Fossil spiders

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ABSTRACT

Over the last three decades, the fossil record of spiders has increased from being previously biased towards Tertiary ambers and a few dubious earlier records, to one which reveals a much greater diversity in the Mesozoic, with many of the modern families present in that era, and with clearer evidence of the evolutionary history of the group. We here record the history of palaeoarachnology and the major breakthroughs which form the basis of studies on fossil spiders. Understanding the preservation and taphonomic history of spider fossils is crucial to interpretation of fossil spider morphology. We also review the more recent descriptions of fossil spiders and the effect these discoveries have had on the phylogenetic tree of spiders. We discuss some features of the evolutionary history of spiders and present ideas for future work.

Key words: amber, Araneae, Cenozoic, history of arachnology, Mesozoic, palaeontology, Palaeozoic.

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I. INTRODUCTION

Spiders (Araneae) have been familiar animals to human cultures since Man first recorded his observations of the natural world; there are drawings of spiders on the walls of caves (Hillyard, 1994; Leroy & Leroy, 2003) and spiders crop up in the mythology of many human societies, commonly as symbols of danger or of clever handiwork (Gertsch, 1949; Cloudsley-Thompson, 2001). Spiders abound in every terrestrial ecosystem (and in some aquatic ones), they are the primary predators of insects, they possess a venom system to assist in prey capture, and they produce and utilize silk in many more ways than any other animal. After the five largest insect orders and mites, Araneae is the most diverse order in modern terrestrial ecosystems, with 40,700 extant species in 3,733 genera and 109 families (Platnick, 2009). All spiders prey on other animals, and they are the most abundant predators on land today. Many different modes of life have developed within the Araneae to enable them to pursue their insect prey in all ecological niches. These include orb-, sheet- and other web weavers, sit-and-wait predators, cursorial hunters, jumping spiders, burrowers, and aquatic spiders. Dispersal by silken threads (ballooning) means that spiders may be found among the aerial plankton. Spider fossils date back to the Palaeozoic era, and may have been part of the first wave of terrestrialization by animals in the mid-Palaeozoic. In this review we seek to shed light upon the changes in abundance and diversity of the Araneae throughout their geological history. We start with a brief review of the history of systematic research in extant spiders, followed by a review of studies on fossil spiders. Finally, we present the current view of the geological history and phylogeny of Araneae, in the form of a phylogenetic diagram, and discuss whether these changes can be linked to biotic and abiotic factors such as mass extinction events, fluctuations in insect diversity (co-radiation), and biogeography.

II. HISTORY OF SPIDER SYSTEMATICS

Spiders hold a unique status in zoological nomenclature in that Clerck's (1757) *Svensk spindlar* (*Aranei suecici*) is deemed by the *International Commission on Zoological Nomenclature* (2000: Art. 3.1) to have been published on 1st January 1758, to enable its inclusion for nomenclatural purposes (the starting point of zoological nomenclature is arbitrarily fixed at 1st January 1758, the presumed publication date of the 10th edition of Linnaeus's *Systema Naturae*). At that time, all spiders were included in a single genus, called *Araneus* by Clerck, *Aranea* by Linnaeus. Later, Latreille (1804) and Walckenaer (1805) defined a number of different genera, most of which correspond to families recognized today. Latreille (1810) created a hierarchical classification for arthropods, including spiders, which was essentially ecological in character. It is interesting to see that in modern books describing the diversity of spiders, such ecological divisions are used as

convenient chapter headings; e.g. in Forster & Forster's (1999) *Spiders of New Zealand* has chapters entitled: Free-living spiders, Crab spiders, Hunting spiders, Jumping spiders, Orbweb spiders, Spaceweb spiders and Seashore spiders.

The first major works to attempt systematic arrangement of spider families were those of Simon (1864, 1874, 1875, 1876, 1878, 1881, 1884a,b, 1892, 1893, 1894, 1895, 1897, 1898, 1901, 1903, 1914, 1926, 1929, 1932, 1937) and Thorell (1869, 1870a,b, 1871, 1872, 1873, 1886) [see Bonnet (1959) for a comprehensive review of these early schemes]. Whilst the foundations of the modern classification of Araneae were established by these authors, there were problems in that many taxa were defined by the presence or absence of single characters, and many of these characters are now recognized as plesiomorphies. For example, Dionycha and Trionycha are two- and three-clawed spiders, respectively; Orthognatha (v. Labidognatha) have orthognath chelicerae; Cribellatae (v. Ecribellatae) are spiders possessing a cribellum; and Dipneumonae and Tetrapneumonae are spiders with two and four book lungs, respectively. Four book lungs and orthognath chelicerae are primitive character states, we now know that the cribellum has been lost many times in araneomorphs, and that the three-clawed state is plesiomorphic in spiders; nevertheless, such characters are still used extensively in modern keys to spider families. At the beginning of the 20th Century, organ systems were used to define major groups. For example, Simon (1892) recognized Haplogynae and Entelegynae primarily on the basis of females possessing simple or complex genitalia, respectively. Petrunkevitch (1933), following the ideas of Bertkau (1878b), created suborders Dipneumonina and Apneumonina for spiders with a pair of book lungs or lacking book lungs, respectively, and also recognized the groups Octostiatae, Sexostiatae and Quadrostiatae on the basis of their possession of eight, six or four cardiac ostia.

In the latter half of the 20th Century, some of the major groupings of Araneae were severely criticized and, indeed, re-organized. Perhaps the biggest change in spider systematics came with the publication of Lehtinen's (1967) monograph on the cribellate spiders. Lehtinen argued, following a suggestion of Petrunkevitch (1933), that all araneomorph spiders were primitively cribellate and that some groups had become secondarily ecribellate. Evidence for this idea came in the form of some closely related families, e.g. Urocteidae and Oecobiidae, which differed merely in the presence or absence of the cribellum and calamistrum (Baum, 1972; Kullmann & Zimmerman, 1976), and later the recognition that among New Zealand spiders there were many cases of cribellate and ecribellate genera in the same family (e.g. Forster, 1970; Forster & Gray, 1979). Not surprisingly, since they questioned a firmly entrenched phylogenetic system, Lehtinen's (1967) conclusions were not without controversy; nevertheless, the fundamental division of araneomorphs into Cribellatae and Ecribellatae was dismantled.

In a series of thought-provoking publications, R. R. Forster and co-workers (Forster, 1967, 1970; Forster & Wilton, 1968, 1973; Forster & Blest, 1979; Forster, Millidge & Court,

1988) made the first attempt to revise the phylogeny of the spiders of New Zealand. Having discovered many cases of closely related cribellates and ecribellates, Forster was a keen protagonist of Lehtinen's (1967) phylogenetic scheme. Moreover, Forster (e.g. 1970) suggested close relationships of a number of families based on their similar tracheal systems. For example, he placed Dictynidae, Hahniidae, Desidae (marine spiders), Cybaeidae, Argyronetidae (the European freshwater spider), Amaurobioididae (another marine spider) and Anyphaenidae (active spiders) together in Dictynoidea on the basis of their shared large tracheal systems. Other authors (e.g. Levi, 1967) have considered the enlargement of the tracheal system to be functionally related to aquatic habitats or an active life. Note that *Argyroneta* is now included with the other cybaeids in the family Argyronetidae, which has priority over Cybaeidae (Jäger, 2007; Jocqué & Dippenaar-Schoeman, 2007; *contra* Platnick, 2009).

Also in the late 20th Century, cladistic methods started to influence spider systematics. Many of the former higher taxa, e.g. Orthognatha, Trionycha, Tetrapneumonae, were clearly recognizable as paraphyletic. One of the consequences of recognizing ecribellate paraphyly was the possibility of rejuvenating Thorell's (1886) concept of orb-weaver monophyly. Under ecribellate monophyly, orb webs, which are produced by both cribellate and ecribellate spiders, were considered by many arachnologists to have evolved convergently at least twice: once in cribellates and once in ecribellates. Opinions in the two decades following Lehtinen's (1967) seminal paper were divided between those who envisaged the orb web as convergent in the cribellate uloborids and the ecribellate araneoids (e.g. Kaston, 1964; Kullmann, 1972; Levi, 1978; Eberhard, 1982; Kovoor & Peters, 1988), and those who considered orb-weavers to be monophyletic (e.g. Brignoli, 1979; Opell, 1979; Levi, 1980). Later, cladistic studies of Coddington (1986*b*, 1990*a*,*b*) confirmed the monophyly of the orb-weaving families and Coddington (1990*a*) resurrected Walkenaer's (1802) term Orbiculariae for the orb-weaver taxon. Excellent reviews of orb-weaver monophyly *versus* convergence were given by Shear (1986, 1994).

The suborders of spiders were the subject of an early cladistic analysis by Platnick & Gertsch (1976). The spider family Liphistiidae had been recognized by Pocock (1892) as the primitive relatives (what we would nowadays call the sister group) to all other spiders. Pocock (1892) erected the suborder Mesothelae for Liphistiidae, whilst all other spiders formed the suborder Opisthothelae. However, Petrunkevitch (1923) and later authors preferred a threefold division into suborders Liphistiomorphae (=Mesothelae), Mygalomorphae and Araneomorphae. Platnick & Gertsch (1976) clearly demonstrated that mygalomorphs and araneomorphs should be considered infraorders within Opisthothelae and thus corroborated Pocock's (1892) findings using cladistic methods. A monograph on Mesothelae was published by Haupt (2003), in which he showed that these spiders lacked a venom gland. Coddington & Levi (1991) reviewed the higher systematics of Araneae, summarizing knowledge, with cladograms,

to that date and suggested avenues for future work. Phylogenetic studies of Recent Araneae based on morphology have continued apace, and cladistic analyses of many major groups have appeared in the succeeding decade. The first major cladistic study of Mygalomorphae (Raven, 1985) was a monumental piece of work given that computer analysis was in its infancy at the time. Goloboff's (1993) update of Raven's work using computer cladistics resulted in some minor adjustments to the phylogeny of the infraorder. Additional cladistic analyses of the Mygalomorphae concern the families Hexathelidae (Raven, 1980), Barychelidae (Raven, 1994), Dipluridae: Ischnothelinae (Coyle, 1995), Nemesiidae (Goloboff, 1995), Theraphosidae: Theraphosinae (Pérez-Miles *et al.*, 1996; Bertani, 2001), Migidae (Griswold & Ledford, 2001) and Rastelloidina (Le Gleut *et al.*, 2004). Hedin & Bond (2006) used nuclear rRNA genes to help elucidate mygalomorph phylogeny. Amongst other conclusions, their results confirmed Atypoidea (Atypidae, Antrodiaetidae, Mecicobothriidae) as a basal lineage sister to all other mygalomorphs, suggested diplurids and hexathelids to form a paraphyletic grade at the base of the non-atypoid clade, and recovered the sampled cyrtaucheniid genera as scattered across the cladogram. Other molecular studies on mygalomorphs have been performed on cyrtaucheniids by Bond & Opell (2002) and Bond & Hedin (2006), and on the genus *Antrodiaetus* by Hendrixson & Bond (2007).

Araneomorphae: Haplogynae is diagnosed by the absence of fertilization ducts in females, so could be considered as a paraphyletic stem group defined on a plesiomorphy. However, Platnick *et al.*'s (1991) analysis showed the group to be monophyletic. Superfamilies within Haplogynae have also been considered. Forster, Platnick & Gray, (1987) reviewed the primitive araneomorph superfamilies Hypochiloidea and Austrochiloidea, concluding that the Hypochilidae are sister group to all other araneomorphs, and the austrochiloids (the unusual antipodean families Austrochilidae + Gradungulidae) are sister to the remaining araneomorphs, the Araneoclada Platnick, 1977. Dysderoid monophyly was confirmed by Forster & Platnick (1985) in their review of the austral spider family Orsolobidae; Platnick *et al.* (1991) demonstrated the close relationship between the dysderoids and two small families, Caponiidae and Tetrablemmidae, and that Filistatidae is sister to all other haplogynes. Ramírez (2000) disagreed with their placement of Tetrablemmidae, considering it sister to Pholcidae+(Plectreuridae+Diguetidae). The remaining haplogynes ['scytodoids' or 'sicarioids' *sensu* Forster (1995)] require more work to be resolved, but a start was made by Lehtinen (1986). In a review of the archaeid spiders—a group first described from fossils (Koch & Berendt, 1854) and later found alive in Madagascar and Africa—a number of disparate families (Mimetidae, Micropholcommatidae, Textricellidae) were placed alongside Archaeidae, which was split to form the four families Archaeidae *sensu stricto*, Mecysmaucheniidae, Holarchaeidae and Pararchaeidae in Palpimanoidea by Forster & Platnick (1984). Thus the size of this superfamily increased considerably, having previously

consisted of only three families: Palpimanidae, Stenochilidae and Huttoniidae. Few subsequent authors have agreed with this concept of the composition of Palpimanoidea [see discussions in Eskov (1987), Coddington & Levi (1991)], which was cut back to its original size by Schütt (2000). In a cladistic analysis of the Symphytognathidae *sensu lato* Schütt (2003) synonymized Micropholcommatidae with Anapidae, but this was not accepted by Platnick (2004) on the grounds that her analysis was based on too few taxa. The most recent analyses which included the Palpimanoidea have, for the most part, corroborated Schütt's hypotheses. The study of entelegyne spider phylogeny by Griswold *et al.* (2005) indicated that the extended Palpimanoidea was likely paraphyletic, with numerous families more probably belonging in Araneoidea. Most likely, the haplogyne palpimanoid families Archaeidae, Huttoniidae, Palpimanidae and Stenochilidae really do belong in that superfamily, while the entelegyne palpimanoids, Holarchaeidae, Pararchaeidae and Mimetidae are araneoids. Huber (2005a), in a study of the evolution from muscular to hydraulic mechanisms in spider palpal bulbs, showed that the Palpimanidae belongs with the Haplogynae. Wunderlich (2004) recognized a number of palpimanoid families within his newly defined and expanded Eresoidea. Other important advances in Haplogynae include Filistatidae (Gray, 1995; Ramírez & Grismado, 1997) and Pholcidae (Huber, 2000, 2001, 2003, 2005b; Bruvo-Mađarić *et al.*, 2005). Clearly, a new phylogenetic study of 'palpimanoids' and their purported sister taxa is necessary to elucidate the relationships of these families.

Whilst Araneomorphae: Entelegynae appears to be monophyletic, reversion to the haplogyne state has occurred a number of times within this group. Within Entelegynae, Orbiculariae have enjoyed the most detailed cladistic studies. In three papers, Coddington (1989, 1990a, b) detailed the evidence which unites the members of the Orbiculariae. Griswold *et al.* (1998) analysed 31 exemplar taxa from 12 families of Araneoidea and used Deinopoidea as the outgroup. They confirmed that the araneoid sheet-web weavers are monophyletic and gave rise to the gumfoot-web weavers (Theridiidae + Nesticidae). In considering the limits of the Araneoidea, Schütt (2000) suggested that the Textricellidae, Micropholcommatidae, Mimetidae and Malkaridae probably also belonged in this superfamily. Scharff & Coddington (1997) produced a phylogenetic analysis of the family Araneidae, the most familiar of the orb-web weavers; their results indicated that there was considerable parallel evolution within this family, including features such as sexual size dimorphism, web decorations (stabilimenta), and the use of silk, rather than venom, to subdue prey. Hormiga (1994b) provided the first major cladistic analysis of linyphiid spiders, concluding that Pimoidae and Linyphiidae were sister taxa and that the monophyly of the linyphiid clade was supported by eight synapomorphies. Other interesting araneoid families have been analysed in the last two decades, such as Theridiosomatidae (Coddington, 1986a), Synotaxidae

(Forster, Platnick & Coddington, 1990; Agnarsson, 2003), Pimoidae (Hormiga, 1994a), Tetragnathidae (Hormiga, Eberhard & Coddington, 1995; Álvarez-Padilla *et al.*, 2009), Linyphiidae: Erigoninae (Hormiga, 2000; Miller & Hormiga, 2004), Cyatholipidae (Griswold, 2001), Symphytognathidae *sensu lato* (Schütt, 2003), Theridiidae (Agnarsson, 2004; Arnedo *et al.,* 2004) and Nephilidae (Kuntner, 2005), which was raised to family rank by this author and then analysed further by Kuntner, Coddington & Hormiga (2008).

Other entelegynes have been subjected to more patchy cladistic analysis. Sac spiders (Clubionidae and related families) were revised by Deeleman-Reinhold (2001). Her work dealt primarily with forest-dwelling spiders from southeast Asia. Bosselaers & Jocqué (2002) undertook a cladistic analysis of 38 genera of Corinnidae and Liocranidae. The ground spiders, Gnaphosoidea, have been the subject of a series of analyses by N. I. Platnick and co-workers, for example, Gallieniellidae (Platnick, 1984), Cithaeronidae (Platnick, 1991), Lamponidae (Platnick, 2000) and too many generic revisions to list here (see Platnick, 2009). In a comparative scanning electron microscopy (SEM) study of the spinnerets of 50 gnaphosoid genera Platnick (1990) redefined the limits of the Gnaphosidae, revalidated and expanded the Prodidomidae, elevated Lamponidae to family rank and dismantled the Platoridae; Trochanteriidae, Ammoxenidae, Gallieniellidae and Cithaeronidae were also treated. A recent book by Murphy (2007), on the gnaphosid genera of the world, was a magnificent compendium of present knowledge of every genus referred to the Gnaphosidae, with detailed drawings by Michael Roberts. This was the first time that any, single, spider family has been treated to such an in-depth monograph. The wolf spiders and their allies, Lycosoidea, were studied by Griswold (1993), who confirmed the monophyly of the superfamily, and of Lycosidae, Trechaleidae, Pisauridae and Zoropsidae, and questioned the monophyly of Ctenidae [polyphyly confirmed through mitochondrial DNA analysis by Huber *et al.* (1993)]. Griswold (1993) also demonstrated the polyphyly of Tengellidae and Miturgidae, and showed that Senoculidae, Oxyopidae, Stiphidiidae and Psechridae together formed a monophyletic group. Many other families have been given cladistic treatments, for example: Anyphaenidae (Ramírez, 1995, 2003), Hersiliidae (Baehr & Baehr, 1993; Rheims & Brescovit, 2004; Foord, 2008), Nicodamidae (Harvey, 1995), Oecobiidae (Bosselaers, 1999), Phyxelididae (Griswold, 1990), Pisauridae: Pisaurinae (Sierwald, 1998; Santos, 2007), Salticidae (Maddison & Hedin, 2003), Sparassidae (Croeser, 1996), Stiphidiidae (Blest & Vink, 2000), Uloboridae (Opell, 1979), Zodariidae (Jocqué, 1991) and Zoropsidae (Bosselaers, 2002). Among the conclusions of the molecular phylogenetic work of Benjamin *et al.* (2008) on the family Thomisidae was that Thomisidae is a well-supported monophyletic taxon, and that the family Borboropactidae Wunderlich, 2004 (later revised by Wunderlich, 2008d) was unsustainable because it is paraphyletic.

Summary cladograms for all Araneae were presented by Coddington & Levi (1991), Griswold *et al.* (1999) and Coddington (2005) and can be viewed at the web-sitehttp://www.gwu.edu/%7Espiders/cladogramsPeet.htm. These are useful in that they show up areas of the phylogeny which are in need of further work (see Coddington & Levi, 1991, for review). These include: within Mygalomorphae, the composition of the Dipluridae and the Nemesiidae (see Goloboff, 1993; Hedin & Bond, 2006); relationships within the haplogynes (the families Scytodidae, Sicariidae, Drymusidae and Loxoscelidae); the origin of the Salticidae; relationships of Theridiidae and the smaller araneoid families in the Araneoidea; the position of Mimetidae. Salticidae is the most diverse spider family alive today; it seems to be geologically young (Cenozoic), but there are at least three hypotheses for the relationship of Salticidae to other spider families: close to Thomisidae (Loerbroks, 1984), among web-builders (Blest, 1985), and in an unresolved trichotomy with Clubionidae and Anyphaenidae, based on their shared secondary loss of cylindrical silk glands (Coddington & Levi, 1991).

None of the studies cited above incorporated fossil taxa in their cladistic analyses. Fossil spiders were included in Bonnet's (1945–1959) *Bibliographia Araneorum* but not in the catalogues of Roewer (1942, 1954*a*, *b*), Brignoli (1983) or Platnick (1989, 1993, 1997, 2004, 2009), although a list of fossil species (Dunlop, Penney & Jekel, 2009) has recently been added to the latest (Platnick, 2009) online version of the catalogue. The known fossil spider fauna was reviewed by Scudder (1886, 1891), Petrunkevitch (1955) and Selden (1993, 1997). McCook (1890) devoted a whole chapter to ancestral spiders and their habits. He compared the known American and European fossil spider faunas and even in this early work, made numerous palaeoecological inferences based on the fossil spider assemblages. Fossil arachnids have been largely overlooked by systematists working on Recent spider faunas; even when they are considered (e.g. Wanless, 1984; Prószyski & Żabka, 1983) it is usually as an aside, and no phylogenetic conclusions are based on fossil evidence because of the concern that important taxonomic characters are not, or are poorly, preserved. However, Prószyski (1985) surveyed the potential of amber Salticidae in comparative investigations with the Recent fauna, commenting that the crucial point of research on amber inclusions is their comparison with extant taxa. The need to consider fossils when revising extant taxa was highlighted in a study of Hersiliidae by Penney (2006*c*) who synonymized an extant genus containing eight species with a previously described fossil genus, which had been overlooked by Rheims & Brescovit (2004) in their revision of the extant neotropical fauna. A recent paper by Harms & Dunlop (2009) is innovative in that it treated amber-preserved spiders in an almost similar way to extant species, although the preservation still prevented a complete cladistic analysis.

III. PRESERVATION AND METHODOLOGY

Spiders are seldom preserved in the fossil record because of their fragility and lack of mineralization. Thus, fossil spiders define the occurrence of a Konservat-Lagerstätte (an exceptional occurrence of well-preserved fossil biota: Seilacher, 1970). One well-known Lagerstätte is amber, the highly polymerized form of fossil tree resin. Living animals become trapped in the sticky resin when it is exuded by the tree and subsequently covered by more resin (e.g. Penney 2002*a*) or become engulfed in less viscous, rapid flowing exudates (Penney, 2005*c*).

Reasons for trees to exude resin are not well known and may be related to wound repair, but many insects, and therefore their predators, are attracted to resin seeps. The resin hardens in contact with the air and, following burial in sediment over millions of years, diagenetic processes turn the resin into the fossilized product amber. Semi-fossilized resin younger than 40,000 years old is softer and is termed copal. Amber preserves fossil inclusions through a process similar to mummification by a combination of rapid and thorough fixation, dehydration and the antibiotic properties of the resin (Henwood, 1993). The degree of preservation is exquisite, and includes fine detail of tissues, cells, and cellular ultrastructure with a startlingly life-like fidelity, as revealed by scanning (SEM) and transmission (TEM) electron microscopy (Grimaldi *et al.*, 1994), detailed for a Baltic amber spider by SEM by Mierzejewski (1976). However, whilst it is commonly possible to identify spider inclusions within the context of Recent spider systematic frameworks, the amber spider fauna is still taxonomically subequal to the Recent fauna (Eskov, 1990); important taxonomic characters are commonly obscured or may not be preserved. It is evident from numerous amber inclusion assemblages (see later) that they represent the remains of warm-temperate to tropical forests. The climate and soil type of similar present-day ecosystems provide poor opportunities for fossilization, yet they contain more than half of the terrestrial species in the world. When one considers the current rate of demise of these forests through anthropogenic factors, the value of fossil amber inclusions for investigating historical ecological changes, and thus possible future consequences of modern deforestation, becomes apparent.

Raw amber can be cut, ground and polished, and viewed directly under a microscope using incident and transmitted light, or smaller pieces can be set in a clear plastic resin prior to grinding for ease of manipulation. Oddly shaped amber pieces can be immersed in mineral oil, which has the same refractive index as amber, to facilitate microscopy by preventing unwanted light reflection and refraction. A method of dissolving amber in chloroform to extract the inclusions has been described (Azar, 1997), but this is not standard practice and inclusions in most ambers would most likely be destroyed by this process. A fully referenced discussion of methods for amber preparation is given in Penney (2008). It is unfortunate that, given the vibrant amber market and the high prices private collectors are

willing to pay, forgeries abound and specimens often get mixed up, making provenance and age difficult to ascertain without employing rigorous tests. Forgeries vary from the making of curios by embedding natural history specimens in Kauri gum (see Fig. 5a in Grimaldi *et al.*, 1994), through accidental or deliberate mixing of ambers and/or copals from different provenances, to elaborate forgeries involving inserting modern specimens into resin-bearing cavities inside real amber (e.g. Ross, 1998). Tests are available to detect real amber, and range from simple examination of other inclusions (e.g. oak stellate hairs and coatings of white emulsion are common in Baltic amber) to more sophisticated techniques such as infra-red spectroscopy, pyrolysis gas chromatography and mass spectroscopy for determining chemical signatures (Grimaldi *et al.*, 1994). However, the excavations of many recently discovered amber deposits (e.g. New Jersey, Spanish, Lebanese, French Eocene and Cretaceous to mention but a few) have been organized by recognized experts in established museums and there is usually no need to question the authenticity of specimens from these sources. There are also Dominican amber fossil dealers who extract directly from the mines and prepare their own material, so this too is unlikely to be contaminated with fakes. Some of the older museum collections would certainly benefit from individual assessment of samples for authenticity, but this would presumably be a time-consuming, costly and laborious exercise, not to mention a potentially embarrassing one.

More rarely, fossil spiders are preserved in terrigenous sedimentary rock strata, and there are nearly as many different preservational styles as there are araniferous Lagerstätten. A number of Mesozoic occurrences are in Plattenkalk (lithographic limestone): thinly bedded, fine-grained limestones usually deposited in still water by settling of calcium carbonate grains. The best-known example of lithographic limestone in the fossil record is Solnhofen, Bavaria, but this deposit is marine in origin and includes no spiders. The early Cretaceous Plattenkalk from Crato, Brazil (Martill, 1993; Mesquita, 1996; Selden, da Casado & Mesquita, 2002, 2006; Dunlop, Menon & Selden, 2007) preserves spiders (as well as a wealth of insects and other organisms) by replacement with goethite (iron hydroxide) within the limestone (Fig. 1F). This is unusual, however, and in most lagoonal and lacustrine limestones the organisms are preserved as organic fragments. When it has been identified (Stankiewicz *et al.*, 2000), this organic matter has been shown to be randomly repolymerized from the original protein–polysaccharide chains to a substance akin to kerogen. Examples of Lagerstätten with spiders preserved as organic matter in fluvial, lagoonal or lacustrine settings include Quaternary diatomite of Italy (Bottali, 1975), the Miocene of Germany (Bertkau, 1878*a*; Heyden, 1859), Miocene of Switzerland (Heer, 1865, 1872, 1876), Miocene of Shanwang, China (Hong, 1985; Zhang, Sun & Zhang, 1994), Eocene of Florissant, Colorado, USA (Licht, 1986), early Cretaceous of Montsech and Las Hoyas, Spain (Selden, 1989, 1990, 1991*a, b*; Selden & Penney, 2003), early Cretaceous

of Siberia and Mongolia (Eskov & Zonstein, 1990), early Cretaceous of South Gippsland, Victoria, Australia (Jell & Duncan, 1986), early Cretaceous of Mexico (Feldmann *et al.*, 1998), Jurassic and Cretaceous of north-east China (P. A. Selden, personal observations), Jurassic of Transbaikalia and Kazakhstan (Eskov, 1984, 1987), Triassic Grès à Voltzia, France (Selden & Gall, 1992), Triassic Molteno Formation of South Africa (Selden *et al.*, 1999; Selden, Anderson & Anderson, 2009), Permian of the Ural Mountains, Russia (Eskov & Selden, 2005), and late Devonian of Gilboa, New York, which has yielded the uraraneid *Attercopus fimbriunguis* Shear, Selden & Rolfe, 1987 (Selden, Shear & Bonamo, 1991; Selden, Shear & Sutton, 2008*b*), formerly thought to be the oldest spider.

More unusual types of preservation include the following. The Bembridge Marls Insect Bed, Eocene of the Isle of Wight, England, in which the fossils occur as external moulds with calcite replacement of internal structures such as muscles and respiratory organs (Selden, 2001, 2002*b*). Fossil spiders from Carboniferous Coal Measures of Europe and North America are generally preserved as external moulds, sometimes infilled with kaolinite, in clay ironstone concretions, for example at Mazon Creek, Illinois (Baird *et al.*). A most peculiar preservation–replacement by silica within calcareous nodules–occurs in the Miocene lacustrine Barstow Formation of California, USA (Palmer, 1957). Coal Measures spiders from Nýřany, Czech Republic, e.g. *Pyritaranea tubifera* Fritsch901, are poorly preserved as pyrite replacement in organic black shale. In the Triassic Solite deposits of Virginia, USA, the spiders are preserved as silver flakes in a black matrix (Selden *et al.*, 1999), and the preservation of the arthropods in the Korean Cretaceous Jinju Formation (Kim & Nam, 2008) is remarkably similar.

Wherever they occur in rock matrices, fossil spiders are a rare example of exceptional preservation. However, there are certain circumstances which are conducive to the preservation of fossil spiders. Most fossils are found in lacustrine or similar quiet-water deposits. Such situations are low energy and so the fragile bodies are not destroyed mechanically. Rapid burial and chemical conditions which lessen the activity of bacteria and other decaying organisms aid preservation; however, the spiders need to get onto the lake floor in the first place. Unlike insects, which are readily trapped by their wings by tensional forces on the water surface, spiders are adept at avoiding landing on water and, should they do so, can normally walk across the surface to safety. Indeed, even floating insects still need to sink to the lake floor to be preserved. It is interesting to note, therefore, that in many of the sedimentary settings in which fossil spiders are common, a large amount of volcanic ash is involved. Volcanic ash could aid their sinking to the lake floor. Another, perhaps related and more likely, means by which insects and arachnids could be transported from the surface film of a lake to the lake floor is by a microbial mat, and such a mechanism has been proposed to explain preservation in, for example, the French Triassic Grès à Voltzia (Gall, 1988) and the late Eocene Florissant deposits of the USA (Harding & Chant,
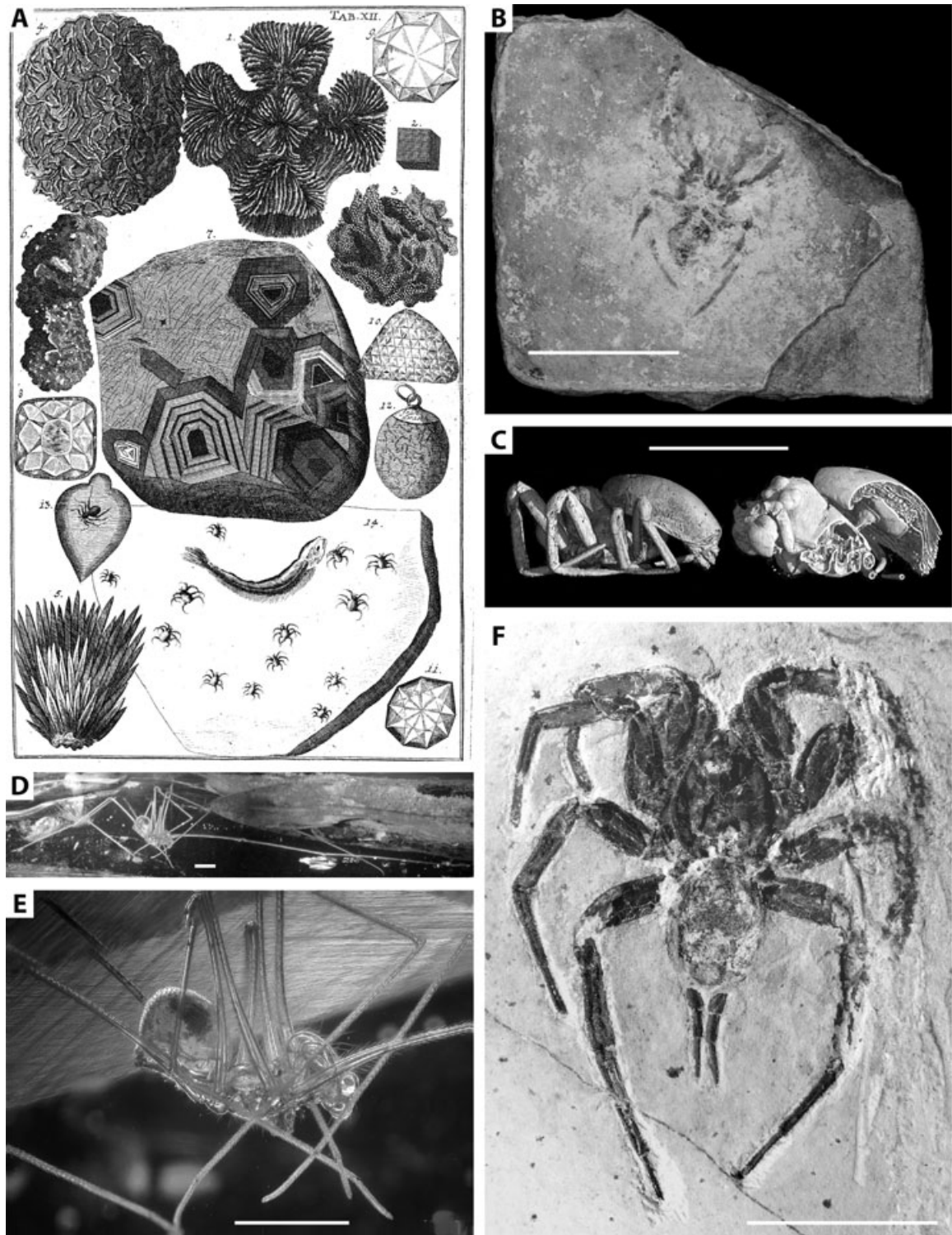
Fig. 1. Examples of fossil spiders. (A) Plate XII of Kundmann (1737) depicting a spider in an amber pendant (labelled 13) and Spinnensteine on a slab of Solnhofen Limestone—in this case the planktonic crinoid *Saccocoma* (14). (B) Holotype of *Theridium bucklandii* Thorell, 1870, Miocene shales of Oeningen, Switzerland, first figured by Buckland (1837, Pl. 46, fig. 12). (C) Holotype of micropholcommatid *Cenotextricella simoni* Penney, 2007, from French Cretaceous amber, computed tomography (CT) scanning image showing very fine detail of both external and internal morphology (Penney *et al.*, 2007). (D, E) Holotype of pholcid *Quamtana huberi* Penney, 2007, from Eocene amber of the Paris Basin (Penney, 2007*c*). (F) Holotype of diplurid mygalomorph *Cratodiplura ceara* Selden, 2006, from Cretaceous Crato Formation of Brazil (Selden, da Casado & Mesquita, 2006). Scale bars: C, D, E = 1 mm; B, F = 1 cm.

2000; O'Brien *et al.*, 2002). In the latter deposit, the diatom blooms responsible for the mats of slime could be correlated with volcanic ash falls which provided nutrients. Examples of other volcanigenic lacustrine sediments with common spiders include the Jurassic–Cretaceous Jiulongshan and Yixian Formations of north-east China [see Zhou, Barrett & Hilton (2003) for a brief review of the Yixian (Jehol) biota], the Jurassic Ichetuy Formation of Transbaikalia (Eskov, 1984), and the Oligocene Canyon Ferry Lagerstätte of Montana, USA (CoBabe *et al.*, 2002). A number of spider fossils are known from crater lake deposits, for example the Cretaceous kimberlite of Orapa, Botswana (Rayner & Dippenaar-Schoeman, 1995; Rayner *et al.*, 1997), the Eocene lake of Grube Messel, Germany (Wunderlich, 1986*a*), the Miocene Randecker Maar of Germany (Schawaller & Ono, 1979; Wunderlich, 1985). The Pliocene lake of Willershausen, Germany, which contains spiders (Schawaller, 1982*b*), owes its origin to salt subsidence.

A number of fossil and sub-fossil spiders are known from late Neogene and younger cold-climate deposits, including a single male palp of a thomisid from late Miocene fluvial sediments beneath a lava flow in Alaska (Leech & Matthews, 1971), a prosoma of an *Erigone* sp. from pond silts dating from an interstadial within the Wisconsin glaciation (Hopkins, Giterman & Matthews, 1976), a thomisid carapace from kettle-hole copropelic sediments dated at 6000 ± 2000 BP from west-central Wyoming (Cutler, 1970), and a range of sub-fossil spider fragments from Holocene peats in Cheshire, UK (Scott, 2003).

Each preservational style requires its own methods of preparation for study. Removal of soft matrix, e.g. in Plattenkalk preservation and to clear kaolinite from ironstone nodules, is best achieved using an aeroneedle (Selden, 2003). Working with this device under a binocular microscope, dislodged debris is gently blown clear of the working site. Gentle dissolution of recalcitrant calcite can be achieved with dilute hydrochloric acid, with great care. To remove the tiny fossils from Devonian clayrocks of New York, hydrofluoric acid is used to macerate the sediment (see Shear *et al.*, 1987; Selden, Shear & Bonamo, 1991), and the resultant organic debris sorted in water under the stereomicroscope.

Standard binocular microscopy is sufficient to study gross morphology, but to view minute details of, for example, tarsal claws or spinneret spigots, it is necessary to use higher magnification. Attempts to utilize SEM (Shear *et al.*, 1987; Selden, 2001) have been generally less successful than use of the compound microscope. Material extracted from the rock matrix, e.g. the Devonian debris from New York (Shear *et al.*, 1987; Selden, Shear & Bonamo, 1991) was studied using Nomarski Interference Contrast transmitted illumination on the compound microscope, whilst reflected light and oil immersion objectives proved invaluable for extracting minute morphological details from spiders in the Montsech Plattenkalk (Selden, 1989, 1990) and Triassic siltstones from north-east France (Selden & Gall, 1992). Another technique involves darkfield, plane-polarized reflected light in dry objectives to achieve high magnification on a compound

microscope without the need for fluid immersion. The recent application of three-dimensional high-resolution computed tomography scanning techniques for the study of fossil insects and spiders (e.g. Grimaldi & Engel, 2005; Penney *et al.*, 2007; Selden, Shear & Sutton, 2008) will prove increasingly useful for future studies of fossil spiders (see Fig. 1C).

Regrettably, sometimes there is a rush by the discoverer to describe a new fossil spider without consulting an expert in palaeoarachnology, which can result in poor primary descriptions. The describer may be a palaeontologist with no arachnological training, an arachnologist without palaeontological knowledge, or neither. Spider fossils which are in need of restudy include Cretaceous araneomorphs from Brazil and China, placed in the genus *Cretaraneus* Selden, 1990 (Mesquita, 1996; Cheng *et al.*, 2008), and possible pisaurids from the Cretaceous of Botswana (Rayner & Dippenaar-Schoeman, 1995) and Korea (Kim & Nam, 2008).

IV. HISTORY OF PALAEOARACHNOLOGY

(1) The earliest references

According to Bonnet's (1945) bibliography, the first mention of a fossil spider in European literature was by Schwenckfeld (1603). Caspar Schwenckfeld was a physician of Hirschberg, Silesia, who published a catalogue of the fossils of Silesia. It is not known whether he was related to the better-known Caspar Schwenckfeld von Ossig (1489–1561), a theologian who brought Lutheranism to Silesia a generation earlier (Schultz 1947). Schwenckfeld the physician's book mentioned spiders on pages 504–510, including fossils on pages 509–510 under the heading Arachnites, and with synonyms *Lapis stellatus*, *Victorialis*, Spinnenstein/Sternstein/Siegstein. He described star-shaped forms in a whitish rock which resemble spiders (hence the common name of Spinnenstein), and their possible medicinal uses, such as the treatment of dropsy. As far as we are aware, this was the first mention of Spinnenstein/Sternstein/Siegstein in the literature, but there are no figures. Spinnensteine turn up in numerous German works after this, but with a variety of meanings. Those in the sense of Schwenckfeld appeared in Kleemann (1755) who correctly identified the Spinnensteine from the Solnhofen Limestone as a kind of sea-star (they are the stemless crinoid *Saccocoma*). In the same year, Knorr (1755) also published plates of the Solnhofen stemless crinoids.

In a different meaning of the word Spinnenstein, Marperger (1699) described how a Cross-spider (or Garden spider, *Araneus diadematus*), placed in a small box for a long time (the German expression *Jahr und Tag*: literally 'year and day'), shrivels into a small 'stone' which, when placed in a ring and worn on the finger changes colour when placed near poison—ideal for a guest at a banquet who is unsure of the host's intentions! The same tale was repeated almost word-for-word by Jablonski (1767). In an excellent review of Spinnensteine, Kundmann (1737) began by describing

gall-stones of domestic animals, as a prelude to discussion of rural myths of spiders containing, or giving birth to, stones which possessed magical powers. He recounted the old wives' remedy of producing spider-stones for medicinal purposes by encrusting a large *Araneus diadematus* with sugar, salt, or coarsely ground Valerian root, and leaving it for a year to shrivel into a hard 'stone' which can then be used to treat various ailments. Kundmann's (1737) review moved on to discuss genuine fossils, including the Solnhofen Spinnensteine and, finally, he described genuine fossil spiders in amber [his plate XII, fig. 13, reproduced here in Fig. 1A]. A more modern review of the Solnhofen Spinnensteine was given by Heller (1961).

In 1682, Edward Lhwyd went up to Jesus College, Oxford, where he studied for five years, but did not finish his degree. He supported himself by assisting Robert Plot (1640–1696), first Keeper of the Ashmolean Museum, and succeeded him as Keeper in 1691. One of Lhwyd's first tasks was to catalogue the new museum's collection, which included many fossils (then called figured stones). He searched the quarries of Oxfordshire, trained quarrymen to recognize fossils, and paid them for their finds. He corresponded with collectors around Britain in order to trade specimens, and also travelled himself in search of fossils for the collection. In 1686, Lhwyd submitted a catalogue of the British fossils in the Ashmolean Museum to the Oxford Philosophical Society, and over the next few years continued to add to it. The catalogue was eventually published in 1699 as *Lithophylacii Britannici Ichnographia* (Lhwyd, 1699). It consists of a catalogue of 1766 minerals and fossils. Designed as a field guide for collectors, it is a handy octavo size, and its profusion of engravings enabled even beginners to recognize their finds. The text is entirely in Latin and thus was accessible to a European readership of the day. Spiders are illustrated on plate 4, but the two specimens shown, together with two insects, are on a plate of Carboniferous seed-ferns entitled 'Lithophyta'. The arthropods are neither numbered nor mentioned in the plate legend or text; they are diagrammatic and lack detail, and appear to be merely decorations to the main plate rather than illustrations of real fossils. However, they were referred to by Roemer (1866), who suggested they may, in fact, be depictions of real fossils from English Coal Measure concretions.

The story of the fake fossils described by Dr Johann Beringer is well known. This Würzburg physician collected figured stones in the early 18th Century. Locals brought interesting objects to the learned doctor and, on 31st May 1725, three stones from a nearby hill were delivered, which showed such objects as worms and astrological designs. Further discoveries included insects, fish, reptiles, amphibians, strange symbols, and spiders, including some with webs. Beringer published descriptions and plates in his *Lithographiae Wirceburgensis* (Beringer, 1726), with spiders dominating plate X. Some figured stones are still in existence, and an unpublished stone shows a spider with an orb web (Jahn & Woolf, 1963). The hoax was uncovered when Beringer found his own name on a stone shortly after the publication of his major work. Embarrassed by the consequences of his publication, Beringer promptly attempted to buy back all of the copies of his book, which was financially ruinous. The perpetrators of the hoax were widely believed to be students. However, Jahn & Woolf (1963), in their Appendix B to a new edition of *Lithographiae Wirceburgensis*, painted a more sinister, but accurate, scenario involving jealous academic colleagues of Beringer who then pinned the blame on the students. Judicial proceedings against the students were started by Beringer on 13th April 1726, but there is no record of the outcome (see Jahn & Woolf 1963 for the whole story).

(2) Amber spiders

(a) Cenozoic

According to Bonnet (1945), the first amber spider was described by Breynio (1726). However, the animal is not described in detail and the figure is too poor to suggest a spider rather than an insect. Kundmann's (1737) plate XII, fig. 13 depicts a genuine spider in amber, whilst Sendel (1742) described and figured many specimens, also including an opilionid, illustrated on his plates V, VII and IX. Bloch (1776) described three specimens of spiders from copal (see Dunlop & Jekel, 2008).

Presl (1822) described two new species of *Araneus* (Araneidae) and Holl (1829) described the new genus and species *Entomocephalus formicoides* from Baltic amber, which was placed in Archaeidae by Petrunkevitch (1958). The location of the specimen on which the description was based is unknown, and the description of the genus consisted of only one sentence; Holl's figure of this specimen (Holl, 1829, plate 8, fig. 68a) is almost certainly a salticid belonging to an ant-mimicing genus such as *Myrmarachne*, even though the figure and description have the specimen with only six eyes (Penney, 2003a, Dunlop & Penney, 2009). Wunderlich (2004, p. 34) suggested the specimen was in Madagascan copal.

Until recently, the main source of fossil spiders was Eocene Baltic amber. The first major work concerning this fauna was the monograph of Koch & Berendt (1854) on spiders and other invertebrates preserved in this fossil resin, published posthumously, with footnotes by Menge (1854). However, many of the species descriptions were vague, and the figures poor. Menge's (1854) additional descriptions in the footnotes, were even more vague, in some cases no more than one line long, nor did he figure any of his new species. In total, 115 new species of spiders in 36 genera (13 new) and 11 families were described, including the first description of the fossil and extant family Archaeidae. Bronn & Roemer (1856) briefly reviewed the species described by Koch & Berendt (1854) and Menge (1854). Giebel (1856) gave descriptions of 107 previously described species and five new species, without figures, from the families Hersiliidae, Araneidae, Agelenidae and Salticidae (two species). Menge (1856) further described some of the specimens described by Koch & Berendt (1854)

and Menge (1854) and erected a number of new genera. The descriptions of *Clostes priscus* (Dipluridae) and *Gerdia myura* (Hersiliidae) by Menge (1869) were somewhat better, with lengthier descriptions and better figures. Thorell (1870*a*) briefly reviewed 30 of the genera proposed by Koch & Berendt (1854) and Menge (1854, 1856, 1869). Simon (1884*c*) described one female *Archaea pougneti* (Archaeidae), which is, as far as we are aware, the only contribution of this most eminent of arachnologists to palaeoarachnology. Reid (1885, 1887) mentioned theridiid and linyphiid spiders in amber from Norfolk, UK, which were later described by Petrunkevitch (1958). Berland (1939) described two new Baltic amber spider species from the families Segestriidae and Theridiidae. The former was suggested as being synonymous with one of Menge's (1854) species by Petrunkevitch (1950).

Petrunkevitch (1942) considered many of Koch & Berendt's (1854) and Menge's (1854) species to be *nomina nuda* due to their inadequate descriptions, but later (Petrunkevitch, 1950) revoked some of these decisions because Menge (1854) seemed to have based his species descriptions on the most distinctive characters. The type material of Koch & Berendt (1854) was considered lost for many years, during which time much work was published on the Baltic amber spider fauna, particularly by Petrunkevitch (1942, 1946, 1950, 1958). Wunderlich (1984) stated that the type material of Koch & Berendt (1854) was in the Palaeontological Museum of Humboldt University, Berlin, but not all of them are present in their collections. The specimens described in the footnotes by Menge (1854) were deposited in the Western European Provincial Museum in Gdańsk (formerly Danzig) (Keilbach, 1982), but their current location is unknown (Kosmowska-Ceranowicz). Because Petrunkevitch (1942) considered many of Koch & Berendt's (1854) and Menge's (1854) species *nomina nuda*, his subsequent publications probably created a large number of junior synonyms, which remain to be identified.

Petrunkevitch (1942) studied 144 specimens of Baltic amber spiders, which he referred to 78 species, in 62 genera and 27 families. Of these, 69 species, 48 genera and five of the families were new. He also briefly discussed methods of study of amber spiders, evolutionary trends in spiders and the relationships of the Baltic amber spider fauna to their Recent relatives. Petrunkevitch (1946) described the Baltic amber spider collection in the American Museum of Natural History, describing 28 specimens in 18 genera (one new) and 21 species (four new). Petrunkevitch (1950) described the 20 families of Baltic amber spiders held in the Museum of Comparative Zoology at Harvard University, erecting one new family, five new genera and 17 new species. Baltic amber spiders in European collections were described by Petrunkevitch (1958) who proposed 19 new genera and 47 new species, including the first descriptions of the families Oxyopidae and Hahniidae from Baltic amber. In all these works the descriptions are extensive and the figures clear (if somewhat diagrammatic), but the photographs are too poor to be of much value. Some of Petrunkevitch's new taxa were suggested as being synonymous with Recent families or subfamilies by Lehtinen (1967), these and more were

synonymized with Recent families and genera by Wunderlich (1984, 1986*b*, 2004). Prószyński & Żabka (1980) examined the relationships between the Baltic amber salticids with the south-east Asian fauna, described one male as the new fossil species *Eolinus tystschenkoi* (Salticidae), and tentatively assigned an immature specimen to the same species. Wunderlich (1981) revised the Baltic amber Oonopidae (see Marusik & Wunderlich, 2008, for a more recent review) and Wunderlich (1986*b*) described ten new species of Baltic amber spiders in four new genera from two Recent families, and mentioned an exuvium which he attributed to the family Ctenizidae. Żabka (1988) described three species of Salticidae (one new) from the Museum of Earth in Warsaw. Eskov (1990) mentioned and Eskov (1992) described *Mimetarchaea gintaras* (which he placed close to Pararchaeidae or Holarchaeidae), a specimen that supposedly possesses key apomorphies of the families Archaeidae *sensu lato* (modified chelicerae and carapace) and Mimetidae (metatarsal macrosetal brush). Eskov (1990) suggested that the families form a sister pair within the Palpimanoidea, and as such, are more closely related than was suggested by Forster & Platnick (1984). However, Wunderlich (2004, p. 1256) concluded that the holotype of *Mimetarchaea gintaras* was a subadult male not an adult, and that the embolus described by Eskov (1992) was the margin of the palpal tarsus. Wunderlich (2004) placed the specimen in Mimetidae, even considering it to belong to the extant genus *Mimetus* and stated that Eskov's speculations regarding the relationships between Archaeidae and Mimetidae were invalid. Fossil Mimetidae were revised by Harms & Dunlop (2009) who confirmed that Eskov's original conclusions were incorrect. Eskov & Marusik (1992) described two new species of *Eopopino* (Nesticidae) from Baltic amber and considered the Acrometidae to be a subfamily of the Nesticidae.

Wunderlich (1993*a, b*) described the first fossil species of the families Cyatholipidae and Scytodidae respectively, from Baltic amber. Griswold (2001) investigated the phylogeny of the extant Cyatholipidae and also studied fossil specimens determined by Wunderlich from the fossil genera *Spinilipus* (Baltic amber) and *Succinilipus* (Bitterfeld amber), but was unable to locate the broad posterior spiracle synapomorphic for the family. As the type specimens were not viewed, their correct placement in this family could not be ruled out, but it would seem unlikely (C. E. Griswold personal communication to D. Penney, 1997). Kulicka (1993) listed the numbers, by family, of the Baltic amber spiders held in the Museum of Earth, Warsaw. The numbers do not add up correctly, but it would seem that the collection contained in excess of 800 specimens, approximately two-thirds of which are unidentified juveniles. Kupryjanowicz (2001) listed 1,187 Baltic amber spiders in the collections of the Museum of the Earth, Warsaw. Resch (1996) reported an unusual piece of amber containing 10 spiders, including Anapidae and Mimetidae, and a small wasp, although none of the inclusions were described. Both Wunderlich (2000) and Eskov & Zonstein (2000) independently described new species of Ctenizidae in Baltic amber. Marusik & Penney (2004) reviewed Baltic amber Theridiidae inclusions, describing six

new species, and the voluminous work of Wunderlich (2004) described approximately 300 new species, including new genera and families. Wunderlich (2008*b*) added more new species to the Baltic amber list, including members of the genera *Ariadna* (Segestriidae), *Orchestina* (Oonopidae), *Pimoa* (Pimoidae), and new tetragnathids, araneids, and zorids. The new Baltic amber family Pumiliopimoidae was erected by Wunderlich (2008*b*) and, in a revision of European Theridiidae, Wunderlich (2008*c*) erected no less than 82 species, many in new genera. A second species of the strictly fossil spider family Spatiatoridae, currently known only from Baltic amber was described by Wunderlich (2006) and a third by Wunderlich (2008*b*). Interesting spider associations described from Baltic amber include a pair of *Orchestina* sp. trapped during copulation (Wunderlich, 1982*b*) and Poinar (2000) described the parasitic mermithid nematode *Heydenius araneus* in the same piece of amber as its supposed crab spider host (Thomisidae).

Other Cenozoic amber sources that yield a reasonable number of spiders include Oligocene–Miocene Chiapas amber from Mexico (Petrunkevitch, 1963, 1971; García-Villafuerte & Vera, 2002; García-Villafuerte & Penney, 2003; García-Villafuerte, 2006*a*, *b*, 2008; Penney, 2006*c*; Dunlop, Harms & Penney, 2008), with approximately 20 described species, and Miocene amber from the Dominican Republic (Wunderlich, 1986*b*, 1988; Penney, 2001), with 156 named spider species and 93 genera in 47 families. Nine of these genera and seven families do not contain named species. None of the families, 27% of the genera and all the species are apparently extinct (Penney & Pérez-Gelabert, 2002; Penney, 2004*e*, 2005*d*, 2006*a*, 2008). However, whether or not all species are extinct must be uncertain, given our poor knowledge of the extant Hispaniolan fauna. Indeed, Penney (2008) suggested that the Dominican amber *Nops lobatus* Wunderlich, 1988 may be synonymous with the extant *Nops blandus* (Bryant, 1942). Geological age is not, of course, a suitable criterion for determining whether or not a fossil belongs to an extinct taxon, though some workers make the erroneous assumption that fossil forms must belong to extinct species.

Poinar & Poinar (1994) provided an interesting historical account of Mexican amber. Biological inclusions in Chiapas, Mexican amber were rediscovered, somewhat accidentally in 1952 and an expedition was launched by scientists from the Department of Entomology and Parasitology, University of California, Berkeley, to collect specimens and geological data for the deposits (Hurd, Smith & Durham, 1962). Twelve spiders from this collection were described by Petrunkevitch (1963), which he placed in seven extant families. Petrunkevitch (1971), published posthumously with additional notes by Harriet Exline, described ten species from 14 specimens in five extant families. Wunderlich (1986*b*, 1988) synonymized some of Petrunkevitch's fossil Mexican amber genera with extant taxa, and considered the specimen identified as Dysderidae by Petrunkevitch (1971) as a dubious identification, but gave no reason for doing so. Penney (2006*c*) revised the Mexican amber Hersiliidae. The recently

discovered lowermost Eocene amber from the Paris Basin, France (Nel *et al.,* 2004) also contains many spiders, but representatives of only four families (Micropholcommatidae, Oonopidae, Selenopidae and Pholcidae) have been described to date (Penney *et al.*, 2007; Penney, 2007*a*, *c*) (see Fig. 1D,E).

Miocene Amber from the Dominican Republic has been known since the end of the 15th Century (Baroni-Urbani & Saunders), but was not brought to the attention of scientists until the 20th Century (Sanderson & Farr, 1960). Ono (1981) described the first spider *Komisumena rosae* (Thomisidae) from this source, Schawaller (1981*a*, 1982*a*, 1984) described the families Hersiliidae, Tetragnathidae, Uloboridae, Dipluridae and Selenopidae, Wunderlich (1982*a*) described five new species from the families Tetragnathidae, Theridiidae, Corinnidae (the extinct genus *Veterator*, originally placed in Gnaphosidae and transferred to Trochanteriidae by Wunderlich (2004); the correct systematic placement of this genus warrants a thorough examination) and Salticidae, and Wunderlich (1987) described a new species of Hersiliidae. Poinar (1987) described an immature male clubionid spider parasitized by an ichneumonid wasp larva. The major taxonomic works on this spider fauna are those of Wunderlich (1986*b*, 1988), who described approximately 130 new, named species. Cutler (1984) provided a short note on Dominican amber Salticidae and new species from this family were described by Reiskind (1989) [synonymized with one of Wunderlich's (1986*b*) species by Penney (2001)] and Wolff (1990). Wunderlich (1998) described new species from the families Mysmenidae and Linyphiidae and Wunderlich (1999) reported the family Archaeidae as present in Dominican Republic amber. However, both these papers were based on specimens that are actually preserved in Madagascan copal (Wunderlich, 2004). Penney (2000*a*) revised the Dominican amber Anyphaenidae, Penney (2000*b*) described Oonopidae and Mysmenidae. Penney (2001) described a new species of Corinnidae, the first indisputable fossil Lycosidae and corrected the taxonomy of numerous other species from this amber. Penney (2005*b*,*c*) described the first fossil Filistatidae, preserved in Dominican amber, and Penney (2005*a*) described the first Caribbean *Floricomus* (Linyphiidae), also from this deposit. Huber & Wunderlich (2006) described a new species of fossil Pholcidae, and Penney (2009) described a specimen of *Plectreurys* (Plectreuridae) from Dominican amber. Extant plectreurids are known only from the south-western USA, Mexico, and parts of the Caribbean, and a specimen from Baltic amber was referred to this family by Wunderlich (2004). A full systematic catalogue, including transfers and synonymies etc., of all fossil Dominican Republic amber spiders described up until 2005 was provided by Penney (2006*b*). This fossil assemblage is very similar to that of the Recent neotropics (Penney & Pérez-Gelabert, 2002; Penney, 2005*d*) and provides an excellent basis for investigations of the historical biogeography (e.g. Penney, 1999, 2007*b*, 2008) and palaeoecology (e.g. Penney, 2002*a*, 2008) of Hispaniolan spiders. The vast bulk of fossil spiders occur in the Cenozoic strata because of their common occurrence in Baltic and Dominican Republic ambers.

A very basic, qualitative comparison of Dominican amber spiders with those from other Cenozoic resins was provided by Schawaller (1981b) and a high-resolution quantitative comparison by Penney & Langan (2006) demonstrated that Dominican and Baltic ambers trapped organisms in the same way, despite an overall larger size of spiders in Baltic amber. A comprehensive synthesis of our current knowledge of Dominican amber (with special reference to spiders) can be found in Penney (2008).

A number of short papers have described one or more species of amber spider from other Cenozoic ambers. Protescu (1937) described two specimens (Theridiidae and Thomisidae) from Romanian amber, and Hickman (1957) described a segestriid spider from what was thought to be the late Neogene, probably Pliocene, amber of Victoria, Australia (the only fossil spider known from that continent). Wunderlich (1981) described two new species of *Orchestina* (Oonopidae) from Kenyan amber. The last two publications may have described extant species preserved in Recent copals (Poinar, 1992). Hong (1982) described a dictynid from the Lower Guchengzi Formation from Fushun coalfield in Liaoning Province, China, and Wunderlich (2004) described pholcid and oonopid spiders from this deposit. Saunders *et al.* (1974) reported but did not describe ten spiders discovered in Claiborne (early Middle Eocene) Arkansas amber. Amber spiders from the families Theridiidae, Linyphiidae, Tetragnathidae, Araneidae, Clubionidae, Thomisidae and Salticidae were reported, but not described, by Barthel & Hetzer (1982) as present in Miocene amber of the Bitterfeld district, Germany, and Wunderlich (1991, 1993a) added new species from the families Leptonetidae and Cyatholipidae to this list. However, the cyatholipids may be misidentifications (Griswold, 2001). There are now 27 families recorded from this amber (e.g. Schumann & Wendt, 1989), including the family Telemidae, which is otherwise unknown in the fossil record. Skalski & Veggiani (1990) listed, but did not describe, spiders as present in Oligocene Sicilian amber and Wunderlich (2004) described the first spiders in amber from Rovno (Ukraine) and commented on the faunal similarities with Baltic amber. Nishikawa (1974) described seven specimens (Oonopidae, Theridiidae, Thomisidae, and four *incertae familiae*) in copal from Mizunami, Japan and Lourenço (2000) described a new sub-fossil species of Archaeidae in Madagascan copal, which was synonymized with an extant species by Wunderlich (2004). Wunderlich (2004, 2008b,c) also described subfossil spiders in copals from Colombia and Madagascar, which included the first records of some extant supraspecific taxa for the island. Bosselaers (2004) described a new species of Selenopidae in copal from Madagascar (see also Penney, Ono & Selden, 2005). Recently, spiders were reported but not described in Eocene amber from India (Alimohammadian *et al.*, 2005). This discovery of an amber deposit is the first on the subcontinent and has important implications for studies of historical biogeography, because it was formed while India was still in its drift phase prior to the India–Asia collision.

(b) Mesozoic

It is only within the last three decades that spiders have been described from Mesozoic amber. Spiders were first reported from Cretaceous ambers of Canada by McAlpine & Martin (1969), France (Schlüter, 1978; Néraudeau *et al.*, 2002; Perrichot, 2005), Spain (Alonso *et al.*, 2000; Peñalver, Delclòs & Soriano, 2007), Myanmar (Burma) (Rasnitsyn & Ross, 2000; Grimaldi, Engel & Nascimbene, 2002), Jordan [Kaddumi, 2005; 2nd edition, Kaddumi (2007) includes some taxonomic descriptions of amber spiders] and Alabama (Bingham *et al.*, 2008). Eskov & Wunderlich (1995) described the new family Lagonomegopidae from two juvenile specimens in amber from Yantardakh, Taimyr, Siberia, and mentioned 50 undescribed specimens from various stages of the Upper Cretaceous of the region. Some of these were placed in the superfamilies Araneoidea, Dysderoidea and Thomisoidea. They also listed spiders as present in fossil resins from Azerbaijan and Armenia. The 47 amber spider specimens mentioned by Zherikhin & Sukatcheva (1973) from Yantardakh, Siberia may now be lost (Eskov & Wunderlich, 1995). Additional lagonomegopid spiders have been described from Cretaceous ambers of New Jersey (Penney, 2002b), Canada (Penney, 2004b), Myanmar (Penney, 2005e) and Spain (Penney, 2006d). Lagonomegopidae are curious in that they have enormously enlarged posterior median eyes, as in Deinopidae, but which are situated on the sides of the cephalic region of the carapace. Moreover, their chelicerae bear only peg-teeth, which places them in the Palpimanoidea. Unfortunately, only juveniles of this family have so far been found.

Other described Cretaceous amber spiders include the families Segestriidae, Oonopidae, Oecobiidae, Dictynidae, Araneidae and Linyphiidae from New Jersey amber (Penney, 2002b, 2004f), Araneidae from Spanish amber (Penney & Ortuño, 2006), Mecysmaucheniidae from French amber (Saupe & Selden, 2009) and Nemesiidae in amber from the Isle of Wight (Selden, 2002a), a family not present in the region today but common in the Mediterranean. Poinar & Milki (2001) cited Wunderlich & Milki (2001) as having described the first spider (Oonopidae) in Lebanese amber, however, their paper was not published until 2004 and the specimen in question was described as belonging to the family Segestriidae (Wunderlich & Milki, 2004). The linyphiid described by Penney & Selden (2002) was the first spider to be described from Lebanese amber and obtained an entry in the 2004 and 2005 editions of the *Guinness Book of World Records* as the oldest spider described from amber. Penney (2003b) described a deinopid spider from the same deposit, but whether or not it would have employed the same net-casting predation strategy as its extant relatives is unclear. New species of Cretaceous amber spiders have been described from Myanmar (Penney, 2003a (Archaeidae), 2004a (Pisauridae), 2006b (Oonopidae)] and Canada [Penney, 2006b (Oonopidae)]. Penney & Selden (2006b) described fossil Huttoniidae from Canadian amber, a family with extant species restricted to New Zealand, though Wunderlich (2008e) has questioned this familial placement.

Fossilized spider silk, including glue droplets have been reported from Mesozoic and Cenozoic ambers by Zschokke (2003, 2004), Wunderlich (2004) and Peñalver, Grimaldi & Delclòs (2006).

In another of his large publications on amber spiders, Wunderlich (2008*a,b,d,e*) turned to the Cretaceous. He described a number of new families, genera and species from Myanmar, Jordanian and Lebanese amber, including the new, extinct families Praeteroleptonetidae (to which he referred *Palaeohygropoda* Penney, 2004*a*), Eopsilodercidae, Plumorsolidae, Micropalpimanidae, Burmascutidae and Salticoididae. He also named new genera and species in extant families from Myanmar amber (Segestriidae, Oonopidae, Archaeidae, Uloboridae, Dictynidae), Jordanian amber (Segestriidae) and Lebanese amber (Segestriidae, Oecobiidae). The full effect of these taxonomic acts awaits further investigation, though we suspect that the new Cretaceous families are simply stem taxa (i.e. they can be referred to modern families but lack the full complement of characters). Wunderlich eschews cladistics and bases his systematic decisions on comparison of many characters between families (Wunderlich, 2008*a*). Such characters need not necessarily be diagnostic, rather it is the combination of observed characters which typify the families and give them their 'jizz' (in ornithological terminology). As a consequence, it is difficult to compare Wunderlich's phylogenies with those of other workers. Since Wunderlich is the most prolific describer of fossil spiders at present, it is important to understand his methodology and its shortcomings.

As an example, Wunderlich (2008*e*) erected the family Eopsilodercidae on the basis of a single adult male, *Eopsiloderces loxosceloides* Wunderlich, 2008, in Myanmar amber. He set up two tribes: Eopsilodercini for *E. loxosceloides* alone, and Furcembolusini for *Furcembolus andersoni* Wunderlich, 2008, and described three other specimens from Myanmar amber as "?Eopsilodercidae *indet.*". Curiously, in the section on relationships of Furcembolusini, Wunderlich (2008*e*, p. 582) wrote that: ". . . the taxon is probably not a member of the Eopsilodercidae."! The family diagnosis of Eopsilodercidae (Wunderlich 2008*e*, p. 577) runs: "(♂;♀ unknown): Cheliceral lamina most probably absent, the anterior margin of the cheliceral furrow bears two tiny teeth, six eyes in a "segestriid" position (so in *Furcembolus*, but not quite sure in the holotype of the type taxon), clypeus not or only fairly protruding, legs without distinct bristles, ♂-pedipalpus (figs. 18, 21, 22): Tibia large, cymbium bristle-less, bulbus simple, originating at the tip of the cymbium." The first character, cheliceral lamina, cannot be confirmed and so must be rejected. The second, two tiny teeth on cheliceral promargin, is not diagnostic at the family level in any spider family. The third character, six eyes in a "segestriid" position, is not known in the type (and only known) specimen and, moreover, five pages further on, Wunderlich (2008*e*, p. 582) suggested that *Furcembolus* is not in Eopsilodercidae anyway! The fourth character, clypeus not or only fairly protruding, refers to a character in the modern *Psiloderces* (Ochyroceratidae), which shows a marked protruberance on the clypeus; Wunderlich (2008*e*, p. 585) erected the new family Psilodercidae for this extant genus alone, and his Eopsilodercidae is based on a comparison with this new extant family. The fifth character, legs without distinct bristles, is ambiguous: *Psiloderces* lacks leg bristles, but the fossil *Eopsiloderces* bears thin bristles on femora and tibia I–II (Wunderlich, 2008*e*, p. 579). The characters of the male palp are distinctive for *Eopsiloderces* but differ from those of *Psiloderces*, which has strong apical bristles on the cymbium. To conclude, the diagnosis is not written in a comparative style, which is unhelpful, and the characters, when investigated, are not present in the type specimen, are irrelevant or ambiguous. In our opinion, erecting new families for single or small collections of fossil specimens, and especially when based on uncertain characters, leads to a plethora of new names but does not help in understanding spider family relationships and evolution.

Also in his latest work, Wunderlich (2008*e*) presented the hypothesis that the Cretaceous period was dominated by Haplogynae and that the majority of modern spider families (ecribellate entelegynes) originated after the K–T boundary; he called the Cretaceous the 'Age of the Haplogynae'. Wunderlich (2008*e*) linked the supposed diversification of modern spider families in the Paleocene with the diversification of ants and angiosperms. The evidence presented derives from: the lack of particular families such as Corinnidae, Salticidae, Thomisidae, and derived araneoids such as Theridiidae and Linyphiidae, in part produced by re-determinations of a number of specimens described by Penney and others from Cretaceous ambers; erection of six new families which, together with two already known, did not survive the K–T extinction; and numerous other behavioural, ecological and geographic aspects which purport to show differences between the Cretaceous and Tertiary spider faunas. From what has been said in the previous paragraph, it will be apparent that our view of spider evolution differs from that of Wunderlich in a number of ways. In our experience many modern families can be traced back to the Cretaceous period, but if the modern family is defined purely on its crown group, then such will not be apparent. This notion allows the erection of new Cretaceous families which differ from modern ones only in the lack of particular characters, as would be expected in a stem-group taxon. A glance at Fig. 2 shows that many modern families are now known from the Cretaceous, and the cladogram predicts that the sister groups of many of these families will also be found in the Cretaceous. The groups of families which have yet to be found in the Mesozoic are those which possibly did originate in the Cenozoic: the Dionycha, for example, have dispensed with prey-capture webs for good reasons (outlined in Dippenaar-Schoeman & Jocqué, 1997). Furthermore, many of the haplogyne families, which were supposed by Wunderlich to typify the Cretaceous (pholcids to sicariids in Fig. 2), are not known from that period (some of these are known from the Mesozoic but have yet to be described). Not only is the Mesozoic era only beginning to be explored in terms of its araneofauna, but
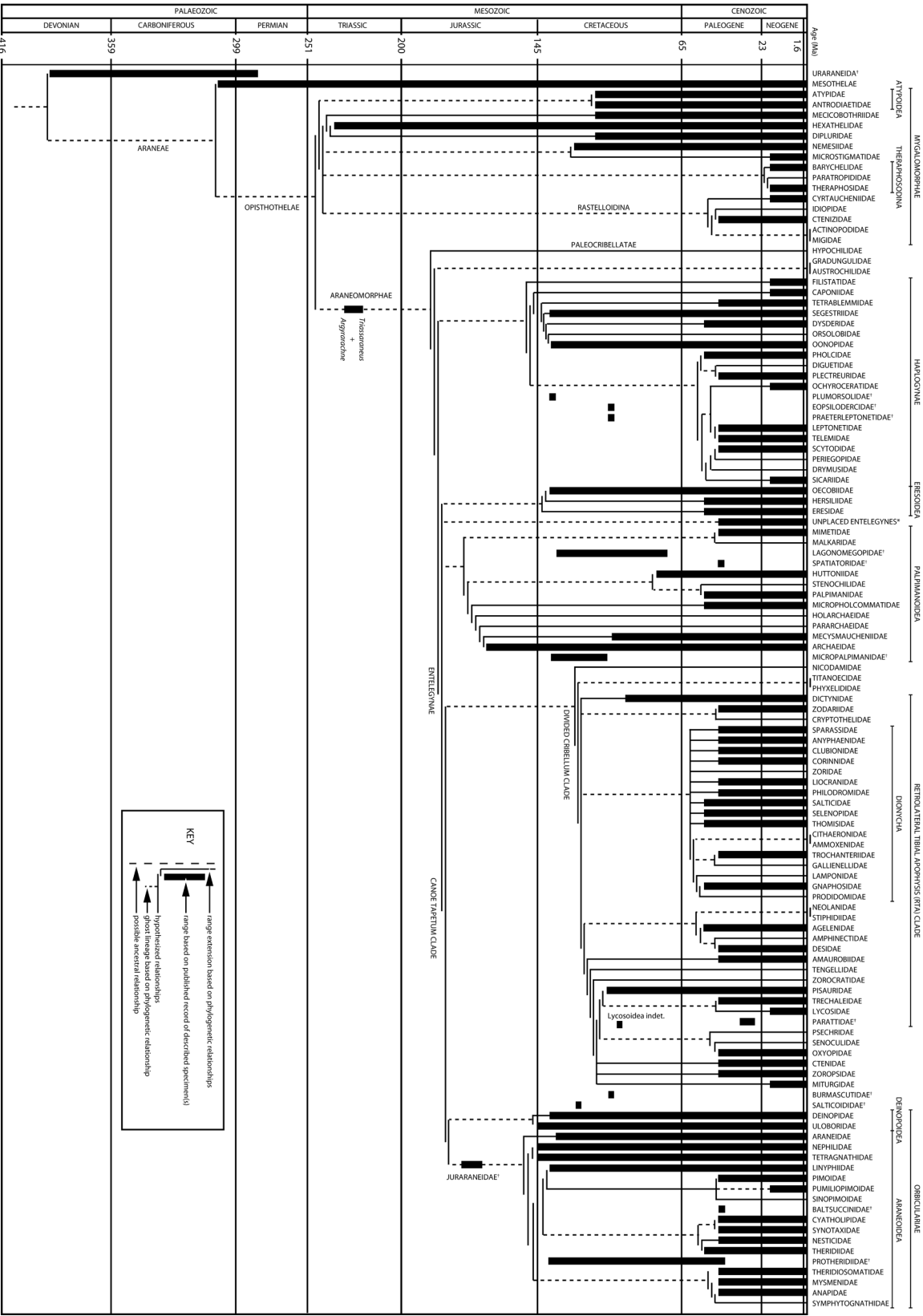
Fig. 2. Legend on next page.

also the Paleocene epoch stands out as being impoverished in spider Lagerstätten, so it is still premature to make sweeping generalizations about faunal turnover in spider evolution. In a parallel example, Eskov & Zonstein (1990) proposed the Mesozoic to be an 'Age of Mygalomorphs', based on the paucity of araneomorph spiders then known from Mesozoic strata; now, Mesozoic records of araneomorphs far exceed those of mygalomorphs, so the concept of a Mesozoic Age of Mygalomorphs has had to be abandoned.

(3) Non-amber spiders

(a) Cenozoic

The second half of the 18th Century was barren of literature references to fossil spiders, but by the early 19th Century, spiders were being mentioned from the Miocene of Aix en Provence (Serres 1818, 1828, 1829). Buckland (1836, 1837, 1858) figured a spider from the Miocene of Aix, and this specimen (BMNH In 43302) was eventually described as *Theridium bucklandii* by Thorell (1870a). Dunlop (1993) figured the specimen as a mygalomorph, without any discussion, but that identification is certainly erroneous. It appears to be the first recognizable non-amber spider to be figured, and is shown here in Fig. 1B. In his comprehensive catalogue of fossils, Giebel (1856) recorded no fossil spiders except those in amber. The Aix fauna continued to be described by Brongniart (1877: *Attoides eresiformis*), most fully by Gourret (1886), and with further additions from Berland (1939). Fossil spiders can still be collected in abundance at Aix (A. Nel, personal communication to P. A. Selden).

The first non-amber spider to be formally described was by Heyden (1859), who studied two specimens from the Miocene Brown Coal of Grube Stoschen, near Linz am Rhein, Germany: *Gea krantzi* (Araneidae) and *Argyroneta antiqua* (Argyronetidae) (BMNH 58824 and 58825, respectively). A few years later, Heer (1865) described 28 specimens belonging to 10 genera, 11 of which he illustrated, from the Miocene lacustrine deposits of Oeningen, on the Swiss/German border (see also Heer, 1872, 1876). Later workers did not accept Heer's identifications; for example, Heywood (footnote in Heer 1876, p. 11) commented on *Argyronecta* [sic.] *longipes* Heer, 1865: 'Unfortunately the two specimens which Prof. Heer received are not sufficiently well preserved for certain determination. The comparative lengths of the legs, the thin filiform palpi, and the rounded form of the sides of the cephalothorax are in favour of it being referred to *Argyronecta*; but the cephalothorax is less prominent in front than in the existing species. A similar form of cephalothorax and legs also occurs in *Tegenaria*. According to Thorell (1870a)

this species does not belong in *Argyronecta*, but seems to form a distinct genus'.

Bertkau (1878a) studied the fossil spider fauna from the Miocene Brown Coal of Rott, Germany. Seven spiders and a millipede were described and illustrated, including three linyphiids, an araneid, an agelenid, a thomisid and, of most interest, numerous specimens of *Argyroneta (Elvina) antiqua* Heyden, 1859. Heyden (1859) had placed his specimen in the European Water Spider genus *Argyroneta* on the basis of its habitus and, presumably, consideration of its preservation in swamp conditions. Thorell (1870a) created the new genus *Elvina*, diagnosed by the palps being thicker than the legs for *Argyroneta antiqua* Heyden, 1859, and suggested that it probably belonged in Tubitelariae (a name no longer in use for a group of spider families including Agelenidae, Gnaphosidae, Clubionidae, Urocteidae, Filistatidae, Dysderidae and, indeed, *Argyroneta*). Petrunkevitch (1946) remarked that the segmentation of the legs was not visible in the holotype. Selden (2001) restudied the specimen and noted that leg segmentation is clearly visible, thus concluding that Petrunkevitch was unlikely to have seen the specimen. Heyden (1859) gave a leg formula of 1234 or 1243; Petrunkevitch (1946) pointed out that the leg formula of the modern *Argyroneta* is 1423 (the fourth legs in this genus are large, possibly modified for swimming). Thus, Heyden's specimen cannot be placed with certainty in the genus *Argyroneta*. Indeed, little can be said about this specimen except that it is a spider, and most likely an araneomorph as evidenced by the large palpal cymbium of this adult male specimen (Selden, 2001).

Scudder described the Oligocene spiders from Florissant, Colorado. In a general paper (Scudder, 1881), dealing with the geological setting, stratigraphy, palaeontology and comparisons with other Tertiary insect faunas, he stated of the spider fauna: 'As a whole the arachnid-fauna appears rather uninteresting, and to have few features in common with that of the Prussian amber.' Of course, one would not expect a volcanic lake to sample the same spider fauna as resin. Uninteresting it is not, however, and Scudder (1890) described some 30 spiders from Florissant (and two indeterminate araneids from Green River, Wyoming) belonging to the families Segestriidae, Clubionidae, Anyphaenidae, Agelenidae, Titanoecidae, Theridiidae, Linyphiidae, Tetragnathidae, Araneidae, Thomisidae and Salticidae. Included under Theridiidae is a spider egg-sac, named *Aranea columbiae*, which has been found not only at Florissant but also in the Green River Formation of Wyoming and Quesnel, British Columbia. They appear to belong to more than one species, and because some of the specimens are stalked, Scudder

Fig. 2. Phylogenetic tree of the spiders (Araneae) produced by combining the fossil record with the cladograms of Coddington & Levi (1991), Griswold (1993), Scharff & Coddington (1997), Griswold *et al.* (1998, 1999), Ramírez (2000), and Álvarez-Padilla *et al.* (2009). Note that, while there have been many objections to the view of Palpimanoidea put forward by Forster & Platnick (1984), there is yet no consensus on where some of its included families should be placed so, for now, we retain the superfamily in its incongruous position. *Unplaced families include Chummidae, Cycloctenidae, Hahniidae, Homalonychidae, Synaphridae, † Ephalmatoridae and † Insecutoridae.

(1890) compared them to the pedunculate egg-sacs of some theridiids (*sensu lato*). McCook (1890, p. 459) reproduced Scudder's (1890) discussion and figures, and compared them to the stalked egg-sacs of the extant genera *Ero* (Mimetidae) and *Theridiosoma* (Theridiosomatidae). The chapter in McCook's (1890, pp. 446–469) book gives a good review of fossil spiders to that date for the non-specialist. McCook (1888) also described a fossil spider, *Eoatypus woodwardii*, from the Eocene Bembridge Marls Insect Bed of the Isle of Wight, England (BMNH In 61271), as an atypid mygalomorph, based on an interpretation of the chelicerae as being particularly large and porrect. The specimen was restudied by Selden (2001) who commented that the appearance of the chelicerae as large is an artefact of fossilization in spiders: the fossils commonly split through the chelicerae, which are sometimes forced upwards through compaction, thus giving the appearance of being much larger and porrect than they would have been in life. He referred *Eoatypus* to Opisthothelae *incertae sedis* (Selden, 2001).

Petrunkevitch (1922) studied the Tertiary spiders of North America, revising some of Scudder's (1890) Florissant species as well as describing new ones. In nearly every case, Petrunkevitch could find little fault with Scudder's description, but disagreed with him in most cases concerning their systematic placement. For example, *Titanoeca*, placed today in Titanoecidae, is a genus of cribellate spiders. Petrunkevitch (1922) could find no cribellum or calamistrum on any of these well-preserved specimens. Scudder (1890) had referred them to this genus on the basis of general similarity to the living genus. Petrunkevitch (1922) referred all of Scudder's (1890) titanoecids to Gnaphosidae (formerly Drassidae) under the new genus *Palaeodrassus*. Scudder (1890) had placed three species in a new genus *Parattus* on account of their resemblance to jumping spiders (Salticidae was formerly known as Attidae), particularly by the presence of large eyes in one row and smaller ones in the second. Scudder created the new genus because no living salticid shows eyes in this pattern, although a third row of eyes (which would be expected in a salticid) could not be discerned in any specimen. Petrunkevitch (1922) demonstrated that referring them to Salticidae could not be sustained, and he was able to make out two rows of four eyes in one specimen (MCZ 118; Fig. 19 in Petrunkevitch, 1922), so created a new family, Parattidae, for them. The family, one of a remarkably few entirely fossil families (Penney & Selden, 2006a), was diagnosed on the basis of round eyes in two rows of four, anterior subequal and fairly equidistant, posterior eyes considerably smaller, with the posterior median eyes between and slightly behind the anterior medians. A re-examination of the type specimen by one of our research students (Richard Cutts) revealed that the fossils are compressed in such a way that what Petrunkevitch (1922) considered to be the anterior eyes are actually the posterior eyes and *vice versa*. The spiders are lycosoids (possibly *Lycosa florissanti* Petrunkevitch, 1922, whose eyes are not discernible, belongs here too), and a manuscript redescribing the type species is in preparation. The new spiders described by Petrunkevitch (1922) are mostly additional species in the same families as noted by Scudder (1890), but one well-preserved specimen is worthy of note: *Eodiplurina cockerelli* Petrunkevitch, 1922 (UCM 17703; BMNH In 25932 is the counterpart) is clearly a mygalomorph, possibly a diplurid. Eskov & Zonstein (1990) referred it to Nemesiidae, but this is untenable because *Eodiplurina* has uniserially dentate tarsal claws whilst nemesiid claws are bipectinate. Licht (1986) produced a short paper for the International Arachnological Congress in Panama on the taphonomy of the Florissant spiders. He concluded that, because the spiders' legs were outstretched, rather than folded up, they must have died in water which was warm or with a low pH value; i.e. related to the volcanic activity at the site. Long experience of one of us (P. A. Selden) in studying fossil spiders in lacustrine deposits has indicated that outstretched legs are quite a common feature of drowned spiders, and warm and/or acidic waters are unnecessary to explain this phenomenon. Spider legs are most likely to curl up due to muscle contraction (spiders have no extensor muscles), perhaps caused by dehydration, and this would not occur in water.

Publication on fossil arachnids in the first half of the 20th Century was almost entirely dominated by the work of Alexander Petrunkevitch; but after his 1922 paper, there was little work published on Cenozoic spiders until near the end of the century. Berland (1939) described one from Aix and four poorly preserved specimens from Alsace, and Petrunkevitch (in Palmer, 1957) described a dictynid from the Miocene Barstow Formation of California. Later works have mainly been short notes on single specimens and/or occurrences by arachnologists dipping a toe into the murky waters of palaeontology. Cutler (1970) and Leech & Matthews (1971) described thomisid fragments from the Pliocene of Wyoming and the Miocene of Alaska, respectively. Schawaller & Ono (1979) recorded a lycosid and a salticid, and Wunderlich (1985) a thomisid, from the Randecker Maar volcanic crater lake deposits in Germany. In the 1980s there were records of a fauna of free-living spiders (Salticidae, Thomisidae and Lycosidae) from the Pliocene of Willershausen, Germany (Schawaller, 1982b), orb-weavers (Araneidae) from the Eocene oil-shale deposits of Messel, Germany (Wunderlich, 1986a), and Selden & Penney (2009) described a pisaurid from Eocene deposits of Horsefly, British Columbia, Canada. Hong (1985) and Zhang *et al.* (1994) described agelenids, araneids, tetragnathids, lycosids, thomisids and salticids from Miocene diatomaceous deposits of Shanwang, China, and Bottali (1975) figured a thomisid and a lycosid from Pleistocene diatomites near Rome, Italy, and Ribera (2003) reported a possible araneid from a Pleistocene cave-fill of Girona, Spain. Not surprisingly, the younger the deposit, the more similar the arachnofauna is to what one would expect to find in a similar habitat today.

(b) Mesozoic

The earliest records of arachnids from the Mesozoic era were misidentifications. Weyenbergh (1869b) described *Hasseltia primigenius* from Solnhofen as a spider, possibly an *Argyroneta*. The name was soon replaced by *Hasseltides*, *Hasseltia* being

preoccupied (Weyenbergh, 1869*a*), and identified as an opilionid by von Hasselt himself (Weyenbergh, 1874*b*; Petrunkevitch, 1949, 1953), but is actually the stemless crinoid *Saccocoma* (Petrunkevitch, 1955). Weyenbergh (1874*a*) also described a supposed pseudoscorpion from Solnhofen, *Chelifer fossilis*, which proved to be a crustacean (Petrunkevitch 1953). Similarly, Münster (in Germar, 1839) described *Phalangites* Münster, 1839 from the Solnhofen Limestone, and the same animal was later described by Roth (1851) as *Palpipes priscus*, both of whom identified it as an opilionid. Seebach (1873) showed it to be a crustacean. *Sternarthron zitteli* Haase, 1890, from Solnhofen, was originally figured as an insect by Oppenheim (1888); Haase (1890) referred it to the Palpigradi, an order of minute arachnids. In spite of Handlirsch's (1906) demonstration that the specimens were indeed insects, and have been referred to Phasmatodea (Carpenter, 1992, p. 188), the palpigrade affinity was accepted by Petrunkevitch (1953, 1955), though he appeared never to have studied the specimens. So, it was not until the late 20th Century that the first Mesozoic spider was described.

Eskov (1984) described the new family Juraraneidae, based on *Juraraneus rasnitsyni* a single adult male from the Jurassic of Transbaikalia, Siberia. The interpretation of *Juraraneus* as an araneoid was based on the complexity of the male palp, with its large paracymbium. Wunderlich (1986*b*) suggested that *Juraraneus* could be accommodated in Araneidae, but did not formally synonymize the families. The original diagnosis of the family was based on a unique combination of morphological characters found in other araneoid families (Eskov, 1984). Eskov (1987) described an archaeid spider, *Jurarchaea zherikhini*, from the Jurassic of Kazakhstan. The find of an archaeid in Jurassic strata was interesting because this family of small, araneophage spiders was already well known from Baltic amber and the Recent Gondwana fauna. Eskov (1987) placed his monotypic Jurarchaeinae somewhat closer to the Pararchaeidae and Holarchaeidae than Archaeidae *sensu stricto*. P. A. Selden restudied the holotypes (and only specimens) of *Juraraneus* and *Jurarchaea*, and is in complete agreement with their description and interpretation as an araneoid and an archaeid *sensu lato*, respectively.

The record of described Mesozoic spiders more than doubled when Selden (1989, 1990) described two tetragnathids and a uloborid from early Cretaceous rocks of the Sierra de Montsech, Spain. These specimens preserved tarsal claws which showed they were orb-web weavers. There had been a controversy raging since the late 1960s regarding whether the cribellate and ecribellate orb-weavers represented convergent evolution or the orb web evolved only once (in cribellates) and then some orb-weavers lost the cribellum (for an excellent review see Shear, 1986). The issue was resolved in the 1980s: orb webs evolved once only and the araneoids lost the cribellum in favour of silk with glue, so the Cretaceous fossils provide a minimum age for the origin of the ecribellate orb because both cribellate and ecribellate orb-weavers occur together in this deposit. Note that in the original description of the Montsech arachnofauna, Selden (1990) was rather cautious in his assignment of the spiders

to modern families. Since at that time there were so few Mesozoic spiders known, and the Palaeozoic forms were seemingly so primitive, there was a concern that Mesozoic forms might not belong to modern families. However, as more Mesozoic spiders came to light, it became apparent that the modern families are well represented in this era and so, in later descriptions of spiders from the Cretaceous of Spain (Selden & Penney, 2003), forms were placed in the modern families Uloboridae and Nephilidae.

The first Mesozoic mygalomorphs were described by Eskov & Zonstein (1990), from localities in the Lower Cretaceous of Siberia and Mongolia. These were placed in the modern families Mecicobothriidae, Antrodiaetidae and Atypidae. The paper aroused much interest, not because of the fossil finds, but because the authors tacked onto the systematic part three short essays on mygalomorph systematics, the evolution of the mygalomorph male palp, and comments on the stratigraphic distribution of mygalomorphs. In the last, Eskov & Zonstein (1990, p. 361) proposed, on the basis of very few data (six specimens) an 'Age of Mygalomorphs' during the late Early Cretaceous, during which short period of time these spiders replaced araneomorphs in the fossil record.

Eskov & Zonstein's (1990) record of the earliest mygalomorphs was soon broken when Selden & Gall (1992) described a dozen specimens of *Rosamygale grauvogeli*, a new species of Hexathelidae from the Triassic of the northern Vosges, France. This was not only the oldest mygalomorph but also the first Triassic spider to be described. It was placed in the modern family Hexathelidae on account of the presence of six spinnerets and other features of fairly primitive mygalomorphs. Hexathelidae occur throughout the Gondwanan region and north as far as southern Europe today, though their greatest diversity occurs in eastern Australia. Raven (1980) postulated a centre of origin in East Antarctica and a dispersal throughout Gondwanaland before its break-up in the Cretaceous. Their presence on the southern shore of the Zechstein Sea in the mid-Triassic indicates a radiation across the supercontinent quite early in the Mesozoic. Also, the presence of a mygalomorph in the Triassic period predicts the presence of its sister group, Araneomorphae, at that time too. Sure enough, the earliest araneomorph spiders were described by Selden *et al.* (1999) from localities in slightly younger Triassic rocks in South Africa and Virginia. Though unmistakably araneomorph, these specimens are too poorly preserved to be identified to family, although an araneoid affinity seems likely.

In recent years, many new specimens of superbly preserved spiders have been recovered from localities in early Cretaceous rocks of Brazil (Mesquita, 1996; Selden, da Casado & Mesquita, 2002, 2006) and Jurassic (Selden, Huang & Ren, 2008) and Cretaceous (Chang, 2004; Cheng *et al.*, 2008) rocks of China and are currently under study. Early observations on these faunas indicate that, not only were modern families present in Jurassic and Cretaceous times but also the same families seem to occur in similar habitats both in the Mesozoic and today: e.g. Tetragnathidae

and Uloboridae seem to be common in the arachnofauna preserved in lacustrine settings (Huang *et al.*, 2006).

(c) Palaeozoic

The first fossil spider to be formally described from Palaeozoic strata was *Protolycosa anthracophila* Roemer (1866). This specimen, from the Coal Measures of Katowice, Poland, was apparently lost during World War II, and could not be found by Petrunkevitch (1953). Information from curators at the museum in Wrocław indicates that this is, indeed, the case. Roemer's drawings clearly show opisthosomal segmentation, but he considered the opisthosoma to be unsegmented in life (perhaps he was unaware of the existence of the extant genus *Liphistius* which has a segmented opisthosoma). Also, *Protolycosa* appeared to bear appendages arising from the anterior part of the opisthosoma. Roemer (1866) and subsequent commentators on *Protolycosa* agreed that this specimen represented a true spider (Araneae), even though its resemblance to the extant genus *Lycosa* is superficial and the segmented opisthosoma with appendages is unusual for spiders. Harger (1874) described a Coal Measure spider from Mazon Creek, Illinois, as *Arthrolycosa antiqua* (YPM 161). He described the fossil as having a segmented opisthosoma and chelate pedipalps; he compared this fossil to the living *Liphistius*, which was described by Schiodte (1849) as having no spinnerets. Harger (1874) preferred not to refer *Arthrolycosa* to Araneae, but considered it as an arachnid showing somewhat primitive features (segmented opisthosoma), with some resemblance to scorpions and opiliones (eye tubercle) and scorpions, pseudoscorpions and uropygids (chelate pedipalps). Harger's original (1874) description was based on an undeveloped specimen (i.e. one in which parts are still embedded in the rock matrix). Scudder (1884) restudied the specimen and concluded that the chelate pedipalps were erroneous; he referred *Arthrolycosa* to Karsch's (1882) order Anthracomarti. Beecher (1889) developed the holotype further to reveal more morphological features, and thus presented a more complete description; he concluded that it should be removed from Anthracomarti and commented that the only character which would exclude *Arthrolycosa* from the four-lunged (mygalomorph) spiders was the segmented opisthosoma.

In a series of papers, Kušta described the Carboniferous Coal Measure arachnid fauna from Rakovnik, Bohemia; the following spiders were described: *Rakovnicia* Kušta, 1885 (Kušta, 1885), *Eolycosa* Kušta, 1886 (Kušta, 1886), *Geralycosa* Kušta, 1888, and *Scudderia* Kušta, 1888. Kušta (1888) placed all of these in Arthrolycosidae Harger, 1874. Frič (1873, 1901, 1904) added more forms from the Bohemian coal basins, and his 1904 monograph summarized and illustrated the known Palaeozoic arachnids to that date. *Palaranea borassifoliae* Frič, 1873 is an interesting specimen. It is clearly a spider compressed onto or under a large leaf of *Cordaites borassifolius* Sternberg; not noticed when first figured, it was Reuss (1854) who first mentioned its presence. Frič (1873) described it, and in 1904 referred it tentatively to *Arthrolycosa*. It was redescribed by Petrunkevitch (1953) in Arthromygalidae Petrunkevitch,

1923, who thought he could see spinnerets on the specimen (see Fig. 199 in Petrunkevitch, 1953), but on Frič's drawing (Frič, 1873, pl. II fig. 78; Frič, 1904, Fig. 7B; Petrunkevitch, 1955, Fig. 99.7) these are shown as right leg 4. A restudy by P. A. Selden indicated spinnerets cannot be confirmed on such a poorly preserved specimen and it is best regarded as Araneae *incertae sedis*.

Frič (1904) referred ten species to Arthrolycosidae and synonymized Kušta's *Scudderia* and *Eolycosa* with *Arthrolycosa*. Arthrolycosidae was placed in suborder Arthrarachnae Haase, 1890. Whereas Haase (1890) included only Arthrolycosidae (*Arthrolycosa, Geralycosa*) in his Arthrarachnae, and placed Protolycosidae (*Protolycosa*) and Liphistiidae (*Eolycosa, Palaranea*) into Tetrasticta Bertkau, 1878*b* [=Tetrapneumones of Latreille (1825)], Frič (1904), redefined Arthrarachnae on a more or less [?] segmented opisthosoma lacking pleurae, and two pairs of book-lungs, and included the Recent *Liphistius* and mygalomorphs (Tetrasticta or Tetrapneumones). He redefined Arthrolycosidae Harger, 1874 on: segmented abdomen lacking pleurae, two tarsal claws and large chelicerae. Frič (1904) established the suborder Pleuraraneae for spiders with granulated rather than hairy exoskeletons, segmented opisthosomas dorsal and ventral, and pleurae. These, which we would now place in Anthracomartidae (Trigonotarbida), included *Hemiphrynus* and *Promygale*. Spiders which Frič (1904) could not place in either suborder included *Perneria, Eopholcus, Pleurolycosa, Brachylycosa* and *Pyritaranea*. The Bohemian specimens are held in the National Museum, Prague.

Pocock (1910) commented on Frič's (1904) monograph; he was critical of Frič's drawings and considered certain misinterpretations were due to Frič's lack of knowledge of the morphology of modern arachnids (see also Pocock, 1911, p. 8). Pocock (1910) synonymized *Promygale* with *Anthracomartus*, and removed all of Frič's Pleuraraneae to Anthracomarti. Pocock (1911) described the British Carboniferous Araneae in a monograph on the British fossil arachnids. He referred two specimens, *Eocteniza silvicola* Pocock, 1911, and *Arthrolycosa* sp. to Mesothelae Pocock, 1892, a suborder restricted to spiders with segmented opisthosomas, and erected the new genus and species *Archaeometa nephilina* (BMNH In 31259) for a supposed araneomorph spider. Here, for the first time, a Palaeozoic spider was referred to the Opisthothelae.

Alexander Petrunkevitch was undoubtedly the major worker on fossil spiders in the 20th Century; his works spanned the period from 1913 to 1971. Petrunkevitch's (1913) monograph listed the known Palaeozoic spiders to that date, redescribed the holotype of *Arthrolycosa antiqua* Harger, 1874, and added a new species of *Arthrolycosa* from the Coal Measure concretions of Mazon Creek, Illinois; photographs as well as drawings were provided. He placed *Arthrolycosa, Protolycosa, Geralycosa, Rakovnicia, Perneria* and *Eocteniza* in Mesothelae: Arthrolycosidae, and not only *Archaeometa* but also *Eopholcus* and *Pyritaranea* in Arachnomorpha (=Araneomorphae). The last reference had been suggested by Pocock (1911), and the referral of all of these genera to Araneomorphae was based primarily on the fact that these specimens have long, thin legs.

Petrunkevitch (1923) erected the family Arthromygalidae to distinguish those Palaeozoic spiders whose eyes were apparently not on a tubercle from arthrolycosids which possess an eye tubercle, with the new genus *Arthromygale* Petrunkevitch, 1923 for *Arthrolycosa fortis* and *A. beecheri*. In a major work on Palaeozoic arachnids, Petrunkevitch (1949) had an opportunity to study European types. In this work he described a new genus and species of mesothele, *Protocteniza britannica*, and a new genus and species of araneomorph, *Arachnometa tuberculata* (BMNH In 13917), both from the Coal Measures of Coseley, England. He erected Archaeometidae for *Archaeometa* and *Arachnometa*. However, it was not until Petrunkevitch (1953) produced a monograph specifically on European Palaeozoic and Mesozoic arachnids that full redescriptions of all available European Palaeozoic Araneae appeared. In this work, the two fossil mesothele families were recognized to contain: *Arthrolycosa* and *Eocteniza*, only, in Arthrolycosidae, and *Arthromygale*, *Protocteniza*, *Palaranea*, *Geralycosa*, *Kustaria* Petrunkevitch, 1953 (for *Scudderia* Kušta, which is preoccupied) and *Rakovnicia* in Arthromygalidae. Interestingly, in his key, Petrunkevitch (1953: 101) described the families Archaeometidae and the new family Pyritaraneidae Petrunkevitch, 1953 as 'Spiders resembling Recent arachnomorph species' which suggests the beginning of some doubt in his mind about their true affinities. *Dinopilio gigas*, classified as an opilionid by Frič (1904), and the new species *D. parvus* Petrunkevitch, 1953, from the Chislet Colliery, Canterbury, England, as well as *Pyritaranea* were included in the latter family. *Eolycosa*, *Palaeocteniza* (see below), and *Pleurolycosa* were placed as Aranei *incertae sedis*. Petrunkevitch's final work on Palaeozoic Araneae was the *Treatise* (Petrunkevitch, 1955), which differed only slightly from his 1953 classification.

The first non-Carboniferous Palaeozoic spider to be described was *Palaeocteniza crassipes* Hirst, 1923, a tiny, poorly preserved specimen (BMNH In 24670) from the Devonian Rhynie Chert of Scotland, which was referred with hesitation to Araneae by Hirst (1923). Petrunkevitch (1953) agreed that its status as a spider was doubtful. After seeing the specimen (Petrunkevitch, 1949) he suggested it could belong to either Araneae or Trigonotarbi, but left it as Araneae *incertae sedis*. In the *Treatise* (Petrunkevitch, 1955, p. P135), however, he put it in Arthromygalidae with the remark 'classification doubtful'. Selden, Shear & Bonamo (1991) restudied the specimen using Nomarski Differential Interference Contrast microscopy. They concluded that the specimen showed no synapomorphies of Araneae and that, given its small size and the abundance of trigonotarbids of all instars in the chert, an identity as a juvenile trigonotarbid was most likely.

Another Devonian supposed spider was described by Størmer (1976) as *Archaeometa? devonica*, from the lower Emsian deposits of Alken an der Mosel, Germany. Reconsideration of Størmer's (1976) tentative identification by Selden, Shear & Bonamo (1991, p. 244) concluded that 'There seems to be no reason to consider *Archaeometa? devonica* as a spider or a fossil arachnid of any sort.' A more convincing Devonian spider was described by Selden, Shear & Bonamo (1991)

as *Attercopus fimbriunguis* (Shear, Selden & Rolfe, 1987), from highly fragmentary material from Givetian shales of Gilboa, New York, USA. Originally described as a possible trigonotarbid (Shear *et al.*, 1987), its probable aranean nature became apparent after a spinneret was discovered in the same beds (Shear *et al.*, 1989), and by comparison of the cuticle ornamentation, the spinneret was related to diverse parts of most of the remaining morphology of the animal. Since then, the status of *Attercopus* has been re-visited, following the discovery of new, conspecific material from South Mountain, near Gilboa, New York. Selden, Shear & Sutton (2008) re-designated *Attercopus* as belonging to a new order, Uraraneida, to which these authors also referred *Permarachne* Eskov & Selden, 2005, previously also described as a spider. Uraraneida possess silk glands and spigots, but these are arranged on ventral plates, not spinnerets. Following the discovery by Haupt (2003) that a cheliceral venom gland opening is absent in the Mesothelae, the supposed venom gland opening on the cheliceral fang of *Attercopus* was reinvestigated, and was found to be absent (Selden, Shear & Sutton, 2008). Furthermore, uraraneids bear a long, post-anal flagellum, unknown in any spider [but present in some other Pantetrapulmonata Shultz, 2007 (Shultz, 2007)]. Uraraneida may be sister group to true spiders, but more work now needs to be done on the relationships of the Pantetrapulmonata. The oldest known spider is therefore Carboniferous in age.

P. A. Selden has studied all available Carboniferous specimens described as spiders, but many of the redescriptions have yet to be published. Preliminary work indicates that *Archaeometa*, *Arachnometa* and *Dinopilio* are arachnids but not spiders, while *Eopholcus* and *Pyritaranea* may be spiders but are not sufficiently well preserved for their affinities to be determined. Synapomorphies of Araneae, such as spinnerets, were generally thought to be missing from Carboniferous spiders (Platnick & Gertsch, 1976), but such have now been found in old specimens after additional preparation, e.g. *Arthrolycosa antiqua* YPM 162 (Petrunkevitch, 1913, pl. VIII, fig. 43; P. A. Selden, unpublished data) and in more recently discovered specimens from the Coal Measures of Montceau-les-Mines, France (Selden, 1996*a*, *b*, 2000). The latter specimens, *Palaeothele montceauensis* (Selden, 1996*a*) (BMNH In 62050 and MHNA 51961/2) were the first which could be definitely identified as mesotheles to be described. Mesothelae are most recognizable by plesiomorphies, synapomorphies of the suborder are harder to see, especially in fossils. Nevertheless, in addition to the segmented dorsal opisthosoma, spinnerets situated in a forward position on the ventral opisthosoma, and anterior medians well developed, two pairs of book-lungs, and orthognath chelicerae–all plesiomorphies–*Palaeothele* exhibits a narrow sternum, a synapomorphy for Mesothelae demonstrated by Raven (1985).

Other Carboniferous fossils attributed to Araneae described in more recent years include a new species of *Protolycosa*: *P. cebennensis* Laurentiaux-Vieira & Laurentiaux, 1963, from the lower Stephanian Coal Measures of Gard,

France (Laurentiaux-Vieira & Laurentiaux, 1963), and the most remarkable *Megarachne servinei* Hünicken, 1980, from the Permo-Carboniferous Bajo de Véliz Formation of San Luis Province, Argentina. The latter was described by Hünicken (1980) as a giant mygalomorph which, with its body length of 339 mm, would have been the largest known spider ever to have lived on Earth. Its identification as a spider was based on interpretations of the shape of the carapace, the position of the eye tubercle, the anterior protrusion of the carapace as a pair of chelicerae, and the posterior circular structure as the abdomen. X-radiography revealed possible morphology hidden in the matrix: cheliceral fangs, sternum, labium and coxae, and so a reconstruction of *Megarachne* as a giant spider was presented. However, difficulties with the interpretation (unusual cuticular ornament, suture dividing the carapace and spade-like anterior border of the chelicera), together with non-preservation of synapomorphies of Araneae, provoked debate about its interpretation as a spider. Whilst many museums around the world had casts of the holotype, the original was locked in a bank vault until this century, when the collector died, it was passed onto the museum in Córdoba and, at around the same time, a new specimen was discovered. Study of the type and the new specimen by P. A. Selden showed that *Megarachne* is not a spider but a bizarre eurypterid, similar to rare forms known from Carboniferous rocks of Scotland and South Africa, close to *Woodwardopterus scabrosus* (Woodward, 1887) (BMNH I1445/6) (Selden, Corronca & Hünicken, 2005).

Until recently, no spiders were recorded from the Permian period. This gap in the fossil record between the mesotheles of the late Carboniferous and the first opisthotheles (both mygalomorphs and araneomorphs are known from the mid-Triassic) was tantalizing, and also enigmatic because some beds in Russia had yielded many thousands of insects but no arachnids (Ponomaryova, Novokshonov & Naugolnykh, 1998). Eskov & Selden (2005) described the first spiders from the Permian: *Permarachne novokshonovi* and an *Arthrolycosa* carapace, from the latest Early Permian insect beds of Perm, Russia. *Permarachne* appeared to show a flagellum emerging from the end of the opisthosoma, which was interpreted by Eskov & Selden (2005) as one of a pair of elongate, pseudosegmented spinnerets. Opisthosomal plates were interpreted as dorsal tergites even though the remainder of the fossil preserved the ventral. Eskov & Selden (2005) concluded that *Permarachne* was a mesothele and probably a weaver of funnel webs, a new mode of life for Mesothelae, and thus shows evidence for a greater diversity of Mesothelae in late Palaeozoic times than today. However, following the find of new material of *Attercopus* (see above) and the recognition of the new order Uraraneida (Selden, Shear & Sutton, 2008), it became apparent that the opisthosomal plates in *Permarachne* were truly ventral and the flagellar structure was a post-anal tail rather than a spinneret. So *Permarachne* belongs in Uraraneida and the *Arthrolycosa* carapace remains the only known record of Permian spiders.

V. DISCUSSION

The fossil record of spiders is still far from complete, as demonstrated quantitatively by Penney (2004*d*). It is not totally inadequate, however, and as the data set of fossil spiders increases and the taxonomy is updated to conform to current hypotheses for Recent Araneae, it is possible to compare the two to investigate evolutionary history (as presented here), palaeobiogeography (e.g. Penney, 1999, 2008), taphonomic/palaeoecological biases of Lagerstätten (e.g. Penney, 2002*a*), the effects of mass extinction events (Penney, Wheater & Selden, 2003) and it also permits direct comparisons of fossil and Recent faunas (Penney, 1999, 2005*d*, 2007, 2008; Penney & Pérez-Gelabert, 2002) and comparisons between different fossil faunas (Penney & Langan, 2006). The fossil record of spiders has been shown to track that of their principal prey, the insects, suggesting a predator–prey co-radiation through geological time (Penney 2004*c*). Certain species, families, or assemblages of extant spiders can be considered indicators for the presence of other species, climatic conditions, certain habitat types, *etc*. Their presence in the fossil record may by used similarly.

The concept of behavioural fixity states that fossil organisms with Recent representatives at genus and in many cases family level, can be predicted to have exhibited similar behaviours to their extant relatives. Selden (1989) provided evidence from spiders preserved in lithographic limestone of north-east Spain, for the antiquity of that most intricate and ubiquitous achievement of spiders, the ability to weave orb webs, back in the early Cretaceous. Recent species of *Mysmenopsis* (Mysmenidae) are usually kleptoparasites in the webs of the funnel-web spider *Ischnothele* (Dipluridae) (Coyle, O'Shields & Perlmutter, 1991). *Mysmenopsis lissycoleyae* described from Dominican amber by Penney (2000*b*) predicts this behaviour and the presence of the diplurid host in the Miocene because of the morphological similarity between the fossil and Recent species; a fossil *Ischnothele* from the same amber source was described by Wunderlich (1988).

Modern phylogenetic (cladistic) analyses of spider taxa have rarely been able to include fossils, for a variety of reasons. One major problem has been the lack of score-able data which can be recovered from fossils. Commonly, characters which are important for systematics are not preserved, eye pattern in rock matrix fossils for example, while other features which are often preserved in fossils have not traditionally been used by neontologists, such as cuticle sculpture or relative sizes and shapes of morphological features. An unsuccessful attempt was made to use morphometrics to quantify the habitus of spiders preserved in rock (Kinchloe Roberts *et al.*, 2008), but amber preservation holds the greatest promise for providing well-preserved fossils for inclusion in cladistic analyses with extant taxa. It is unfortunate, then, that the bulk of the descriptive work on amber spiders has been done without regard to modern methods of analysis (e.g. Wunderlich 2008*a*–*e*). The authors of a recent paper revising the fossil mimetids (Harms & Dunlop, 2009), though lacking sufficient data of both sexes of the taxa they studied to

perform a cladistic analysis, nevertheless recognized the inadequacy of earlier work, were able to compare many important characters between fossil and living specimens, and thus remove the fossils from monotypic, fossil genera and refer them to extant taxa. In the future, it is likely that workers trained in modern phylogenetic methods, combined with new techniques for the extraction of data from fossils (e.g. micro-CT scanning; Penney *et al.*, 2007), will be able to more fully integrate fossils with extant taxa in phylogenetic analyses.

In contrast to phylogeny, where fossils play a subordinate role, they are of paramount importance in studies of historical biogeography, and can play a decisive part in the falsification of proposed hypotheses (Eskov, 1990). For example, the current Gondwanan distribution of the extant spider family Archaeidae supports the 'theory of mobilistic biogeography' i.e. that the fragmentation of Gondwanaland and the subsequent continental drift can explain their current distribution. However, because fossils of this family occur in Baltic amber (Koch & Berendt, 1854), French amber (D. Penney, personal observations), Burmese amber (Penney, 2003*a*) and from the Jurassic of Kazakhstan (Eskov, 1987) and China (Selden, Huang & Ren, 2008), the palaeontological data contradict this hypothesis and a different explanation is required. The 'theory of ousted relicts' (e.g. Eskov & Golovatch, 1986) proposes that austral disjunctions result from southerly movement of populations from formerly more northern distributions due to climatic change (most likely Eocene–Oligocene or Pleistocene). A more likely explanation is that the present-day Gondwanan distributions represent relicts from a formerly pancontinental distribution reduced in extent by extinctions in northern areas. There is a considerable amount of palaeontological data, in the form of fossil representatives of Recent austral taxa in the northern hemisphere, which tends to be the rule rather than the exception, to support this hypothesis (Eskov, 1987). Reiskind (1989) investigated the phylogeny and biogeography of the fossil (Dominican Republic amber) and extant species of the jumping spider genus *Lyssomanes* (Salticidae) in the West Indies and proposed three scenarios based on cladistics, ecology and the fossil record for the observed distributions. One of these scenarios concluded that at one time, two lineages co-existed on Hispaniola, but the fossil species was not ancestral to the extant species. Wunderlich (1988) described two species of *Lyssomanes* from Dominican amber [one of which was a senior synonym of Reiskind's species (Penney, 2001)], which were not included in Reiskind's (1989) analysis because the work was not published when his paper went to press. It may be that the second species of Wunderlich (1988) represents the ancestral lineage of the Recent species but a re-analysis is required to confirm this.

Penney (1999) compared the Dominican Republic amber fossil spider record with that of the Recent Hispaniolan spider fauna, which is, at present, poorly known (Penney & Pérez-Gelabert, 2002, Penney 2004*e*). The families Cyrtaucheniidae, Microstigmatidae, Nemesiidae, Ochyroceratidae, Tetrablemmidae, Palpimanidae, Hersiliidae, Symphytognathidae *sensu lato*, Anapidae, Mysmenidae, and Hahniidae, known from the fossil, but not Recent, fauna were predicted to be components of the Recent Hispaniolan fauna (Penney, 1999). Subsequently, Rheims & Brescovit (2004) reported the presence of extant Hispaniolan Hersiliidae for the first time. Based on a terrestrial invertebrate species longevity of less than ten million years, the presence of endemic and non-endemic species, and the assumption that Hispaniola has suffered no major ecological disruption that would cause the amber lineages to become extinct, the following hypotheses were made: Filistatidae and Desidae colonized Hispaniola after the Miocene amber formation; Drymusidae, Amaurobiidae, and Deinopidae were present on Hispaniola during the Cenozoic, but avoided capture, or have yet to be found in the amber; and Scytodidae, Oecobiidae, Uloboridae, Dictynidae and Clubionidae colonized Hispaniola since the Miocene amber formation but these families, which were present on Hispaniola during the period of amber formation, contain undiscovered endemic species (Penney, 1999). Some of these hypotheses are unequivocally falsifiable through the future discovery of the families in Dominican amber as has occurred with Mysmenidae [Penney, 2000*b*; the specimens described by Wunderlich (1998) are actually in Madagascan copal (Wunderlich, 2004)] and Filistatidae (Penney, 2005*b*). More recently, Penney (2008) conducted a more thorough investigation of the biogeographic origins of the Hispaniolan spider fauna, based on an integrated approach, which analysed both neontological and palaeontological data. He suggested that, on the whole, the origins were probably from South America *via* a temporary landspan rather than by overwater dispersal. It should be noted that the above examples of the application of palaeontological data to investigations of biogeography are suggestive, being based solely on comparisons of past and present distributions. More comprehensive cladistic analyses to determine how the fossil and extant species are related will be required to determine whether or not they hold any substance. We emphasize that fossil data cannot be ignored as they so often are in neontological revisionary studies that also seek to propose origins for specific groups.

Extant spider family assemblages can be indicators of climatic conditions; certain families are more common in northern temperate regions e.g. the sheet-weaving spiders (Linyphiidae), whereas others occur solely in the tropics and the southern hemisphere e.g. the net-casting spiders (Deinopidae). In Lagerstätten, which provide a large number of fossil spiders, the relative proportions of the different families can often be used to make predictions regarding the climate of the region at that point in geological time. For example, Wunderlich (1994) discussed the biogeographical relationships of the extant and fossil central European spiders to the tropical and subtropical faunas. The families Archaeidae, Deinopidae and Cyatholipidae (these may be misidentifications; Griswold, 2001) known as fossils in Baltic amber have extant species only in the tropics and

southern hemisphere. Some of the families and genera found in the fossil record of central Europe are today only found in southern Europe or are rare in central Europe; for example, Ctenizidae, Dipluridae, Leptonetidae, Hersiliidae, Oecobiidae and *Orchestina* (Oonopidae). The above assemblage points to a sub-tropical climate in central Europe during the Cenozoic (Wunderlich, 1994) (but see also Archibald & Farrell, 2003). Penney (1999, 2005*d*, 2008) and Penney & Pérez-Gelabert (2002) pointed to a high degree of similarity between the spider assemblages present on Hispaniola during the Miocene and those of today, which supports the idea of a tropical climate for the Caribbean at the time of Dominican Republic amber formation.

(1) Current work

Penney & Selden (2006*a*) provided a review of the strictly fossil spider families. At that time, 20 strictly fossil spider families (including Archaeidae which was originally described as a fossil family) had been described and the expectation was that more awaited discovery. Of these families, one (Archaeidae) had extant species discovered subsequently and it is not unreasonable to expect the same may happen with other families, highlighting the need for neontologists to consider palaeontological data when describing new higher taxa because they may already exist as fossils. Of the Palaeozoic families, none of the specimens attributed to Archaeometidae are spiders and of the remaining families all but Permarachnidae are poorly defined and in need of revision. However, at this stage it would appear that they consist solely of primitive mesothele spiders. The Mesozoic families as currently delimited are acceptable, although discovery of new material may demonstrate that *Juraraneus* belongs in Araneidae.

The majority of strictly fossil spider families described from the Cenozoic were established by A. I. Petrunkevitch, who often based his new taxa on juvenile specimens. This is the case for the families Adjutoridae, Arthrodictynidae, Inceptoridae and Insecutoridae (all from Baltic amber); the type specimens require formal systematic scrutiny before the validity of these families (including their proposed synonymies) can be determined. Ephalmatoridae and Spatiatoridae (Baltic amber), also established by Petrunkevitch have been revised by Wunderlich (1986*b*, 2004) and are currently considered valid, although the systematic affinities of the former are unclear. Wunderlich (2004) erected the families Baltsuccinidae and Protheridiidae from Baltic amber (the latter now also known from Cretaceous Lebanese amber: Wunderlich, 2008*e*), and Wunderlich (2008*e*) erected the family Pumiliopimoidae from Baltic amber and the families Praeterleptonetidae, Eopsilodercidae, Plumorsolidae, Micropalpimanidae, Burmascutidae and Salticoididae from Cretaceous ambers; these have yet to be critically assessed. The following fossil families have been synonymized with extant taxa: Acrometidae = Synotaxidae, Mithraeidae = Uloboridae, Mizaliidae = Oecobiidae (all Baltic amber); and recent unpublished data have shown that Parattidae are lycosoid spiders.

Palaeoarachnologists recognize the taxonomic subequality of fossil spiders to the Recent fauna (e.g. Eskov, 1990; Selden, 1996*a*) and accept that fossils must usually play a secondary role in phylogenetic analyses. Even the latest methods of visualization, e.g. micro-CT scanning (Penney *et al.*, 2007), cannot resolve all morphological detail of fossils, such as trichobothria, leg spines, setae, and cuticle ultrastructure. In addition, and for reasons unknown, when using this technique some amber fossils are better revealed than others. Two amber fossils that appear similar under light microscopy can provide very different qualities of image when scanned using micro-CT. Whilst the technique is a great step forward it is not perfect. However, fossils are of immense value in the construction of evolutionary trees, the next logical step in understanding the phylogenetic history of a group, once robust cladograms have been established (Selden, 1996*a*; Selden & Penney, 2001). Evolutionary or phylogenetic trees are constructed by superimposing well-supported and accepted cladograms of hypothesized phylogenetic relationships, derived from work on extant taxa, over stratigraphic data from the fossil record (Smith, 1994). Three assumptions are made when constructing these trees: (1) the cladogram is robust and provides the best available evidence for phylogenetic relationships of the taxa; (2) demonstrably monophyletic taxa have not given rise to other taxa; (3) stratigraphic range extensions should be kept to a minimum. The known ranges provided by the fossil taxa, and the subsequent range extensions (the extra stratigraphic range added to the observed range of a taxon to make the evolutionary tree concordant with the phylogenetic hypotheses) of sister taxa and ghost lineages (a branch of an evolutionary tree with no fossil data but which needs to be hypothesized after combining cladistic and biostratigraphic data) and proposed ancestral lineages (which result here from the addition of fossil metataxa), show the evolutionary history of a group over geological time. This technique, fully explained by Smith (1994) provides minimum dates for the hypothesized dichotomies, and provides a graphical representation of origination, divergence and extinction events, of taxa through geological time. The calibration of these trees using fossils can also provide useful minimum-age baseline data for investigations into conservation, convergence and divergence of genetic sequences observed in extant organisms, e.g. spider silk fibroin sequences (Gatesy *et al.*, 2001), and can falsify molecular clock estimates (Dunlop & Selden, 2009). The cladograms used here to produce the phylogenetic tree for spiders (Fig. 2) are based on Coddington & Levi (1991), with amendments, e.g. Griswold (1993), Scharff & Coddington (1997), Griswold *et al.* (1998, 1999), Ramírez (2000). Schütt (2000) suggested a number of changes to this phylogeny, based on a small number of morphological characters from seven families, but did not undertake a new cladistic analysis; her changes are not included here. Le Gleut *et al.* (2004) did not resolve convincingly the phylogeny of the Rastelloidina so no changes based on their work are incorporated. Schütt (2003) synonimized Micropholcommatidae with Anapidae, but this

was not accepted by Platnick (2004) because of the limited number of taxa included in her analysis. Our placement of Micropholcommatidae follows Coddington & Levi (1991). Wunderlich (2004) suggested many additional changes to the currently accepted spider phylogeny but these are not included here because he did not rigorously test his hypotheses and these remain to be confirmed. Ultimately, it is hoped that the Assembling the Tree of Life—Spiders project (http://research.amnh.org/atol/files/index.html) which incorporates morphological, molecular and fossil data (Penney & Selden, 2006a) will provide a robust and accurate phylogeny.

(2) Results of recent work: the phylogenetic tree

The evolutionary tree of spiders (Fig. 2) clearly illustrates the geological longevity and the early major radiations of this group and demonstrates that most extant families have been documented in the fossil record. Arachnids have used silk since at least Devonian times and, indeed, the use of silk by spiders for the capture of prey may have been the impetus for the evolution of flight in insects (Vollrath & Selden, 2007). Spiders existed long before the dinosaurs evolved and many of the spider families familiar to us today existed alongside them. Qualitative observations of all fossil spiders in conjunction with a quantitative analysis of spiders preserved only in amber (Penney *et al.*, 2003) have demonstrated that spider families passed relatively unaffected through the extinction event that eliminated the dinosaurs. The combination of their high global diversity, generalist predatory nature and their ability to enter a state of metabolic torpor in times of low food availability probably facilitated their survival (Penney & Selden, 2007).

The early Cretaceous saw the origin of flowering plants (angiosperms) and an explosive radiation of modern insect groups concurrently. The major radiations of obligate anthophilous insects probably occurred during the late Early to Late Cretaceous, because this period is consistent with the appearance of entomolophilous syndromes in Cretaceous flowers (Grimaldi, 1999). Although not all spiders weave webs, silk use for prey capture is unique to spiders and there is a great deal of variation in how they employ this strategy, which in turn helps explain their high diversity and ubiquitous nature today. The orb-web typifies spiders to scientists and laypersons alike and this architecturally complicated and highly efficient prey-capture strategy was already being employed by spiders in the early Cretaceous (Selden, 1989; Penney & Ortuño, 2006). Spiders probably evolved the ability to weave orb-webs in the Jurassic or earlier, thus allowing them to co-radiate alongside their insect prey without the need for a catch-up lag phase.

VI. CONCLUSIONS

(1) There are currently 1099 recognized fossil spider species (Dunlop, Penney & Jekel, 2009), but the taxonomic descriptions of many of these are poor when compared to current standards for extant spiders.

(2) For many of the amber specimens described by Koch & Berendt (1854) and Menge (1854) the whereabouts of the holotypes is unknown and most must now be considered lost. For most of their species the descriptions are inadequate for designating neotypes.

(3) Alexander Petrunkevitch published a great deal of work on all fossil arachnids and described many fossil spiders during the mid-20th Century. Some of his taxonomic practices were unacceptable by modern standards. For example, on several occasions he erected new fossil spider families based on a single specimen of a poorly preserved, juvenile spider. Fortunately, his holotypes are available for study, although they are widely dispersed in various museums.

(4) Many new fossil spider species (e.g. from Dominican and Baltic ambers) have been described in non-peer-reviewed journals and this practice continues to cause problems in the fossil spider literature (see discussions in Harms & Dunlop, 2009).

(5) Whilst many fossil species (often placed in new fossil genera) described recently may be misidentified, their family identifications are, on the whole, most probably correct. In this respect, we have confidence in the minimum dates for our evolutionary tree (Fig. 2).

(6) It is only within the last 25 years that our knowledge of pre-Cenozoic spiders has increased substantially, extending the range of many extant spider families to before the end-Cretaceous extinction event that eliminated the dinosaurs and many other groups. New Mesozoic fossil localities are still being discovered and many are yielding interesting spider fossils. Some have already been described, whereas research on others is currently in progress.

(7) As the data set of fossil spiders is refined as a result of new taxonomic and systematic studies and is updated to conform to current hypotheses for Recent Araneae, it will become more useful to both palaeontologists and neontologists, including ecologists, biogeographers, and other biologists.

VII. APPENDIX: INSTITUTIONAL ABBREVIATIONS

BMNH: The Natural History Museum, London; MCZ: Museum of Comparative Zoology, Harvard; MHNA: Museum d'Histoire Naturelle, Autun; UCM: University of Colorado Museum; YPM: Yale Peabody Museum.

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X. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1: Table of known fossil spider localities, with stratigraphic position, probable age, sedimentology, palaeoenvironment, araneofauna, and main references.

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