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THE OLDEST LINYPHIID SPIDER, IN LOWER CRETACEOUS LEBANESE AMBER (ARANEAE, LINYPHIIDAE, LINYPHIINAE)

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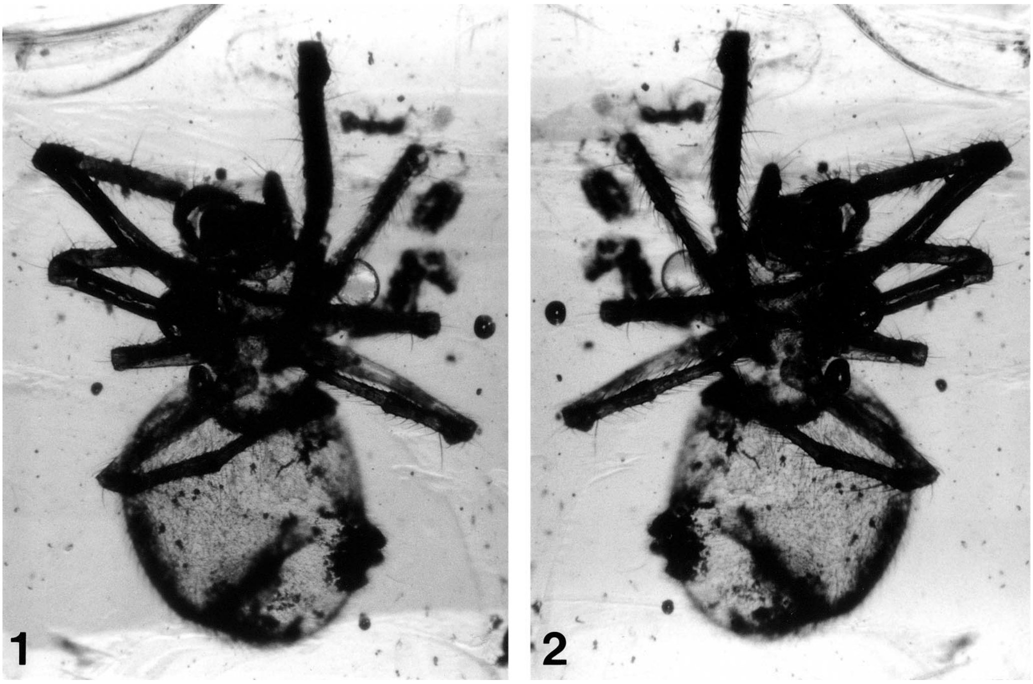
ABSTRACT. A new fossil Linyphiidae: Linyphiinae is described from 125–135 Ma old (Upper Neocomian–basal Lower Aptian) Cretaceous amber from the Kdeirji/Hammana outcrop, Lebanon. This is the oldest known linyphiid as well as the oldest described amber spider. The first major radiation of the linyphiid subfamilies occurred in the early Cretaceous, if not before, and the presence of Linyphiidae in this period predicts the presence of Pimoidae then too. Current evidence, which suggests the higher araneoids did not radiate and diversify until after the end-Cretaceous mass extinction event may be an artefact of sample size.

Keywords: Linyphiidae, Linyphiinae, Lebanese amber fossil

The spider family Linyphiidae contains 4,129 extant species in 550 genera (Platnick 2001), which represents approximately nine percent of total spider species diversity. It ranks second, after Salticidae, in terms of number of described species, but first for number of genera (Platnick 2001). However, many of these genera are monotypic and would probably not withstand phylogenetic scrutiny (Hormiga 2000). The family consists mainly of very small spiders, mainly sheet-web builders. It has a global distribution, but linyphiids are most diverse in northern temperate regions (Coddington & Levi 1991). Their niche may be occupied by Theridiidae in the lower and southern latitudes (e.g. Nentwig 1993: table 8). There are six recognized extant linyphiid subfamilies: Dubiaraneinae Millidge 1993, Erigoninae Emerton 1882, Linyphiinae Blackwall 1859, Micronetinae Hull 1920, Mynogleninae Lehtinen 1967, and Stemonyphantinae Wunderlich 1986 (A. Tanasevitch pers. comm.), although the Linyphiinae are considered by some (e.g. Hormiga 2000) to consist of two tribes: Micronetini and Linyphiini, reducing the number to five (e.g. Hormiga 1994a, 2000).

Fossil linyphiids have been described from Tertiary ambers from the Dominican Republic (Miocene, 15–20 Ma) (Wunderlich 1988), Mexico (Miocene–Oligocene, 19–27 Ma) (Petrunkevitch 1971), the Baltic region (Eocene, 44 Ma) (Petrunkevitch 1942, 1958; see also taxonomic comments of Wunderlich 1986) and from Upper Cretaceous (Turonian, 90–94 Ma) amber from New Jersey (Penney in press). Wunderlich (1998) described a linyphiid from what was thought to be Dominican Republic amber, but has since been shown to be Madagascan copal (J. Wunderlich, pers. comm.), which is semi-fossilized resin less than two million years old. A non-amber fossil linyphiid was described by Berland (1939) from the Oligocene of Alsace, France. The specimen in Mexican amber is an exuvium from an immature spider, and the French specimen is poorly preserved. Both were described and named as linyphiids, but we consider their current placement in the Linyphiidae to be unreliable. Fossil linyphiids have been reported as present, but not described, from Eocene Bitterfeld amber (44 Ma) (Schumann & Wendt 1989) and Upper Cretaceous Canadian amber (65–83 Ma) (McAlpine & Martin 1969).

This paper describes the oldest known linyphiid spider from upper Neocomian–basal Lower Aptian (c. 125–135 Ma) Cretaceous Lebanese amber from the Kdeirji/Hammana outcrop, which represents one of the oldest insect inclusion-bearing amber deposits (Azar 1998). This specimen is the oldest described amber spider, the previous being a new genus and species of Nemesiidae described in Barremian amber from the Isle of Wight, UK (Selden in press).



Figures 1–2.—Female linyphiine in Lebanese amber, photomicrographs of holotype. 1. Dorsal view x50; 2. Ventral view x50.

METHODS

Preservation.—The spider is preserved in a very small piece (3 x 3 x 1 mm) of clear, yellow-colored amber. There are a few air bubbles of varying size and a small number of organic and inorganic syninclusions.

Methods.—The amber piece had been prepared by being set in a clear synthetic resin disc (22 mm diameter x 2 mm thick), and polished prior to receipt by the authors. The specimen was studied, drawn and photographed, using both transmitted and incident light, using a Nikon Optiphot stereomicroscope, with a camera lucida drawing tube and a Nikon FX–35DX camera attached by means of a phototube. An Olympus SZH stereozoom microscope with incident light revealed additional detail of the specimen. All measurements are in mm.

Abbreviations used in the text and figures.—ab = air bubble; at = anal tubercle; ch = chelicera; co = colulus; cx = coxa; ep = epigyne; fe = femur; la = labium; mx = maxilla; mt = metatarsus; op = opisthosoma; pa = patella; pp = pedipalp; sp = spinneret; st = sternum; ta = tarsus; ti = tibia; tr = trichobothria; 1–4 = walking legs 1–4. In the leg formula (e.g. 4123), the legs are ranked in order of length (longest first). Tm1 and Tm4 are measurements of the distance that a trichobothrium is located along the lengths of metatarsi 1 and 4 respectively, relative to the length of the leg segment, e.g. Tm1 = 0.3 indicates that the trichobothrium is located three tenths of the way along metatarsus 1, from the proximal end of the segment.

SYSTEMATIC PALAEONTOLOGY

Family Linyphiidae Blackwall 1859
Subfamily Linyphiinae Blackwall 1859
gen. et sp. indet.
Figs. 1–3

Distribution.—Upper Neocomian–basal Lower Aptian (c. 125–135 Ma) Cretaceous Lebanese amber from the Kdeirji/Hammana outcrop, Lebanon.

Only known specimen.—Female, specimen No. 491 preserved in Cretaceous Lebanese amber, held in the Laboratoire d'Entomologie, Muséum National d'histoire Naturelle, Paris (MHNP), examined.

Description.—*Measurements:* body length 1.86; carapace ground away (Fig. 1), but the

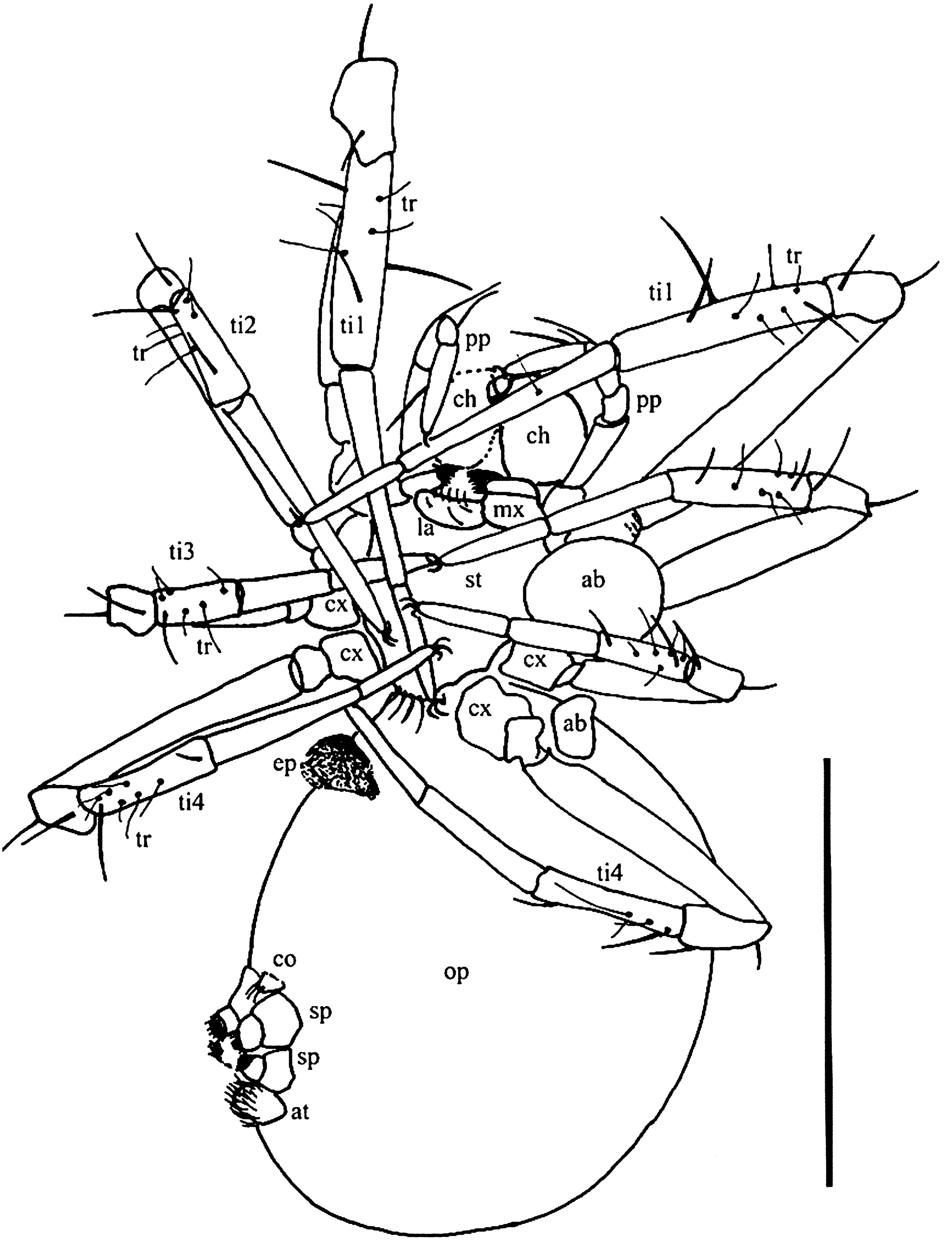


Figure 3.—Female linyphiine in Lebanese amber, camera lucida, ventral view. Scale bar = 1 mm.

chelicerae are in place so it is possible to determine the body length. Detailed structure and dentition of chelicera are not visible, but it appears unmodified and lacks stridulatory striae on the ectal surface. Maxilla wider than long with distinct serrula and a transverse row of dark, chitinized denticles; labium slightly rebordered, much wider than long. Sternum 0.43 long, 0.40 wide, smooth, with sparse covering of setae; margin slightly incised to accommodate coxae, sharply truncated posteriorly where it extends between fourth coxae; five erect setae along the truncated edge. Opisthosoma 1.23 long, 1.00 high, sub-spherical, without tubercles or scuta, covered with short setae; the right side has collapsed inwards. Anterior lateral and posterior lateral spinnerets with numerous spigots, posterior median spinnerets not visible. Colulus relatively large, with at least three bristles. Anal tubercle distinct (Figs. 2, 3). Epigyne projects ventrally, appears domed in lateral view (a clear ventral view is not possible because of the position of the spider in the amber matrix so the detailed structure is not clear). Epigyne heavily sclerotized, with a single opening and a flat dorsal margin; lateral margins appear rounded and project slightly posteriorly.

Leg formula 1423. Leg 1 fe 0.71, pa 0.19, ti 0.43, mt 0.41, ta 0.33, total 2.07; leg 2 fe 0.57, pa 0.16, ti 0.29, mt 0.26, ta 0.24, total 1.52; leg 3 fe 0.41, pa 0.14, ti 0.21, mt 0.19, ta 0.17, total 1.12; leg 4 fe 0.63, pa 0.16, ti 0.33, mt 0.31, ta 0.21, total 1.64; all segments with distinct setae and annulate distally. Coxae and trochantera without modifications; fe 1 and possibly fe 2 with short median dorsal spine, apparently lacking on fe 3 and 4; fe 1 with long prolateral spine located just distal to midpoint; all patellae with proximal and distal dorsal spines; tibial spination 2, 2, 2, 2; ti 1 also with median, long prolateral spine; metatarsi and tarsi without spines (Figs. 1–3). All tibiae with trichobothria equal to or longer than the tibial diameter (Fig. 3); Tm1 = 0.3, Tm4 lacking. Tarsi with three simple, untoothed claws and accessory setae, unpaired claw long, pedipalp with a single simple claw.

Remarks.—It is well appreciated that amber spiders are taxonomically subequal to Recent spiders (e.g. Eskov 1990). In many fossils it is difficult to identify and study those characters considered important as diagnostic for extant taxa. The specimen described here cannot be diagnosed by any putative autapomorphies, so a specific epithet is not assigned, nor can it be placed with certainty in an extant genus. This female linyphiine, it is the oldest representative of the Linyphiidae recorded, and is also the oldest described amber spider.

DISCUSSION

The superfamily Araneoidea comprises twelve extant families (Griswold et al. 1998) and the extinct families Ephalmatoridae Petrunkevitch 1950, redefined by Wunderlich (1986) from Baltic amber, and Juraraneidae Eskov 1984 from the Jurassic of Kazakhstan. The phylogenetic scheme for the Araneoidea (Fig. 4) follows Griswold et al. (1998), except for the placement of the fossil taxa. According to Griswold et al. (1998) the unambiguous synapomorphies for the linyphioid families, which includes Linyphiidae and its sister taxon Pimoidae (see Hormiga 1994b), are stridulating striae ectally on the male chelicerae, patella–tibia autospasy, and an enlarged base on the basal posterior lateral spinneret cylindrical gland spigot. The fossil specimen is female, all legs are intact, and the fine detail of the spigots is not clear. The fossil is excluded from the Pimoidae on account of its size, considerably smaller than 5 mm, the lower end of the range given by Hormiga (1994b), the epigyne does not protrude posteriorly beyond the epigastric furrow as it appears to in many pimoid species, femur 4 lacks dorsal spines, and the legs lack long setae which are curved at their distal end (e.g. Hormiga 1994b). The systematic placement of many genera within linyphiid subfamilies is based solely on autapomorphies derived from male secondary genital organs and in some cases no unambiguous diagnostic character states have been established for female specimens. Therefore, we tentatively place this specimen in the Linyphiidae: Linyphiinae, based on the remaining somatic and genitalic morphology, for example the legs spination and trichobothrial patterns, but to which tribe (Micronetini or Linyphiini) it belongs is uncertain. We accept that this placement is not based on any putative autapomorphies and are unaware of any studies, which provide reliable diagnostic or phy-

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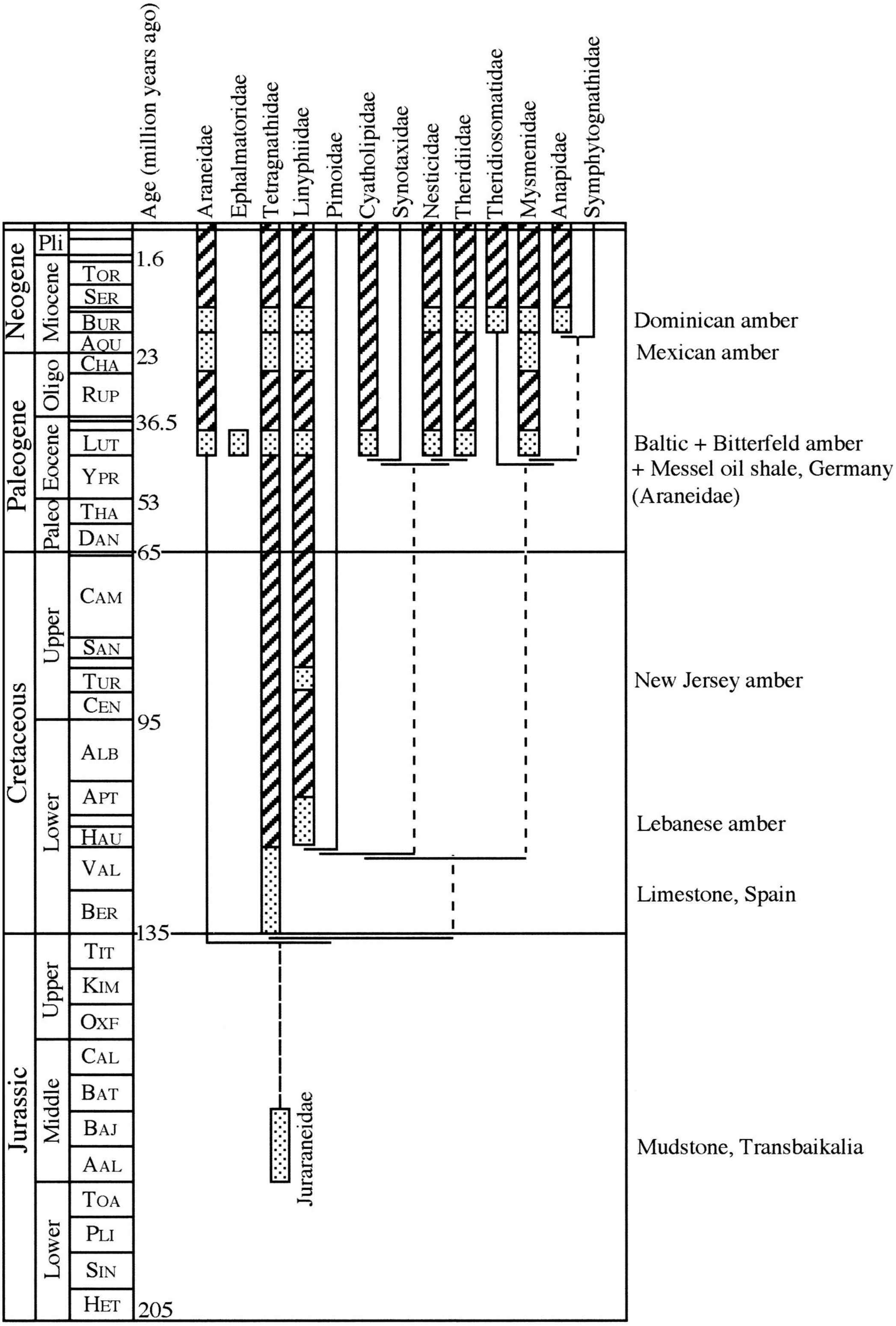
Figure 4.—Evolutionary tree of the Araneoidea. Dotted fill = described fossil, striped fill = known geological range, vertical solid lines = range extension, horizontal solid lines = phylogenetic relationships, tight dashed lines = ancestral lineage, loose dashed lines = ghost lineage, Lagerstätten on right side. Terminology follows Smith (1994).


Age (million years ago)
Araneidae
Ephalmatoridae
Tetragnathidae
Linyphiidae
Pimoidae
Cyatholipidae
Synotaxidae
Nesticidae
Theridiidae
Theridiosomatidae
Mysmenidae
Anapidae
Symphytognathidae
Juraraneidae
Neogene
Paleogene
Cretaceous
Jurassic
Pli
Miocene
Oligo
Eocene
Paleo
Upper
Lower
Middle
Tor
Ser
Bur
Aqu
Cha
Rup
Lut
Ypr
Tha
Dan
Cam
San
Tur
Cen
Alb
Apt
Hau
Val
Ber
Tit
Kim
Oxf
Cal
Bat
Baj
Aal
Toa
Pli
Sin
Het
1.6
23
36.5
53
65
95
135
205
Dominican amber
Mexican amber
Baltic + Bitterfeld amber
+ Messel oil shale, Germany
(Araneidae)
New Jersey amber
Lebanese amber
Limestone, Spain
Mudstone, Transbaikalia

logenetic chaetotaxy or trichobothrial patterns. However, paleoarachnologists are often confronted with fossils which are unique and do not possess, or clearly exhibit, the characters used in Recent spider taxonomy and systematics, but important specimens of great antiquity such as this warrant description and placement as far as is possible.

The presence of fossil Linyphiidae in the upper Neocomian–basal Lower Aptian (c. 125–135 Ma) predicts the presence of Pimoidae, otherwise unknown in the fossil record, in the Cretaceous. It also predicts the occurrence of the spineless femur clade and the symphytognathoids, or their ancestors approximately a further 35 Ma back in the fossil record, from the oldest known described fossil Linyphiidae in Turonian New Jersey amber (Penney in press) (Fig. 4). A number of authors e.g. Wunderlich (1986), Millidge (1993) and Hormiga (1994a, 2000) have provided various hypotheses regarding the subfamilial phylogenetic relationships within the Linyphiidae. These were compared and contrasted by Hormiga (2000) whose favored cladogram had the Linyphiinae (Micronetini and Linyphiini) as a sister group to the remaining linyphioid taxa, excluding Millidge's (1993) Dubiaraneinae, which Hormiga considered a dubious taxon. However, it remains to be seen whether these proposed relationships withstand future phylogenetic analyses incorporating more linyphiid species and more character states (Hormiga 2000). Accepting Hormiga's (2000) cladogram, which can be represented in parenthical notation as: ((((Stemonyphantinae) (Mynogleninae)) (Erigoninae)) ((Micronetini) (Linyphiini))), as the most reliable indication of the intrafamilial phylogeny currently available, then this fossil is direct evidence that the first major radiation, which separated the Linyphiinae from the remaining linyphiid taxa, occurred in the early Cretaceous, if not before.

The current fossil evidence (Fig. 4) gives the impression that the more derived, higher araneoids radiated and diversified in the Tertiary after the end-Cretaceous mass extinction event. However, we suspect that this observation is a sampling artefact. Thousands of Tertiary amber spiders, particularly from the Baltic and the Dominican Republic, have been studied over the last century and a half, whereas probably fewer than 50 specimens of Cretaceous spiders, many of which are poorly preserved and not identifiable to family, account for the only three publications to date (Eskov & Wunderlich 1994; Penney in press; Selden in press) that describe Cretaceous amber spiders. The relatively large number of Recent spider families being discovered in rocks and amber of Mesozoic age suggests a great antiquity of modern spider families (Selden & Penney 2001), we would expect to find some of these families given enough Cretaceous specimens and are currently working through this material.

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