily from Cenozoic deposits (SAUPE & SELDEN, 2011; MAGALHAES et al., 2020). In these deposits, spiders preserve fine details of their morphology, and many can be attributed to extant genera and families. However, the oldest ambers containing spiders date back to the Cretaceous (DUNLOP et al., 2023). Spiders may also be found in rock matrices, with different types of preservation. However, such occurrences are extremely rare: in several deposits, insects outnumber spiders in ratios that exceed 1000 to 1 (SELDEN et al. 2009). These fossils are the source of knowledge into the diversity of species from older periods, but their preservation is often not as good as in amber, making taxonomic placement difficult in some cases.

This review aims to offer a comprehensive and up-to-date synthesis of the current understanding of Mesozoic spiders in non-amber deposits. Specifically, it seeks to discuss their taxonomic attributions, identify patterns among different deposits and trends in their preservation, distribution and diversity, as well as discuss future directions for research on fossil spiders.

MATERIAL AND METHODS

We performed an extensive literature review on Google Scholar using the terms "Araneae" or "spider" combined with "Mesozoic," "Cretaceous," "Jurassic," and "Triassic", encompassing all papers documenting valid records of Mesozoic Araneae (between 1984 and 2024). Species described from amber deposits were not considered. To ensure inclusivity, we included data from two additional resources: the World Spider Catalog (DUNLOP et al. 2024) and The Paleobiology Database (https://paleobiodb.org/) were also consulted. Each record was systematically organized into a spreadsheet, detailing the estimated age in millions of years, locality of the deposit and original placement. However, several fossils likely do not belong in the taxa where they were originally placed. We thus also included in the table a suggested revised taxonomic placement in the light of current knowledge. Geological ages were correlated to the International Chronostratigraphic Chart (v. 2023-09; COHEN et al., 2013). Original placements considered were those on Dunlop et al. (2024) catalog of fossil spiders, with the exception of the records in Rayner and Dippenaar-Schoeman (1995), Cifuentes-Ruiz et. al. (2005), Selden (2020) and Downen and Selden (2021), which were not on the catalog. In these cases, classifications considered were those on the original papers.

For discussion, data were categorized according to periods, from the Triassic to Cretaceous, and palaeogeographic maps were made on Gplates with PaleoAtlas (SCOTESE, 2016) to illustrate the diversity of major systematic groups. The first occurrences of superfamilies and families are discussed, such as localities that represent notable points of diversity. Potential future prospects and possibilities for studying spider fossils are also discussed.

RESULTS AND DISCUSSION

TRIASSIC SPIDERS

The Triassic period, ranging from 252–201 million years ago, witnessed the emergence of some of the oldest known spider lineages. Five species are currently known (Table 1), but despite being few, these records are important as they break a 20-million-year gap on the spider fossil record: apart from the Carboniferous spiders and a single record from the Permian (SELDEN, 2021), spiders only reappear in the fossil record during the Middle Triassic.

The first spider described from this period is also the oldest record of the suborder Opisthothelae and the infraorder Mygalomorphae: *Rosamygale grauvogeli* Selden and Gall, 1992, from the Grès à Meules Formation, a Middle Triassic (Anisian) deposit in France. *Rosamygale* can be assigned to the clade Avicularioidea based on the lack of an abdominal scutum and well-separated posterior lateral spinnerets. Originally, it was attributed to Hexathelidae, which was shown to be non-monophyletic (HEDIN et al., 2018; OPATOVA et al., 2020). The specimens lack synapomorphic characters of any extant family, so its familiar placement remains unknown.

Some of the *Rosamygale* specimens shows an interesting feature: a tridimensionally preserved abdomen, which is not common on fossil spiders, cast in calcium phosphate. This exemplifies the distinct taphonomic pathway of the Grès à Meules Formation, which is believed to have been a deltaic sedimentary environment: a rapid phosphatization takes place. This is a rare process in invertebrates due to the rapid recycling of phosphate in organic tissues. Then, the acidic conditions created by decaying organic matter release free calcium ions, which react with phosphate and precipitate apatite. The resulting phosphatic nodules preserve the three-dimensional morphology, preventing its flattening during subsequent sediment compaction processes (SELDEN; NUDDS, 2012).

Other Triassic mygalomorphs include *Friularachne rigoi* Dalla Vecchia and Selden, 2013, from the Italian Dolomia di Forni, and *Edwa maryae* Raven, Jell, Knezour, 2015 from the Australian Blackstone Formation, both from the Upper Triassic (Norian). The Dolomia di Forni Formation was deposited in an anoxic marine basin (ROGHI; MIETTO; DALLA VECCHIA, 1995). Although no other terrestrial arthropods are found in this locality, it is known that Dolomia di Forni was surrounded by a shallow water carbonate platform, where spiders must have lived, supported by the presence of terrestrial plants and vertebrates (DALLA VECCHIA, 1997). On the other hand, the Blackstone Formation is known for its deposits that suggest a floodplain environment dominated by migrating point bars within large meandering river systems (ERIKSSON, 1984) and is an important locality for the study of fossil arthropods, yielding the richest paleoentomofauna Triassic assemblage (ANDERSON; KOHRING; SCHLÜTER, 1998).

Friularachne, a single spider specimen discovered in the Dolomia di Forni Formation of northeast Italy, was attributed to the Atypoidea clade, based on the large size of the chelicerae, slender legs with inconspicuous setation, and a dorsal scutum on the anterior part of the opisthosoma. As a single, poorly preserved specimen, it was not attributed to any atypoid family.

Edwa maryae was placed within the Masteriinae (Dipluridae), supported by a molariform palpal bulb with a long paraembolic process, similar to the extant *Masteria* Koch, 1873. Recent phylogenies have shown that Dipluridae is not a monophyletic group, and has been splitted into different families (Dipluridae, Ischnothelidae, Euagridae, Microhexuridae) (OPATOVA et al., 2020). Although Masteriinae has not been reviewed in this context, it is predicted that this subfamily may eventually be recognized as a standalone family (OPATOVA et al., 2020). Therefore, at present, *Edwa* remains within the Dipluridae family.

Regarding araneomorph spiders, two Triassic species were described by Selden et al. (1999), *Triassaraneus andersonorum* Selden, 1999 and *Argyarachne solitus* Selden, 1999 from the Upper Triassic (Carnian) of the Cow Branch Formation in the United States and the South African Molteno Formation, respectively. The Cow Branch Formation exhibits a mix of lacustrine and fluvial sediments, with fine-grained shales and siltstones indicative of tranquil lake settings, alongside coarser sandstones and conglomerates from more dynamic river systems (LIUTKUS; FRASER; HECKERT, 2014), and holds an insect *Lagerstatte* (FRASER et al., 1996). In contrast, the Molteno Formation is predominantly fluvial, characterized by thick, cross-bedded sandstones from high-energy river channels and finer siltstones and mudstones from associated floodplains (ERIKSSON, 1984).

Both species described by Selden (1999) are poorly preserved specimens, hindering their assignment to any higher taxonomic classification. Later, Selden et al. (2009) presented another representative of *Triassaraneus*, confirming its placement within Araneomorphae, the oldest record of the infraorder. The presence of small claws and the absence of tarsal scopulae and claw tufts suggest that *Triassaraneus* was a web-dwelling spider rather than a ground-dweller (SELDEN; ANDERSON; ANDERSON, 2009). On the other hand, *Argyrarachne* is known from a single juvenile specimen. Like *Triassaraneus*, *A. solitus* is clearly identifiable as a spider based on its leg and podomere arrangement. The short, dentate tarsal claws are common among web weavers. In any case, none of the specimens can be classified beyond Araneomorphae.

Table 1. A summary of the Triassic fossil record of spiders on rock matrices, with most recent placement and the suggested on this work. Ma: Millions of years.

Age (Ma)	Taxa	Reference	Location	Placement in Dunlop et al. (2023)	Suggested placement
247.2-243	*Rosamygale grauvogeli*	Selden and Gall, 1982	Grés a Meules Formation (France)	Hexathelidae	Avicularioidea *incertae sedis*
237-227	*Argyrarachne solitus*	Selden et al., 1999	Cow Branch Formation (USA)	Araneomorphae *incertae sedis*	Araneomorphae *incertae sedis*
237-227	*Triassaraneus andersonorum*	Selden et al., 1999	Molteno Formation (South Africa)	Araneomorphae *incertae sedis*	Araneomorphae *incertae sedis*
227-208.5	*Friularachne rigoi*	Dalla Vecchia and Selden, 2013	Dolomia di Forni Formation (Italy)	Atypoidea *incertae sedis*	Atypoidea *incertae sedis*
227-208.5	*Edwa maryae*	Raven et al., 2015	Blackstone Formation (Australia)	Dipluridae	?Dipluridae: ?Masteriinae

JURASSIC SPIDERS

Noteworthy geological and environmental events characterized the Jurassic, with particular reference to the accretion of paleooceanic fragments along the eastern margin of the Asian continent (KEMKIN; JINGENG, 2006) and the intense volcanic eruptive activities (HESSELBO et al., 2002; LUTTINEN et al., 2022). These events possibly impacted on the preservation of fossil spiders, such as the distribution of some lineages, as changes in climate and habitat would have influenced their survival and diversification. In comparison to the Triassic fauna, Jurassic spiders present a relatively diverse Araneomorphae assemblage (Table 2). No records of Mygalomorphae from the Jurassic are currently known.

Juraraneus rasnitsyni Eskov, 1984, the first Jurassic spider described, was later redescribed by Selden (2012) who reinterpreted the spider morphology and identified a functional calamistrum (although no cribellum is visible). It was assigned to the monotypic family Juraraneidae. The Ichetuy Formation, where the specimen was found, consists of a thick volcanic sequence interbedded with mudstones and is believed to have been deposited in lakes in a mountainous region, preserving numerous arthropods, mainly insects (ARNOLDI et al., 1977). In the same year, *Mesarania hebeiensis* Hong, 1984, was the first spider to be described from the Chinese Daohugou area and was initially classified as an additional Araneoidea. According to Selden et al. (2020), it is likely that this spider belongs to the cribellate genus *Zhizhu* Selden, Ren & Shih, 2016, which is an Entelegynae spider of uncertain affinities, but the holotype has been lost, so a re-study of this specimen is not possible.

A noteworthy group among Jurassic spiders is the Palpimanoidea superfamily. Although molecular clock analyses suggest a Triassic origin (KALLAL et al., 2021), their fossils first appeared and diversified in the Jurassic, with half of all spider records from this period being palpimanoids. The oldest palpimanoid known is *Seppo koponeni* Selden and Dunlop, 2014, from the Lower Jurassic of the Grimmen strata, Germany. The specimen possesses an enlarged chelicerae with peg teeth, a cheliceral furrow devoid of true teeth and the presence of a distal trichobothrium on metatarsus I, aligning with Palpimanoidea (WOOD; GRISWOLD; GILLESPIE, 2012; WOOD; WUNDERLICH, 2023). Other terrestrial arthropods are found at Grimmen, including scorpions, grylloids, grylloblattoids and dermapterans (ANSORGE, 2003). Unlike most other rock-matrix fossil spiders, *Seppo* is preserved in calcium carbonate sediments. This rare preservation in marine clay is possibly explained by different modes of transportation, such as ballooning, severe weather events, or transportation via floating vegetation (ANSORGE, 2003).

Jurarchaea zherikhini Eskov, 1987, from the Karabastau Formation on Kazakstan has been recently confirmed as a primitive archaeid (WOOD; WUNDERLICH, 2023). The highly laminated claystone of the Karabastau deposits represents the remains of a large, stable, freshwater lake and provides exceptional preservation of fossil arthropods (SZWEDO; ŻYŁA, 2009; YAN, 2009).

Jurassic palpimanoids mainly occur in the Daohugou biota, which is known as the ‘early assemblage’ of the chinese Yanliao Biota (LIAN; CAI; HUANG, 2021). It yields a diverse array of fossil arthropods (GIRIBET et al., 2012; HUANG; SELDEN; DUNLOP, 2009; WANG; REN, 2009), including at least 700 spider specimens (SELDEN; REN; SHIH, 2016).

The Daohugou area was a near-shore shallow lacustrine basin with a warm, humid climate and diverse vegetation (WANG et al., 2019). The fine volcanic ash produced by frequent volcanic activity during the Middle Jurassic may have influenced the preservation of the Daohugou biota (GUO et al., 2022). Mechanisms such as microbial processes and pyritization, along with the unique fossilization environment created by clay minerals, also contributed to the exceptional preservation (WANG et al., 2009).

Selden et al. (2008) described two palpimanoid species from the Daohugou area, *Patarchaea muralis* Selden, Huang & Ren, 2008, an archaeid (WOOD; WUNDERLICH, 2023), and *Sinaranea metaxyostraca* Selden, Huang & Ren, 2008, with uncertain familiar affinities. The holotype of *Sinaranea* was described as an adult male (which is dubious, as no palpal sclerite is visible) and placed on Palpimanoidea based on its cheliceral peg-teeth. Although displaying characters observed in Palpimanidae and Huttoniidae, it is not possible to assign the fossil to any family.

Other palpimanoids from the Daohugou beds were later described by Selden et al. (2020): *Caestaranea jurassica* Selden, Huang & Garwood, 2020, *Onychopalpus thomisoides* Selden, Huang & Garwood, 2020, and *Sinaranea brevicrus* Selden, Huang & Garwood, 2020. All of them have palpimanoid synapomorphies such as a chelicera with peg teeth, but cannot be assigned to any family.

A further species from the Daohugou beds is *Eoplectreurys gertschi* Selden and Huang, 2010, a small haplogyne spider originally assigned to Plectreuridae based on the chelicerae fused at the base, clasping setae on the first leg of males and general shape of the body and male palp. Although sharing similarities with extant plectreurid genera, those traits are homoplasious (MAGALHAES et al., 2020) and no convincing synapomorphies of the family are preserved on the fossil.

Zhizhu daohugouensis Selden, Shih and Dong (2015) was initially classified as a stem Deinopoidea, which has been recovered as a non-monophyletic group (FERNÁNDEZ et al., 2018; WHEELER et al., 2017). Its classification is difficult, as the absence of a tibial apophysis excludes *Zhizhu* from the RTA clade, and the specimen also lacks typical characteristics of Araneoidea.

A large female spider from the Daohugou beds was initially described as *Nephila jurassica* Selden, Shih & Ren, 2011 (SELDEN; SHIH; REN, 2011) and placed within the modern genus *Nephila* Leach, 1815, due to morphological similarities. However, a few years later, an adult male specimen was discovered, and by its palpal morphology, those specimens were reclassified into a new genus, *Mongolarachne* Selden, Shih and Ren, 2013, and a new monotypic family, Mongolarachnidae Selden, Shih and Ren, 2013, was erected within Araneoidea.

Records from other localities include *Talbragaraneus jurassicus* Selden and Beattie, 2013 from the Late Jurassic (latest Oxfordian–Tithonian) Talbragar Fossil Fish Bed, located in central New South Wales, Australia. The depositional environment is interpreted as a shallow-water deposit close to the shoreline and it's characterized by tuffaceous siltstone with opaline silica, suggesting a volcanic influence, like other Jurassic *Lagerstätten* (BEATTIE; AVERY, 2012). The species exhibits distinctive features including an inward curved calamistrum on the fourth metatarsus, indicative of Uloboridae. Its presence in a Late Jurassic context aligns with molecular phylogenetic studies, suggesting an early emergence of orb-weaving spiders (DIMITROV et al., 2011). According to Frese et al. (2017), a second spider specimen from Talbragar exists, but has not been described.

Table 2. A summary of the Jurassic fossil record of spiders on rock matrices, with most recent placement and the suggested on this work. Ma: Millions of years.

Age (Ma)	Taxa	Reference	Location	Placement in Dunlop et al., (2023)	Suggested placement
182.7-174.1	*Seppo koponeni*	Selden and Dunlop, 2014	Grimmen beds (Germany)	Palpimanoidea *incertae sedis*	Palpimanoidea *incertae sedis*
166.1-157.3	*Jurarchaea zherikhini*	Eskov, 1987	Karabastau Formation (Kazakhstan)	Archaeidae	Archaeidae
166.1-157.3	*Mesarania hebeiensis*	Hong, 1984	Daohugou beds (China)	Araneoidea *incertae sedis*	Araneoidea *incertae sedis*
166.1-157.3	*Patarchaea muralis*	Selden et al., 2008	Daohugou beds (China)	Archaeidae	Archaeidae
166.1-157.3	*Sinaranea metaxyostraca*	Selden et al., 2008	Daohugou beds (China)	Palpimanoidea *incertae sedis*	Palpimanoidea *incertae sedis*
166.1-157.3	*Caestaranea jurassica*	Selden et al., 2020	Daohugou beds (China)	Palpimanoidea *incertae sedis*	Palpimanoidea *incertae sedis*
166.1-157.3	*Onychopalpus thomisoides*	Selden et al., 2020	Daohugou beds (China)	Palpimanoidea *incertae sedis*	Palpimanoidea *incertae sedis*
166.1-157.3	*Sinaranea brevicrus*	Selden et al., 2020	Daohugou beds (China)	Palpimanoidea *incertae sedis*	Palpimanoidea *incertae sedis*

Age (Ma)	Taxa	Reference	Location	Placement in Dunlop et al., (2023)	Suggested placement
166.1-157.3	*Eoplectreurys gertschi*	Selden and Huang, 2010	Daohugou beds (China)	Plectreuridae	Synspermiata *incertae sedis*
166.1-157.3	*Zhizhu daohugouensis*	Selden et al., 2016	Daohugou beds (China)	“Deinopoidea”	Araneomorphae *incertae sedis*
166.1-157.3	*Mongolarachne jurassica*	Selden et al., 2013	Daohugou beds (China)	Mongolarachnidae	Mongolarachnidae
163.5-157.3	*Juraraneus rasnitsyni*	Eskov, 1984	Ichetuy Formation (Russia)	Juraraneidae	Juraraneidae (within Araneomorphae *incertae sedis*)
152.1-145	*Talbragaraneus jurassicus*	Selden and Beattie, 2013	Talbragar Formation (Australia)	Uloboridae	?Uloboridae

CRETACEOUS SPIDERS

Cretaceous paleontological records provide important data on the origin, evolution and distribution of various groups, as it was marked by important geological and biological events that led to a broad biotic reorganization (GALE et al., 2020). Most Mesozoic spiders date back to the Cretaceous, and their study has revealed a great diversity through the description of several species distributed among various groups, especially in the last two decades (Table 3).

Selden (1990) described three spider species from the Lower Cretaceous of the Sierra de Montsech, Spain. The depositional environment is interpreted as the evolution of a coastal lake transitioning from profundal to littoral lacustrine environments. The spider-bearing sequence, known as the Lithographic Limestones, represents a particularly tranquil lacustrine depositional episode, suggesting an anoxic lake bottom (GIL-DELGADO et al., 2023). *Palaeouloborus lacasae* Selden, 1990, was initially classified within "Deinopoidea" based on characteristics such as femoral trichobothria, the presence of a calamistrum and a cribellum, and plumose hairs. By the lack of distinctive synapomorphies of Deinopidae, Selden and Penney (2003) placed *Palaeouloborus* within Uloboridae. However, Deinopoidea has shown to be a non-monophyletic group (WHEELER et al., 2017), so these criteria must not be considered. The other two species, *Cretaraneus vilaltae* Selden, 1990 and *Macryphantes cowdeni* Selden, 1990, were classified within Araneoidea. *Cretaraneus vilaltae* is characterized by a distinctive pedipalp with a long, slightly twisted embolus, a feature typical of *Nephila* Leach, 1815 (SELDEN, 1990). Consequently, Selden and Penney (2003) assigned the species to Nephilinae (Araneidae) based on its distinctive pedipalp morphology. *Macryphantes* was described as a tetragnathid based on the femoral trichobothria, which, alone, cannot be used to confirm this familiar placement. Additionally, Wunderlich (2015) proposed that *Macryphantes* should be considered a synonym of *Paleouloborus*.

From the same locality, Selden (2014) described *Montsecarachne amicorum* Selden, 2014, originally placed within Plectreuridae. The species shares similarities with the Jurassic genus *Eoplectreurys* but differs in several morphological aspects, including a shorter embolus and the absence of a tibial spur on the first pair of legs of males. Such as *Eoplectreurys,* its assignment to Plectreuridae is based on generalist characters.

A slightly older locality than Montsec, Las Hoyas, also in Spain has fossiliferous beds which consist of laminated limestones produced by microbial communities, deposited in a lake system with shallow carbonate water and no marine influence (DELGADO BUSCALIONI; POYATO-ARIZA, 2016). Among its diverse fauna, an araneoid spider, *Huergina diazromerali*

Selden and Penney, 2003, was classified as a tetragnathid. Few distinguishable characters are preserved on this specimen, and this assignment was based on general characters such as body size and leg proportions.

Eskov and Zonshtein (1990) reported the first Cretaceous mygalomorphs from two different localities: Semyon creek (Barremian-Aptian) in Transbaikalia, Russia, and Bon-tsagan (Aptian) in Mongolia. Four atypoid species were described: *Cretohexura coylei* Eskov and Zonshtein, 1990 and *Cretomegahexura platnicki* Eskov and Zonshtein, 1990, originally placed within Mecicobothriidae, *Cretacattyma raveni* Eskov and Zonshtein, 1990, placed in Antrodiaetidae, and *Ambiortiphagus ponomarenkoi* Eskov and Zonshtein, 1990, originally placed in Atypidae. The presence of a cheliceral apophysis on the male of *Cretacattyma* indeed suggests its placement within Androdiaetidae, and *Cretomegahexura* presents a carapace with expanded pleurites at the posterior lateral corners of the carapace, thus being a representative of Megahexuridae. None of the other two specimens presents actual synapomorphies of any atypoid family (HEDIN et al., 2019).

Other records of mygalomorphs were documented in the Lower Cretaceous Crato Formation, Northeast Brazil, by Selden, Casado and Mesquita (2006), who described two species classified as Dipluridae. The depositional environment is interpreted as lacustrine with calm and anoxic waters, and the Nova Olinda beds, where spiders occur, is dated as Aptian (COIMBRA; FREIRE, 2021). *Cretadiplura ceara* Selden, 2006 and *Dinodiplura ambulacra* Selden, 2006 were referred to Dipluridae based on their elongated posterior spinnerets. Selden et al (2006) suggested that both species belonged to Diplurinae based on the unsegmented distal article of the posterior spinnerets and a recurved fovea. On the other hand, Raven et al. (2015) suggested a placement within Euagrinae, based on the enlarged mating spines (megaspines) on tibia II of males. The allotype of *Dinodiplura ambulacra*, originally classified as a female of the species, was reanalyzed by Raven et al (2015). The analysis revealed modifications in the palp, indicative of distinct reproductive structures, suggesting that the specimen is a male belonging to another genus and species. As a result, the specimen was redescribed and the new species *Seldischnoplura seldeni* Raven, Jell, Knezour, was proposed. Diplurid monophyly has been tested in recent years (HEDIN et al., 2018; OPATOVA et al., 2020) and several subfamilies are now ranked as families. With this, these Crato specimens cannot be assigned to a family with certainty.

Additional taxa from the Crato Formation include the araneomorphs *Cretaraneus martinsnetoi* Mesquita, 1996, an araneoid which appears to be the most abundant species in this locality, and *Cretapalpus vittari* Downen and Selden, 2021, a palpimanid. *Cretaraneus martinsnetoi* was described based on a single specimen and assigned to the genus through comparison with *Cretaraneus vilaltae* Selden, 1990, found in a Cretaceous deposit in Spain (SELDEN, 1990). However, differences observed among the holotype, other Crato specimens, and the Spanish species suggest that this Crato araneoid does not belong to the same genus, and a reanalysis of this species is necessary. *Cretapalpus vittari* shows typical Palpimanidae features such as an inflated first leg femur, a heavily sclerotized scutum, and two spinnerets encircled by a sclerotized ring, being the oldest reported Mesozoic occurrence of the family (DOWNEN; SELDEN, 2021). It is known that several undescribed Crato specimens exist, so it is expected that future studies help to solve questions regarding the *Cretaraneus* placement, as well as the description of new taxa.

A locality with a noticeable paleoaraneofauna is The Lower Cretaceous Jinju Formation, the most fossiliferous of the Gyeongsang Supergroup, Korea. The depositional environment is interpreted as fluvio-lacustrine, mainly comprising grey to black shale intercalated by packets of sandstones (CHOUGH; SOHN, 2010). By far, the most common fossils from the Jinju Formation are arthropods, such as ostracods, conchostracans, isopods, insects, and spiders (PAIK et al., 2019). *Korearachne jinju* Selden, Nam, Kim and Kim, 2012, was found preserved in a dark grey shale slab with albuiform fish, dipteran insects, and possible crustacean fragments, suggesting a mass-mortality event. It was assigned to Lycosoidea, but the absence synapomorphies of this superfamily put this placement into doubt. Wunderlich (2012) suggested it could be a haplogyne spider, possibly Pholcoidea or Leptonetoidea, but the fossil displays no characters to ensure a confident familiar classification.

Additionally, other spiders from the Jinju Formation have been described, including two new species, *Koreamegops samsiki* Park, Nam and Selden, 2019, and *Jinjumegops dalingwateri* Park, Nam and Selden, 2019, both lagonomegopids. Other specimens are also described, but could not be assigned to a family, genus, or species, being determined as one Palpimanoidea *incertae sedis*, two undetermined Entelegynae, one Araneomorphae *incertae sedis* and one Mygalomorphae *incertae sedis* (PARK et al., 2019).

The Lower Cretaceous Yixian Formation in China is renowned for its Jehol biota, which contains finely laminated lacustrine strata characterized by abundant volcanic ash layers (PAN et al., 2011), encompassing a diverse range of terrestrial and freshwater organisms (PAN et al., 2013; ZHANG; WANG; FANG, 2010; ZHOU, 2014), including spiders. Selden et al. (2015) described *Zhizhu jeholensis* from this locality, and it differs from the Jurassic *Zhizhu* *daohugouensis* primarily by the morphology of the pedipalp, which is shorter and bears a planispiral embolus rather than a conispiral one. Chang (2004) described several spider species attributed to extant genera *Araneus* Clerck, 1757, *Gnaphosa*, and *Theridion*. These generic assignments are highly dubious, the descriptions provided are succinct and only comprise the general body shape, and the illustrations lack in details, making it impossible to reclassify those specimens even at family level. Therefore, a reanalysis of this material is necessary, and we suggest treating those specimens as Araneomorphae incertae sedis. *Cretadromus liaoningensis* Cheng, Shen & Gao, 2009 was classified as a member of Philodromidae. We did not had access to the original paper, so this species is not reviewed here, but its placement in Philodromidae is unlikely and should be further investigated.

The Zazinskaya Formation of Transbaikalia, a Lower Cretaceous deposit, is also known as the Baissa locality and represents an inter-montane lake situated within a granite massif, with oxygen deficiency and high hydrogen sulfide levels in the hypolimnion. It yields an abundant fossil insect fauna, along with crustaceans, gastropods and exceptionally preserved spiders (ZHERIKHIN et al., 1999). *Eocoddingtonia eskovi* Selden, 2010, an araneoid spider, was described from six specimens preserved as organic material in fine clayrock. *E. eskovi* exhibits typical characteristics of a small araneoid spider, with a globular opisthosoma positioned well forward over the prosoma. The sternum and labium conform to the typical morphology observed in other theridiosomatids. However, the presence of sternal pits, although suggested in some specimens, is not confirmed and cannot be used to assign the fossil to the family.

A younger record (Late Albian) is *Atocatle ranulfoi* Feldmann, Vega, Applegate and Bishop, 1998, from the Tlayua Formation in Mexico. It has been interpreted as shallow marine shelf deposits (JUAREZ et al., 2023). Fossils in this formation are found on red laminated limestones, preserving a rich assembly of plants, vertebrates and invertebrates, including arachnids (APPLEGATE et al., 2006). Unfortunately, the specimen is poorly preserved, making it impossible to assign any classification beyond order. Another Mexican record comes from the Cerro del Pueblo Formation, which is younger than Tlayua (EBERTH et al., 2004). This formation was deposited in lakes or small ponds, associated with the deltaic system prevalent in northeastern Mexico during Campanian times (EBERTH et al., 2004). As *Atocatle,* the Cerro del Pueblo specimen is poorly preserved and classified as Opisthothelae *incertae sedis* (CIFUENTES-RUIZ et al., 2006). It is also known that a single, poorly preserved specimen occurs in the Lower Cretaceous Orapa Mine, in Central Botswana (RAYNER; DIPPENAAR-SCHOEMAN, 1995), but classification beyond Araneae is impossible.

Table 3. A summary of the Cretaceous fossil record of spiders on rock matrices, with most recent placement and the suggested on this work. Ma: Millions of years.

Age (Ma)	**Taxa**	**Reference**	**Location**	**Placement in Dunlop et al., (2023)**	**Suggested placement**
129.4-125	*Cretaraneus vilaltae*	Selden, 1990	Sierra de Montsec (Spain)	Araneidae	?Araneidae: ?Nephilinae
129.4-125	*Macryphantes cowdeni*	Selden, 1990	Sierra de Montsec (Spain)	Tetragnathidae	Entelegynae *incertae sedis*
129.4-125	*Palaeouloborus lacasae*	Selden, 1990	Sierra de Montsec (Spain)	Uloboridae	Entelegynae *incertae sedis*
129.4-125	*Araneus beipiaoensis*	Chang et al., 2004	Yixian Formation (China)	Araneidae	Araneomorphae *incertae sedis*
129.4-125	*Araneus liaoxiensis*	Chang et al., 2004	Yixian Formation (China)	Araneidae	Araneomorphae *incertae sedis*
129.4-125	*Araneus aethus*	Chang et al., 2004	Yixian Formation (China)	Araneidae	Araneomorphae *incertae sedis*
129.4-125	*Araneus reheensis*	Chang et al., 2004	Yixian Formation (China)	Araneidae	Araneomorphae *incertae sedis*
129.4-125	*Gnaphosa liaoningensis*	Chang et al., 2004	Yixian Formation (China)	Gnaphosidae	Araneomorphae *incertae sedis*

129.4-125	*Theridion atalus*	Chang et al., 2004	Yixian Formation (China)	Theridiidae	Araneomorphae *incertae sedis*
129.4-125	*Cretaraneus liaoningensis*	Cheng et al., 2008	Yixian Formation (China)	Araneidae	?Araneidae
129.4-125	*Cretadromus liaoningensis*	Cheng et al., 2009	Yixian Formation (China)	Philodromidae	Entelegynae *incertae sedis*
129.4-125	*Zhizhu jeholensis*	Selden et al., 2016	Yixian Formation (China)	"Deinopoidea"	Araneomorphae *incertae sedis*
129.4-125	*Huergina diazromerali*	Selden and Penney, 2003	Las Hoyas (Spain)	Tetragnathidae	Araneomorphae *incertae sedis*
129.4-125	*Montsecarachne amicorum*	Selden, 2014	Las Hoyas (Spain)	Plectreuridae	Synspermiata *incertae sedis*
125-113	*Cretohexura coylei*	Eskov and Zonshtein, 1990	Semyon Creek (Russia)	Mecicobothriidae	Atypoidea *incertae sedis*
125-113	*Cretomegahexura platnicki*	Eskov and Zonshtein, 1990	Bon-Tsagan Lake (Mongolia)	Mecicobothriidae	Megahexuridae
125-113	*Cretacattyma raveni*	Eskov and Zonshtein, 1990	Bon-Tsagan Lake (Mongolia)	Antrodiaetidae	Antrodiaetidae
125-113	*Ambiortiphagus ponomarenkoi*	Eskov and Zonshtein, 1990	Bon-Tsagan Lake (Mongolia)	Atypidae	Atypoidea *incertae sedis*

125-113	*Eocoddingtonia eskovi*	Selden, 2010	Zazinskaya Formation (Russia)	Theridiosomatidae	Araneoidea *incertae sedis*
115-110	*Cretaraneus martinsnetoi*	Vianna Mesquita, 1996	Crato Formation (Brazil)	Araneidae	?Araneidae
115-110	*Cretadiplura ceara*	Selden et al., 2006	Crato Formation (Brazil)	Dipluridae	Avicularioidea *incertae sedis*
115-110	*Dinodiplura ambulacra*	Selden et al., 2006	Crato Formation (Brazil)	Dipluridae	Avicularioidea *incertae sedis*
115-110	*Seldischnoplura seldeni*	Raven et al., 2015	Crato Formation (Brazil)	Dipluridae	Avicularioidea *incertae sedis*
115-110	*Cretapalpus vittari*	Downen and Selden, 2021	Crato Formation (Brazil)	Palpimanidae	Palpimanidae
113-100.5	*Atocatle ranulfoi*	Feldmann et al., 1998	Tlayua Formation (Mexico)	Araneae *incertae sedis*	Araneae *incertae sedis*
113-100.5	*Korearachne jinju*	Selden et al., 2012	Jinju Formation (South Korea)	Lycosoidea *incertae sedis*	Araneomorphae *incertae sedis*
113-100.5	*Koreamegops samsiki*	Park et al., 2019	Jinju Formation (South Korea)	Lagonomegopidae	Lagonomegopidae
113-100.5	*Jinjumegops dalingwateri*	Park et al., 2019	Jinju Formation (South Korea)	Lagonomegopidae	Lagonomegopidae

113-100.5	Entelegynae *incertae sedis*	Park et al., 2019	Jinju Formation (South Korea)	Entelegynae *incertae sedis*	Entelegynae *incertae sedis*
113-100.5	Entelegynae *incertae sedis*	Park et al., 2019	Jinju Formation (South Korea)	Entelegynae *incertae sedis*	Entelegynae *incertae sedis*
113-100.5	Palpimanoidea *incertae sedis*	Park et al., 2019	Jinju Formation (South Korea)	Palpimanoidea *incertae sedis*	Palpimanoidea *incertae sedis*
113-100.5	Araneomorphae *incertae sedis*	Park et al., 2019	Jinju Formation (South Korea)	Araneomorphae *incertae sedis*	Araneomorphae *incertae sedis*
113-100.5	Mygalomorphae *incertae sedis*	Park et al., 2019	Jinju Formation (South Korea)	Mygalomorphae *incertae sedis*	Mygalomorphae *incertae sedis*
86.3-100.5	Araneae *incertae sedis*	Rayner and Dippenaar-Schoeman, 1995	Orapa mine (Botswana)	Araneae *incertae sedis*	Araneae *incertae sedis*
83.6-72.1	Opistothelae *incertae sedis*	Cifuentes-Ruiz et al., 2006.	Cerro del Pueblo Formation (Mexico)	Opistothelae *incertae sedis*	Opistothelae *incertae sedis*

SYSTEMATIC PALEONTOLOGY

Order Araneae Clerck, 1757

Suborder Opisthothelae Pocock, 1892

Infraorder Mygalomorphae Pocock, 1892

Clade Avicularioidea Simon, 1874

Avicularioidea *incertae sedis*

***Rosamygale* Selden and Gall, 1992**

***Rosamygale grauvogeli* Selden and Gall, 1992**

Type specimens: Holotype AR11; paratypes AR1, AR8 and AR12 (Grauvogel-Gall Collection – Institut de Géologie, Université Louis Pasteur, Strasbourg, France).

Remarks: This species is classified as an avicularioid on the basis of its well-separated posterior lateral spinnerets and the absence of an abdominal scutum. It was originally placed in Hexathelidae, but the family has been reviewed and redelimited since then, and none of the specimens presents synapomorphies of any extant family. This species is here placed as Avicularioidea *incertae sedis*.

***Dinodiplura* Selden, 2006**

***Dinodiplura ambulacra* Selden, 2006**

Type specimens: Holotype SMNK-PAL.3995 part (Staatliches Museum für Naturkunde, Karlsruhe, Germany) and MPSC A883 counterpart (Museu de Paleontologia Plácido Cidade Nuvens, Santana do Cariri, Ceará, Brazil). Allotype F1417 ⁄ SAN ⁄ AR ⁄ DIP ⁄CJW (Jörg Wunderlich private collection, Hirschberg, Germany) [this allotype has been later re-classified as the holotype of *Seldischnoplura seldeni* by Raven et al. (2015)].

***Cretadiplura* Selden, 2006**

Cretadiplura ceara Selden, 2006

Type specimens: Holotype MB.A.979 (Museum für Naturkunde der Humboldt-Universitat Berlin, Berlin, Germany), Allotype A11 (Laboratório de Geociências, Universidade Guarulhos, São Paulo, Brazil).

Seldischnoplura Raven, Jell, Knezour, 2015

Seldischnoplura seldeni Raven, Jell, Knezour, 2015

Type specimen: Holotype (allotype of *Dinodiplura ambulacra*), F1417/SAN/AR/DIP/CJW (Jörg Wunderlich private collection, Hirschberg, Germany).

Remarks: The three species above can be assigned to Avicularioidea based on the lack of an abdominal scutum, and were originally placed in Dipluridae. The family has been reviewed and redelimited since then, and none of the specimens can be classified with certainty to family level, although a placement in Euagridae has been suggested by Raven et al. (2015) and should be considered upon re-study of the original specimens. There species are here classified as Avicularioidea *incertae sedis*.

Clade Atypoidea Simon, 1874

Atypoidea *incertae sedis*

Cretohexura Eskov and Zonshtein, 1990

Cretohexura coylei Eskov and Zonshtein, 1990

Type specimen: Holotype PIN 2385/418 (Mesozoic Arachnida collection, Paleontological Institute of the Russian Academy of Science, Moscow, Russia).

Remarks: This species can be assigned to Atypoidea based on the presence of abdominal sclerites and a conductor on the male palp. It was originally placed in Mecicobothriidae, but the family has been reviewed and redelimited since then, and no synapomorphies of extant families were preserved on the specimen. This species is here placed as Atypoidea *incertae sedis*.

***Ambiortiphagus* Eskov and Zonshtein, 1990**

***Ambiortiphagus ponomarenkoi* Eskov and Zonshtein, 1990**

Type specimen: Holotype PIN 3559/5764 (Mesozoic Arachnida collection, Paleontological Institute of the Russian Academy of Science, Moscow, Russia).

Remarks: This species can be assigned to Atypoidea based on the presence of an abdominal sclerite. It was originally placed in Atypidae, but family has been reviewed and redelimited since then, and no synapomorphies uniting the fossil to Atypidae or other extant family were preserved. This species is here placed as Atypoidea *incertae sedis*.

Family Megahexuridae Hedin and Bond, 2019

***Cretomegahexura* Eskov and Zonshtein, 1990**

***Cretomegahexura platnicki* Eskov and Zonshtein, 1990**

Type specimens: Holotype PIN 3559/5763, paratypes PIN 3559/5760 and PIN 3559/5761 (Mesozoic Arachnida collection, Paleontological Institute of the Russian Academy of Science, Moscow, Russia).

Remarks: This species can be assigned to Atypoidea based on the presence of an abdominal sclerite. It was originally placed in Mecicobothriidae, but the family has been reviewed and redelimited since then, and a new family, Megahexuridae, was erected. *Cretomegahexura* has expanded pleurites at posteriolateral corners of the carapace, which are consistent with this family. This species is here placed within Megahexuridae.

Infraorder Araneomorphae Pocock, 1892

Araneomorphae *incertae sedis*

***Zhizhu* Selden, Ren and Shih, 2016**

***Zhizhu daohugouensis* Selden, Ren and Shih, 2016**

Type specimens: Holotype: NIGP151720a,b, allotype: NIGP151716a,b, paratypes: NIGP151717a,b, NIGP151718, NIGP151719a,b, NIGP151721a,b and NIGP151722 (Nanjing Institute of Geology and Palaeontology, Nanjing, China).

Remarks: This species was originally placed as a “Deinopoidea” *incertae sedis*, but this group has shown to be non-monophyletic. The specimens cannot be classified as Entelegynae with certainty as well, and they lack synapomorphies of any extant family, so this species is here placed as Araneomorphae *incertae sedis*.

Korearachne **Selden, Nam, Kim and Kim, 2012**

Korearachne jinju **Selden, Nam, Kim and Kim, 2012**

Type specimen: TSH-0808 (Jeju World Natural Heritage Center of Korea, Daejeon, South Korea).

Remarks: This species was tentatively placed in the superfamily Lycosoidea, but it lacks synapomorphies of this group and of any other spider family. This species is here placed as Araneomorphae *incertae sedis*.

Araneus **Clerck, 1757**

Araneus beipiaoensis **Chang, 2004**

Type specimen: Holotype ZH005 (Jilin University collection, Changchun, China).

Araneus liaoxiensis **Chang, 2004**

Type specimen: Holotype ZH002 (Jilin University collection, Changchun, China).

Araneus aethus **Chang, 2004**

Type specimen: Holotype ZH004 (Jilin University collection, Changchun, China).

Araneus reheensis **Chang, 2004**

Type specimen: Holotype ZH003 (Jilin University collection, Changchun, China).

Remarks: Those species were originally placed within the family Araneidae, but due to the lack of synapomorphies uniting the fossils to any extant family, this species is here placed as Araneomorphae *incertae sedis*. A redescription of these species is necessary for re-allocation in another genus, as they are misplaced in *Araneus*.

Gnaphosa **Latreille, 1804**

Gnaphosa liaoningensis **Chang, 2004**

Type specimen: Holotype ZH006 (Jilin University collection, Changchun, China).

Remarks: This species was originally placed within the family Gnaphosidae, but due to the lack of synapomorphies uniting the fossil to any extant family, this species is here placed as Araneomorphae *incertae sedis*. A redescription of this species is necessary for re-allocation in another genus, as it is misplaced in *Gnaphosa*.

Theridion **Walckenaer, 1805**

Theridion atalus **Chang, 2004**

Type specimen: Holotype ZH007 (Jilin University collection, Changchun, China).

Remarks: Those species were originally placed in the family Theridiidae, but due to the lack of synapomorphies uniting the fossil to any extant family, this species is here placed as Araneomorphae *incertae sedis*. A redescription of this species is necessary for re-allocation in another genus, as it is misplaced in *Theridion*.

Huergina **Selden and Penney, 2023**

Huergina diazromerali **Selden and Penney, 2023**

Type specimen: Holotype ADR-001-ARa,b (Museo del Instituto Tecnologico GeoMinero, Madrid, Spain).

Remarks: This specimen was originally assigned to Tetragnathidae, but due to the lack of synapomorphies uniting the fossil to any extant family, or superfamily, it is here placed as Araneomorphae *incertae sedis*.

Cretaraneus **Selden, 1990**

Cretaraneus liaoningensis **Cheng, Meng and Wang, 2008**

Remarks: Those species were originally placed in the family Araneidae, but due to the lack of synapomorphies uniting the fossil to any extant family, this species is here placed as Araneomorphae *incertae sedis*. A redescription of this species is necessary for re-allocation in another genus.

Family Juraraneidae Eskov, 1984

Juraraneus Eskov, 1984

Juraraneus rasnitsyni Eskov 1984

Remarks: The position of the family within Araneoidea is questionable. *Juraraneus* possesses a calamistrum, being thus a cribellate spider, which suggests this family may be distantly related to the superfamily. We suggest the removal of Juraraneidae from Araneoidea, being here placed as Araneomorphae *incertae sedis.*

Synspermiata *incertae sedis*

Eoplectreurys Selden and Huang, 2010

Eoplectreurys gertschi Selden and Huang, 2010

Type specimens: Holotype NIGP151720a,b; allotype: NIGP151716a,b; paratypes: NIGP151717a,b; NIGP151718; NIGP151719a,b; NIGP151721a,b; NIGP151722 (Nanjing Institute of Geology and Palaeontology, Nanjing, China).

Montsecarachne Selden, 2014

Montsecarachne amicorum Selden, 2014

Type specimens: Holotype, LC-3780 IEI A,B (part and counterpart); paratype LC-2936 IEI A,B (part and counterpart) (Institut d’Estudis Ilerdencs, Lleida, Spain).

Remarks: The two species above can be assigned to Synspermiata based on the palp form, and both were originally placed in Plectreuridae. The specimens lack synapomorphies uniting the fossil to any extant family, so both species are here placed as Synspermiata *incertae sedis*, although the possibly fused chelicerae of *M. amicorum* would suggest it may belong to the stem lineage of Pholcoidea + Scytodoidea (see MAGALHAES et al. 2020).

Entelegynae *incertae sedis*

Palaeouloborus Selden, 1990

Palaeouloborus lacasae Selden, 1990

Type specimen: Holotype LP 1755 AP (Institut d'Estudis Ilerdencs, Lérida, Spain).

Remarks: This species was originally placed in Uloboridae, but due to the lack of synapomorphies uniting the fossil to any extant family, this species is here placed as Entelegynae *incertae sedis*.

Macryphantes **Selden, 1990**

Macryphantes cowdeni **Selden, 1990**

Type specimen: Holotype LC 1753 APa,b; paratype LC 1754 APa,b (Instituí d'Estudis Ilerdencs, Lérida, Spain).

Remarks: This species was tentatively placed in Tetragnathidae, but due to the lack of synapomorphies uniting the fossil to any extant family, this species is here placed as Entelegynae *incertae sedis*.

Superfamily Araneoidea

Eocoddingtonia **Selden, 2010**

Eocoddingtonia eskovi **Selden, 2010**

Type specimens: Holotype PIN 3064/8593; allotype: PIN 4210/5463, PIN3064–8591, PIN4210/5461, PIN4210/5462, PIN 3064/8594 (Mesozoic Arachnida collection, Paleontological Institute of the Russian Academy of Science, Moscow, Russia).

Remarks: This species can be assigned to the superfamily araneoidea based on its general habitus (globose opisthosoma, epigyne and spinnerets close together ventrally), and was originally placed in Theridiosomatidae. The specimens lack synapomorphies of this family (the presence of sternal pits cannot be confirmed) and of any other extant family. Thus, this species is here placed as Araneoidea *incertae sedis*.

THE DIVERSITY OF FOSSIL SPIDERS

The fossil record is inherently biased and incomplete, presenting considerable difficulties for large-scale studies even in organisms with a high propensity to fossilize (DONOVAN; PAUL, 1998). Regarding spiders, it is evident that these gaps are even larger, particularly concerning their distribution over certain periods and/or localities. As a result, ecological responses of spiders to major geological, climatic and biological events are still not very clear.

The morphology of a fossil spider may sometimes be difficult to interpret. Additionally, in many groups morphological homoplasy is rampant (e.g., araneids, mygalomorphs). Combined, these two factors often lead to misclassification. It is noteworthy that the absence of certain characters on a specimen does not necessarily represent their absence on the organism original morphology, but may be a taphonomic-controlled bias (ALLISON; BOTTJER, 2010). Due to their rarity on the fossil record, it is common for many new spider taxa to be described on the basis of single specimens. In some cases, those specimens are poorly preserved, thus being impossible to assign to lower taxonomic ranks. However, they are still important as many represent the only record of that time span or locality (e.g. SELDEN, 1999). Several fossil spider species have been described and classified as members of extant families, often justified on combinations of plesiomorphic characters. These placements must be approached with caution, as the erroneous classification of fossil species within certain families result in inaccurate calibration points for molecular clocks and other evolutionary timelines (MAGALHAES et al., 2020).

Along the Triassic, mygalomorphs appear to be more abundant than araneomorphs (Figure 2A). One representative of Atypoidea and two Avicularioidea are known, and with the exception of a dubious Dipluridae, no classification within those clades is possible. Both araneomorph species cannot be assigned to any classification beyond infraorder. Thus, considering the scarcity of known species, it is difficult to estimate spider diversity during this period.

Jurassic spiders are twice more diverse than Triassic ones, with a fauna dominated by araneomorphs, as no mygalomorphs are known from this time range (Figure 2B). 69% of all records are from the same location, the Daohugou fossil beds in China. The main representatives are the palpimanoids (53,8%), and it is also the first time the superfamily appears on the fossil record. It also contains the oldest records of Archaeidae, which is indeed the oldest confirmed record of any still extant family. Cribellate orb-weavers (Uloboridae) are also present during that time, being also the only Jurassic spider from the Southern Hemisphere.

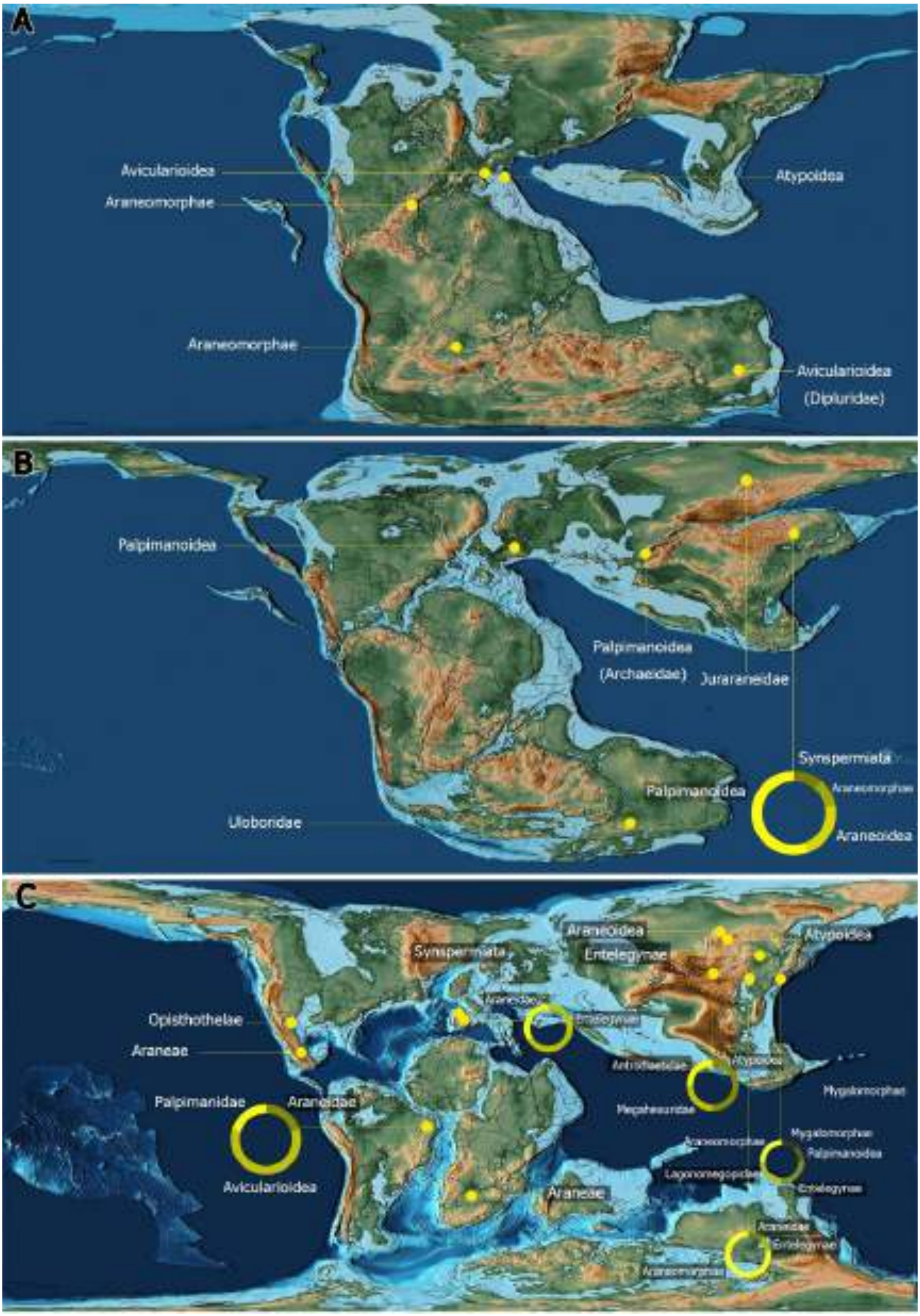
The presence of a large number of Palpimanoidea representatives in Jurassic strata might be influenced by the establishment of a warm temperate climate, similar to the ecological preferences of extant palpimanoids (GRÖCKE et al., 2003). Despite the fossil record pointing to an eastern Laurasia limited occurrence, the current distribution of certain families, including Archaeidae, along with divergence dating studies, suggests a broader range in the past (WOOD; WUNDERLICH, 2023).

The Cretaceous exhibits even greater diversity, with more than thirty records in rock matrices, predominantly araneomorphs (68,57%) (Figure 2C). At the time of the Early

Cretaceous greenhouse, fossil sites that preserve spiders were numerous and scattered over the globe. This is likely reflected by, again, the expansion of temperate and tropical zones that culminated in the Late Jurassic-Early Cretaceous (GRÖCKE et al., 2003). Analyses by SHAO & LI (2018) indicate that spiders diversified during this period. The distribution of families varied considerably, and their presence and diversity can be observed in various deposits with a considerable number of records, such as the Aptian Crato Formation in Brazil, the Barremian Yixian Formation in China and the Albian Jinju Formation in South Korea. These deposits reveal a wealth of spider genera and species over time, suggesting changes in the composition of communities during different intervals. The oldest records of the Palpimanidae and Araneidae families date from Cretaceous rock-matrices, as well as the Antrodiaetidae mygalomorphs. Lagonomegopidae, an extinct family, was also described from this period. It should be noted that many other extant spider families also have their oldest records in the Cretaceous, although in these cases only from amber deposits: Oonopidae, Psilodercidae, Tetrablemmidae, Pacullidae, Leptonetidae, Theridiidae, Oecobiidae and Hersiliidae (MAGALHAES et al. 2020).

Regarding the geographical distribution of Cretaceous records, the scenario is similar to the Jurassic: only 17% are described from Gondwanan deposits. Those are the Crato Formation in Brazil and the Upper Cretaceous of the Orapa Diamond Mine in Botswana, which yields a single poorly preserved specimen. This demonstrates the importance of continuous research on the Crato paleoaraneofauna, which contains numerous as yet undescribed specimens.

Figure 2. Distribuition of fossil spiders throughout the Mesozoic. (A), Triassic, (B), Jurassic, (C) Cretaceous. Maps were adapted from PaleoAtlas (SCOTESE, 2016) on GPlates.



PRESERVATION PATHWAYS OF FOSSIL SPIDERS

Fossil spiders in rock matrices are a rare example of exceptional preservation (SELDEN; PENNEY, 2010). The main reason for the limited data on fossil spiders, compared to other groups, is the lack of well-preserved terrestrial deposits where spider specimens can be found. The occurrence of spiders is considered to identify a fossil deposit as a *Konservat-Lagerstätte* or conservation deposit (Seilacher, 1970).

Lagerstätten with fossil spiders include diverse preservational modes associated with claystones, dolostones, shales, tuff, mudstones, siltstones and lithographic limestones, although it is the fine-grained, laminate, lacustrine deposits, that provides the most numerous and well-preserved specimens. Diagenetic minerals such as pyrite, carbonates, phosphates, and silica, commonly associated with exceptional preservation, have been observed in fossil spiders.

The rapid burial and chemical conditions that reduce bacterial activity on lacustrine deposits leads to exceptional preservation (BRIGGS, 2003). The chitinous cuticle of spiders belongs to a group known as structural polysaccharides (POLITI et al., 2021), which exhibit considerable resistance to degradation (BAAS et al., 1995). The permineralization of soft tissues, including refractory structures like chitin, occurs under specific early mineralization conditions that can preserve fine anatomical details, such as setae (ALLISON, 1988). The preservation of those delicate structures is essential for detailed comparison with recent taxa and correct taxonomic classification.

The oxygenation of the sedimentation environment also affects decomposition processes, with oxygen depletion leading to different chemical reactions that influence the preservation of organisms (ALLISON, 1988). Most fossil spiders are found in lacustrine or similar quiet-water deposits, where low energy environments prevent the mechanical destruction of fragile bodies, with rare exceptions on marine strata. Many sedimentary settings where fossil spiders are found also involve a significant amount of volcanic ash, potentially aiding their sinking to the lake floor (SELDEN; PENNEY, 2010). The controls on the preservation of spiders, as soft-bodied fossils, are more complex than those on hard skeleton, and they include organic matter input, microbial activity, and environmental geochemistry (DOWNEN et al., 2022; OLCOTT et al., 2022).

FUTURE DIRECTIONS

The preservational patterns of fossil spiders seem to be similar to other terrestrial arthropods, thus, it is not unexpected to find spiders in *Lagerstätten* with those organisms on its fauna. Some examples are the Triassic deposits where spiders are found: the three of them are all variations on the same fluvio-lacustrine theme: the Molteno formation having been laid down in an intracontinental basin, the Ipswich group in a small intramontane depression and the Cow Branch in a series of grabens (ANDERSON et al. 1998). It is known that the Triassic insect assemblage of Argentina (Potrerillos and Los Rastros formations) has a similar depositional setting, and its arthropod fauna is virtually identical with that of the Ipswich Series in Australia (GIOIA; GALLEGO; MELCHOR, 2003), so we predict that spiders could also occur on this locality.

Additionally, it is known that the Lower Cretaceous Khasurty location of Transbaikalia yields several undescribed spider specimens that were discovered in the last years (KOPYLOV et al., 2021). New expectable spider finds, along with the re-study of previously known specimens utilizing micro-CT and SEM techniques could give us a more accurate picture of the distribution of the Mesozoic spider fauna, as well as the pathways involved in their preservation.

CONCLUSIONS

The Mesozoic fossil record of spiders in rock-matrices comprises 5 Triassic, 13 Jurassic and 34 Cretaceous occurrences, and the most representative group are the araneomorphs, particularly the palpimanoids. The geological distribution of these occurrences, mainly concentrated on the Northern Hemisphere, highlights the importance of further studies in deposits in the Southern Hemisphere, such as the Brazilian Crato Formation. Fossil spiders are often preserved in lacustrine deposits, although they can also occur in marine strata. We suggest continued work on previously known deposits, exploring of potential spider-bearing deposits, and the reanalysis of described taxa. These approaches will increase the knowledge on the origin and distribution of several groups, and help elucidating their preservational pathways.

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CHAPTER TWO: ARANEOID SPIDERS FROM THE CRATO FORMATION, LOWER CRETACEOUS OF THE ARARIPE BASIN, BRAZIL.

ABSTRACT

The superfamily Araneoidea composes a large portion of known modern spider diversity, with its members exhibiting varied morphologies and behaviors. Those spiders are relatively common in the fossil record of the Crato Formation of Brazil, with exceptionally preserved specimens. Here, 46 fossil spiders were analyzed, and from those, 7 were described, providing additional data on the morphology of *Cretaraneus martinsnetoi* Mesquita, 1996, that illuminate its taxonomic placement. Additionally, two distinct species were identified and described, but despite their general appearance resembling araneoids, they could not be assigned with certainty to any known family. Thus, both specimens were attributed to Araneomorphae *incertae sedis*. Some of the specimens preserved cuticular microstructures hitherto not recorded in fossil spiders before, attesting the exceptional taphonomic conditions of the Crato Formation and its importance as one of the few Gondwanan *Lagerstätte* that preserves fossil spiders.

KEY WORDS: Fossil spider; Taxonomy; Taphonomy; *Lagerstatten*.

INTRODUCTION

The superfamily Araneoidea is a well-supported group of spiders composed of 17 families (DIMITROV et al., 2017), which represent more than 25% of all spiders described (HORMIGA; GRISWOLD, 2014). Araneoids exhibit a wide diversity of morphologies, behaviors, and web architectures, such as the true orb-weavers (Araneidae), sheet webs (e.g., Linyphiidae) or cobwebs (e.g., Theridiidae), adapting to diverse habitats worldwide. Their ecological role as insect predators contributes significantly to maintaining ecosystem balance (BLACKLEDGE; KUNTNER; AGNARSSON, 2011).

Araneoids are estimated to have a Jurassic origin (BOND et al., 2014), although the oldest reliable record is from the Lower Cretaceous (PENNEY; ORTUÑO, 2006). Besides the abundance of extant species, the fossil record of araneoids, as the fossil spider record in general, is scarce, due to their fragility and lack of mineralization, which hamper fossilization (SELDEN; PENNEY, 2010). The Crato Formation in Northeast Brazil preserves spiders, along with a diverse range of insects and other organisms replaced by goethite (BARLING et al., 2015). The Crato biota is composed of highly abundant fossils which often preserves soft tissues with fine details of its internal and external morphology (DIAS; CARVALHO, 2020;

FIELDING; MARTILL; NAISH, 2005; STORARI et al., 2024; VAREJÃO et al., 2019). This geological unit is particularly important for studying fossil arachnids, with specimens often better preserved than other Mesozoic shale records and sometimes easier to study than those in amber inclusions (DUNLOP; MENON; SELDEN, 2007). Dating back to the time of the Gondwana breakup, this geological unit is of considerable interest for understanding the biogeographical history of spiders throughout the Mesozoic era.

Currently, five spider species are known from the Crato Formation, one palpimanidae (*Cretapalpus vittari* Downen and Selden, 2021), three mygalomorphs (*Dinodiplura ambulacra* Selden, 2006, *Cretadiplura ceara* Selden, 2006, and *Seldischnoplura seldeni* Raven, Jell and Knezour, 2015) and one araneoid (*Cretaraneus martinsnetoi* Mesquita, 1996). Most of the undescribed specimens appear to be araneoids conspecific with *Cretaraneus martinsnetoi*, but the placement of the species within the genus is questionable. Until now, the only formally described specimen is the holotype, which is poorly preserved and provides limited information about the species. Here, we analyzed 46 fossil spider specimens from the Crato Formation, of which nine araneoid representatives were identified and described. Their taxonomic affinities were discussed, as well as their preservational patterns.

MATERIAL AND METHODS

All specimens come from the Lower Cretaceous (Aptian) Nova Olinda Member of the Crato Formation, northeast Brazil from quarries at Nova Olinda, Ceará Province, Brazil. A total of 46 specimens were analyzed (Table 1). The fossils are part of the collections of the Laboratório de Paleontologia da URCA (LPU), Museu de Paleontologia Plácido Cidade Nuvens (MPSC), and Coleção Paleontológica da Universidade Federal Rural de Pernambuco (UFRPE). Those with few visible morphological characters or preservation artifacts hindering their identification were not considered in the taxonomic study. Instead, they were classified solely as Araneomorphae *incertae sedis*.

In the Crato Formation, fossils are commonly found in two types of limestone. The first type is yellowish limestone, which often appears as an orange and friable material, making it easily damaged. This type of preservation is the most common in this geological unit and results from the replacement of the original cuticle by goethite (limonite) (MENON; MARTILL, 2007). The second type of limestone is grayish in color, and fossils found within it are generally black and more delicate. This grayish limestone is essentially a weathered version of the yellowish limestone. The original substitution mineral, likely an iron sulfide phase with carbonaceous material, underwent *in situ* oxidation over an extended period, resulting in the transformation of the material (BARLING et al., 2015). In the analyzed specimens, both states of preservation were observed.

The fossils were prepared mechanically using fine needles to remove the excess of rock matrix, followed by the methodology outlined by SELDEN (2003). This method involves the use of an "Aeroneedle", a preparation tool crafted using aquarium pumps and hypodermic needles, which removes surface layers of sediment and minute debris through air jets. For this study, the tool was adapted using bivolt InalaPOP inhalers and insulin needles with a 0.25 mm caliber. Following preparation, the fossils were measured using electronic calipers and examined under a stereomicroscope with an Opton digital camera attached to capture images. Some of the specimens were lightly wetted with water to enhance the contrast of the fossil with the matrix rock and facilitate the visualization of structures not easily seen when dry.

Micrographs of the specimens were obtained using a SU3500 scanning electron microscope. Regions of interest in the fossilized samples were imaged using a backscattered electron (BSE) detector, allowing for the acquisition of surface images with a three-dimensional character (BSE-3D), a result of the overlapping signals of topographic and compositional BSE contrast. The specimens were analyzed without any special preparation, maintaining the microscope chamber under low vacuum (100 Pa) to prevent surface sample charging. The micrographs were acquired using an electron acceleration voltage of 20 kV and a current of 18 μA.

Morphological analyses were conducted, where specimens were compared with existing paleoarachnological literature, and their taxonomic affinities were determined. All measurements are in millimeters. The symbol '+' following a measurement indicates a body part that is not fully visible. Abbreviations: fe-femur, pa-patella, ti-tibia, mt-metatarsus, ta-tarsus, AME-anterior median eyes, ALE-anterior lateral eyes, PME-posterior median eyes, PLE-posterior lateral eyes.

Table 4. A summary of all fossils analyzed.

Specimen	**Classification**	**Sex**	**Leg flexure**	**View**
LPU 447	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral
LPU 448	Araneomorphae *incertae sedis*	Undefined	Curled	Ventral
LPU 449 A/B	*Cretaraneus martinsnetoi*	Female	Curled	Ventral

LPU 897A/B	*Cretaraneus martinsnetoi*	Female	Curled	Dorsal
LPU 1078	*Araneomorphae* incertae sedis	Undefined	Curled	Ventral
LPU 1088	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral
LPU 1407	Araneomorphae *incertae sedis*	Undefined	Curled	Ventral
LPU 1478	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral
LPU 1596	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
LPU 1598 A/B	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
LPU 1599 A/B	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
LPU 1674 A/B	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
LPU 1675	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
LPU 1704	*Cretaraneus martinsnetoi*	Female	Extended	Dorsal
LPU 1788	*Cretaraneus martinsnetoi*	Female	Extended	Dorsolateral
LPU 1919	Araneomorphae incertae sedis	Undefined	Curled	Ventral
LPU 1920 A/B	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
LPU 1597	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
MPSC A4414	Nephilinae	Female	Extended	Ventral
UFRPE 5308 A/B	*Cretaraneus martinsnetoi*	Male	Curled	Ventral
MPSC A6856	Araneomorphae *incertae sedis*	Undefined	Curled	Ventral
MPSC A6855	Araneomorphae *incertae sedis*	Undefined	Curled	Ventral
MPSC A6853	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral

MPSC A6850	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
MPSC A6843	*Cretaraneus martinsnetoi*	Female	Extended	Dorsal
MPSC A6861	Araneoidea	Female	Curled	Dorsolateral
MPSC A6845	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral
MPSC A6840	Araneomorphae *incertae sedis*	Undefined	Curled	Ventral
MPSC A6847	*Cretaraneus martinsnetoi*	Undefined	Curled	Dorsal
MPSC A6846	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
MPSC A6830	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral
MPSC A 6839	*Cretaraneus martinsnetoi*	Undefined	Curled	Ventral
MPSC A6865	*Cretaraneus martinsnetoi*	Undefined	Curled	Dorsal
MPSC A6848	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
MPSC A6836	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
MPSC A6858	*Cretaraneus martinsnetoi*	Undefined	Curled	Dorsal
MPSC A6857	*Cretaraneus martinsnetoi*	Undefined	Curled	Dorsal
MPSC A6866 A/B	*Cretaraneus martinsnetoi*	Female	Curled	Dorsal
MPSC A6859	*Cretaraneus martinsnetoi*	Female	Curled	Dorsal
MPSC A6834	*Cretaraneus martinsnetoi*	Female	Curled	Ventral
MPSC A6852	*Cretaraneus martinsnetoi*	Female	Curled	Dorsal
MPSC A6868	Araneomorphae *incertae sedis*	Female	Curled	Ventral
MPSC A6854	*Cretaraneus martinsnetoi*	Undefined	Curled	Dorsal
MPSC A6835	*Cretaraneus martinsnetoi*	Female	Curled	Dorsal
MPSC A6867	*Cretaraneus martinsnetoi*	Undefined	Extended	Dorsal

MPSC A6869	Araneomorphae *incertae sedis*	Undefined	Curled	Ventral

RESULTS AND DISCUSSION

Out of the 46 specimens analyzed, nine could not be classified at the level of superfamilies, families, genera, or species, and were thus defined as Araneomorphae *incertae sedis*. Most spiders, totaling 35 specimens, are representatives of *Cretaraneus martinsnetoi*, predominantly composed of females and juveniles arranged ventrally. Only one male was identified. Along with six females, those with better preservation, this male was described in this study, highlighting characteristics of both the ventral and dorsal views of the species. Additionally, two clearly distinct species were described here, although their preservation is poor and no classification beyond Infraorder was possible.

SYSTEMATIC PALEONTOLOGY

Order Araneae Clerck, 1757
Suborder Opisthothelae Pocock, 1892
Infraorder Araneomorphae Smith, 1902
Araneomorphae *incertae sedis*

Material: MPSC A6861, lateral view (Figures 3 and 4).

Description: Medium-sized araneomorph spider, possibly a female. Carapace oval-shaped, longer than wide, length 2.83, width 1.71. Chelicerae massive, without a lateral boss or a stridulating area (Figure 4A). Thin palps, unmodified, length 1.28. Palpal claw not visible. Rounded opisthosoma, setose (Figure 4B), largest at median area, length 2.86, width 2.13. Both legs III missing. Macrosetae on fe, pa, mt (Figure 4C). Podomere lengths: Leg I fe 5.74, pa 0.95, ti 6.08, mt 5.02, ta 1.53; Leg II fe 4.62, pa 0.80, ti 5.01, mt 5.8; Leg IV fe 5.80, pa 1.02, ti 4.86, mt 5.89, ta 1.59.

Remarks: MPSC A6861 clearly differs from other araneomorphs of the Crato Formation by the different proportions of the cephalotorax and legs, which are slender, have smaller patella and longer tibia. The habitus and general body shape resembles many families of different major groups as Pholcidae, Drymusidae, and several araneoids, including Linyphiidae, Nesticidae, Pimoidae and Synotaxidae. Pholcids have a pseudosegmented tarsi, which the specimen lacks, and most linyphiid and pimoid species have stridulatory striae on the chelicerae. No tarsal claws or eyes are visible, making classification difficult. Based on the known characters, it is not possible to assign this spider to any of these families or any major group with certainty. Thus, we here classify it as Araneomorphae *incertae sedis*.

Figure 3. MPSC A6861, dorsolateral view. Scale bar= 2 mm.

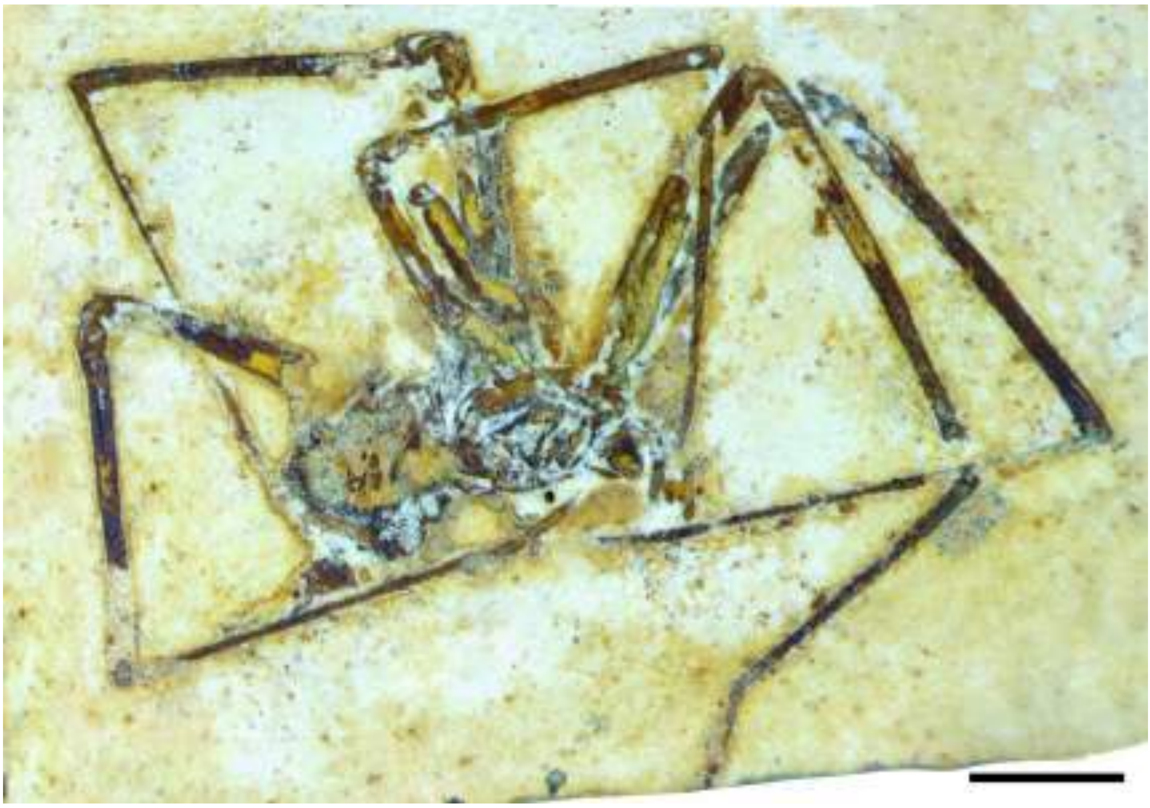

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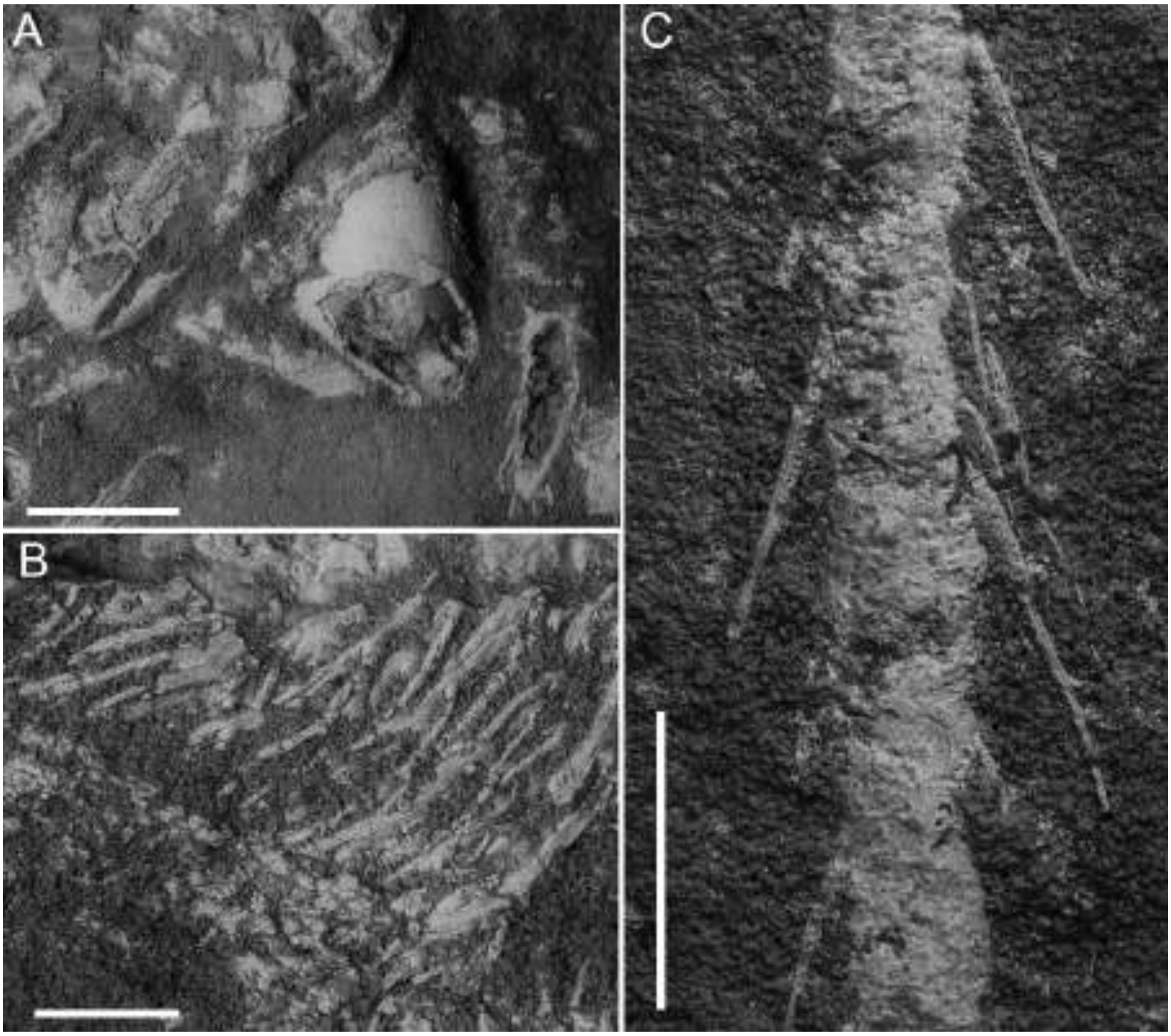
Figure 4. MPSC A6861, micrographs. A, chelicerae, scale bar: 500 µm; B, setae insertions on opisthosoma, scale bar: 200 µm; C, macrosetae on mt IV, scale bar: 300 µm.



Material: MPSC A4414, ventral view (Figure 5).

Description: Large araneomorph spider. Total length: 38.2, including legs. Carapace longer than wide, oval shaped, length 4.31, width 2.73; palp thin, length 3.60. Palpal claw not visitble. Subtriangular sternum. Abdomen length 5.89, width 3.13, tapering posteriorly. Very long first pair of legs (2.5x the size of the body); few setae on legs. Podomere lenghts: Leg I fe 8.31, pa 1.80, ti 6.88, mt 7.04, ta 2.07; Leg II fe 4.99, pa 1.24, ti 3.64, mt 3.62, ta 2.51; Leg III fe 3.37, pa 0.74, ti 2.03, mt 2.64, ta 1.22; Leg IV fe 4.44, pa 1.28; ti 3.60, mt 2.73, ta 1.83.

Remarks: MPSC A4414 clearly differs from the other specimens analyzed, mainly by its larger size. Although many parts of the fossil are missing, such as the initial portion of the femur, almost all tarsi, and the opisthosoma, these areas can be delineated through impressions, suggesting that these missing portions may have been preserved in an unknown counterpart. The overall size and a long, tapering abdomen are characters similar to some modern

Nephilinae, such as *Nephilengys* Koch, 1872 and *Nephila* Leach, 1815. However, the specimen is poorly preserved and lacks characters useful to a secure classification. Therefore, the specimen is classified as Araneomorphae *incertae sedis*.

Figure 5. MPSC A4414, ventral view. Scale bar= 4 mm.

Superfamily Araneoidea Latreille, 1806

Family Araneidae Clerck, 1757

Araneidae *incertae sedis*

Cretaraneus martinsnetoi Mesquita, 1996

Cretaraneus martinsnetoi Mesquita, 1996: 25, fig. 2, plates I–III (holotype female from outcrops in Fazenda Tatajuba, Santa Formation, Araripe Basin, Ceará, Brazil, deposited in Coleção Paleontológica do Departamento de Geociências da Universidade Guarulhos, UnG/1T-50, not examined); Dunlop et al. 2007: 106, fig. 9.1.

Diagnosis. Araneoid spiders with subelliptical carapace; subtriangular sternum; small, subtriangular labium; macrosetae on patella.

Remarks. This species was hitherto known only from the holotype. Below, we present descriptions and information of several additional specimens assigned to this species.

Material: UFRPE 5308A/B, ventral view (Figures 6, 7).

Description: Subadult male. Total length: 7.17, including legs. Rounded carapace, setose, longer than wide, length 2.45, width 1.91. Abdomen length 2.56, width 1.84. Subtriangular sternum wider at the anterior margin, subtriangular labium; chelicerae rounded; eight eyes arranged in two simple rows of four (Figure 6D), pedipalps swollen (Figure 6A); legs I and II robust in femur, patella, and tibia, slender in metatarsus and tarsus; macrosetae on the tibia and metatarsus; legs III and IV strongly curved, details of the podomeres cannot be defined A pair of book lungs is visible. Eye diameters: AME 0.10, PME 0.10, PLE 0.10. Distance between eyes: AME–ALE 0.20, AME–AME 0.20, PME–PLE 0.29, PME–PME 0.28, ALE–PLE 0.17, AME–PME 0.16. Podomere lengths: Leg I fe 3.77, pa 1.07, ti 3.15, mt 3.40, ta 0.76; Leg II fe 2.93, pa 0.94, ti 2.18, mt 2.42, ta 0.80; Leg III fe 1.25+; Leg IV fe 1.76, pa 0.38, ti 0.88+.

Figure 6. UFRPE 5308, A, part and B, counterpart. Scale bars= 2 mm.

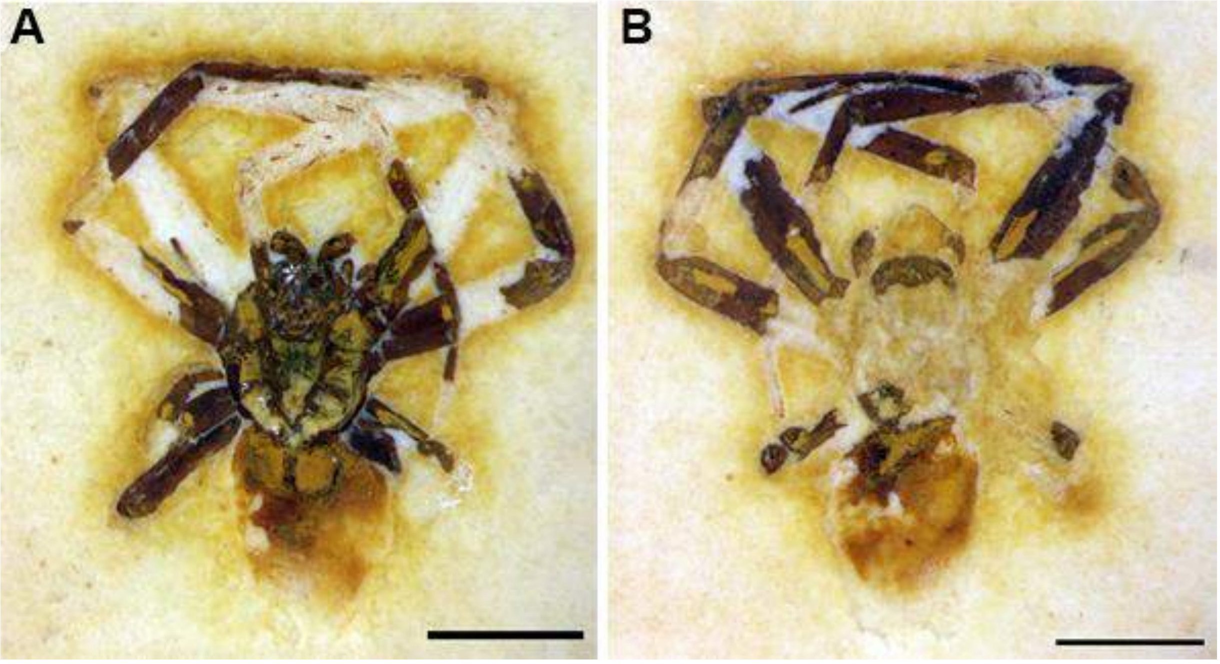
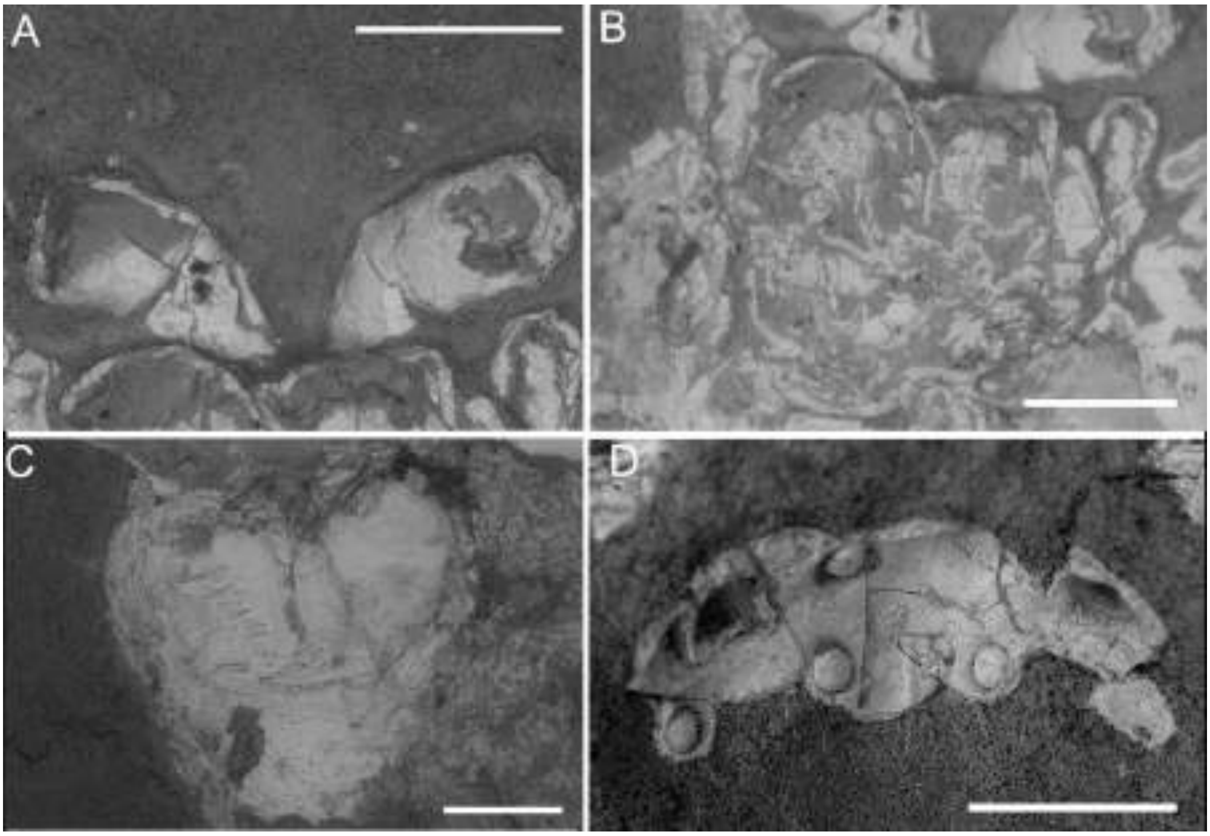


Figure 7. UFRPE 5308 micrographs. A, swollen palps, B, anterior margin of cephalotorax, C, opisthosoma, D, details of eyes. Scale bars: 500 µm.

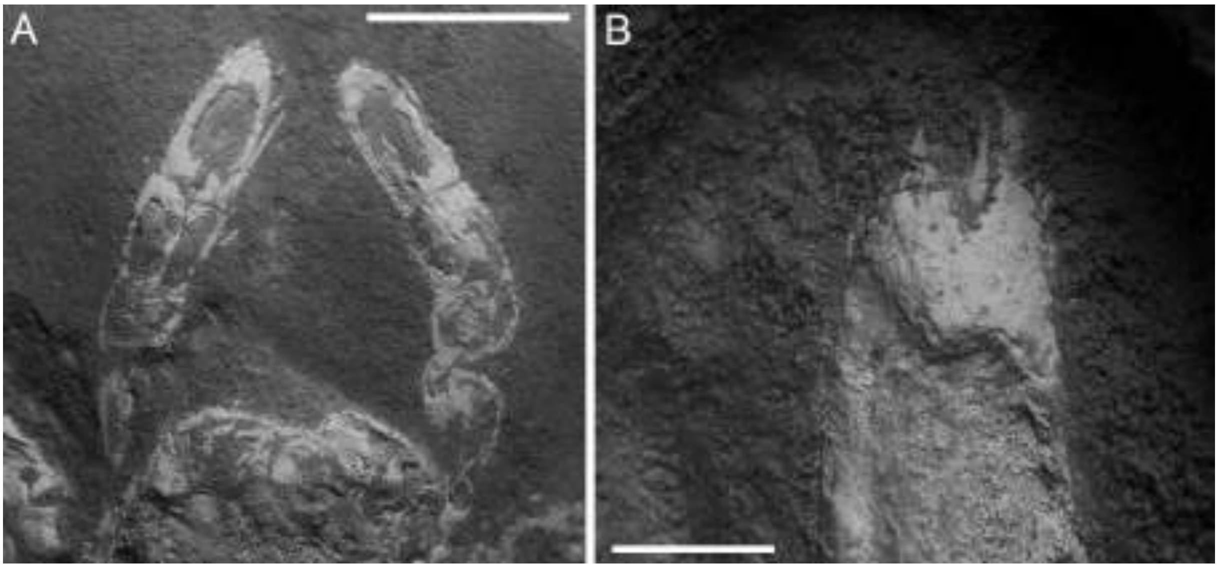


Material: LPU 1704, dorsal view (Figures 6, 7).

Description: Female. Total length 23.22, including legs. Pedipalps with macrosetae, fe 0.63, pa 0.41, ti 0.50, ta 0.75; oval carapace, length 3.23, width 2.13; oval-shaped abdomen, length 3.56, width 2.37; all legs are preserved, sparse, with macrosetae along the tibia and patella, and fine setae on the tibia, patella, metatarsus, and tarsus. Three tarsal claws are visible on leg III (Fig. 9B). Podomere lengths: Leg I fe 4.12, pa 1.21, ti 2.93, mt 3.59, ta 1.47; Leg II fe 3.36, pa 1.06, ti 2.10, mt 2.70, ta 1.22. Leg III fe 1.70, pa 0.60, ti 1.28, mt 1.33, ta 0.87; Leg IV fe 2.42, pa 0.76, ti 1.83; mt 2.06, ta 0.81.

Figure 8. LPU 1704, dorsal view. Scale bar= 3 mm.

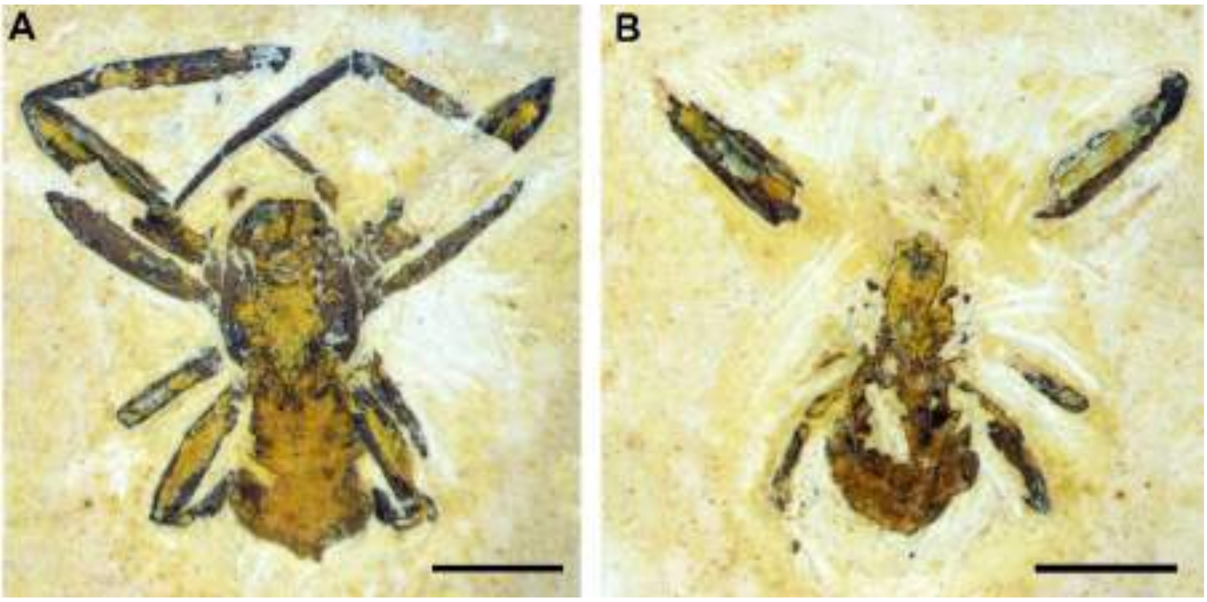
Figure 9. LPU 1704, A, detail of palp with macrosetae, B, tarsus III showing tarsal claws. Scale bars, A = 1 mm, B= 100 μm.



Material: LPU 897 A/B, dorsal view (Figure 10).

Description: Female. Pedipalps partially preserved (length 1.01); oval carapace, longer than wide, length 4.36, width 3.35; raised cephalic area; oval abdomen, longer than wide, length 4.27, width 3.45; all pairs of legs are present, however, incomplete and curved; impressions of setae can be easily visualized in the regions of the legs that were removed/lost, as well as macrosetae along the tibia; posterior spinnerets are visible. Podomere lenghts: Leg I fe 6.54, pa 1.84, ti 4.67, Leg II fe 6.48+, ti 3.24+, mt 3.72, ta 1.78; Leg III fe 2.91+, Leg IV fe 3.94+, pa 0.88.

Figure 10. LPU 897, ventral view, A, part, B, counterpart. Scale bar= 3 mm.



Material: LPU 1088, ventral view (Figures 11, 12).

Description: total length 9.25, including legs. Oval carapace, partially preserved, longer than wide, length 1.63+, width 1.57; oval abdomen, longer than wide, length 2.20, width 1.68, a pair of book lungs is visible, lamellae observable under SEM (Fig. 12D). No impression of epigyne or spermathecae visible under SEM (Fig. 12C), although a cuticular fold uniting both booklungs is present. Circular sclerotized area at the posterior margin of abdomen, possibly internal impression of spinnerets; only legs I, II, and IV are preserved, curved, with fine setae visible along the tibiae, metatarsus, and tarsus, in the form of impressions. Podomere lenghts: Leg I fe 2.01, pa 0.67, ti 2.54, mt 2.33, ta 0.57; Leg II fe 1.54, pa 0.40, ti 1.61, mt 1.37, ta 0.54; Leg IV fe 1.32, pa 0.31, ti 1.05, mt 1.03.

Figure 11. LPU 1088, ventral view. Scale bar= 3 mm.

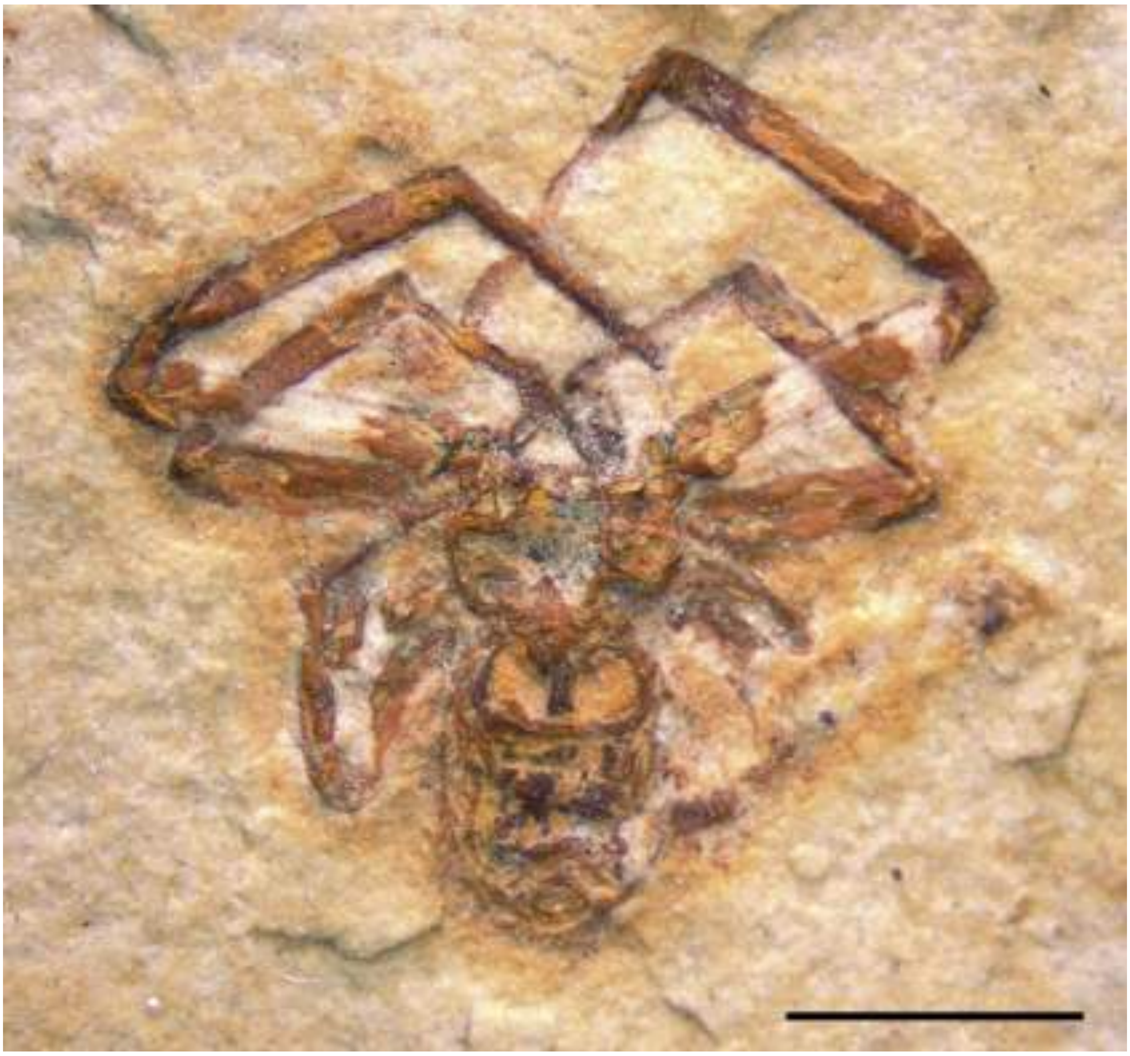
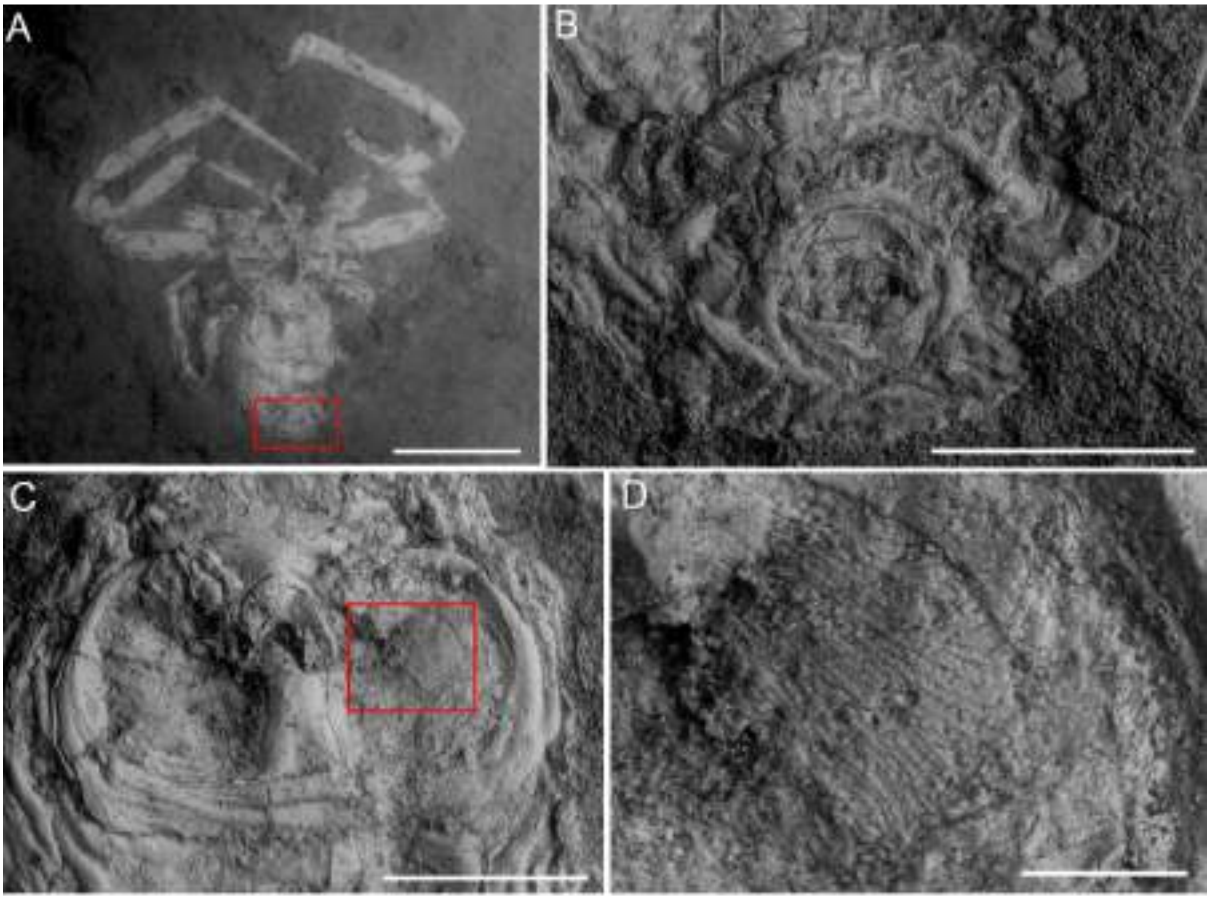


Figure 12. LPU 1088, micrographs. A, overview, B, spinnerets, C, book lungs and D, book lung lamellae. Scale bars= A, 2mm; B, C, 500 µm; D, 100 µm.



Material: LPU 1596, ventral view (Figures 13, 14).

Description: Female. Total length 10.16, including legs. Rounded and large chelicerae, pedipalps partially preserved, length 2.48; carapace partially preserved, oval shaped, length 3.16, width 3.53; labium wider than long, length 0.43, width 0.69; subtriangular sternum, longer than wide, length 1.75, width 0.97; oval-shaped abdomen, longer than wide, slightly narrower in the anterior region, length 3.94, width 2.73; all legs are preserved, however, incomplete; coxae are visible on both sides. Podomere lengths: Leg I fe 4.70, pa 1.15, ti 4,48+; Leg II fe 3.37+; Leg III fe 2.26; pa 0.92+; Leg IV fe 3.63, pa 1.07, ti 1.19+. Impressions of setae observable under SEM in the cuticle of the palps, labium, legs and sternum. Genital region swollen between the booklungs but with no observable epigyne (Fig. 14B).

Figure 13. LPU 1596, ventral view. Scale bar= 3 mm.

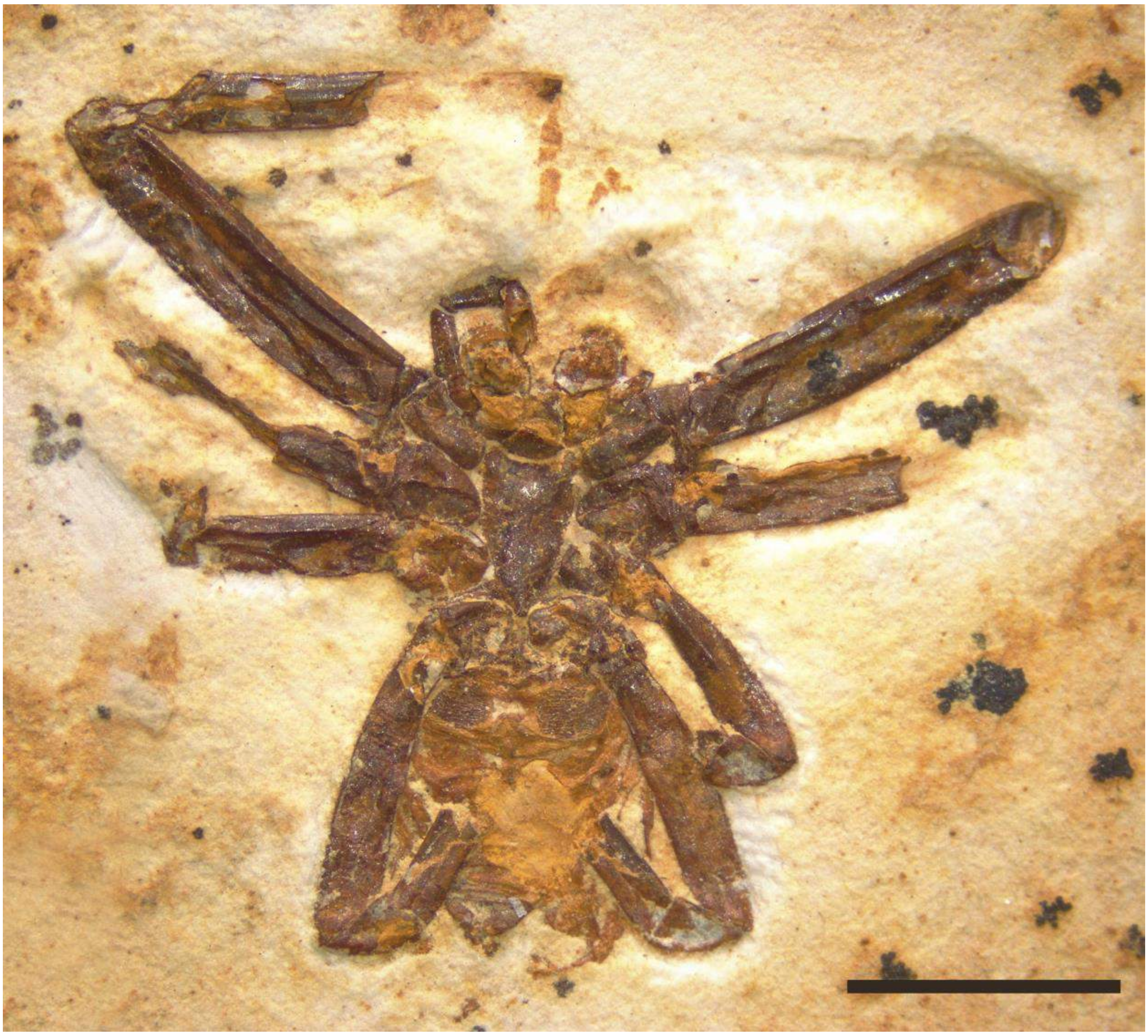
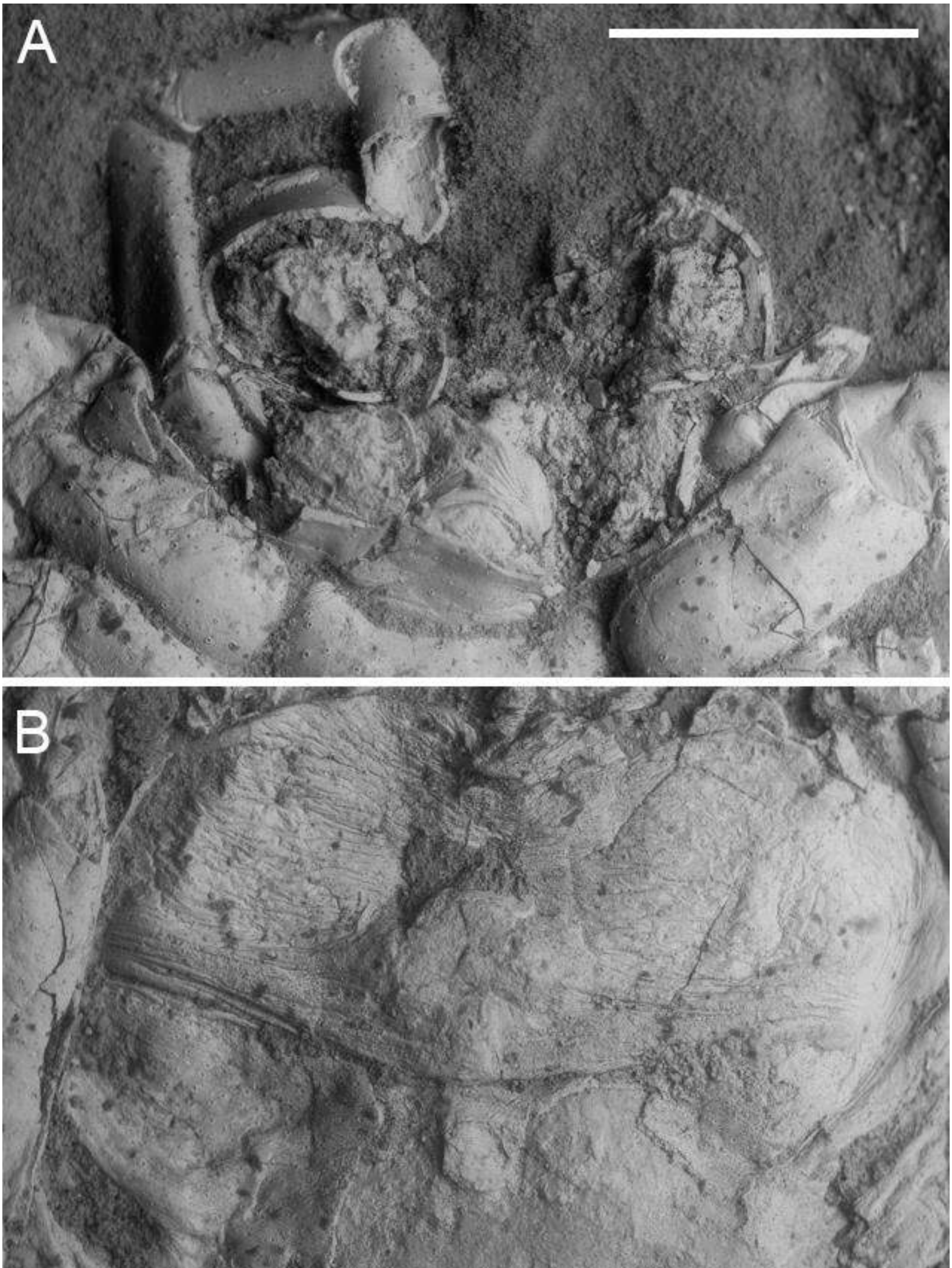


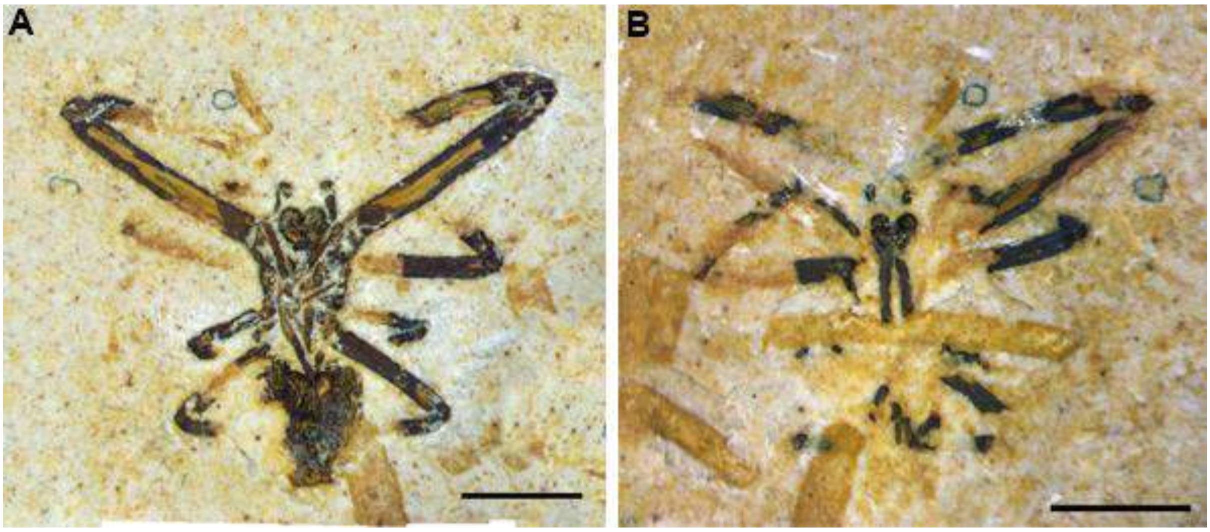
Figure 14. LPU 1596 micrographs. A, details of palp and mouthparts; B, epigastric furrow and book lungs. Scale bars= 1 mm.



Material: LPU 1674 A/B, ventral view (Figure 15).

Description: Female. Total length 5,52, including legs. Oval carapace, partially preserved, longer than wide, length 1.75, width 1.49; rounded and large chelicerae, thin palps partially preserved, length 0.69, labium subtriangular; wide and stout maxillae; oval-shaped opisthosoma, longer than wide, length 2.61, width 1.79. All legs are preserved, curved over the cephalothorax. Podomere lengths: Leg I fe 3.69, pa 0.73, ti 2.97+; Leg II fe 2.37, pa 0.51, ti, mt, ta; Leg III fe 1.48; pa 0.28, Leg IV fe 2.18, pa 0.50.

Figure 15. LPU 1674 (A), part and (B), counterpart. Scale bars= 2 mm.



Material: MPSC A6854, dorsal view (Figures 16, 17, 18, 19).

Description: Total length 7.82, including legs. The palps are curled down the body, so it is not possible to determine if a male or female. Carapace oval-shaped, setose, length 2.37, width 2.09. Opisthosoma oval-shaped, length 3.21, width 2.12. A pair of book lungs is visible. All legs are preserved, curled under the body. Slit sensilla are visible on the mt of leg IV (Fig. 17). Podomere lengths: Leg 1 fe 3,44; pa 0,96; ti 2,77; mt 2,92; ta 0,97+. Leg 2 fe 2,44; pa 0,82; ti 1,87; mt 2,12. Leg 3 fe 1,42; pa 0,55. Leg 4 fe 1,81.

Figure 16. MPSC A6854, dorsal view. Scale bar= 2 mm.

Remarks: UFRPE 5308, LPU 1704, LPU 897, LPU 1088, LPU 1596, LPU 1674 and MPSC A6854 are considered conspecific with *Cretaraneus martinsnetoi* based on the general shape of cephalothorax and opisthosoma, leg proportions and the presence of macrosetae on patella. Those specimens provide additional data on the morphology of the species. The Crato spider *Cretaraneus martinsnetoi* was defined based on *Cretaraneus vilaltae* Selden, 1999, an araneoid spider described by a single specimen from the Lower Cretaceous of Spain, and it is characterized by several shared characters with specimens from the Crato Formation, such as the subelliptical/oval carapace, a raised cephalic area, subtriangular sternum and labium, and abundant fine setae. However, as pointed out by Dunlop, Menon and Selden (2007), some inconsistencies are noted regarding the placement of this species within the genus *Cretaraneus*, with the most clearly visible distinguishing character being the length of the legs: whereas in *Cretaraneus* Selden, 1990, the legs are relatively equal in size (about three times the length of carapace); in the specimens described here, legs I is noticeably longer (at least 3x the cephalotorax length), while leg III is shorter (walking leg formula 1243), besides the presence of macrosetae on the patella. It is impossible to compare the male palp morphology between the Crato species and *Cretaraneus* Selden, 1990, as the only male identified, UFRPE 5308, is a subadult with no distinguishable palpal sclerites, but based on the known characters, it is evident that the two species do not belong to the same genus.

Cretaraneus was initially placed within the family Nephilidae, which was later reclassified as a subfamily of Araneidae (Nephilinae). The Crato specimens indeed exhibit characteristics suggestive of araneids, such as the legs with numerous macrosetae, a walking formula 1243 and tarsi with three tarsal claws, a labium wider than long, a subtriangular sternum, and shape of the abdomen, but there is not enough evidence that these spiders belong to the Nephilinae subfamily. The posterior median eyes are well separated (more than one PME diameter), a character from all nephilines, but also present in other genera within Araneidae. PLE size is equal than PME, differing from *Clitaetra*, certain *Nephila*, *Herennia* and *Argiope*. Therefore, we suggest here that Crato spiders be classified as Araneidae *incertae sedis*. In order to reclassify the species at a generic level, a redescription of the holotype would be advisable. It is not done here, as we did not have access to the specimen.

TAPHONOMY

The specimens studied here exhibited a three-dimensional preservation, or at the very least, partial preservation with minimal compaction, contrasting to the compression fossils of most other lacustrine deposits (e.g. PARK; NAM; SELDEN, 2019). Most spiders also showed complete and articulated bodies and appendages. It is uncommon to encounter arthropods in a complete yet disarticulated state, indicating the likelihood of rapid burial, or possibly bacterial sealing as suggested by Briggs and Gall (1990), which would have prevented disintegration on the lagoon floor. Such high-quality preservation implies minimal transport distance under aggressive regimes, swift descent to the lagoon floor, and limited or negligible decay during transportation. Scavenging during transport must have been minimal or absent, and burial or sealing processes must have been rapid. The circumvention of these processes likely characterized the prevailing conditions in the spider setting of the Crato Formation.

The preservation of soft tissues is a rare occurrence and typically requires mineralization processes to outpace degradation (BRIGGS, 2003). Various taphonomic processes contribute to exceptional preservation, including silicification, phosphatization, pyritization, aluminosilicification, and preservation by carbonate minerals (MUSCENTE et al., 2017). In *Lagerstätte* deposits, animal and plant tissues are often finely preserved, capturing high-quality details and organic structures such as internal organs, integument, feathers and muscle fibers (VAREJÃO et al., 2019). Consequently, organic structures such as internal organs (MUSCENTE et al., 2017) can be found.

Barling et al. (2015) proposed that a specimen can be deemed exceptionally well preserved if it exhibits delicate morphological features, such as fine setae, and if it retains fabrics resulting from decomposition and other taphonomic processes. Non-cuticular soft tissues, such as muscles, are typically preserved as replacements by apatite minerals (MENON; MARTILL, 2007). SEM analyses showed that the Crato spiders exhibit a remarkable degree of morphological fidelity. The specimen MPSC A6854 shows both macroscopic and microscopic anatomical features, along with mineralization of cuticular regions and internal soft tissues. Lyriform organs, a precise assembly of stress detecting cuticular slit sensilla, was found on the patella of leg IV (Figure 17B). The specimen also showed diverse textures and surfaces on the abdomen that could represent putative remains of fine cuticular structures of the book lungs, such as a pilate trabeculae (Figure 18B), and an arbuscular-reticulate atrium wall (Figure 18C). Those structures are morphologically consistent with those found in araneomorph spiders (KÜNTZEL; DUNLOP; SCHOLTZ, 2019). The same specimen also shows distinct honeycomb-shaped structures right above the spinnerets (Figure 19B). In solifugae, it is known that similar structures represent the epicuticle of large tracheae (FRANZ-GUESS; STARCK, 2016), but those were not studied in spiders until now. It could also represent the openings of the fusulas of a cribellum, and that would indicate that the spider is not an araneoid. In any case, further analyses of this structures are necessary, and by the moment, remains an enigma.

The Crato Formation preserves spiders, along with a wealth of insects and other organisms, through an unusual replacement with goethite (iron hydroxide) or hematite within the limestone (BARLING et al., 2015). In most lagoonal and lacustrine limestones, organisms are typically preserved as organic fragments. The primary components of spider cuticle are polysaccharide chitin linked to proteins, which can vary across distinct regions of the cuticle (POLITI et al., 2021). Taphonomic processes in arthropods typically result in a depolymerization of chitin-protein chains into a substance resembling kerogen. However, original chitin may sometimes be identified through geochemical analysis (CODY et al., 2011).

It has been proposed that the remarkable preservation of fossils within the laminated carbonates of this unit may be attributed to the organic mediation of microorganisms, particularly bacteria, which are immersed in a polysaccharide matrix within microbial mats (VAREJÃO et al., 2019), forming a microbial sarcophagus and the subsequent mineralization of organic remains (DIAS; CARVALHO, 2020, 2022).

Figure 17. A, patella IV of MPSC A6854, B, close up showing slit sensilla. Scale bars= A, 500 µm, B, 100 µm.

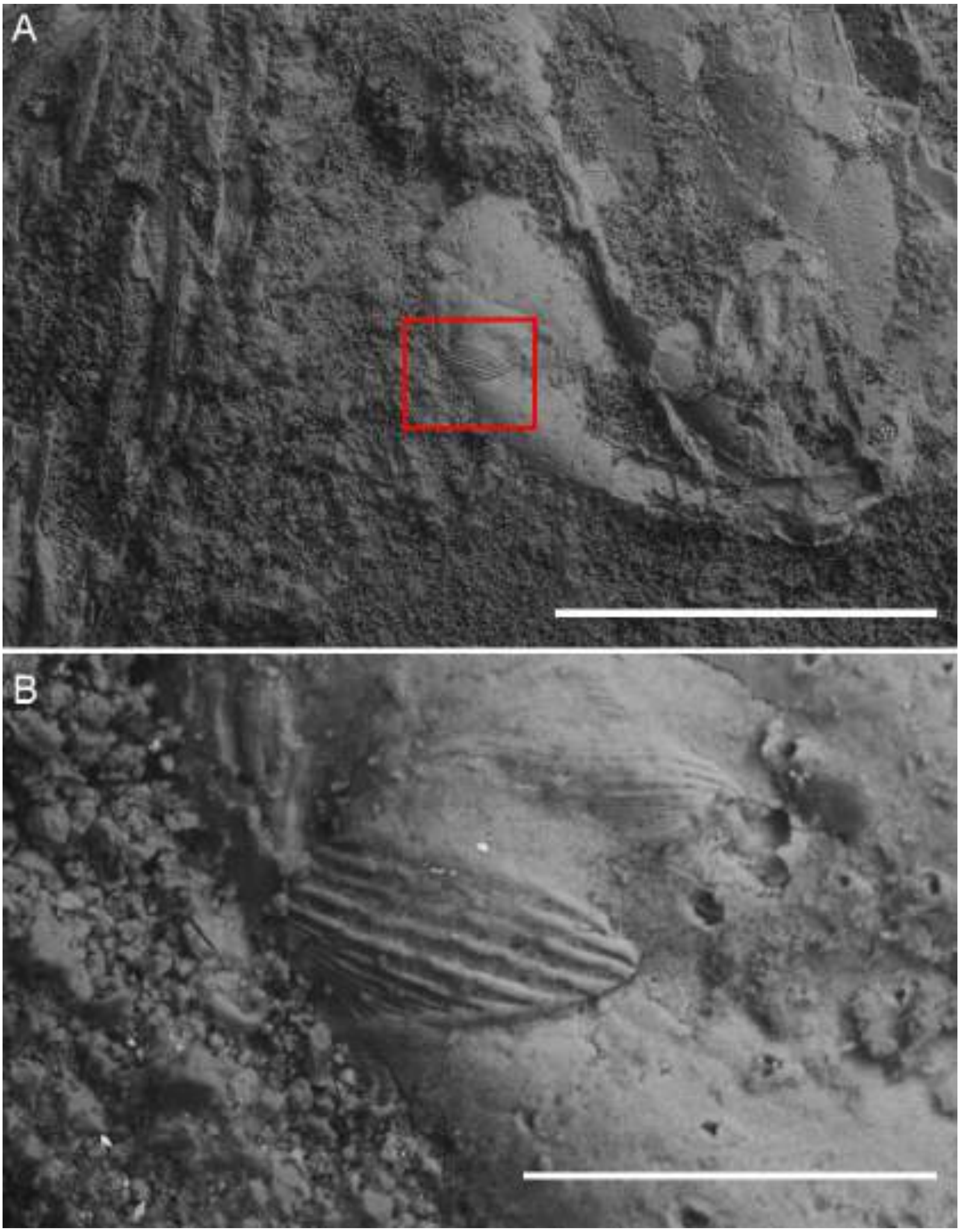


Figure 18. MPSC A6854, fine morphology of the book lungs. A, overview of the abdomen, B, pilate trabeculae, C, atrium wall. Scale bars= A, 1 mm, B, 25 µm, C, 20 µm.

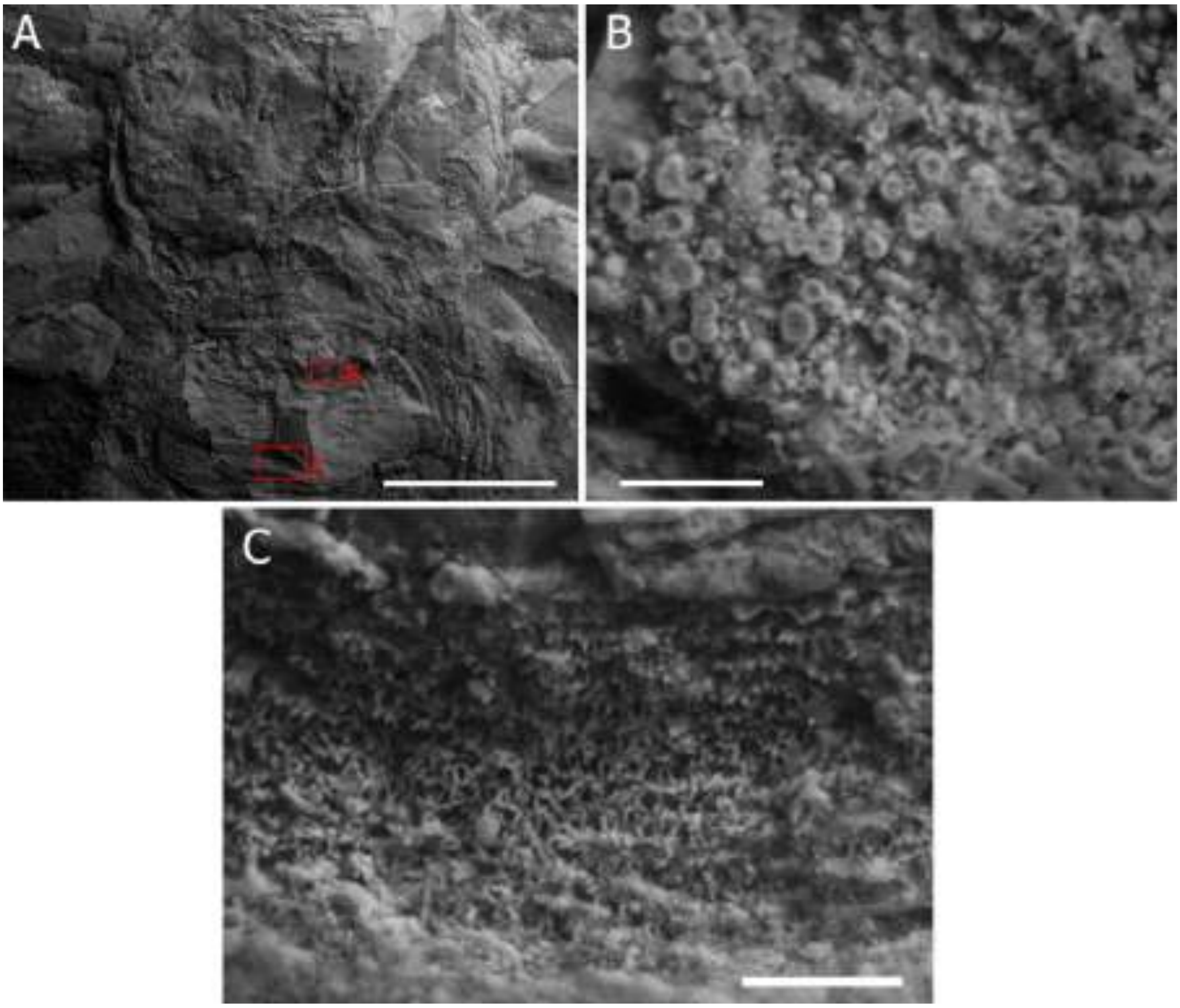
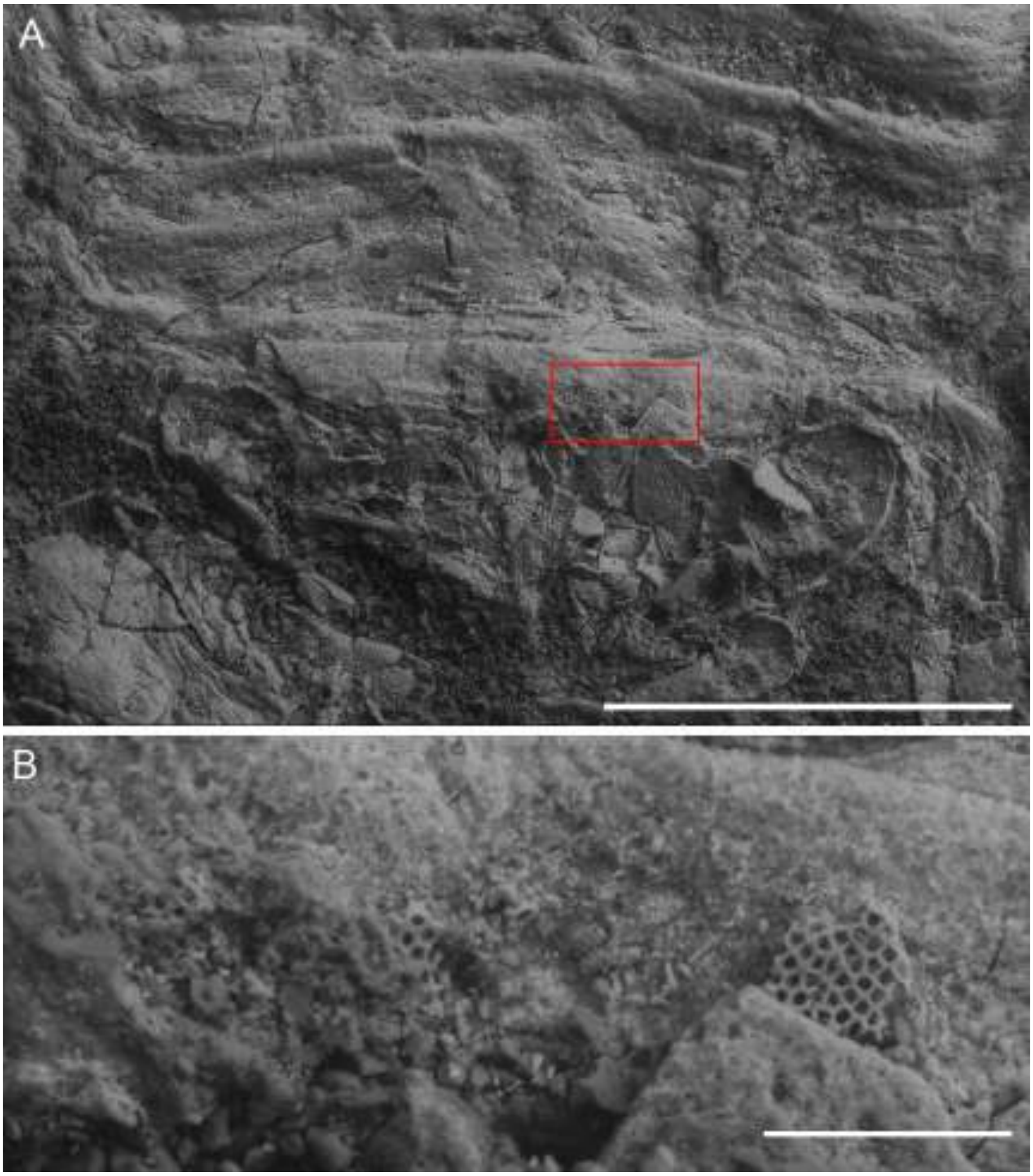


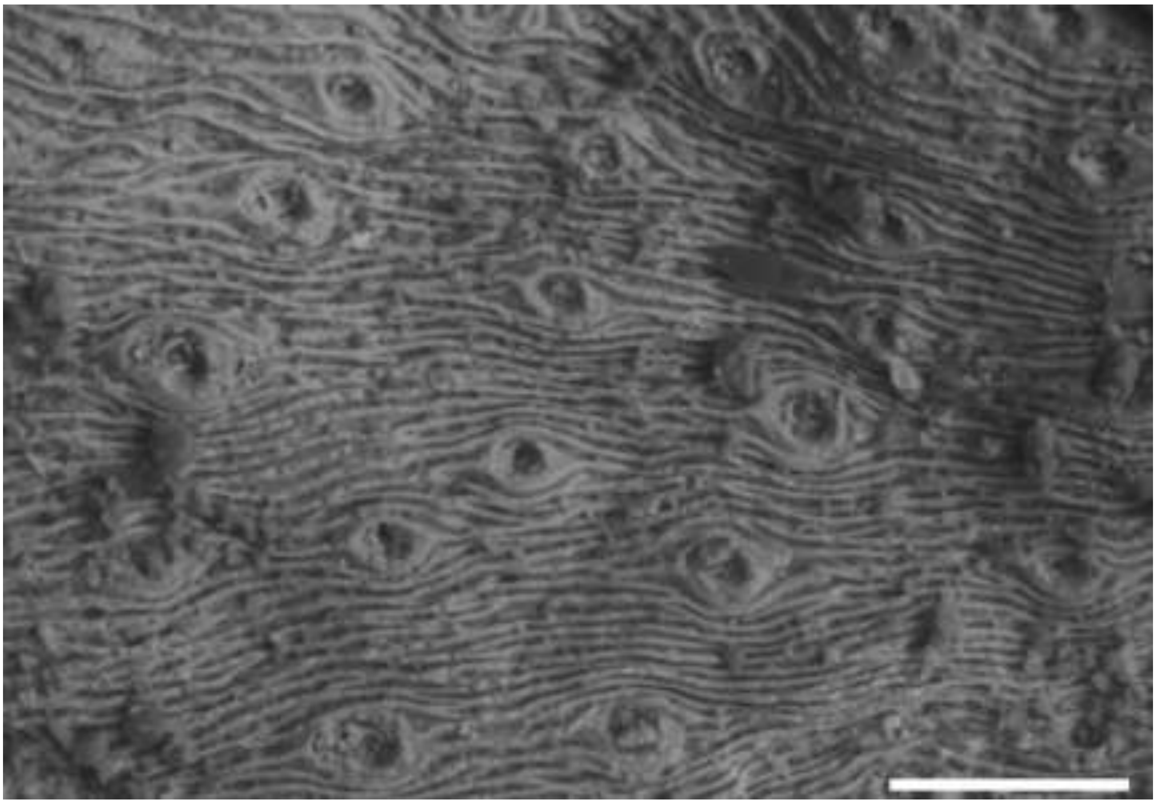
Figure 19. MPSC A6854, region of spinnerets in dorsal internal view, epicuticle of tracheae? Scale bars= A, 500 µm, B, 50 µm.



Spiders are relatively abundant within the fauna of the Crato Formation. As terrestrial arthropods, a transportation from their natural habitats to the lake is needed for their preservation. The presence of fine details and articulated specimens implies that this transportation likely occurred over short distances and under non-aggressive conditions. Consequently, this suggests a proximity between the lake and the habitats of these spiders. Moreover, most spiders from the Crato Formation display morphological resemblances to modern orb-weaving spiders, implying that these organisms probably constructed their webs in the proximity of or around the lake.

It was also observed that most of the spiders analyzed here (89%) were preserved with their legs curled over their bodies. When preserved with the dorsal side facing up, it becomes impossible to observe most of the leg podomeres, which makes it difficult to discern many of the diagnostic characteristics. This leg curvature serves as evidence of the hypersalinity of the paleolake in the Crato Formation. According to Downen et al. (2015), spiders deposited in normal freshwater typically exhibit fully extended legs, but as salinity increases, their legs become increasingly curved. Therefore, a plausible explanation for the pattern of curved legs in most specimens would be the spiders' death on land or while floating on the water's surface, causing their legs to bend in their natural post-mortem position. Subsequently, they were deposited in the hypersaline lake, where the high salinity prevented the legs from extending again (DOWNEN et al., 2015). The Crato spiders’ abdomens have a shrunken appearance (Figure 20), which is also evidence for hypersalinity in the lake. The abdomen of spiders is softer and much less sclerotized than other parts of its exoskeleton (WHITEHEAD; REMPEL, 1959), allowing it to expand and contract in digestion, respiration and reproduction processes. This flexible nature also accommodates the silk glands and spinnerets used for web-building and other functions. In a hypersaline lake, water would draw out of the organism’s body through osmosis, leading to dehydration and a shrunken appearance.

Figure 20. SEM image of LPU 1596 abdomen, showing shrunken appearance. Scale bar= 50 µm.



FINAL CONSIDERATIONS

This study has expanded the knowledge of the fossil spiders from the Crato Formation by reviewing and adding new data on the morphology of *Cretaraneus martinsnetoi* and describing two distinguishable new specimens. Additionally, the identification of microstructures attests the exceptional preservation and high fidelity of the Crato spiders, providing evidence of a hypersaline depositional environment. Continued analysis, including the description of additional specimens and revisiting already described taxa, holds the potential to further enhance the knowledge about these organisms.

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FINAL GENERAL CONSIDERATIONS

Fossil spiders are often found in lacustrine deposits, and many of the described taxa needs to be revised, as their taxonomic classifications are often based on characters that do not ensure their positioning. This includes the fossil spiders from the Crato Formation, one of the few Gondwanan deposits to preserve such organisms. The description of new specimens provided additional data on the morphology of *Cretaraneus martinsnetoi*, the most abundant spider species at this site, which has an unclear taxonomic placement. The presence of cuticular microstructures not previously recorded also indicates exceptional taphonomic conditions on the Crato Formation.

Thus, this research not only expands the knowledge about fossil spiders but also establishes a pathway for future investigations that may lead to new discoveries and deepen the understanding of the evolution of this group. The Crato Formation remains an important research focus that should be continuously explored and preserved.

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