

Calibrating the chelicerate clock: a paleontological reply to Jeyaprakash and Hoy

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Abstract Divergence times inferred for major lineages of Chelicerata (scorpions, spiders, mites, pycnogonids and xiphosurans) in a recent paper on mitochondrial phylogeny by Jeyaprakash and Hoy are compared to the known stratigraphical occurrences of these groups. Erroneous statements concerning fossil date estimates in the original study are corrected. We emphasize that the fossil record of chelicerates is more complete than is sometimes assumed, and that paleontology plays a key role in dating cladogenesis by setting minimum divergence times, which can and do falsify molecular clock estimates where the inferred divergence is substantially younger than the known fossil record. The oldest representatives of each chelicerate order are documented here, together with similar data for the major mite lineages down to family level. Through these, we hope to provide a robust framework and reference points for future molecular systematic studies of this nature.

Keywords Chelicerata · Fossil record · Molecular clocks · Phylogeny

Introduction

In a recent paper, Jeyaprakash and Hoy (2009) used a mitochondrial phylogeny to infer provisional divergence times for some of the major lineages of Chelicerata: namely scorpions, spiders, mites, pycnogonids and xiphosurans. While we welcome these

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increasingly sophisticated approaches towards resolving ingroup relationships among arachnids and their relatives, as well as their times of cladogenesis, we feel that the Jeyaprakash and Hoy analysis suffers from its cursory treatment of paleontological source material. Key studies seem to have been overlooked and consequently some of the fossil dates cited—such as the oldest spider supposedly being Cretaceous in age—are inaccurate. This is unfortunate because fossils, when used properly, have much potential to help calibrate estimates of divergence time based on molecular clocks (reviewed by Donoghue and Benton 2007), but this can only be done successfully if the paleontological dataset is handled as carefully as the mitochondrial or nuclear gene data.

As Jeyaprakash and Hoy noted, the arachnid fossil record is not perfect (see especially Selden 1993a, b for detailed summaries), but it is markedly better for some groups than for others. Fossils play a valuable role in documenting the oldest occurrences of particular groups or lineages, and thus provide a minimum age for cladogenesis. In this way fossils can easily falsify a hypothesized divergence time derived from other sources if this estimate turns out to be substantially younger than the oldest specimen(s) documented in the literature. A putative scorpion–spider split in the Devonian, proposed as an initial divergence time estimate by Jeyaprakash and Hoy (2009), is a case in point and is falsified by the presence of Silurian scorpions; which have been known since the late nineteenth century.

Here, we briefly compare the initial mitochondrial-based estimates offered by Jeyaprakash and Hoy (2009) with the current fossil record. Discrepancies are highlighted and discussed. We further note the relatively restricted taxon sampling across Chelicerata, in which eight orders are missing from the original analysis (harvestmen, palpigrales, pseudoscorpions, solifuges, ricinuelids, whipspiders, whipscorpions and schizomids) compared to the six actually tested (scorpions, spiders, actinotrichid and anactinotrichid mites, pycnogonids and xiphosurans). We feel there is also a wider issue about using mitochondrial versus nuclear sequence data for reconstructing deep chelicerate phylogeny and this is coupled with an apparent reluctance on the part of the authors to consider alternative patterns of relationships (Wheeler and Hayashi 1998; Giribet et al. 2002; Shultz 2007). Potentially relevant literature seems to have been overlooked (Bernini 1986; Selden 1993a; de la Fuente 2003; Dunlop and Arango 2005) and for these reasons some of Jeyaprakash and Hoy's more controversial suggestions—like terrestrial origins for pycnogonids—should be treated with caution.

Finally, Donoghue and Benton (2007) advocated a non-adversarial approach to resolving discrepancies between 'rocks and clocks' and provided examples of the strengths and limitations of both methods with regard to dating the evolutionary origins of modern groups. In this spirit, and in the hope of encouraging more integrative and collaborative approaches within arachnology in future, we also offer a summary, with citations, of the oldest reliable stratigraphical records in the literature for both the chelicerate orders (Table 1) and the major lineages down to family level of both anactinotrichid (Table 2) and actinotrichid mites (Table 3). We also wish to draw attention to a medium-term goal of having all fossil chelicerates listed down to species level as an online resource, as has already been accomplished for spiders (Dunlop et al. 2008a).

Methods

Paleontological data was compiled from available summaries and the original literature where appropriate. Details of the primary sources consulted can be found in Dunlop et al.

Table 1 Oldest occurrences of the chelicerate orders in the fossil record based on the current literature

Taxon	Oldest record	Ma	Source reference(s)
Pycnogonida	Cambrian, Furongian	c. 501	Waloszek and Dunlop (2002)
Xiphosura	Ordovician, ‘Richmondian’	c. 445	Rudkin et al. (2008)
Chasmataspida ^a	Ordovician, Llanvirn ^b	c. 465?	Caster and Brooks (1956)
Eurypterida ^a	Ordovician, Caradoc	c. 460	Størmer (1951)
Scorpiones	Silurian, Llandovery	c. 428	Laurie (1899); Kjellesvig-Waering (1986)
Opiliones	Devonian, Pragian	c. 410	Dunlop et al. (2003)
Phalangiotarbida ^a	Devonian, ‘Siegenien’	c. 411	Poschmann et al. (2005)
Pseudoscorpiones	Devonian, Givetian	c. 392	Shear et al. (1989)
Solifugae	Carboniferous, Westphalian	c. 308	Petrunkévitch (1913)
Palpigradi	Neogene, Pliocene	c. 5?	Rowland and Sissom (1980)
Acari	Devonian, Pragian	c. 410	Hirst (1923); Dubinin (1962); see also Table 3
Ricinulei	Carboniferous, Namurian	c. 319	Brauckmann (1987)
Trigonotarbida ^a	Silurian, Přidolí	c. 419	Jeram et al. (1990)
Uraraneida ^a	Devonian, Givetian	c. 392	Selden et al. (2008)
Araneae	Carboniferous, Westphalian	c. 312	Pocock (1911)
Haptopoda ^a	Carboniferous, Westphalian	c. 312	Pocock (1911)
Amblypygi	Carboniferous, Westphalian ^c	c. 312	Pocock (1911)
Thelyphorida	Carboniferous, Namurian	c. 319	Brauckmann and Koch (1983)
Schizomida	Paleogene, Oligocene	c. 34	Lin et al. (1988)

^a Indicates an extinct group

^b Oldest body fossil; resting impressions probably assignable to this extinct, aquatic group are known from the late Cambrian

^c There are also some mid Devonian cuticle fragments which express a potential synapomorphy in their trichobothrial position with Amblypygi

(2008c), who used essentially the same dataset to generate species counts for all fossil chelicerates (see their Table 1). In this study, 1952 valid species of fossil chelicerate were gleaned from the literature, 1593 of them arachnids. These included 979 fossil spiders—to which about a hundred more have since been added by Wunderlich (2008)—as well as 111 scorpions and 294 mites (mostly actinotrichids and including many subfossil oribatids assigned to living species; see especially Karppinen et al. 1979 and Solhøy and Solhøy (2000) and references therein). For the purposes of the present paper, oldest occurrences of individual lineages are largely derived from the relevant chapter of *The Fossil Record 2* (Selden 1993b), with the present lists (Tables 1–3) updated to accommodate discoveries and/or reinterpretations published after this date. While some groups of fossil arachnids have been formally cataloged (e.g., scorpions, Fet et al. 2000), accessibility to modern and accurate raw paleontological data including taxonomic lists and relevant literature can be a problem. Thus, as part of a larger project preparing for a revised issue of the chelicerate volume of the *Treatise on Invertebrate Paleontology* (PAS, JAD), provisional lists of species have been compiled by JAD and collaborators. The fossil spider data is already available online (Dunlop et al. 2008a) as an appendix to the *World Spider Catalog* and with Norman Platnick’s permission (pers. comm. to JAD 2008) the intention is to upload species lists and references for other chelicerate orders here in due course. In the meantime JAD is happy to make the provisional data available for research purposes on a fair use basis.

Table 2 Oldest occurrences of anactinotrichid (parasitiform *s. l.*) mite families in the arachnid fossil record based on the current literature

Taxon	Oldest record	Ma	Source reference(s)
<i>Opilioacarida</i>			
Opilioacaridae	Paleogene, Eocene	c. 44–49	Dunlop et al. (2004)
<i>Gamasida</i>			
Sejidae	Paleogene, Eocene	c. 44–49	Koch and Berendt (1854)
Zerconidae	Quaternary, ?Pleistocene	>2.6	Błaszak et al. (1995)
Uropodidae	Quaternary, Holocene	>0.01	Ramsay (1960)
Parasitidae	Paleogene, Eocene	c. 44–49	Witlanski (2000)
Podocinidae	Quaternary	>2.6	Aoki (1974)
Macrochelidae	Quaternary, Holocene	>0.01	Ramsay (1960)
Digamasellidae	Neogene, Miocene	c. 16	Hirschmann (1971)
<i>Holothyrida</i>			
	Recent (no fossil record)	–	–
<i>Ixodida</i>			
Argasidae	Cretaceous, Turonian	c. 90–94	Klompen and Grimaldi (2001)
Ixodidae	Cretaceous, Albian	c. 100	Poinar and Brown (2003); Poinar and Buckley (2008)

Families not listed can be assumed to have no fossil record. Major groups and nomenclature based primarily on the Tree of Life project and the lists compiled by Joel Hallan <<http://insects.tamu.edu/research/collection/hallan/>>

Results and discussion

One of the major, novel conclusions proposed by Jeyaprakash and Hoy 2009, p. 15) was that the arachnid groups they investigated “...all originated in the late Paleozoic Era and diversified in the Mesozoic Era, soon after the “Cambrian explosion”, which is much earlier than indicated by the fossil record.” Yet, with the exception of palpigrades and anactinotrichid mites, the fossil record clearly does indicate that all arachnid orders were present in a recognizable form by the middle to late Paleozoic (Table 1; Fig. 1) and figures showing exactly this pattern of distribution have long been available in the literature (e.g., Selden 1993a, b). We do not accept that the late Paleozoic (c. 300 Ma) is really that ‘soon’ after the Cambrian explosion (c. 530 Ma); being separated by a gap of some 230 million years.

Scorpions

Jeyaprakash and Hoy (2009, pp. 2, 14) implied that the oldest known scorpions originate from the Buntsandstein of France which they cited both (correctly) as Triassic and (incorrectly) as Jurassic within their paper. Their given age estimate of 200 Ma (which is indeed close to the Jurassic–Triassic boundary) is, however, incorrect and the title of Lourenço and Gall’s (2004) original description clearly stated that the fossils are early Triassic (i.e., 251–245 Ma). In any case, Jeyaprakash and Hoy made no reference to standard monographs (Kjellesvig-Waering 1986) or catalogs (Fet et al. 2000) which document much older material. In fact, scorpions may be the oldest known arachnids and their Paleozoic record is actually richer in species than either the Mesozoic or the

Table 3 Oldest occurrences of actinotrichid (acariform) mite families in the arachnid fossil record based on the current literature

Taxon	Oldest record	Ma	Source reference(s)
<i>Sphaerolichida</i>			
Alicorhagiidae	Devonian, Pragian	c. 410	Hirst (1923); Dubinin (1962)
Alycidae	Devonian, Pragian	c. 410	Hirst (1923); Dubinin (1962)
Nanorchestidae	Devonian, Pragian	c. 410	Hirst (1923); Dubinin (1962)
<i>Eupodina</i>			
Bdellidae	Cretaceous, Campanian	c. 78	Ewing (1937)
Eriophyiidae	Paleogene, Eocene	c. 40	Southcott and Lange (1971)
Phytoptidae ^b	Paleogene, Oligocene	c. 25	von Heyden (1860, 1862)
Penthalodidae	Paleogene, Eocene	c. 44–49	Koch and Berendt (1854)
Rhagidiidae	Paleogene, Eocene	c. 44–49	Judson and Wunderlich (2003)
Tydeidae	Devonian, Pragian	c. 410	Hirst (1923); Dubinin (1962)
<i>Eleutherengona</i>			
Acarophenacidae	Cretaceous, Albian–Cenoman.	c. 94–112	Magowski (1994)
Tarsonemidae	Quaternary	>2.6	Aoki (1974)
Cheyletidae	Cretaceous, Albian	c. 100	Cockerell (1917)
Camerobiidae	Paleogene, Eocene	c. 44–49	Bolland and Magowski (1990)
Cryptognathidae	Paleogene, Eocene	c. 44–49	Koch and Berendt (1854)
Tetranychidae	Paleogene, Eocene	c. 44–49	Koch and Berendt (1854)
<i>Anystae</i>			
Anystidae	Cretaceous, Albian–Cenoman.	c. 94–112	Zacharda and Krivoluckij (1985)
Caeculidae	Paleogene, Eocene	c. 44–49	Coineau and Magowski (1994)
<i>Parasitengona</i> ^b			
Arrenuroidea ^c (fam. uncertain)	Miocene, Neogene	c. 12?	Cook in Palmer (1957)
Trombidiidae	Paleogene, Eocene	c. 50	Koch and Berendt (1854)
Erythraeoidea (fam. uncertain)	Cretaceous, Aptian	c. 115	Dunlop (2007)
Erythraeidae	Paleogene, Eocene	c. 44–49	Koch and Berendt (1854)
Protoerythraeidae ^a	Cretaceous, Campanian	c. 78	Vercammen-Grandjean (1973)
Smarididae	Paleogene, Eocene	c. 44–49	Kulicka (1990)
<i>Oribatida</i> ^d			
Adelphacaridae	Carboniferous, Brigantian	c. 326–330	Subías and Arillo (2002)
Ctenacaridae	Devonian, Frasnian	c. 375–385	Subías and Arillo (2002)
Devonacaridae ^a	Devonian, Givetian	c. 392	Norton et al. (1988)
Protochthoniidae ^a	Devonian, Givetian	c. 392	Norton et al. (1988)
Hypochthoniidae	Carboniferous, Brigantian	c. 326–330	Subías and Arillo (2002)
Cosmochthoniidae	Carboniferous, Brigantian	c. 326–330	Subías and Arillo (2002)
Protoplophoridae	Carboniferous, Brigantian	c. 326–330	Subías and Arillo (2002)
Gehypochthoniidae	Carboniferous, Brigantian	c. 326–330	Subías and Arillo (2002)
Collohmanniidae	Paleogene, Eocene	c. 44–49	Sellnick (1919); Norton (2006)
Camisiidae	Cretaceous, Albian–Cenoman.	c. 94–112	Bulanova-Zachvatkina (1974)
Crotoniidae	Neogene, Pliocene	c. 2.6–5	Womersley (1957)
Nothridae	Paleogene, Eocene	c. 44–49	Karsch (1884); Sellnick (1919)

Table 3 continued

Taxon	Oldest record	Ma	Source reference(s)
Phthiracaridae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Euphthiracaridae	Quaternary, Holocene	>0.01	
Oribotritidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Hermannidae	Paleogene, Eocene	c. 44–49	Norton (2006)
Malaconothridae	Quaternary, Holocene	>0.01	
Mucronothridae	Quaternary, Holocene	>0.01	
Trhypochthoniidae	late Jurassic	c. 145–161	Krivolutsky and Krasilov (1977)
Nanhermannidae	Quaternary, Holocene	>0.01	
Ameronothridae	Quaternary, Holocene	>0.01	
Caleremaeidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Carabodidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Otocephidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Cepheidae	Cretaceous, Aptian	c. 115–121	Arillo and Subías (2002)
Eremaozetidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Cymbaeremaeidae	Jurassic, Callovian	c. 161–165	Selden et al. (2008)
Micreremidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Damaeidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Eremaeidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Astegistidae	late Jurassic	c. 145–161	Krivolutsky and Krasilov (1977)
Gustaviidae	Quaternary, Holocene	>0.01	
Liacaridae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Peloppiidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Tenuialidae	Quaternary, Holocene	>0.01	
Gymnodamaeidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Hermannellidae	Paleogene, Eocene	c. 44–49	Sellnick (1919, 1931)
Hydrozetidae	Jurassic, Sinemurian	c. 197	Sivhed and Wallwork (1978)
Limnozetididae	Quaternary, Holocene	>0.01	
Liodidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Neoliodidae	Paleogene, Eocene	c. 44–49	Sellnick (1919)
Autognetidae	Quaternary, Holocene	>0.01	
Oppiidae	Paleogene, Eocene	c. 44–49	Sellnick (1919, 1931)
Suctobelbidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Thyrisomidae	Quaternary, Holocene	>0.01	
Plateremaeidae	Cretaceous, Albian–Cenoman.	c. 94–112	Krivolutsky and Ryabinin (1976)
Tectocephaeidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Archaeorchestidae ^a	Cretaceous, Aptian	c. 115–121	Arillo and Subías (2002)
Achipteriidae	late Jurassic	c. 145–161	Krivolutsky and Krasilov (1977)
Tegoribatidae	Quaternary, Holocene	>0.01	
Ceratozetidae	Paleogene, Eocene	c. 44–49	Koch and Berendt (1854); Sellnick (1931)
Chamobatidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Euzetidae	Quaternary, Holocene	>0.01	
Mycobatidae	Quaternary, Holocene	>0.01	

Table 3 continued

Taxon	Oldest record	Ma	Source reference(s)
Zetomimidae	Quaternary, Holocene	>0.01	
Galumnellidae	Quaternary, Holocene	>0.01	Aoki (1974)
Galumnidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Licneremaeidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Passalozetidae	Quaternary, Holocene	>0.01	
Scutoverticidae	Neogene, Miocene	c. 16	Woolley (1971); Norton and Poinar (1993)
Oribatellidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Phenopelopidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Haplozetidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Mochlozetidae	Neogene, Miocene	c. 16	Woolley (1971); Norton and Poinar (1993)
Oribatulidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Oripodidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Parakalummidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Scheloribatidae	Paleogene, Eocene	c. 44–49	Sellnick (1931)
Tubulozetidae	Quaternary, Holocene	>0.01	
<i>Astigmata</i>			
Winterschmidtidae	Neogene, Miocene	c. 16	Türk (1963)
?Tyroglyphidae ^c	Neogene, Miocene	c. 16	Pampaloni (1902)

^a Indicates an extinct group. Families not listed can be assumed to have no fossil record. Major groups and nomenclature based primarily on the Tree of Life project and the lists compiled by Joel Hallan <<http://insects.tamu.edu/research/collection/hallan/>>

^b Questionable record based on fossilized galls only

^c A further putative fossil water mite from Rott in Germany (von Heyden 1962) has been regarded as an insect larva (e.g., Bertkau 1878, p. 346) and is not included here

^d Bernini et al.'s (2002) controversial record from the early Ordovician (ca. 475 Ma) of Sweden was assigned to Oribatida as "...intermediate between the cymbaeremid and ameronothroid families..."

^e Familial position of Pampaloni's extinct genus merits confirmation

Cenozoic. The oldest scorpion comes from the mid Silurian Pentland Hills of Scotland (Laurie 1899) which is dated to c. 428 Ma (Fig. 1). Other slightly younger Silurian scorpions are well-known from the literature (e.g., Dunlop et al. 2008b, and references and synonymy lists therein).

The Pentland Hills material is not especially well-preserved, but it is recognizably a scorpion and is particularly significant because Jeyaprakash and Hoy (2009) provisionally estimated the scorpion–spider split at early Devonian (393 ± 23 Ma). This result must be an underestimate, since even the oldest limit of their proposal is still 12 million years younger than the oldest fossil scorpion. The alternative scenario would be to have spiders evolving in the Devonian from within the scorpion lineage: a scenario which we find extremely unlikely and which would involve numerous major morphological reversals. In general, the position of the scorpions has proved to be one of the more controversial aspects of arachnid evolution. Traditionally placed as basal arachnids or even as sister-group of the extinct sea scorpions (Eurypterida), current datasets usually resolve them close to, or even as sister-group to, the harvestmen (Opiliones) (Shultz 2007). The

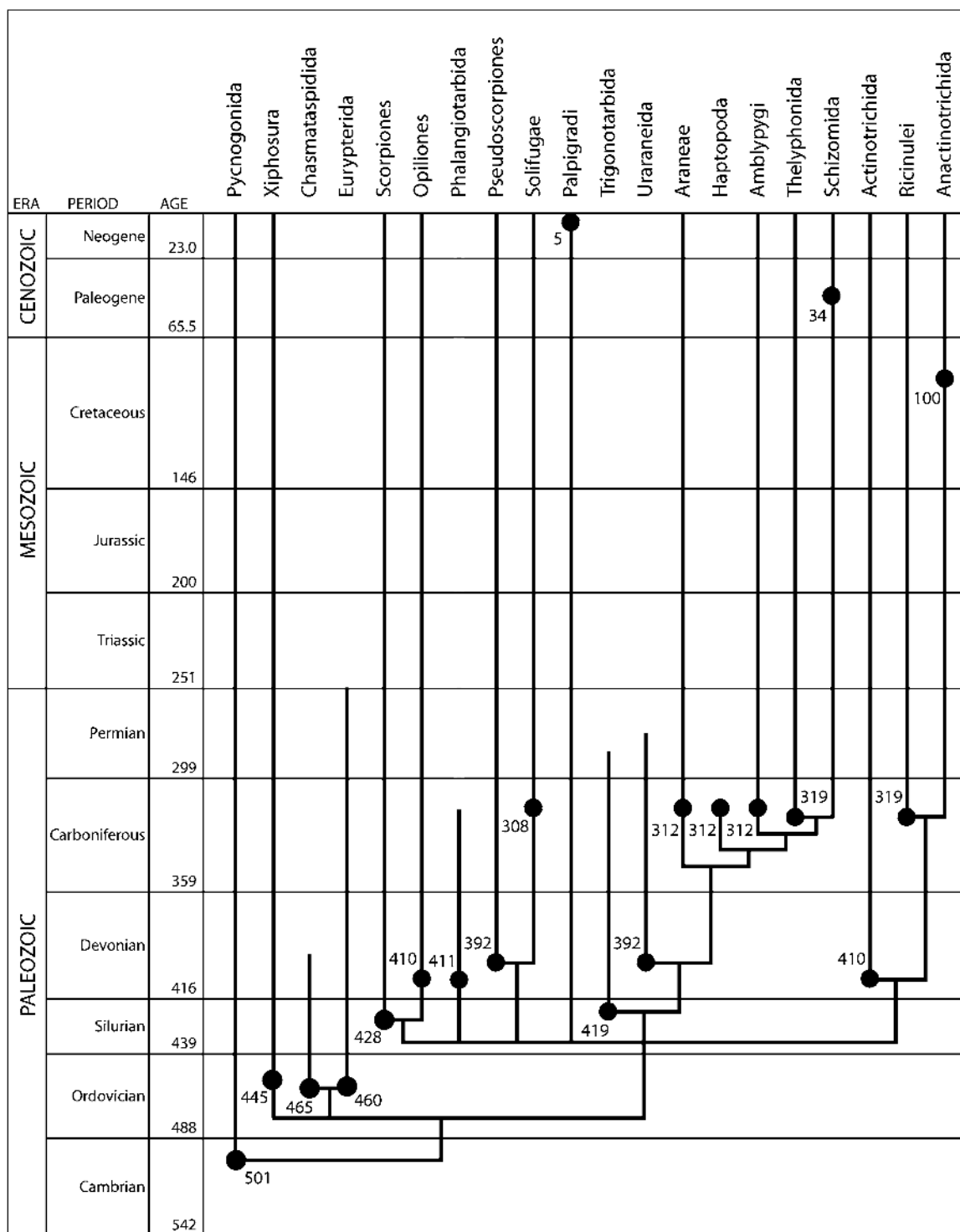


Fig. 1 Phylogenetic tree of the arachnids and their relatives showing reliable earliest fossil occurrences (see Tables 1, 2 for details). Cladogram based on Shultz (2007) and geological dates from the IUGS International Stratigraphic Chart (Gradstein et al. 2004). Compare with Fig. 2 in Jeyaprakash and Hoy (2009)

incomplete taxonomic sampling of the Jeyaprakash and Hoy study meant that this hypothesis could not be tested here and we feel it would be very worthwhile to compare a scorpion–spider divergence estimate with a scorpion–harvestman one. The oldest harvestman is from the early Devonian (c. 410 Ma) Rhynie chert of Scotland (Dunlop et al. 2003).

Spiders

Jeyaprakash and Hoy (2009, p. 2) stated that the oldest spider is Cretaceous in age; this is incorrect. Carboniferous spiders have been described since the late nineteenth century (e.g., Roemer 1866; Harger 1874; Pocock 1911; Petrunkevitch 1913) (Fig. 1) and while the exact status of some of these Paleozoic forms is questionable (Penney and Selden 2006), at least one late Carboniferous example is an unequivocal mesothele (Selden 1996). The previous oldest spider was described from Devonian rocks of New York by Selden et al. (1991) as *Attercopus*, but recently this animal has been shown to be more primitive than true spiders (Selden et al. 2008) and has now been raised to a separate arachnid order Uraraneida. Nevertheless, it had silk glands and other characteristics typical of true spiders. In the Mesozoic era, true spiders (Opisthothelae) are known from the middle Triassic of Virginia and South Africa (Selden and Gall 1992; Selden et al. 1999), and belong to modern families. The Jurassic has few described spiders, but these also belong to modern families (Eskov 1984, 1987; Selden et al. 2008). By the end of the Cretaceous, numerous modern families had become well established (Vollrath and Selden 2007 and references therein; see also Wunderlich 2008).

Mites

Jeyaprakash and Hoy (2009) estimated the split between mites and pycnogonids (see below) as late Silurian (424 ± 21 Ma) and placed the split between the two major mite clades (actinotrichids and anactinotrichids) in the early Devonian (394 ± 24 Ma). In support of this, the authors correctly alluded to oribatid mites from the mid Devonian of Gilboa, New York (Norton et al. 1988). Further oribatids from the late Devonian and early Carboniferous (Subías and Arillo 2002) could also be mentioned in this context. However, these oribatids are not the oldest record of mites. Older material comes from the early Devonian (c. 410 Ma) Rhynie Chert of Scotland (Hirst 1923; see also Bernini 1986) and is currently assigned to both Sphaerolichida and Eupodina (Dubinin 1962) (Table 3). A putative oribatid mite assigned to a derived, ‘higher’ lineage from the early Ordovician (c. 475 Ma) of Sweden (Bernini et al. 2002) is controversial. The brief original description lacked photographic documentation. Although the authors argued that it is not a younger contaminant mixed up in an Ordovician sediment sample, additional material would be welcome to confirm the oldest putative record of Arachnida. The oldest unequivocal mites (Tables 1, 3; Fig. 1) are thus the early Devonian specimens from Rhynie.

Compared to actinotrichids, the paucity of the anactinotrichid fossil record—which consists of about a dozen species and only goes back as far as the late Cretaceous—remains one of the puzzles of arachnid evolution. As pointed out to us in review, many anactinotrichid lineages seem to show ‘Gondwanan’ trends, whereas the majority of the productive fossil localities found so far come from the northern hemisphere. Whether ticks diverged as far back as 300 ± 27 , as suggested by Jeyaprakash and Hoy (2009), and whether their first hosts were amphibians or reptiles remain interesting lines of inquiry. Paleontological data can currently contribute nothing here. de la Fuente (2003) offered further insights into the possible origins and fossil record of the ticks. It should be noted that Klompen and Grimaldi’s (2001) argasid tick from New Jersey amber is no longer the oldest record of the group (Table 2). It has been superseded by two slightly older (c. 100 Ma) Cretaceous hard ticks from Myanmar (=Burmese) amber (Poinar and Brown 2003; Poinar and Buckley 2008).

Pycnogonids

Perhaps one of the more controversial aspects of Jeyaprakash and Hoy's (2009) results is the grouping of pycnogonids and mites (thus rendering Euchelicerata paraphyletic), with an estimated mite–pycnogonid divergence time in the late Silurian (424 ± 21 Ma) and a mite–pycnogonid–scorpion–spider divergence in the late Ordovician (459 ± 18 Ma). Although historically pycnogonids and mites were indeed sometimes placed together (see Dunlop and Arango 2005 for a review), this was usually based on rather superficial resemblances like attempts to homologize the pycnogonid proboscis with the sucking mouthparts of ticks. These have not translated into convincing modern synapomorphies. There are, however, some interesting similarities such as larval stages with fewer limbs than the adult (i.e., anamorphic development) and the possible retention of the euarthropod head, in the form of a principal anterior body tagma—the (actinotrichid) mite proterosoma and the pycnogonid cephalosoma—with only four pairs of appendages. However, both of these could be interpreted as plesiomorphic (Hassanin 2006; Dunlop and Alberti 2008) and cladistic analysis based on morphology almost invariably recovers Pycnogonida as either the sister group of Euchelicerata or of other Euarthropoda in general (reviewed in Dunlop and Arango 2005). Even if the relationships proposed by Jeyaprakash and Hoy (2009) were to prove correct, their provisional divergence estimates are inconsistent with the fossil record. Waloszek and Dunlop (2002) were cited in passing as evidence for the aquatic origins of Pycnogonida, but the same paper explicitly focuses on the oldest putative fossil sea spider which derives from the late Cambrian (c. 501 Ma) Orsten of Sweden (Fig. 1). This is over 50 million years before the maximum mite–pycnogonid divergence date derived from the mitochondrial evidence and almost 25 million years before the putative arachnid/pycnogonid split.

Nevertheless, it is notable that many mitochondria-based studies have resolved pycnogonids within Arachnida—at least under some parameters of analysis—and specifically closest to mites (e.g., Wheeler and Hayashi 1998, Fig. 6; Giribet et al. 2002, Fig. 6; Hassanin 2006, Figs 1–3; Podsiadlowski and Braband 2006, Fig. 3; Jeyaprakash and Hoy 2009, Fig. 1). These results have a certain consistency and require explanation. Podsiadlowski and Braband (2006), for example, felt that long-branch attraction and homoplastic changes within the mitochondrial DNA may be generating an artifact and both these authors and Hassanin (2006) noted that nuclear genes tend to concur with morphology and recover the more traditional Pycnogonida–Euchelicerata hypothesis (see also Regier and Shultz 2001; Mallatt et al. 2004; Regier et al. 2005). Domes et al. (2008) reiterated the point that mitochondrial genomes evolve faster than nuclear ones, and that the resulting saturation of the phylogenetic signal can be problematic when attempting to resolve deep splits. By contrast, Jeyaprakash and Hoy (2009) felt that mites and pycnogonids could be a real result and suggested that long-branch attraction was less likely in their own study using slower-evolving sequences.

Taking up an earlier thought experiment by Podsiadlowski and Braband (2006), Jeyaprakash and Hoy promoted a scenario in which pycnogonids and mites shared a common terrestrial ancestor, with the sea spiders invading the marine environment secondarily. The many reductive characters associated with pycnogonids make any interpretation of their evolutionary history difficult, but we find a secondarily aquatic mode of life unlikely. It seems to be based on (a) an over-reliance on mitochondrial gene data to the exclusion of nuclear genes and morphology, (b) an unproven assumption that the common ancestor of mites and/or arachnids was fully terrestrial and (c) the need to ignore the Cambrian 'Orsten' larva which came from an unequivocally marine environment. Furthermore, the

hatching larvae of modern sea spiders lack walking legs (e.g., Gillespie and Bain 2006), expressing instead stubby larval limbs comprising only two articles plus a long distal spine. Unless there were major reversals back to an aquatic type of larva, it is hard to envisage a terrestrial ancestor of sea spiders producing young of this nature.

Finally, one of the most enduring hypotheses based on morphology recovers mites with ricinuleids. Shultz (2007) recognized a tree of the form (Actinotrichida (Anactinotrichida + Ricinulei)); i.e., mites resolve here as paraphyletic (Fig. 1). This broad Acaromorpha clade is based principally on the presence of a hexapodal larva and, less convincingly, similarities in the mouthparts (reviewed in Dunlop and Alberti 2008). Jeyaprakash and Hoy did not include ricinuleids in their analysis, but a recent study of an oribatid mitochondrial genome (Domes et al. 2008) recovered [Anactinotrichida (Actinotrichida + Ricinulei)]; although they did not test the position of pycnogonids. As both Domes et al. and Jeyaprakash and Hoy noted, a more integrated picture of relationships requires broader taxon sampling of the mt genome, both across the diversity of mites and for all major lineages of Chelicerata.

Xiphosurans

Xiphosurans (horseshoe crabs) are often regarded as classic examples of living fossils. Anderson and Selden (1997) excluded a number of problematic early Paleozoic merostome fossils from Xiphosura sensu stricto. These authors recognized a paraphyletic stem-lineage of so-called synziphosurines—extinct forms, the oldest of which is Silurian—and a crown group Xiphosurida which at that time first appeared in the Carboniferous. More recently, Rudkin et al. (2008) described the oldest horseshoe crab from the late Ordovician of Manitoba, Canada (Fig. 1). This remarkable find has the opisthosomal tergites fused into a single plate or thoracetron and is thus assignable with some confidence to the more derived xiphosurid lineage. It implies quite a deep split between stem- and crown-group xiphosurans. The Manitoban fossils are dated to c. 445 Ma. The oldest fossil thus falls within the 475 ± 53 Ma range predicted by Jeyaprakash and Hoy (2009) for the xiphosuran divergence from the remaining chelicerates.

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