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Spider Origin and Evolution in Fossil Environments

José de la Fuente[1,2*]

Abstract

The origin and evolution of arthropods is preserved in fossil amber and limestone inclusions. Amber with syninclusions represent fossil environments. The study used fossil arthropods *Guangweicaris spinatus* from Cambrian (ca. 518 Mya) and extinct spider-like *Eophrynus* sp. from Upper-Carboniferous Pennsylvanian (ca. 310 Mya) to represent the origin of arthropods. Then, spiders (Class Arachnida, Order Araneae), Families Linyphiidae, Hersiliidae in Burmese amber from Cretaceous (ca. 99 Mya), Family Linyphiidae in Baltic amber from *Eocene (ca. 38-54 Mya)* and Family Salticidae in Dominican amber from Oligocene (*ca. 25-38 Mya*) were used as the reference organisms to characterize lifecycle and environment with coexistence and possible interactions with other arthropods such as mosquitoes, ants, flies, beetles, fleas, lacewing and gnat. An inclusion with a land snail mollusk (Class Gastropoda, Order Architaenioglossa, Family Cyclophoridae) was also identified in Burmite. Fossils from different locations and epochs represent spider origin and evolution.

Keywords: Amber; Arthropod; Evolution; Fossil; Insect; Spider

Introduction

Arthropods are estimated to originate in the Cambrian period (ca. 485-541 million years ago; Mya) with worm-like lobopodians with annulated appendages as the earliest stem-group [1]. Arthropods are also considered the most diverse animal phylum with abundant fossil record. Spiders (Phylum Arthropoda, Subphylum Chelicerata, Class Arachnida, Order Araneae, Clerck 1757) are arthropods with morphological characteristics of two body parts and the absence of antennae sensory organs and chelicerae structures for feeding [2]. Arachnids are considered to have evolved from an ancestor like eurypterids marine chelicerates (order Eurypterida) found in the seas from 500 to 245 Mya during the Ordovician to Permian periods [3]. Spiders are proposed to originate from at least 380 Mya with possible increased number of species during Triassic period after "Great Dying" extinction event (https://www.nationalgeographic.com/science/article/triassic) with more than 45,000 extant species [3-5].

Spiders have been represented in traditional African folklore, Greek and Roman mythology and in other cultures popular myths and symbolism. As approached in this study, fossil arachnids including spiders and mites are preserved in limestones and amber inclusions to provide information on the evolution and environment of these organisms, which have been also included in cultural representations and (e.g., [6-10]).

Affiliation:

[1]Health and Biotechnology-SaBio. Instituto de Investigación en Recursos Cinegéticos IREC-CSIC-UCLM-JCCM, Ronda de Toledo 12, 13005 Ciudad Real, Spain

[2]Department of Veterinary Pathobiology, College of Veterinary Medicine, Oklahoma State University, Stillwater, OK 74078, USA

***Corresponding author:**

José de la Fuente, Health and Biotechnology-SaBio. Instituto de Investigación en Recursos Cinegéticos IREC-CSIC-UCLM-JCCM, Ronda de Toledo 12, 13005 Ciudad Real, Spain.

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Methodology

All fossils used in this study are authentic following reported considerations [8] and came from author´s KGJ Collection (Ciudad Real, Spain). As previously reported [8,10], images of fossil pieces were captured using a Leica Microsystems (Wetzlar, Germany) M80 routine stereomicroscope with a 1× PLAN objective and a 2X–6X zoom (https://www.leica-microsystems.com/products/light-microscopes/stereo-microscopes/p/leica-m80/) and a Carl Zeiss stereomicroscope (SteREO Discovery V12, Munich, Germany) using the ZEN 2 pro software. Microscope images were analyzed using the Image J program (https://imagej.net/ij/), and interpretative camera drawings were generated using the BeFunky application (https://www.befunky.com/features/photo-to-sketch/) and critically checked and edited. Morphological classifications were based on artificial intelligence (AI)-powered paleontology tool, Fossil Identifier (https://www.identifyrock.net/tools/fossil-identifier) and scientific references. Depending on the quality of preserved organisms and obtained images, classifications were provided at different levels with priority given to spiders, and in some cases should be considered as "putative classification".

Results

Arthropod and worm in Chinese Cambrian limestone, ca. 518 Mya

Rare and special fossils were identified in a Cambrian limestone fund in Yunnan, China (Figures 1A and 1B). The extinct arthropod *Guangweicaris spinatus* (Order Fuxianhuiida†, Family Fuxianhuiidae†, Genus *Guangweicaris*†) [11] (Figure 1A) was identified together with the extinct *Cricocosmia jinningensis* palaeoscolecid worm (Class Palaeoscolecida†, Family Cricocosmiidae†, Genus *Cricocosmia*†, Huo and Sun 1988) [12] (Figure 1B). Focusing on the arthropod, key morphological tergites were preserved in the fossil [13], features of segmented body and telson that are interpreted as early, primitive versions of those found in later arthropods (Figure 1A).

Guangweicaris spinatus is one of the earliest known arthropods that originated significantly before spiders during early Cambrian period (ca. 510-515 Mya). *Guangweicaris* are then considered a stem-group arthropod and a very early relative to modern chelicerates such as spiders (Order Araneae), which appeared during the Devonian period about 380 Mya, over 100 million years after *Guangweicaris*. Accordingly, *G. spinatus* and spiders are phylogenetically connected through their positions on the arthropod evolutionary tree.

Spider-like in Upper Carboniferous Pennsylvanian limestone, ca. 310 Mya

An extinct spider-like (not true spiders) *Eophrynus* sp. (Order Trigonotarbida†, Family Eophrynidae†, Genus *Eophrynus*†, Woodward 1871) was identified in a Poland limestone from the Upper Carboniferous Pennsylvanian period (Figures 1A-1C). The spider-like Trigonotarbids arachnids show segmented abdomens divided into three or five plates with dorsal tergites. These morphological features are associated with likely predatory behavior requiring protection [14-20].

Spiders in fossil syninclusions in Cretaceous Burmese amber, ca. 99 Mya

Fossil amber *syninclusions* represent multiple organisms preserved together within the same piece with coexistence and possible interactions [10]. Spiders are represented in amber syninclusions as shown here in Burmese amber from Cretaceous period (ca. 99 Mya) (Figures 3-5).

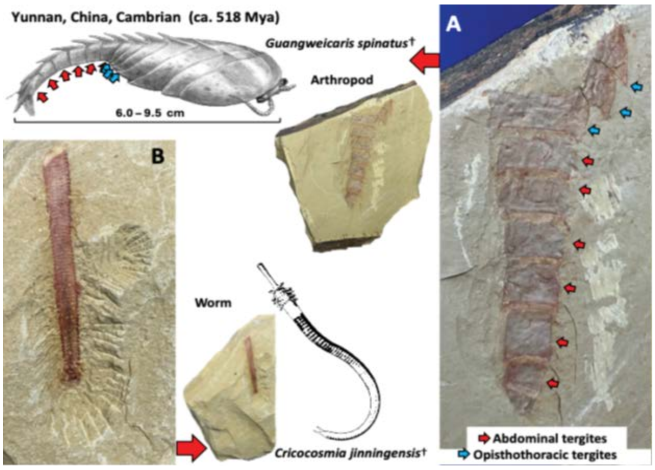

Figure 1: Arthropod and worm from early Cambrian period. (A) Extinct arthropod *Guangweicaris spinatus* with preserved abdominal (n=6) and opisthothoracic tergites (n=3). (B) Extinct *Cricocosmia jinningensis* palaeoscolecid worm. Locality: Yunnan, China. Matrix dimensions ca. 10 x 7 x 2 cm.

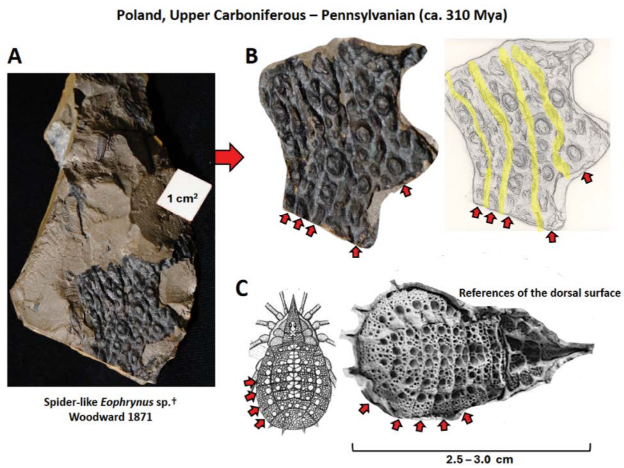

Figure 2: Spider-like from Upper-Carboniferous Pennsylvanian period. (A) Fossil limestone with extinct spider-like *Eophrynus* sp. (B) Abdomens plates with dorsal tergites. (C) References of the dorsal surface. Locality: Poland, GZW Upper Silesia Coal Basin. Matrix dimensions ca. 8.5 x 4.0 x 2.0 cm.

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Figure 3: Spider with mosquito, ants, land snail and lacewing syninclusions in Burmite

A fossil spider (Class Arachnida, Order Araneae, Infraorder Araneomorphae, Superfamily Araneoidea, Family Linyphiidae, Blackwall 1859) was identified with multiple organism syninclusions including mosquito, ants, land snail and lacewing.

The Linyphiidae spider displays the characteristic body proportions of a sheet weaver spider, specifically the prominent, bulbous pedipalps visible at the front. In male linyphiids, these palps are often complex and enlarged to house reproductive organs, which matches the distinct, club-like structures extending forward from the cephalothorax in the image. The general leg morphology and the relative size of the prosoma to the opisthosoma are also diagnostic for this family within Cretaceous-aged Burmese amber.

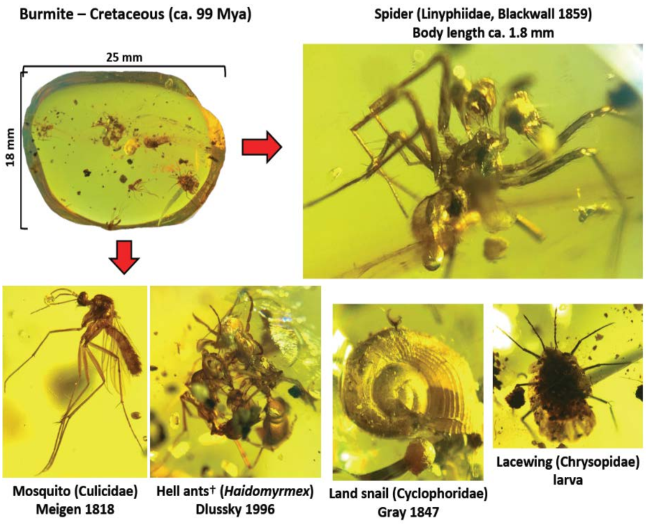

Figure 3: Spider with mosquitoes, ants, land snail and lacewing syninclusions in Burmite. Locality: Hukawng Valley in Kachin State, northern Myanmar. Amber dimensions ca. 25 x 18 cm.

The Culicidae mosquito (Class Insecta, Order Diptera, Superfamily Culicoidea, Family Culicidae, Meigen 1818) exhibits the distinct morphology of a mosquito with a slender body, extremely long and thin legs, a single pair of functional wings, and a prominent proboscis used for feeding.

The Hell ants (Class Insecta, Order Hymenoptera, Family Formicidae, Subfamily Haidomyrmecinae†, Genus Haidomyrmex†, Diussky 1996) display the characteristic morphology of the extinct Hell ants with prominent, scythe-like upward-directed mandibles with position of the head and orientation of elongated mouthparts relative to the clypeus typical of the Genus Haidomyrmex† found in Cretaceous Burmese amber.

A land snail mollusk (Class Gastropoda, Order Architaenioglossa, Family Cyclophoridae, Gray 1847) displays a characteristic planispiral or low-spired discoidal shell morphology typical of many terrestrial operculate snails found in Burmese amber. The visible radial growth lines on the whorls and the overall compact, flattened shape strongly match the diagnostic features of the family Cyclophoridae, which are frequently preserved in Cretaceous amber deposits from Myanmar.

The lacewing larva (Class Insecta, Order Neuroptera, Family Chrysopidae) was identified based on the broad, flattened, oval-shaped body with lateral tubercles, which are hallmark features of these "trash-carrying" insects. The elongated, prominent, sickle-shaped mandibles are clearly visible, projecting anteriorly from the head, which is typical for their predatory lifestyle.

Figure 4: Stem ant†, Crane fly, spider, snakefly and mosquito syninclusions in Burmite

In a different Burmite, a spider (Class Arachnida, Order Araneae, Infraorder Araneomorphae, Family Hersiliidae, Thorell 1869) was identified with ant and winged insect syninclusions.

The spider displays the extremely long, prominent posterior lateral spinnerets that are the diagnostic hallmark of the family Hersiliidae, often referred to as two-tailed spiders. The body proportions, flattened appearance, and the leg structure captured in this Burmese amber piece align with known Cretaceous fossils within this family.

A mosquito was classified as Culicidae (Class Insecta, Order Diptera, Family Culicidae, Meigen 1818) based on the elongated proboscis, slender multi-segmented legs, and characteristic wing venation and hair-like scales typical of a mosquito preserved in amber. The presence of the

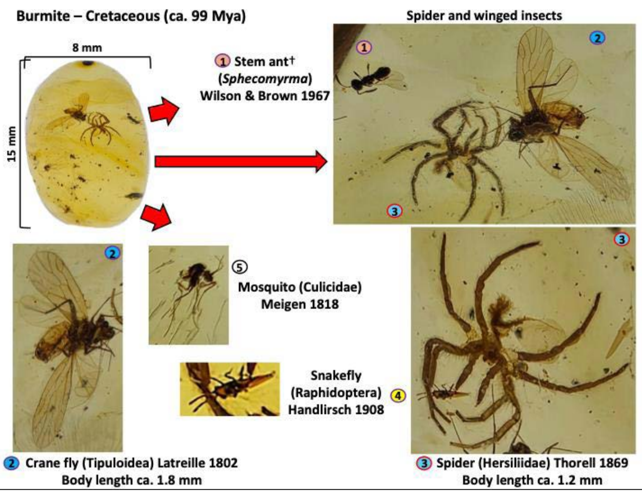

Figure 4: Stem ant† (1), Crane fly (2), spider (3), snakefly (4) and mosquito (5) syninclusions in Burmite. Locality: Hukawng Valley in Kachin State, northern Myanmar. Amber dimensions ca. 15 x 8 x 5 mm.

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long, forward-projecting mouthparts is the most diagnostic feature of this family within the order Diptera found in mid-Cretaceous Burmese amber inclusions.

An ant inclusion was morphologically identified as a Stem ant† (Class Insecta, Order Hymenoptera, Family Formicidae, Genus *Sphecomyrma*†, Wilson and Brown 1967) based on the combination of an ant-like metapleural gland and a petiolate waist alongside wasp-like features such as the wing venation pattern and the structure of the head and antennae. Its preservation in Burmese amber is consistent with the primary fossil record for this extinct genus.

The Crane fly (Class Insecta, Order Diptera, Superfamily Tipuloidea, Latreille 1802) showed classic morphological characteristics for these insects including long slender legs and large, membranous wings with a distinct venation pattern in a delicate structure and body proportions characteristic of the Tipulidae family often found in Cretaceous amber.

A putative snakefly (Class Insecta, Order Raphidioptera, Handlirsch 1908) was difficult to characterize but the elongated prothorax, which separates the head from the rest of the body creating the distinctive neck-like appearance with long, slender antennae and the positioning of the appendages in the amber matrix were used for classification.

Interestingly, both crane fly and snakefly were found near the spider mouthparts (chelicerae and pedipalps), raising the question of possible predator (spider)-prey (crane fly) and predator (spider)-predator (snakefly) interactions [21] (Figure 4, numbers 3-2 and 3-4 together, respectively).

Figure 5: Spider, ants and Crane fly syninclusions in Burmite

In the third Burmite, a spider (Class Arachnida, Order Araneae, Clerck 1757) with clear division between the cephalothorax and the abdomen, along with multiple long, jointed walking legs radiating from the central body and fine hairs or setae on the legs was identified with ants, Crane fly and beetle syninclusions. A possible ant-eating spider predatory behavior (e.g., [22]) may be represented in this fossil amber (Figure 5, numbers 1-2 together).

At least three ants (Class Insecta, Order Hymenoptera, Superfamily Formicoidea, Latreille 1809) were identified in this amber piece. The specimens show a clear division into three distinct body segments consisting of a head, thorax, and abdomen. It possesses long, segmented antennae characteristic of Hymenoptera and multiple jointed legs emerging from the thorax. The inclusion in Figure 5 (number 3) was assigned to either ant or spider. For ant, the specimen shows a clear three-part body structure consisting of a head, thorax, and a distinctively shaped abdomen with six articulated legs and long antennae, which are characteristic morphological features of the order Hymenoptera, specifically ants. However, the specimen also displays a

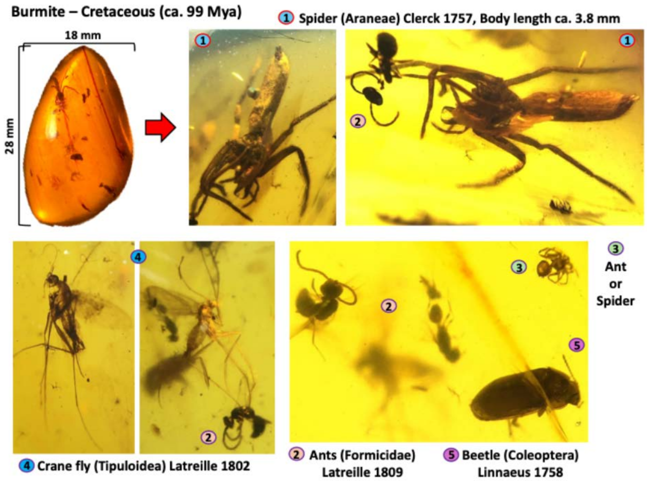

Figure 5: Spider (1), ants (2) and Crane fly (4) syninclusions in Burmite. An ant or spider (3) was also identified. Locality: Hukawng Valley in Kachin State, northern Myanmar. Amber dimensions ca. 28 x 18 x 8 mm, weight 2.2 g.

distinct cephalothorax and abdomen, along with long, jointed appendages characteristic of arachnids with a body plan and limb arrangement suggesting spider. In these cases, additional detailed morphological analyses with high resolution images are required to define the inclusion organism classification.

The Crane fly (Class Insecta, Order Diptera, Superfamily Tipuloidea, Latreille 1802) exhibits classic morphological characteristics as the specimen described in Figure 4 with an elongated body, very long and slender legs, and a distinctively shaped thorax. The presence of a single pair of functional wings visible in the amber preservation is consistent with the order Diptera, to which crane flies belong. However, in this case it could be considered as a different member of the superfamily Tipuloidea such as a member of the Limoniidae family, which are often smaller and can look very similar to crane flies in amber inclusions.

The beetle syninclusion (Class Insecta, Order Coleoptera, Linnaeus 1758) displays the classic anatomical structure of a coleopteran with hardened forewings known as elytra that meet in a straight line down the back, a distinct head with visible antennae, and a segmented body typical of beetles.

Spiders in fossil syninclusions in Eocene Baltic amber, ca. 38-54 Mya

Eocene Baltic amber is an important source for the study of fossil animals. In this study, five Baltic amber pieces with spider syninclusions with other organisms were characterized (Figures 6-9).

Figure 6: Fly and spider with web syninclusions in Baltic amber

The spider (Class Arachnida, Order Araneae, Clerck 1757) displays classic anatomical features including a

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cephalothorax, an abdomen, and multiple long, articulated walking legs. The presence of pedipalps near the front, the specific arrangement of the limb segments, and the overall body plan within the Baltic amber matrix confirm it is an arachnid of the order Araneae. The spider web displays the characteristic irregular, geometric, and intersecting fine-thread structure typical of silk spun by arachnids. The radial tension and multiple nodal connections where individual threads meet are consistent with how spider silk is preserved under tension within resin before polymerization. Although with less possible, it could also be considered an internal resin cracking or "stress fractures" that can mimic the appearance of a web, as can some types of fungal mycelium or crystalline inclusions that grow in branch-like patterns within the amber matrix.

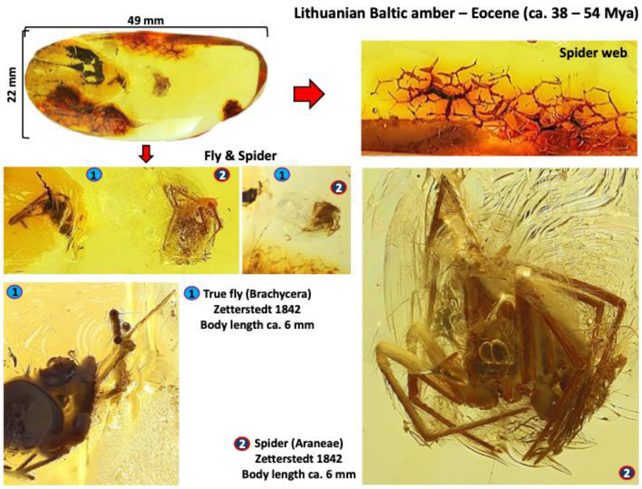

Figure 6: Fly (1) and spider (2) syninclusions in Baltic amber. Spider web was also identified. Locality: Lithuania. Amber dimensions ca. 49 x 22 x 10 mm, weight 6.9 g.

Figure 7: Spider and click beetle in Baltic amber

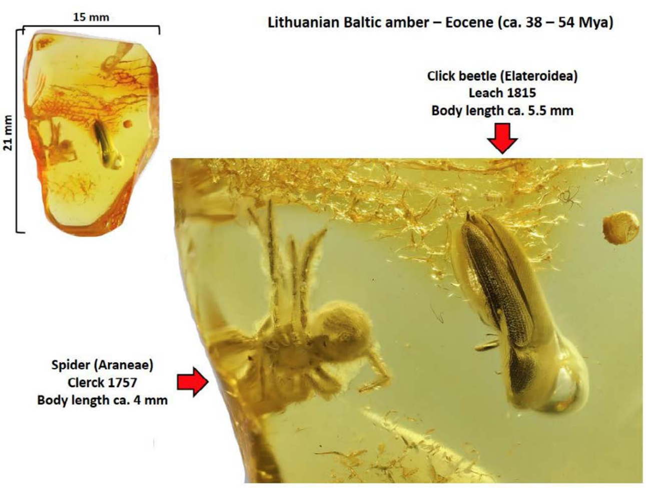

Figure 7: Spider and click beetle syninclusions in Baltic amber. Locality: Lithuania. Amber dimensions ca. 21 x 15 x 5 mm, weight 1.0 g.

The fly (Class Insecta, Order Diptera, Suborder Brachycera, Zetterstedt 1842) displays key morphological features diagnostic of true flies such as the presence of a distinct, multi-faceted compound eye and the characteristic prominent, bristle-bearing thoracic structures. The articulated appendages and the structural alignment of the head capsule are highly consistent with the anatomical layout of Nematocera or Brachycera flies preserved in Baltic amber.

The spider inclusion (Class Arachnida, Order Araneae, Clerck 1757) is preserved in amber and exhibits the clear morphological characteristics of an arachnid. It possesses a distinct cephalothorax and abdomen, along with multiple jointed, hairy legs extending from the central body mass. The presence of fine setae (hairs) on the legs and body is a hallmark of many spider species.

The click beetle (Class Insecta, Order Coleoptera, Family Elateridea, Leach 1815), also known as elaters, snapping beetles, spring beetles, or skipjacks was identified close to the spider with elongated, narrow, and parallel-sided with dark coloring, and hard wing covers (elytra) (e.g., [23]).

Figure 8: Swarm of spiderlings in Baltic amber

As represented in this Baltic amber, spiderlings are immature newly hatched spiders that disperse from their hatching site using ballooning as a method to climb high and use silk strands to float on air currents. The egg case of the spider serves to protect the enclosed offspring during the early stages of their lives to resist threats such as predator/parasitoid invasion and temperature fluctuations while the spiderlings must be able to exit it in the appropriate season in the absence of the mother, which often dies shortly after egg case construction [24].

Figure 9: Spider exuvia in Baltic amber

A spider exuvia (Class Arachnida, Order Araneae, Family Linyphiidae, Blackwall 1859) was identified in Baltic amber. Spider morphological classification was based on characteristic long, slender, spiny legs typical of sheet-web spiders. The body proportions, with a relatively small cephalothorax and elongated, spindly appendages, strongly match the morphology of various extinct and extant genera within the family Linyphiidae, which are among the most common spider fossils discovered in Baltic amber. The possibility of spider being of the family Theridiidae, which also features long-legged forms often preserved in Baltic amber should be considered.

The spider exuvia (or exuviae or exuvium) word comes from the Latin *exuviae*, meaning "things stripped from a body" and is found only in the plural [25]. Exuviae are rare in amber and represent the empty, cast-off exoskeleton appearing as a pale, fragile, or paper-thin replica of the spider including legs, hairs, and fangs left behind after ecdysis when

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spider molts to grow [25]. Exuviae in amber represent a fossil environment in which spiders were active and growing.

Spiders in fossil syninclusions in Oligocene Dominican amber, ca. 25-38 Mya

The Dominican amber represents a different fossil environment in which spiders and in particular ant-mimicking jumping spiders found here are rare findings relevant for scientific studies (e.g., [26]).

Figure 10: Spider and insect syninclusions in Dominican amber

An ant-mimicking spider (Class Arachnida, Order Araneae, Family Salticidae, Blackwall 1841) was identified with distinct cephalothorax and abdomen separated by a narrow pedicel. The leg arrangement and the presence of what appear to be pedipalps near the head region are diagnostic of arachnids. Its elongated, slender profile is a classic example of Batesian mimicry found in Salticidae, where spiders evolve to look like ants to avoid predators or infiltrate colonies.

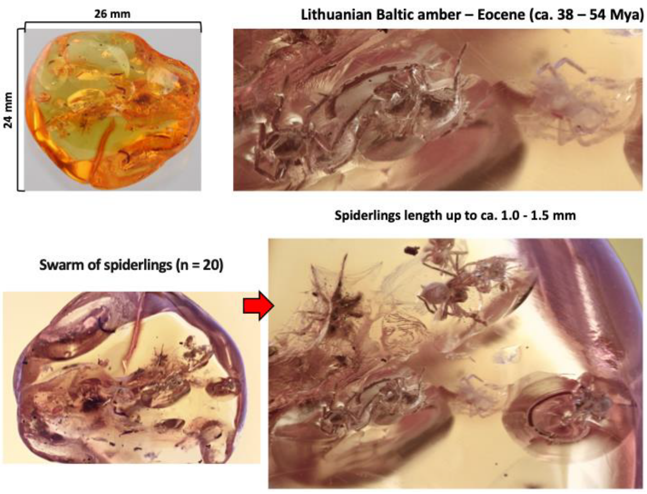

Figure 8: Swarm of spiderlings in Baltic amber. Locality: Lithuania. Amber dimensions ca. 26 x 24 x 11 mm, weight 3.6 g.

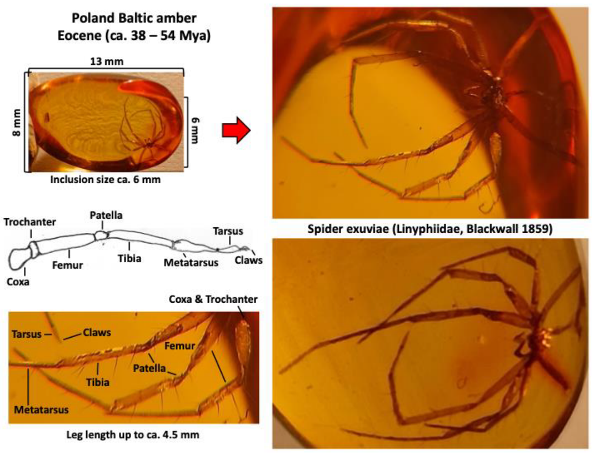

Figure 9: Spider exuvia in Baltic amber. Locality: Poland. Amber dimensions ca. 13 x 8 x 6 mm, weight 3.4 g.

Three Crown ants (Class Insecta, Order Hymenoptera, Family Formicidae) were identified with limited resolution based on characteristic tripartite body structure of an ant, consisting of a distinct head, a mesosoma (thorax), and a gaster (abdomen). The attachment of the legs to the mesosoma and the overall silhouette are highly indicative of Formicidae. The size, posture, and morphological proportions observed in the amber matrix are consistent with common ant inclusions found in Dominican amber. Another specimen was assigned to a putative classification (Class Insecta, Order Hymenoptera, Suborder Apocrita).

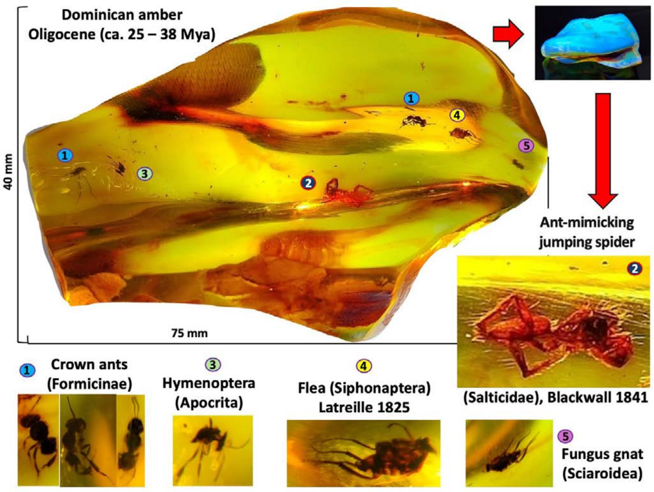

Figure 10: Spider and insects in Dominican amber. An ant-mimicking jumping spider 2) was identified with syninclusions of crown ants (1), Hymenoptera Apocrita (3), flea (4) and fungus gnat (5). Locality: Dominican Republic. Amber dimensions ca. 75 x 40 x 30 mm, weight 31 g.

A flea (Class Insecta, Order Siphonaptera, Latreille 1825) was morphologically identified with a laterally compressed body shape and highly developed, enlarged hind legs adapted for jumping. The orientation of the legs in relation to the thorax and the overall proportions are diagnostic of a flea trapped in amber.

A fungus gnat (Class Insecta, Order Diptera, Superfamily Sciaroidea) was putatively classified based on characteristic long, slender legs, delicate wing venation remnants, elongated antennae and the distinct hump-backed thorax typical of the superfamily Sciaroidea found frequently in Dominican amber.

Discussion

The study of fossil inclusions in limestone and amber provides information on the origin and evolution of spiders (Figure 11). As supported by fossil record (Figures 1 and 2), arthropods originated in the Cambrian period ca. 485-541 Mya and Arachnids evolved from an ancestor such as Eophrynidae† during the Ordovician to Permian periods ca.

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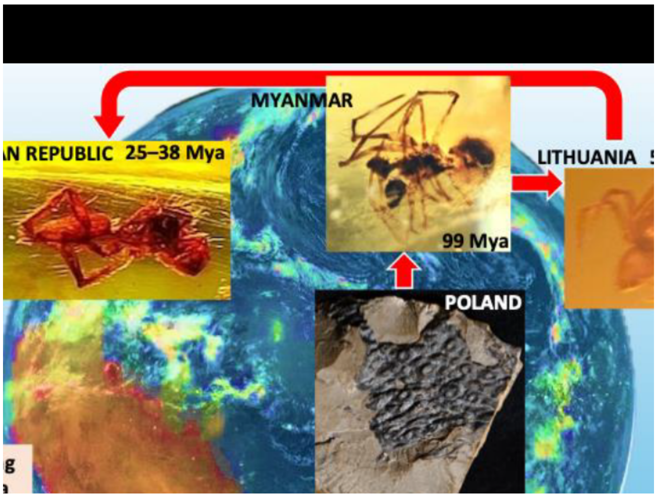

Figure 11: Evolution of arthropods in the fossil record. Images obtained from author´s KGJ Collection (Ciudad Real, Spain).

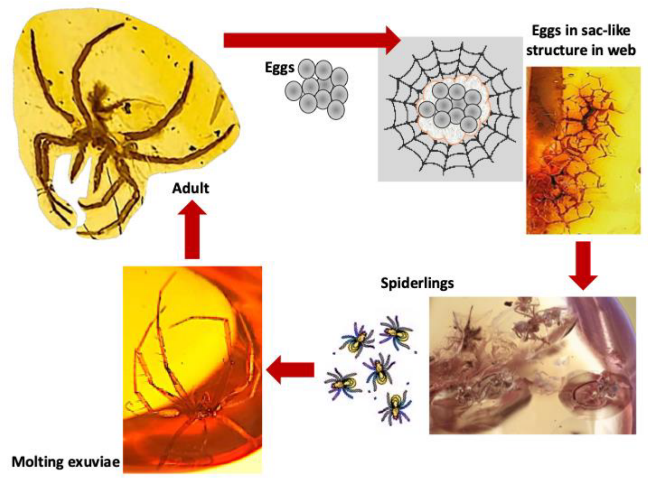

Figure 12: Spider life cycle. Fossils derived from Figures 6 (spider web), 8 (spiderlings) and 9 (exuviae).

252-485 Mya. Spiders then appeared at least 380 Mya with possible increased number of species during Triassic period after the Permian-Triassic "Great Dying" extinction event ca. 251.9 Mya, as represented in Burmese Cretaceous (ca. 99 Mya), Baltic Eocene (*ca. 38-54 Mya*) and Dominican Oligocene (*ca. 25-38 Mya*) amber (Figures 3-10).

Fossil syninclusions in amber represent fossil environments with coexistence between ants and other arthropods and organisms such as land snail mollusks. In some cases, fossil syninclusions may be considered as possible interactions between spiders and other arthropods with possible predator (spider)-prey (crane fly), predator (spider)-prey (ant) and predator (spider)-predator (snakefly) interactions (Figures 4 and 5).

Spiders in amber also represent the Arachnida lifecycle [27] (Figure 12) as shown here with spider fossil web (Figure 6), spiderlings (Figure 8) and exuviae (Figure 9).

In conclusion, Fossils from different locations and epochs represent spider origin and evolution.

Competing Interests

The author declares that no competing interests exist.

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