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How many species of fossil arachnids are there?

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Abstract. The species-level diversity of fossil Chelicerata is summarized for each order. 1952 valid species of fossil chelicerates are currently recognized, of which 1593 are arachnids. In order of abundance they are: Araneae (979 fossil species), Actinotrichida (283), Eurypterida (241), Scorpiones (111), Xiphosura (96), Trigonotarbida (71), Pseudoscorpiones (38), Phalangiotarbida (30), Opiliones (25), Ricinulei (15), and Anactinotrichida (11). Other groups are represented by ten fossil species or fewer. Based on published descriptions, spiders thus appear to dominate the fossil arachnid species assemblage, making up a greater proportion of paleodiversity than their Recent diversity would predict. Scorpions are also overrepresented, particularly in the Paleozoic, compared to their modern diversity. By contrast, groups like mites, harvestmen, pseudoscorpions and solifuges are noticeably under-represented as fossils when compared to modern patterns of diversity.

Keywords: Chelicerata, Arachnida, diversity, fossil, species counts

Harvey (2002: table 1) reported a total – to December 2000 – of 97,682 valid species of Recent Arachnida; with the caveat that many more probably remain to be described. But how many species of fossil arachnids are there? Older figures of 366 valid fossil arachnid species names can be culled from Scudder (1891) and, some sixty years later, Petrunkevitch (1955: 48) had cataloged 505. Since that time there have been important developments in our understanding of arachnid paleontology (see, e.g., Selden 1993). New localities continue to yield new species, while amber spiders (e.g., Wunderlich 2004) have proved to be the major source of new names in recent years. That said, revision of historical types usually lowers diversity once synonyms or erroneously assigned fossils have been recognized. Here, we offer a modern summary of crude fossil arachnid diversity (Table 1) and the most important localities (Table 2) as a baseline for future paleoarachnological research. 1593 valid fossil arachnid species are recognized here from 1776 published names. For completeness we have expanded our review to cover the entire Chelicerata, resulting in a grand total of 1952 valid fossil species from 2283 published names.

METHODS

No single modern catalog of fossil arachnids and their relatives exists, thus data had to be compiled from various sources as outlined for each group below. Where available, we drew on existing catalogs and/or summary papers, plus additions to the fauna since these publications. Data were cross-referenced to the primary literature wherever possible. Also valuable were lists on Joel Hallan's website <http://insects.tamu.edu/research/collection/hallan/>. Here, we restrict counts of valid species to published names and revisions only; i.e., excluding thesis work or papers in progress. The total number of described names incorporates synonyms, *nomina dubia*, *nomina nuda*, and incorrectly assigned material. For some groups – spiders, mites and the extinct orders in particular – species numbers had to be largely compiled from the primary literature and, due to space limitations, not all sources could be included here in the citations. We eventually hope to produce a more detailed list including taxa, authors, localities, type repositories and references, either as a printed catalog or internet resource. In the meantime the authors are happy to make our provisional lists available on a ''fair use'' basis upon request.

RESULTS

Pycnogonida.—Nine fossil sea spiders have been described (Poschmann & Dunlop 2006; Charbonnier et al. 2007): one late Cambrian larva from the ''Orsten'' of Sweden, a Silurian species from the Herefordshire Lagerstätte, UK, four from the early Devonian Hunsrück Slate of Germany and three from the Jurassic of France. Putative fossil sea spiders described from the Jurassic of Germany appear to be misidentified crustaceans.

''Euchelicerata''.—An enigmatic Silurian fossil from the Herefordshire Lagerstätte, UK was described as having ''chelicerate affinities'' (Orr et al. 2000). Since it has opisthosomal opercula – a defining character of Euchelicerata – it can probably be assigned to this clade. Four further species are provisionally listed as ''euchelicerates'' in our database, but they are primarily there because they are poor fossils of indeterminate affinity.

Xiphosura.—Horseshoe crabs are unique among living chelicerates in that there are far more fossil species than the four living ones. That said, the temporal distribution of these species throughout their geological history suggests an overall

Table 1.—Valid fossil species of Chelicerata described to March 2008, divided into geological eras. See text for details of sources. Data includes subfossil (Quaternary: Holocene) occurrences of Recent species, of which 127 involve actinotrichid (oribatid) mites.

Group	Paleozoic	Mesozoic	Cenozoic	Total
Pycnogonida	6	3	—	9
"Euchelicerata"	5	—	—	5
Xiphosura	75	20	1	96
Chasmataspidida	8	—	—	8
Eurypterida	241	—	—	241
Scorpiones	79	16	16	111
Opiliones	7	1	17	25
Phalangiotarbida	30	—	—	30
Pseudoscorpiones	1	2	35	38
Solifugae	2	1	2	5
Acari: Anactinotrichida	—	1	10	11
Acari: Actinotrichida	15	15	253	283
Palpigradi	—	—	1	1
Ricinulei	15	—	—	15
"Pantetrapulmonata"	3	—	—	3
Trigonotarbida	71	—	—	71
Araneae	18	31	930	979
Haptopoda	1	—	—	1
Amblypygi	5	1	3	9
Uropygi	6	1	—	7
Schizomida	—	—	4	4
all Chelicerata	588	92	1272	1952
Arachnida only	253	69	1271	1593

diversity at any given time in the past similar to that seen today. In earlier studies various Paleozoic fossils vaguely resembling horseshoe crabs were assigned to Merostomata or even Xiphosura. Anderson & Selden (1997) excluded a number of these problematic taxa in their study of Paleozoic Xiphosura. These can be divided into a synziphosurine stem-lineage and a crown group Xiphosurida; the latter recently shown to extend back to the Ordovician (Rudkin et al. 2008). Data for Mesozoic and Cenozoic xiphosurids are mostly derived from Hauscke & Wilde (1991) and references therein. Currently, 96 xiphosuran species can be recognized, although revisions of Pennsylvanian genera (Anderson 1994, 1997) resulted in quite dramatic reductions in overall diversity. Most species-rich fossil genera appear to be over-split (Anderson 1996), with names based on preservational differences rather than convincing biological features. Further synonyms can be expected and the current total figure is probably an overestimate.

Chasmataspidida.—These little-known late Cambrian–mid Devonian marine euchelicerates are characterized by a long postabdomen of nine segments, but share prosomal features with both eurypterids and xiphosurans, rendering their monophyly and affinities uncertain. Seven chasmataspids were listed by Tetlie & Braddy (2004:table 1) and another was added by Poschmann et al. (2005). Both papers include further references and discussions of their morphology and relationships.

Eurypterida.—The extinct eurypterids, or sea scorpions, are the most diverse Paleozoic chelicerates. They ranged from the Ordovician to the Permian, with a clear peak of diversity in the Silurian. Tetlie (2007) provided a recent overview of their distribution and phylogeny. Tollerton (2004) proposed that some 29 Ordovician species are pseudofossils; i.e., sedimentary structures that fortuitously resemble animal material. Excluding these, our provisional list – drawing largely on Tetlie (2004) – documents 241 currently valid eurypterid species names. However, previous workers had a habit of assigning poor-quality specimens to common genera and Tetlie's study suggests that about fifty of these names are potentially synonyms, or otherwise based on non-diagnostic material. Thus, a final figure of c. 190 species may prove more realistic. Further revisions are needed, especially among the families Pterygotidae – which includes the largest recorded arthropods – and Adelophthalmidae, which are common in Coal Measures environments.

Scorpiones.—Whereas the fossil record of most (extant) arachnid orders is skewed towards the Cenozoic by large numbers of amber species, the scorpion fossil record is uniquely more diverse in the Paleozoic (Table 1). Drawing on the comprehensive posthumous monograph of Kjellesvig-Waering (1986), Fet et al. (2000) recognized 97 valid fossil scorpion species. Scorpions are the only arachnid order with a well-defined (Paleozoic) stem- and crown-group fossil record. A major question is whether the large number of Mississippian–Pennsylvanian taxa reflects a genuine period of radiation and experimentation – at least three major lineages appear to co-occur during this time – or to what extent this is an artifact of fossil abundance. Kjellesvig-Waering's monograph is problematic in that many Paleozoic specimens were not merely described as new species, but assigned their own family and/or superfamily group. A recent revision by Dunlop et al. (2008) synonymized two Silurian species, and with them eight superfluous higher taxa. Compared to their Paleozoic record, Mesozoic and Tertiary scorpions are quite rare. However, recent work has recovered increasing numbers from amber (Santiago-Blay et al. 2004; Lourenço & Weitschat 2005; and references therein), yielding a current total for all fossil scorpions of 111 valid species.

Opiliones.—The harvestman fossil record was reviewed by Dunlop (2007) who recognized 25 valid species and discussed the status of a number of fossils erroneously assigned to this group. The oldest harvestman is a eupnoid from the Rhynie chert and this is followed by a handful of Mississippian and Pennsylvanian species from Europe and North America. A single named Mesozoic example is known from Myanmar (Burmese) amber. The largest species assemblages come from Cenozoic ambers and the Florissant in Colorado, USA. Representatives of all four major lineages (or suborders) have now been found. The putative Pennsylvanian arachnid order Kustarachnida – with effectively only one valid species – is a misidentified harvestman and has thus been included in the Opiliones data. Descriptions of new species from amber are currently in preparation.

Phalangiotarbida.—This extinct order ranges from the Early Devonian to the Early Permian and is most common in the Coal Measures of Europe and North America. Petrunkevitch (1953) listed 24 species, plus one dubious taxon (excluded from Table 1); all under the order name Architarbi. There has been no formal revision of this species assemblage, but at least one (lost) fossil managed to get itself named three times which is fairly indicative of the quality of work thus far; see Rößler et al. (2003) for details. A posthumous Kjellesvig-Waering

Table 2.—Significant localities yielding fossil Chelicerata referred to in the text, including details of their stratigraphic position and approximate age in millions of years (Ma). Ages based primarily on the geological time chart of the British Geological Survey <http://www.bgs.ac.uk/education/britstrat/home.html>.

Locality	Country	Period	Epoch	Ma
Onyx Marble, Arizona	USA	Neogene	Pliocene?	2–5?
Dominican amber	Dominican Republic	Neogene	Miocene	16
Chiapas (Mexican) amber	Mexico	Neogene	Miocene	16
Randecker Maar	Germany	Neogene	Miocene	17
Aix-en-Provence	France	Palaeogene	Oligocene?	22?
Florissant, Colorado	USA	Palaeogene	Eocene	34
Baltic amber	Baltic coast of Europe	Palaeogene	Eocene	44–49
Canadian amber	Canada	late Cretaceous	Campanian	c. 78
Sierra de Montsech	Spain	late Cretaceous	Santonian	84
New Jersey amber	USA	late Cretaceous	Turorian	90–94
Myanmar (Burmese) amber	Myanmar	late Cretaceous	Albian	c. 100
Crato Formation	Brazil	early Cretaceous	Aptian	115
Álava amber	Spain	early Cretaceous	Aptian	115–121
Lebanese amber	Lebanon	early Cretaceous	Nec.–Aptian	130
Coal Measures	Europe / N. America	Pennsylvanian	Nam.–Steph.	327–290
Gilboa, New York State	USA	mid Devonian	Givetian	380
Hunsrück Slate	Germany	early Devonian	Emsian	390
Rhynie Chert, Scotland	UK	early Devonian	Pragian	410
Herefordshire Lagerstätte	UK	Silurian	Wenlock	425
"Orsten"	Sweden	late Cambrian	—	c. 500

manuscript mentioned in Selden (1993) proposed a number of synonymies, but was never formally published. Since Petrunkevitch's monographs a few new descriptions have been published, including the oldest record (Poschmann et al. 2005), such that 30 valid species can currently be recognized.

Pseudoscorpiones.—Harvey (1991) listed 32 valid fossil pseudoscorpions derived from Myanmar, Chinese, Baltic, and Dominican amber (see also Spahr 1993:12–20). Two further species were treated as *nomina dubia* by Harvey. Also not included as a valid species here is a questionable assignment, listed in Spahr, of a fossil in Romanian amber with affinities to an extant species. Since Harvey's catalogue, we can add the oldest record of the group from the mid Devonian of Gilboa, New York State (Schawaller et al. 1991). This, and further amber records (e.g., Henderickx 2005; Judson 2007), yield a current total count of 38 valid fossil species.

Solifugae.—Five fossil camel spider species are known, including a putative stem-group species from the Mississippian of Poland, a poorly-preserved example from the Coal Measures of Mazon Creek, Illinois, USA, one from the Cretaceous Crato Formation of Brazil, and two in Baltic and Dominican amber respectively; see Dunlop et al. (2004) for further details and literature.

Anactinotrichida.—Fossil anactinotrichid mites (Parasitiformes in some terminologies) are surprisingly rare given their modern diversity – eleven fossil species in total – and currently have a record no older than the late Cretaceous. They include an opilioacarid from Baltic amber (Dunlop et al. 2004), five named gamasid (or mesostigmatic) species from Baltic and Mexican amber (e.g., Witlański 2000), and five ticks (reviewed by Fuente 2003), mostly from various Mesozoic and Tertiary ambers.

Actinotrichida.—Actinotrichid mites (Acariformes in some terminologies) have a much more diverse, and a much older, fossil record. A putative Ordovician oribatid was not formally named, thus the oldest described actinotrichids come from the Rhynie chert of Scotland and from Gilboa, New York, USA (both Devonian). Further Devonian and Mississippian mites have been recovered from macerates (Subías & Arillo 2002), after which there is a considerable hiatus in the fossil record until mites begin to be formally described again in the mid Mesozoic. Amber is a major source of taxa and Spahr (1993) listed 129 actinotrichids across all ambers. A few amber species have been described since (e.g., Judson & Wunderlich 2003; Norton 2006), while various non-amber sources, like Aix-en-Provence in France (Gourret 1887), contribute to the fossil record too. Taxonomically, the best represented group are oribatids; presumably thanks to their often strongly sclerotized bodies. Their fossil record was reviewed by Krivolutsky & Druck (1986), and Norton (2006) partially revised the Baltic amber species. It is also worth noting that there is an extensive record of subfossil (Holocene) oribatid mites (e.g., Karpinen et al. 1979) from ancient soils and peats only hundreds or thousands of years old. All can be assigned convincingly to Recent species and comprise 127 of the fossil names in our data. Whether they should truly be considered fossils is a moot point, but we have included them in our calculations for completeness. Together with the other (extinct) species this gives a total fossil record of 283 actinotrichid names. Frequent reports of unnamed mites, particularly from various Mesozoic ambers, suggest that this number is a serious underestimate.

Palpigradi.—A single, ?Pliocene, fossil palpigrade has been described from the Onyx Marble of Arizona, USA (Rowland & Sissom 1980). A putative record from the Jurassic of Germany is a misidentified insect; see also Harvey (2002).

Ricinulei.—Fossil ricinuleids were revised by Selden (1992). All originate from the Pennsylvanian Coal Measures of Europe and North America. Fifteen valid fossil species in four genera and two families were recognized and no new taxa have been described since.

"Pantetrapulmonata".—Three Devonian arachnid species could not be assigned to any specific order, but were listed – partly for convenience – as probable members of this clade (Dunlop et al. 2006).

Trigonotarbida.—This extinct order ranges from the late Silurian to the early Permian and is most common in the Pennsylvanian Coal Measures of Europe and North America. Petrunkevitch (1953) listed 52 valid species – combining data for Trigonotarbida and its synonym Anthracomartida – plus five dubious taxa; at least one of which has since been revalidated (Dunlop & Rössler 2002). There has been considerable movement since Petrunkevitch's monographs, both in terms of revising older taxa and describing new ones. More remains to be done, especially among the common and clearly over-split Anthracomartidae (see comments in Dunlop & Rössler 2002), but our dataset recognizes 71 currently valid species names.

Araneae.—Penney & Selden (2007) provided a brief, general review of the spider fossil record. The oldest example comes from the Devonian of Gilboa, New York, USA (Selden et al. 1991) and a number of Pennsylvanian mesothele-like taxa have been recorded, the affinities of which are currently being revised (P. Selden, pers. comm.). The oldest unequivocal mesothele is late Pennsylvanian and both mygalomorphs and araneomorphs have now been recorded from sedimentary deposits in the Triassic. The vast majority of fossil spiders, c. 820 species, originate from amber. Around 540 species have been recorded from Eocene Baltic amber alone and Wunderlich (2004:203) speculated that three times this number may eventually be recovered from this one deposit. Miocene Dominican amber ranks second with approximately 170 named species (Penney 2006a) and the geographically and stratigraphically contemporary Chiapas (Mexican) amber yields about twenty (e.g., Petrunkevitch 1971). Other Cenozoic ambers – e.g., Parisian (France), Bitterfeld (Germany), Rovno (Ukraine) and China – are beginning to yield spiders too, as are various younger resins or copals; see studies in Wunderlich (2004). Significantly, an increasing number of species have been described in recent years from Cretaceous ambers such as Taimyr, Siberia (Eskov & Wunderlich 1995), Manitoba, Canada, Myanmar (= Burma) (Penney 2006b), New Jersey (Penney 2004a), the Isle of Wight, UK (Selden 2002); Álava (Spain) (Penney & Ortuño 2006) and Lebanese amber (Penney 2003).

Non-amber fossil spiders are much less common, but also derive from a wide range of localities. In addition to the Coal Measures, the most species-rich of these include the Cretaceous of Mongolia and Siberia (Eskov & Zonshtein 1990), Sierra de Montsech, Spain (Selden & Penney 2003), and the Brazilian Crato Formation (Selden et al. 2006). Also significant are the Cenozoic localities of Aix-en-Provence, France (Gourret 1887; Berland 1939), Florissant, Colorado, USA (Petrunkevitch 1922), Shanwang, Shandong, China (Zhang et al. 1994) and the Randecker Maar, Germany (Schawaller & Ono, 1979). Subfossil spiders from peat bogs can also be identified and assigned to extant species (Scott 2003) and these records have been included in our lists. Our total dataset for amber and non-amber spiders yields 979 fossil species; thus spiders show the highest levels of paleodiversity – approaching three times as many species as the next largest chelicerate groups (Table 1).

Haptopoda.—This extinct, monotypic, Coal Measures order was restudied by Dunlop (1999). Its status as a distinct order was confirmed, but no further species have been assigned to it.

Amblypygi.—Six species of fossil whip spider are listed in Harvey (2003:22, 30–32), four from the Coal Measures of Europe and North America and two in extant families from Mexican and Dominican amber respectively. Following Harvey, a dubious record from Aix-en-Provence (Gourret 1887) has been excluded. An overlooked Coal Measures name, a new species from the Crato Formation of Brazil (Dunlop & Martill 2002), and one from Mexican amber (Poinar & Brown 2004) bring the total number of currently valid species to nine.

Uropygi.—Nine species of fossil whip scorpion are listed by Harvey (2003:73–74, 79–80); and one further Pennsylvanian species was overlooked. Tetlie & Dunlop (2008) recognized only six species from the Coal Measures of Europe and North America (one of which may actually be a stem-group schizomid). There is a further species from the Crato Formation of Brazil (Dunlop & Martill 2002), yielding a current total of seven, but a putative species from the Miocene of California, USA is a misidentification.

Schizomida.—Four Tertiary species of fossil schizomid in three genera have been described. Three come from the Onyx Marble of Arizona, USA and one from the Oligocene of China. Further details can be found in Harvey (2003:103, 129). No further species have since been recorded, although schizomids from Dominican Republic amber will be described shortly.

DISCUSSION

Comparing measures of fossil (Table 1) and Recent (Harvey 2002) biodiversity, our species counts imply that the arachnid fossil record is biased in favor of spiders and scorpions. These two orders make up a greater percentage of total fossil diversity compared to their relative abundance in modern ecosystems today. Correspondingly, the fossil record is biased against mites, harvestmen, pseudoscorpions and solifuges. Mites make up almost half of all living arachnid species, but less than a fifth of the fossil paleodiversity. Part of the explanation must be the greater intensity of work on fossil spiders (cf. Wunderlich 2004 and references therein) and to a lesser extent scorpions (Kjellesvig-Waering 1986). By contrast we recognize a corresponding lack of effort, or expertise, when it comes to members of the Acari, Opiliones, Pseudoscorpiones, and the "minor" orders. Physically small taxa, like mites and pseudoscorpions, are generally less likely to be preserved (or noticed). Solifuges tend to be associated today with dry habitats and conditions for fossilization are most favorable where there are substantial bodies of water into which animals can fall and be buried.

It is important to stress that these crude species counts encompass the entire fossil record and to caution against over-interpreting data combined from different time periods and under different conditions of fossilization. Arachnids, and other chelicerates, lack a mineralized exoskeleton, thus their fossil record is sporadic and relies heavily on "windows" of exceptional preservation (Table 2). This makes it difficult to trace changes in their biodiversity over geological time with any accuracy, since apparent peaks of species-level diversity in the raw data largely reflect productive fossil localities like the Coal Measures or intensively investigated ambers. Nevertheless, superimposing the fossil record onto well-supported cladograms allows the construction of "evolutionary trees." Since a given taxon must be as old as its sister-group (which may not be preserved) these trees have considerable value in predicting which lineages should have been present during any given time period. They allow quantitative studies of faunal change, such as Penney et al.'s (2003) demonstration that spider families were not affected by the K-T mass extinction event, or Penney's (2004b) use of richness estimates to show how spider radiations seem to track the radiation of their insect prey over geological time. It is our hope that the raw data we are assembling here can allow similar quantitative studies to be expanded and applied to Chelicerata as a whole.

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LITERATURE CITED

Anderson, L.I. 1994. Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek, Illinois. Proceedings of the Geologists' Association 105:265–275.

Anderson, L.I. 1996. Taxonomy and taphonomy of Palaeozoic Xiphosura. Unpublished Ph.D. thesis. The University of Manchester, UK. 413 pp.

Anderson, L.I. 1997. The xiphosuran *Liomesaspis* from the Montceau-les-Mines Konservatt-Lagerstatte, Massif Central, France. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 204:415–436.

Anderson, L.I. & P.A. Selden. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. Lethaia 30:19–31.

Berland, L. 1939. Description de quelque araignées fossiles. Revue Française d'Entomologie 6:1–9.

Charbonnier, S., J. Vannier & B. Riou. 2007. New sea spiders from the Jurassic La Voulte-sur-Rhone Lagerstätte. Proceedings of the Royal Society of London B 274:2555–2561.

Dunlop, J.A. 1999. A redescription of the Carboniferous arachnid *Plesiosiro madeleyi* Pocock, 1911 (Arachnida: Haptopoda). Transactions of the Royal Society of Edinburgh: Earth Sciences 90:29–47.

Dunlop, J.A., S.R. Fayers, H. Hass & H. Kerp. 2006. A new arthropod from the early Devonian Rhynie chert, Aberdeenshire (Scotland), with a remarkable filtering device in the mouthparts. Palaeontologische Zeitschrift 80:296–306.

Dunlop, J.A. & D.M. Martill. 2002. The first whipspider (Arachnida: Amblypygi) and three new whipscorpions (Arachnida: Thelyphonida) from the Lower Cretaceous Crato Formation of Brazil. Transactions of the Royal Society of Edinburgh: Earth Sciences 92:325–334.

Dunlop, J.A. & R. Rössler. 2002. The trigonotarbid arachnid *Anthracomartus voelkelianus* (Anthracomartidae). Journal of Arachnology 30:211–218.

Dunlop, J.A., O.E. Tetlie & L. Prendini. 2008. Reinterpretation of the Silurian scorpion *Proscorpius osborni* (Whitfield): integrating data from Palaeozoic and Recent scorpions. Palaeontology 52:303–320.

Dunlop, J.A., J. Wunderlich & G.O. Poinar, Jr. 2004. The first fossil opilioacariform mite (Acari: Opilioacariformes) and the first Baltic amber camel spider (Solifugae). Transactions of the Royal Society of Edinburgh: Earth Sciences 94:261–273.

Eskov, K.Y. & J. Wunderlich. 1995. On the spiders of Taimyr ambers, Siberia, with the description of a new family and with general notes on the spiders from the Cretaceous resins (Arachnida: Araneae). Beiträge zur Araneologie 4:95–107.

Eskov, K.Y. & S. Zonshtein. 1990. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata: Araneae). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 178:325–368.

Fet, V., W.D. Sissom, G. Lowe & M.E. Braunwalder. 2002. Catalog of the Scorpions of the World (1758–1998). The New York Entomological Society, New York. 690 pp.

Fuente, J. de la. 2003. The fossil record and origin of ticks (Acari: Parasitiformes: Ixodida). Experimental and Applied Acarology 29:331–344.

Gourret, P. 1887. Recherches sur les Arachnides Tertiaires d'Aix en Provence. Recueil Zoologique Suisse 4(3):431–496.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester University Press, Manchester, UK & New York. 726 pp.

Harvey, M.S. 2002. The neglected cousins: what do we know about the smaller arachnid orders? Journal of Arachnology 30:357–372.

Harvey, M.S. 2003. Catalogue of the Smaller Arachnid Orders of the World. CSIRO Publishing, Collingwood, Victoria, Australia. 385 pp.

Hauschke, N. & V. Wilde. 1991. Zur Verbreitung und Ökologie mesozoischer Limuliden. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 183:391–411.

Henderickx, H. 2005. A new *Geogarypus* from Baltic amber (Pseudoscorpiones: Geogarypidae). Phegea 33:87–92.

Judson, M.L.I. 2007. First fossil record of the pseudoscorpion family Pseudochiridiidae (Arachnida, Chelonethi, Cheiridioidea) from Dominican amber. Zootaxa 1393:45–51.

Judson, M.L.I. & J. Wunderlich. 2003. Rhagidiidae (Acari, Eupodoidea) from Baltic amber. Acta zoologica cracoviensa 46(suppl.–Fossil Insects):147–152.

Karpinen, E., D.A. Krivolutsky, M. Koponen, L.S. Kozlovskaja, L.M. Laskova & M. Viitasaari. 1979. List of subfossil oribatid mites (Acarina, Oribatei) of northern Europe and Greenland. Annales Entomologici Fennica 45:103–108.

Kjellesvig-Waering, E.N. 1986. A restudy of the fossil Scorpionida of the world. Palaeontographica Americana 55:1–287.

Krivolutsky, D.A. & A.Y. Druck. 1986. Fossil oribatid mites. Annual Review of Entomology 31:533–545.

Lourenço, W.R. 2004. Description of a further species of fossil scorpion in Baltic amber. *In* Fossil Spiders in Amber and Copal. (J. Wunderlich, ed.). Beiträge zur Araneologie 3:1886–1889.

Norton, R.I. 2006. First record of *Collohmannia* (*C. schusteri* n. sp.) and *Hermannia* (*H. sellnicki* n. sp.) from Baltic amber, with notes on Sellnick's genera of fossil oribatid mites (Acari: Oribatida). Acarologia 46:111–125.

Orr, P.J., D.J. Siveter, D.E.G. Briggs, D.J. Siveter & M.D. Sutton. 2000. A new arthropod from the Silurian Konservat-Lagerstätte of Herefordshire, UK. Proceedings of the Royal Society of London B 267:1497–1504.

Penney, D. 2003. A new deinopoid spider from Cretaceous Lebanese amber. Acta Palaeontologica Polonica 48:569–574.

Penney, D. 2004a. New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda, Araneae). Palaeontology 47:367–375.

Penney, D. 2004b. Does the fossil record of spiders track that of their principal prey, the insects? Transactions of the Royal Society of Edinburgh: Earth Sciences 94:275–281.

Penney, D. 2006a. An annotated systematic catalogue, including synonymies and transfers, of Miocene Dominican Republic amber spiders described up until 2005. Revista Ibérica de Aracnología 12:25–52.

Penney, D. 2006b. Fossil oonopid spiders in Cretaceous ambers from Canada and Myanmar. Palaeontology 49:229–235.

Penney, D. & V.M. Ortuño. 2006. Oldest true orb-weaving spider (Araneae: Araneidae). Biology Letters 2:447–450.

Penney, D. & P.A. Selden. 2007. Spinning with the dinosaurs: the fossil record of spiders. Geology Today 23:230–236.

Penney, D., C.P. Wheater & P.A. Selden. 2003. Resistance of spiders to Cretaceous–Tertiary extinction events. Evolution 57:2599–2607.

Petrunkevitch, A. 1922. Tertiary spiders and opilionids of North America. Transactions of the Connecticut Academy of Arts and Sciences 25:211–279.

Petrunkevitch, A.I. 1953. Palaeozoic and Mesozoic Arachnida of Europe. Memoirs of the Geological Society of America 53:1–128.

Petrunkevitch, A.I. 1955. Arachnida. Pp. 42–162. *In* Treatise on Invertebrate Paleontology, Part P, Arthropoda 2. (R.C. Moore, ed.). Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Petrunkevitch, A.I. 1971. Chiapas amber spiders, II. University of California Publications in Entomology 63:1–44.

Poinar, G.O., Jr. & A.E. Brown. 2004. A new whip spider (Arachnida: Amblypygi), *Phrynus mexicana*, is described from Mexican amber. *In* Fossil spiders in Amber and Copal. (J. Wunderlich, ed.). Beiträge zur Araneologie 3:1881–1885.

Poschmann, M., L.I. Anderson & J.A. Dunlop. 2005. Chelicerate arthropods, including the oldest phalangiotarbid arachnid from the Early Devonian (Siegenian) of the Rhenish Massif, Germany. Journal of Paleontology 79:110–124.

Poschmann, M. & J.A. Dunlop. 2006. A new sea spider (Pycnogonida) with a flagelliform telson from the Lower Devonian Hünsruck Slate, Germany. Palaeontology 49:983–989.

Rössler, R., J.A. Dunlop & J.W. Schneider. 2003. A redescription of some poorly known Rotliegend arachnids from the Lower Permian (Asselian) of the Ilfed and Thuringian Forest Basins, Germany. Paläontologische Zeitschrift 77:417–427.

Rowland, J.M. & W.D. Sissom. 1980. Report on a fossil palpigrade from the Tertiary of Arizona and a review of the morphology and systematics of the order. Journal of Arachnology 8:69–86.

Rudkin, D.M., G.A. Young & G.S. Nowlan. 2008. The oldest horseshoe crab: a new xiphosurid from late Ordovician Konservat-Lagerstätten deposits, Manitoba, Canada. Palaeontology 51:1–9.

Santiago-Blay, J., V. Fet, M.E. Soleglad & S.R. Anderson. 2004. A new genus and subfamily of scorpions from Lower Cretaceous Burmese amber (Scorpiones: Chaerilidae). Revista Ibérica de Aracnología 9:3–14.

Schawaller, W. & H. Ono. 1979. Fossile Spinnen aus miozänen Sedimenten des Randecker Maars in SW-Deutschland (Arachnida: Araneae). Jahreshefte der Gesellschaft für Naturkunde in Württemberg 134:131–141.

Schawaller, W., W.A. Shear & P.M. Bonamo. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). American Museum Novitates 3009:1–24.

Scott, A.G. 2003. Subfossil spiders from Holocene peat cores. Journal of Arachnology 31:1–7.

Scudder, S.H. 1891. Index of the known fossil insects of the world including myriapods and arachnids. Reports of the U.S. Geological Survey 71:1–744.

Selden, P.A. 1993. Fossil arachnids–recent advances and future prospects. Memoirs of the Queensland Museum 33:389–400.

Selden, P.A. 2002. First British Mesozoic spider, from Cretaceous amber of the Isle of Wight, southern England. Palaeontology 45:973–983.

Selden, P.A., F.C. Casado & M.V. Mesquita. 2006. Mygalomorph spiders (Araneae: Dipluridae) from the Lower Cretaceous Crato Lagerstätte, Araripe Basin, north-east Brazil. Palaeontology 49:817–826.

Selden, P.A., W.A. Shear & P.M. Bonamo. 1991. A spider and other arachnids from Devonian of New York, and reinterpretations of Devonian Araneae. Palaeontology 34:241–281.

Spahr, U. 1993. Ergänzungen und Berichtigungen zu R. Keilbachs Bibliographie und Liste der Bernsteinfossilien – verschiedene Tiergruppen, ausgenommen Insecta und Araneae. Stuttgarter Beiträge zur Naturkunde B 194:1–77.

Subías, L.S. & A. Arillo. 2002. Oribatid mite fossils from the Upper Devonian of South Mountain, New York and the Lower Carboniferous of County Antrim, Northern Ireland (Acariformes, Oribatida). Estudios del Museo de Ciencias Naturales de Alava 17:93–106.

Tetlie, O.E. 2004. Eurypterid phylogeny with remarks on the origin of arachnids. Unpublished Ph.D. thesis. The University of Bristol, UK. 320 pp.

Tetlie, O.E. 2007. Distribution and dispersal history of Eurypterida (Chelicerata). Palaeogeography, Palaeoclimatology, Palaeoecology 252:557–554.

Tetlie, O.E. & S.J. Braddy. 2004. The first Silurian chasmataspid, *Loganamaraspis dunlopi* gen. et sp. nov. (Chelicerata: Chasmataspidida) from Lesmahagow, Scotland, and its implications for eurypterid phylogeny. Transactions of the Royal Society of Edinburgh: Earth Sciences 94:227–234.

Tetlie, O.E. & J.A. Dunlop. 2008. *Geralinura carbonaria* (Arachnida; Uropygi) from Mazon Creek, Illinois, USA, and the origin of subchelate pedipalps in whip scorpions. Journal of Paleontology 82:299–312.

Tollerton, V.P., Jr. 2004. Summary of a revision of New York State Ordovician eurypterids: implications for eurypterid palaeoecology, diversity and evolution. Transactions of the Royal Society of Edinburgh: Earth Sciences 94:235–242.

Witlański, W. 2000. *Aclerogamasus stenocornis* sp. n., a fossil mite from Baltic amber (Acari: Gamasida: Parasitidae). Genus 11:619–626.

Wunderlich, J.W. (ed.). 2004. Fossil spiders in Amber and Copal. Beiträge zur Araneologie 3:1–1908.

Zhang, J., B. Sun & X. Zhang. 1994. Miocene insects and spiders from Shanwang, Shandong. Science Press, Beijing. 298 pp. [In Chinese with English Summary].

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