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Assembling the Tree of Life—Phylogeny of Spiders: a review of the strictly fossil spider families

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Abstract: The project Assembling the Tree of Life (AToL)—Phylogeny of Spiders is an ambitious, collaborative, six-year project, which aims to construct a robust cladogram for all spider families. The resulting phylogeny will be based on morphological, molecular, behavioural and palaeontological data. Fossil spiders are not considered in current systematic catalogues. As a first step to compiling the required palaeontological data for the AToL project, this paper reviews all previously described fossil spider families. To date, twenty strictly fossil spider families have been described. One has subsequently had extant species discovered (Archaeidae), others have been synonymized with extant families (Acrometidae, Adjutoridae, Arthrodictynidae, Mithraeidae, Mizaliidae), some are valid taxa (Permarachnidae, Juraraneidae, Lagonomegopidae, Baltsuccinidae, Ephalmatoridae, Insecutoridae, Protheridiidae, Spatiatoridae) and others are in need of revision (Arthrolycosidae, Arthromygalidae, Pyritaraneidae, Inceptoridae, Parattidae). None of the fossil specimens attributed to Archaeometidae are spiders.

Key words: amber, Araneae, fossil record, palaeontology

Introduction

The project Assembling the Tree of Life (AToL)—Phylogeny of Spiders is an ambitious six-year project funded by the US National Science Foundation (NSF), which aims to construct a robust cladogram for all spider families (Hormiga *et al*. 2004; http://research.amnh.org/atol/files/index.html). The resulting phylogeny will be inferred from a character matrix of unprecedented dimensions (>20 million cells) and will consist of morphological, molecular, behavioural and palaeontological data. Including fossils in such a large-scale and multi-disciplinary approach sets an important precedent for future projects on other groups. Although taxonomically subequal to Recent specimens, some fossils, particularly those in amber, are often preserved with life-like fidelity. Strictly fossil families may share character states with extant families and help resolve their correct placement in the resulting phylogeny. The fossil taxa from extinct families will be scored as far as possible and included in the data matrix. More importantly, fossils form a means by which the final tree can be calibrated over geological time, by providing minimum dates for the observed phylogenetic dichotomies. The age–clade congruence of the tree can be used to provide additional support for the final phylogeny.

As a first step to compiling the required palaeontological data, this paper reviews all previously described strictly fossil spider families. Early reviews of the spider fossil record (Scudder 1886, 1891, Petrunkevitch 1955) were based on different classification schemes to that which exists at present. In addition, the taxonomy of many earlier workers clearly warrants reassessment (see discussion in Selden 1993a). Since these earlier works, many more fossil spiders have been described and recent reviews (e.g. Selden 1993b, 1996, Selden, Penney in prep.) included fossils from both extant and extinct families but at most provided 'first and last' occurrence data, and thus

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did not provide complete species listings for each family. The aim here is to update these works by presenting a complete list of all species (including holotype repository data) originally placed in strictly fossil spider families and by commenting on their current taxonomic status.

The Strictly Fossil Spider Families

Occasionally, fossil spiders are described that do not show enough features to assign them to extant families, yet new genera are erected e.g. *Palaeouloborus* Selden, 1990, *Macryphantes* Selden, 1990, *Attercopus* Selden, Shear, 1991 (in Selden *et al*. 1991), *Triassaraneus* Selden, 1999 (in Selden *et al*. 1999) and *Argyrarachne* Selden, 1999 (in Selden *et al*. 1999). The temptation might be to assign these taxa to new fossil families based on plesiomorphic characters as was done for example by Eskov (1984) with the family Juraraneidae. Because of a lack of autapomorphic features, the temptation then is to synonymize these metataxa (sensu Smith 1994) with the closest available extant taxa, thus generating an awkward circular argument, not to mention unnecessary feeble names. For geologically old fossils, synonymizing these metataxa with extant taxa will increase the hypothesized range extensions for related taxa when constructing evolutionary trees (see Penney *et al*. 2003: Fig. 2), thus reducing the overall parsimony of the tree, whereas metataxa can be placed as 'ancestral' lineages. New material examined in light of previously described specimens may demonstrate that previously unplaced genera belong in extant families, e.g. *Palaeouloborus* belongs in Uloboridae and *Macryphantes* in Tetragnathidae (Selden, Penney 2003). Thus, the authors are happy to retain the currently unplaced (in terms of family) fossil spider taxa as *incertae sedis* within the systematic limits of their original taxonomic assignment.

Abbreviations: AMNH = American Museum of Natural History, New York; BA = Baltic amber; BSPHGM = Bayerische Staatssammlung für Paläontologie und Historische Geologie, Münich; CCU = Crosby Collection of Cornell University; Fl = Florissant Shales, Colorado; G = Institute and Museum of Geology and Palaeontology of the Georg-August-University, Göttingen; LUM = Lille University Museum; MCZ = Museum of Comparative Zoology, Harvard; MfN = Museum für Naturkunde Institut für Paläontologie, Humboldt Universität zu Berlin; MGUH = Mineralogical and Geological Museum, Copenhagen; NHM = Natural History Museum, London; NMP = Prague National Museum; PCFK = personal collection of F. Kernegger, Hamburg; PCJW = personal collection of Jörg Wunderlich, Hirschberg-Leutershausen; PIN = Palaeontological Institute of the Russian Academy of Sciences, Moscow; PIP = Palaeontological Institute, Paris; SMUC = Sedgwick Museum, University of Cambridge, UK; UMMP = University of Michigan Museum of Paleontology; YPM = Peabody Museum of Yale University; * = type species of the genus.

Palaeozoic Families

Remarks: All verifiable Palaeozoic spiders belong to the suborder Mesothelae or show more plesiomorphic character states (Eskov, Selden 2005). A monograph on Palaeozoic spiders is in preparation by PAS, in which the taxonomy of the numerous genera used for Palaeozoic mesotheles will be clarified. Therefore, the taxonomic status of these families has yet to be challenged.

Family ARCHAEOMETIDAE Petrunkevitch, 1949

(Fig. 1)

Age: Carboniferous (Westphalian B–Westphalian C)

Current status: Not valid, the fossils are not spiders

Species originally included: *Archaeometa nephilina* Pocock, 1911* (Fig. 1), Coseley, Dudley, UK (holotype sex not mentioned, originally described from the personal collection of Mr W. Egginton, current specimen location NHM In. 31259); *A.*? *devonica* Størmer, 1976, Alken-an-

der-Mosel, Germany (holotype sex unknown SMF); *Arachnometa tuberculata* Petrunkevitch, 1949*, Coseley, Dudley, UK (holotype sex not mentioned NHM I. 13917); *Eopholcus pedatus* Fritsch, 1904*, pyrite of Nýřaný, Czech Republic (holotype sex not mentioned NMP CGH 3184, Inv. 835). Each of the above species is known from a single specimen.

Remarks: Petrunkevitch's (1949, p. 107) diagnosis of this family – 'Arachnomorph spiders with prograde legs, and segmented abdomen' seems bizarre, considering the former character is widespread in araneomorphs [arachnomorphs] and the latter is plesiomorphic in Araneae and lost in Opisthothelae. The diagnosis and composition of the family was repeated in the *Treatise* (Petrunkevitch 1955), and no formal changes have yet been made. However, Selden and Shear studied *A. nephilina* and *A.? devonica*, and concluded (Selden *et al*. 1991) that they are not spiders, let alone araneomorphs. Subsequent study of *Arachnometa* and *Eopholcus* (PAS, unpublished) has indicated that these, too, show no diagnostic characters of Araneae, and the latter genus shows none of the diagnostic characters of the family.

Family ARTHROLYCOSIDAE Fritsch, 1904

Age: Carboniferous (Westphalian B)–Permian (Capitanian)

Current status: Valid, but poorly defined and in need of revision

Species currently included: *Arthrolycosa antiqua* Harger, 1874* (holotype sex indeterminate YPM No. 161), Francis Creek Shale, Mazon Creek, USA; *A. danielsi* Petrunkevitch, 1913 (holotype sex not mentioned, originally described from the personal collection of Mr L.E. Daniels, current specimen location UMMP 7219), Francis Creek Shale, Mazon Creek, USA; *Eocteniza silvicola* Pocock, 1911*, Coseley, Dudley, UK (holotype sex not mentioned, originally described from the personal collection of Mr W. Egginton, current specimen location NHM In. 31245). See also remarks under Arthromygalidae.

Remarks: Considered a family in the suborder Mesothelae by Petrunkevitch (1949: 275), and accepted by Eskov, Selden (2005) who described an isolated carapace, which they assigned to *Arthrolycosa*. Petrunkevitch rediagnosed this family as mesotheles with a distinct eye tubercle; modern mesotheles have an eye tubercle, so the family is poorly defined.

Family ARTHROMYGALIDAE Petrunkevitch, 1923

(Fig. 3)

Age: Carboniferous (Westphalian B–Stephanian)

Current status: Valid, but poorly defined and in need of revision

Species currently included: *Arthromygale fortis* (Fritsch, 1904)*, Rakovnik, Czech Republic (holotype sex not mentioned NMP CGH 1937, Inv. 804); *A. beecheri* (Fritsch, 1904), Rakovnik, Czech Republic (holotype sex not mentioned NMP CGN 1939, Inv. 805); *Protocteniza britannica* Petrunkevitch, 1949*, Coseley, Dudley, UK (holotype sex not mentioned NHM In. 14015); *Protolycosa anthracophila* Roemer, 1866, Upper Silesia (holotype sex unknown; this specimen was in Wrocław but is now lost [since WWII]); *P. cebennensis* Laurentiaux-Vieira, Laurentiaux, 1963, couche Le Pin, La Grand'Combe, Cévennes, France (holotype sex unknown LUM); *Palaranea borassifoliae* Fritsch, 1873*, Bohemia, Czech Republic (holotype sex not mentioned NMP); *Geralycosa fritschi* Kusta, 1888* (Fig. 3), Rakovnik, Czech Republic (holotype sex not mentioned NMP CGH 1943 and 1945, Inv. 811); *Kustaria carbonaria* (Kusta, 1888)*, Rakovnik, Czech Republic (holotype sex not mentioned NMP CGH 1933, Inv. 806); *Rakovnicia antiqua* Kusta, 1884*, Rakovnik, Czech Republic (holotype sex not mentioned NMP CGH 610, Inv. 810); *Eolycosa lorenzi* Kusta, 1885*, Rakovnik, Czech Republic (holotype sex not mentioned NMP CGH 1941 and 1948, Inv. 809).

Species no longer included: *Palaeocteniza crassipes* Hirst, 1923*, Rhynie Chert, Scotland (Devonian) (holotype sex not mentioned NHM In. 24670) (=?trigonotarbid exuvium).

Remarks: Considered a family in the suborder Mesothelae (e.g. Petrunkevitch 1949: 275). Petrunkevitch (1913) referred all Carboniferous spiders to Arthrolycosidae Fritsch, 1904 but, in 1923, he erected Arthromygalidae to accommodate the Carboniferous taxa listed above, and distinguished them from Arthrolycosidae by their eye arrangement. Petrunkevitch (1953) placed *Palaeocteniza crassipes* and *Eolycosa lorenzi* in 'Aranei incertae sedis', but in the *Treatise* (Petrunkevitch 1955) he listed both under Arthromygalidae, the former doubtfully. Subsequent work (Selden *et al*. 1991) has shown that *Palaeocteniza crassipes* Hirst, 1923 is most likely a moulted exoskeleton of a juvenile trigonotarbid and hence removed it from Araneae. The other genera can mostly be considered as spiders belonging to Mesothelae, but study of the specimens (PAS, unpublished) shows that Petrunkevitch's eye characters are quite fictitious.

Family PERMARACHNIDAE Eskov, Selden, 2005

Age: Permian (Cisuralian)

Current status: Valid

Species currently included: *Permarachne novokshonovi* Eskov, Selden, 2005*, Koshelevka Formation, Russia (holotype ?exuvium part and counterpart, PIN 4909/12).

Remarks: Easily distinguished from all other mesotheles by the presence of an elongated, cylindrical, multisegmented, distal article of one of the spinnerets (Eskov, Selden 2005).

Family PYRITARANEIDAE Petrunkevitch, 1953

(Fig. 2)

Age: Carboniferous (Westphalian B–Westphalian C)

Current status: Valid, but poorly defined and in need of revision

Species currently included: *Dinopilio parvus* Petrunkevitch, 1953, Chislet Colliery, Canterbury, UK (holotype sex not mentioned NHM In. 37101); *D. gigas* Fritsch, 1904* (Fig. 2), Rakovnik, Czech Republic (holotype sex not mentioned NMP CGH 1949, Inv. 816); *Pyritaranea tubifera* Fritsch, 1899*, Nýřaný, Czech Republic (holotype sex not mentioned NMP CGH 3170, Inv. 775).

Remarks: Petrunkevitch (1953) erected this family for supposed araneomorphs with laterigrade legs (cf. Archaeometidae, above) and segmented abdomens. The former character is widespread in Araneae, whilst the latter is plesiomorphic in spiders and would suggest Mesothelae. More recent study of these specimens (PAS, unpublished) indicates that *Dinopilio parvus* and *Pyritaranea tubifera* could be spiders but are too poorly preserved to assign to family, whilst *D. gigas* is most likely a large mesothele.

Mesozoic Families

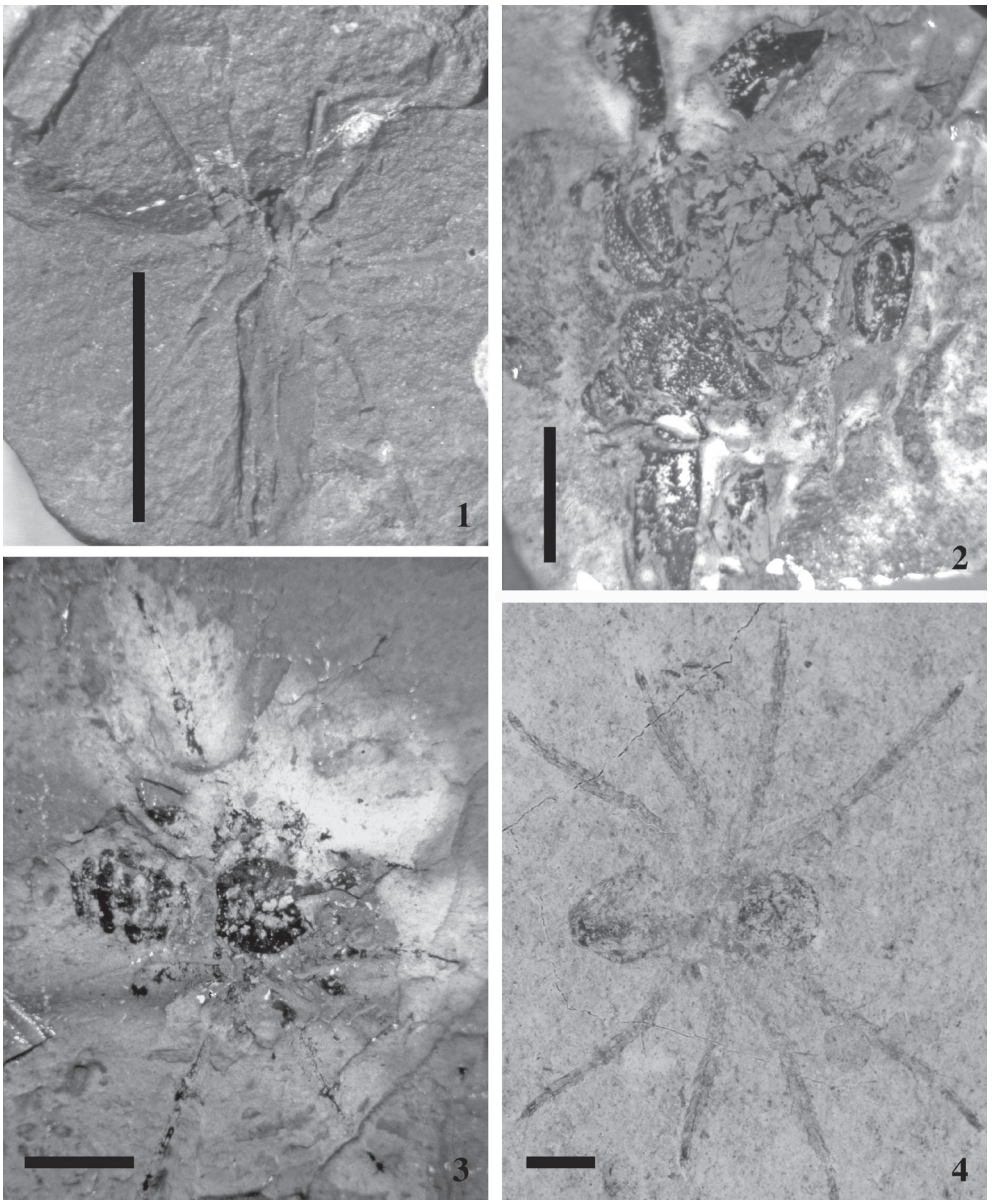
Family JURARANEIDAE Eskov, 1984

Age: Jurassic (Middle?)

Current status: Valid, but possibly synonymous with Araneidae

Species currently included: *Jurararaneus rasnitsyni* Eskov, 1984*, Buryat, Siberia (holotype, male part and counterpart, PIN 3000/3000).

Remarks: Wunderlich (1986: 95, 138) proposed that this family might be synonymous with Araneidae, but did not formally synonymize them. The original diagnosis of the family was not



Figs 1-4. Holotypes of non-amber fossil spiders: 1 – *Archaeometa nephilina* Pocock, 1911 (Archaeometidae); 2 – *Dinopilio gigas* Fritsch, 1904 (Pyritaraneidae); 3 – *Geralycosa fritschi* Kusta, 1888 (Arthromygalidae); 4 – *Parattus resurrectus* Scudder, 1890 (Parattidae). Scale lines: approximately 1 mm.

based on unique apomorphies but on a combination of morphological characters found in other araneoid families (Eskov 1984).

Family ARCHAEIDAE Koch, Berendt, 1854

Age: Jurassic (Callovian–Kimmeridgian)–Recent

Current status: Valid

Species originally included (i.e., when known from fossil species only): *Archaea hyperoptica*

Menge, 1854 (holotype female lost, possibly in MfN [Keilbach 1982: 180]); *A. incompta* Menge, 1854 (holotype female lost); *A. laevigata* Koch, Berendt, 1854 (holotype juvenile MfN MB.A 1083); *A. paradoxa* Koch, Berendt, 1854* (holotype male/female lost); *A. sphinx* Menge, 1854 (holotype juvenile lost); *Baltarchaea conica* (Koch, Berendt, 1854)* (holotype juvenile lost).

Remarks: Although no longer a strictly fossil family Archaeidae is included here because it was first described from fossils in Baltic amber, with extant species discovered in Madagascar and South Africa a quarter of a century later (Pickard-Cambridge 1881). Wunderlich (2004: 780) considered *A. incompta*, *A. laevigata* and ?*A. sphinx* to be synonyms of *A. paradoxa*. *A. hyperoptica* was placed as the type species of *Eoarchaea* Forster, Platnick, 1984 (not accepted by Eskov 1992, but accepted by Wunderlich 2004). *A. conica* was transferred to the new genus *Baltarchaea* Eskov, 1992 in the family Mecysmaucheniidae by Eskov (1992). This genus was placed in Archaeidae: Archaeinae by Wunderlich (2004). Fossil species are also known in Cretaceous amber from Burma (Penney 2003), from the Jurassic of Kazakhstan (Eskov 1987), and the family has been recorded in Tertiary amber from Paris (Penney 2006a). Wunderlich (2004) described new fossil taxa from Baltic amber and reported the presence of this family in Eocene amber from the Ukraine (Rovno).

Family LAGONOMEGOPIDAE Eskov, Wunderlich, 1995

Age: Cretaceous (Aptian–Campanian)

Current status: Valid

Species currently included: *Burlagonomegops eskovi* Penney, 2005*, Burmese amber (holotype juvenile AMNH Bu–707, paratype juvenile AMNH Bu–1353); *B. alavensis* Penney, 2006, Spanish amber (holotype juvenile MCNA 8635 [CRLV 03]); *Grandoculus chemahawinensis* Penney, 2004*, Canadian amber (holotype juvenile, MCZ A 5000); *Lagonomegops americanus* Penney, 2005, New Jersey amber (holotype juvenile, AMNH NJ–556 [KL–297]); *L. sukatchevae* Eskov, Wunderlich, 1995*, Siberian amber (holotype juvenile, PIN 3311/564, location currently unknown, K. Eskov, pers. comm. 2004).

Remarks: This family is currently known only from juvenile specimens and is characterized by having cheliceral peg teeth and large eyes situated antero-laterally. *G. chemahawinensis* has such an eye arrangement, but is sufficiently different from the other genera in many other features that it may belong to a new fossil family (Penney 2004).

Cenozoic Families

Family ACROMETIDAE Wunderlich, 1979

Age: Tertiary (Eocene)

Current status: Not valid, a synonym of Nesticidae or Synotaxidae

Species originally included: *Acrometa cristata* Petrunkevitch, 1942*, BA (holotype male NHM In. 18724 [Klebs 481, No. 13408], four paratype males NHM In. 18713 [Klebs 467, No. 13430], In. 18728 [Klebs 485, No. 13458], In. 18750 [Klebs 508, No. 13453], In. 18752 [Klebs 510, No. 13461]; *A. samlandica* (Petrunkevitch, 1942), BA (holotype juvenile female NHM In. 18943, one exuvium NHM In. 17629); *A. minutum* (Petrunkevitch, 1942), BA (holotype juvenile SMUC No. C 6650); *A. robustum* (Petrunkevitch, 1942), BA (holotype juvenile CCU No. 8); *A. setosus* (Petrunkevitch, 1942), BA (holotype male NHM In. 18118); *A. succini* (Petrunkevitch, 1942), BA (holotype female NHM In. 18943); *Anandrus inermis* (Petrunkevitch, 1942), BA (holotype male NHM In. 18743 [Klebs 501, No. 13441]; *A. infelix* (Petrunkevitch, 1950)*, BA (holotype male MCZ 7002); *A. quaesitus* (Petrunkevitch, 1958), BA (holotype male MfN [zoology] no number assigned); *A. redemptus* (Petrunkevitch, 1958), BA (holotype male MGUH

9995); *Cornuanandrus maior* Wunderlich, 1986, BA (holotype male PCJW no number assigned): *Pseudoacrometa gracilipes* Wunderlich, 1986, BA (holotype male BSPHGM no number assigned, paratype male PCJW no number assigned).

Remarks: *Acrometa* Petrunkevitch, 1942 and *Anandrus* Menge, 1856 (sub *Elucus* Petrunkevitch, 1942) were originally placed in Araneidae (Metinae) and Theridiosomatidae respectively by Petrunkevitch (1942). Petrunkevitch (1958) placed both genera in Araneidae. Wunderlich (1979) considered *Acrometa* a tetragnathid and to be synonymous with the extant genera *Metella* Fage, 1931, *Pimoa* Chamberlin, Ivie, 1943 and *Louisfagea* Brignoli, 1971. This synonymy was rejected by Brignoli (1979) and *Metella* and *Louisfagea* are now considered junior synonyms of *Pimoa* (Pimoidae) (e.g. Platnick 2006). Wunderlich (1986) revised *Acrometa* and *Anandrus* and synonymized *Theridiometa* Petrunkevitch, 1942, *Liticen* Petrunkevitch, 1942, *Eogonatium* Petrunkevitch, 1942 and *Viocurus* Petrunkevitch, 1958 with *Acrometa* (Wunderlich 1986: 131). Wunderlich (1986: 124) suggested Acrometidae might be closely related to Nesticidae or Malkaridae. The family was considered a synonym of the former by Eskov, Marusik (1992) and of Synotaxidae (separated from Theridiidae by Forster *et al*. 1990) by Wunderlich (2004: 1195) based on the structure of the male pedipalp. Wunderlich (2004: 1822) reported the presence of *A. cristata* in Eocene amber from the Ukraine (Rovno).

Family ADJUTORIDAE Petrunkevitch, 1942

(Fig. 5)

Age: Tertiary (Eocene)

Current status: Not valid, synonymous with Zodariidae and Sparassidae

Species originally included: *Adjutor mirabilis* Petrunkevitch, 1942* (Fig. 5), BA (holotype juvenile female NHM In. 18945); *A. deformis* Petrunkevitch, 1958, BA (holotype juvenile female PIP no number assigned); *Adjunctor similis* Petrunkevitch, 1942*, BA (holotype juvenile female NHM In. 18085); *Admissor aculeatus* Petrunkevitch, 1942*, BA (holotype juvenile female NHM In. 18946).

Remarks: Lehtinen (1967: 397) proposed araneoid affinities for this family based on the figures and descriptions of Petrunkevitch, all of which were based on juvenile specimens. Wunderlich (1984), without elaboration, placed the subfamily Adjutorinae in Zodariidae: ?Zodariinae (see also Wunderlich 1986: 23, 2004: 1702), and the subfamily Adjunctorinae in Sparassidae: Eusparassinae (see also Wunderlich 1986: 29, 2004: 1702). *Adjunctor* Petrunkevitch, 1942 is not a junior synonym of *Sosybius* Koch, Berendt, 1854 as proposed by Wunderlich (1986: 29) (Wunderlich 2004: 1702).

Family ARTHRODICTYNIDAE Petrunkevitch, 1942

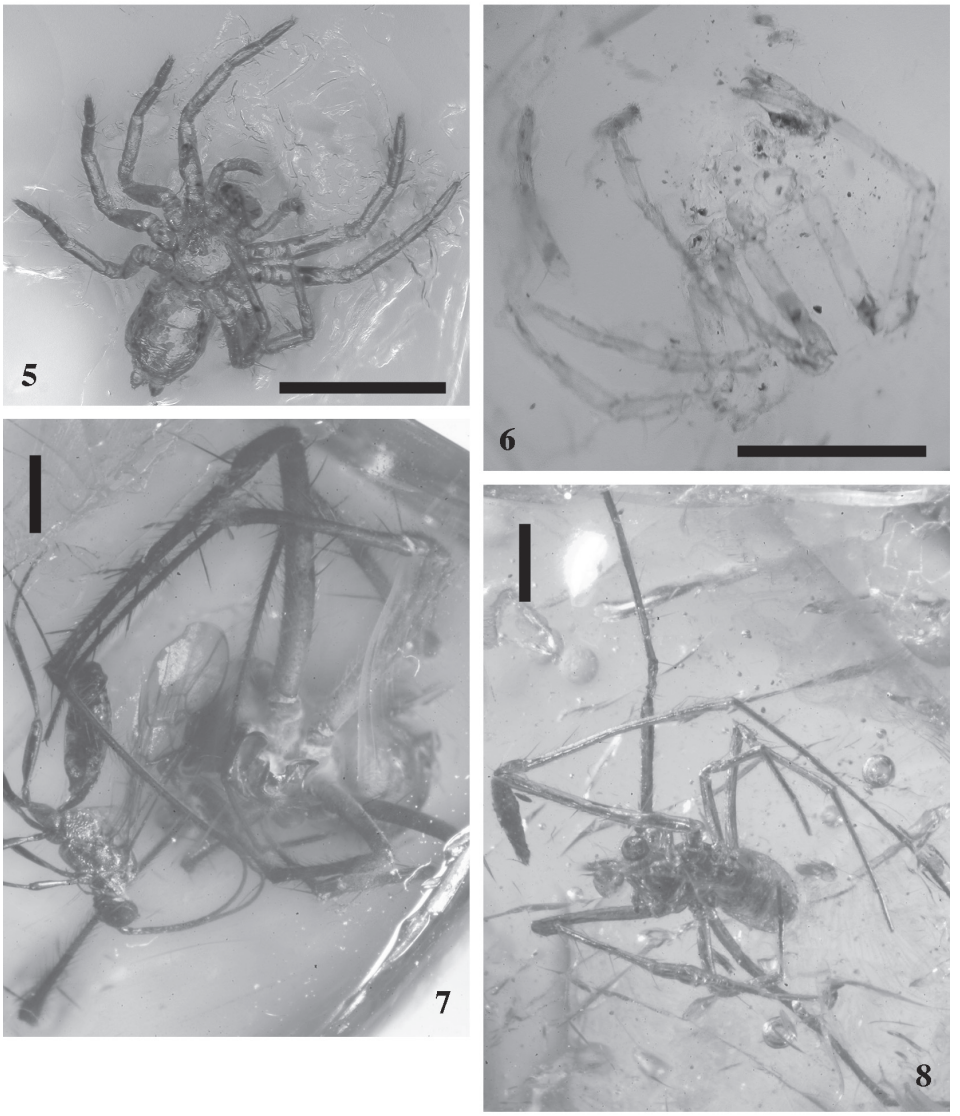
(Fig. 6)

Age: Tertiary (Eocene)

Current status: Not valid, synonymous with Dictynidae

Species originally included: *Arthrodictyna segmentata* Petrunkevitch, 1942* (Fig. 6), BA (holotype juvenile NHM In. 18950).

Remarks: The holotype and only known specimen is juvenile, incomplete and poorly preserved (Petrunkevitch 1942). Based on the figures and description by Petrunkevitch (1942), Lehtinen (1967: 397) considered the correct placement of this taxon problematic. The family was synonymized with Dictynidae by Wunderlich (1984); see also Wunderlich (1986: 24). This synonymy was considered tentative by Wunderlich (2004: 1428). A formal redescription of the type material is in preparation by DP.



Figs 5-8. Holotypes of amber fossil spiders: 5 – *Adjutor mirabilis* Petrunkevitch, 1942 (Adjutoridae); 6 – *Arthrodictyna segmentata* Petrunkevitch, 1942 (Arthrodictynidae); 7 – *Baltsuccinus flagellaceus* Wunderlich, 2004 (Baltsuccinidae); 8 – *Praetheridion fleissneri* Wunderlich, 2004 (Protheridiidae). Scale lines: approximately 1 mm.

Family BALTSUCCINIDAE Wunderlich, 2004

(Fig. 7)

Age: Tertiary (Eocene)

Current status: Valid, but warrants independent assessment (original publication not peer-reviewed)

Species currently included: *Baltsuccinus flagellaceus* Wunderlich, 2004* (Fig. 7), BA (holotype male PCJW F40/BB/AR/BAL; *B. similis* Wunderlich, 2004, BA (holotype male G 359).

Remarks: Placed in the Araneoidea, but its systematic position within this superfamily is

unclear (Wunderlich 2004: 1130). The original diagnosis was primarily a list of plesiomorphic characters. A diagnostic apomorphy may be the bipartite paracymbium with a large, heavily sclerotized, trough-shaped portion and a separate long, slender setose branch (Wunderlich 2004).

Family EPHALMATORIDAE Petrunkevitch, 1950

Age: Tertiary (Eocene)

Current status: Valid

Species currently included: *Ephalmator bitterfeldensis* Wunderlich, 2004, BA (Bitterfeld) (holotype male MfN 569); *E. calidus* Wunderlich, 2004, BA (holotype male PCFK 8/38); *E. debilis* Wunderlich, 2004, BA (holotype male PCJW F337/BB/AR/EPH); *E. distinctus* Wunderlich, 2004, BA (holotype male PCJW F338/BB/AR/EPH, paratype male PCJW F592/BB/AR/EPH); *E. ellwangeri* Wunderlich, 2004, BA (holotype male PCJW F557/BB/AR/EPH); ?*E. eximius* Petrunkevitch, 1958, BA (holotype juvenile female MGUH 9988); *E. fossilis* Petrunkevitch, 1950*, BA (holotype male MCZ 7882, paratype male MCZ 7188); *E. kerneggeri* Wunderlich, 2004, BA (holotype male PCFK 196/94); *E. petrunkevitchi* Wunderlich, 2004, BA (*Eophalmator* a lapsus calami) (holotype male PCJW F322/BB/AR/EPH); *E. ruthildae* Wunderlich, 2004, BA (holotype male PCJW F321/BB/AR/EPH, paratype male F336/BB/AR/EPH); *E. trudis* Wunderlich, 2004, BA (holotype male PCJW F339/BB/AR/EPH, three paratype males in a single piece of amber F340/BB/AR/EPH); *E. turpiculus* Wunderlich, 2004, BA (holotype male PCJW F325/BB/AR/EPH).

Remarks: Wunderlich (1986: 26) provided a revised diagnosis of this monogeneric family and Wunderlich (2004: 1559) revised Ephalmatoridae suggesting that *E. eximius* Petrunkevitch, 1958, described from a juvenile, was misplaced in this family. Unfortunately, Wunderlich (2004) did not provide a distinct diagnosis based on autapomorphic characters, but gave a combined diagnosis and description, which was based on the combination of a large number of different characters. Lehtinen (1967: 397) was unable to place this family, but Wunderlich (2004) proposed that it might be most closely related to Corinnidae, Zodariidae, Nicodamidae or Chummidae. The only known female specimen from this family was described, but not named by Wunderlich (2004: 1570).

Family INCEPTORIDAE Petrunkevitch, 1942

Age: Tertiary (Eocene)

Current status: Not valid, possibly synonymous with Agelenidae

Species originally included: *Inceptor aculeatus* Petrunkevitch, 1942*, BA (holotype juvenile CCU number 5); *I. dubius* Petrunkevitch, 1946, BA (holotype female AMNH 26267).

Remarks: The original description of this family was based on a single juvenile specimen with no unusual outstanding features. Lehtinen (1967: 397) was unable to place this family, but Wunderlich (1984) synonymized it with Agelenidae: Ageleninae. Wunderlich (1986) retained this view but suggested these fossils may also have affinities with Zodariidae. This family was not mentioned by Wunderlich (2004) and is in need of revision.

Family INSECUTORIDAE Petrunkevitch, 1942

Age: Tertiary (Eocene)

Current status: Valid, but possibly synonymous with Pisauridae

Species currently included: *Insecutor aculeatus* Petrunkevitch, 1942*, BA (holotype juvenile female NHM In. 18741 [Klebs 499, No. 13456], paratype juvenile/?female NHM In. 18723 [Klebs 480, No. 13447]); *I. mandibulatus* Petrunkevitch, 1942, BA (holotype juvenile female NHM In. 18742 [Klebs 500, No. 13456], paratype juvenile female NHM In. 18721 [Klebs 478,

No. 13434]); ?*I. pecten* Wunderlich, 2004, BA (holotype male PCJW F644/BB/AR); *I. rufus* Petrunkevitch, 1942, BA (holotype juvenile female NHM In. 18123) ?*I. spinifer* Wunderlich, 2004, BA (holotype male PCJW F642/BB/AR, paratype male PCJW F643/BB/AR).

Remarks: Petrunkevitch (1942) considered this family most closely related to Pisauridae. Additional specimens were described/mentioned by Petrunkevitch (1956, 1958), including a mature male of *I. mandibulatus* (AMNH 26258: 2), but its conspecificity is uncertain (Wunderlich 2004: 1526). Lehtinen (1967: 397) was unable to place this family, but Wunderlich (1984, 1986: 25) synonymized it with Agelenidae: Ageleninae and Wunderlich (2004: 1524) provided a revised diagnosis, without discernable autapomorphies and proposed that it might be synonymous with Pisauridae, but nonetheless maintained it as a separate family. The males described by Wunderlich (2004) were only tentatively placed in *Insecutor*. Wunderlich (2004: 1525) suggested that *Thyelia* Koch, Berendt, 1854 may be a senior synonym of *Insecutor* Petrunkevitch, 1942 but was unable to locate the type material of Koch and Berendt required to confirm this. The systematic status of this family is unclear.

Family MITHRAEIDAE Koch, Berendt, 1854

Age: Tertiary (Eocene)

Current status: Not valid, synonymous with Uloboridae

Species originally included: *Androgeus militaris* Koch, Berendt, 1854, BA (holotype male MfN MB.A 1111 [cabinet P1287, drawer 115]); *A. triqueter* Koch, Berendt, 1854*, BA (holotype male MfN MB.A 1112 [cabinet P1287, drawer 115]).

Remarks: Petrunkevitch (1955: 152) was unable to place *Androgeus* Koch, Berendt, 1854 in any known family, but later considered Mithraeidae to be synonymous with Uloboridae (Petrunkevitch 1958). Wunderlich (1986: 27) synonymized *Androgeus* with the extant uloborid genus *Hyptiotes* Walckenaer, 1837 and transferred *A. militaris* to *Eomysmena* Petrunkevitch, 1942 (Theridiidae).

Family MIZALIIDAE Thorell, 1870

Age: Tertiary (Eocene)

Current status: Not valid, synonymous with Oecobiidae

Species originally included: *Mizalia rostrata* Koch, Berendt, 1854*, BA (holotype male lost, not found in collection of MfN). *M. truncata* Menge, 1854, BA (holotype sex and location unknown).

Remarks: The family was erected for the genus *Mizalia* Koch, Berendt, 1854, which had originally been placed in Theridiidae. The only species formally listed in this family by Thorell (1870) was *M. rostrata*. Some other species listed in *Mizalia* by Koch, Berendt (1854) had been transferred from this genus by Menge (1854) prior to the erection of the new family. Petrunkevitch (1955: 152) was unable to place *Mizalia* Koch, Berendt, 1854 in any known family. Mizaliini was considered a tribe in Oecobiidae: Urocteinae by Wunderlich (1986) and as a subfamily of Oecobiidae by Wunderlich (2004: 831). Wunderlich (1986) synonymized *Paruroctea* Petrunkevitch, 1942 with *Mizalia* and Wunderlich (2004) described the new Baltic amber species *M. gemini* Wunderlich, 2004 and *M. spirembolus* Wunderlich, 2004.

Family PARATTIDAE Petrunkevitch, 1922

(Fig. 4)

Age: Tertiary (Eocene)

Current status: Valid, but probably synonymous with a lycosoid family

Species currently included: *Parattus evocatus* Scudder, 1890, Fl (holotype female MCZ Scudder Coll. No. 12005 [renumbered 66]); *P. latitatus* Scudder, 1890, Fl (holotype sex not mentioned MCZ Scudder Coll. No. 9823 [renumbered 67]); *P. oculatus* Petrunkevitch, 1922, Fl (holotype female MCZ Scudder Coll. No. 118); *P. resurrectus* Scudder, 1890* (Fig. 4), Fl (holotype male MCZ Scudder Coll. No. 1081 [renumbered 64], paratype female MCZ Scudder Coll. No. 8459 and 8282 [renumbered 65]).

Remarks: Because the specimens are poorly preserved, this ecribellate, entelegyne family was originally diagnosed by the 'unusual' eye arrangement as follows: eyes round, in two rows of four, anterior subequal and fairly equidistant, posterior eyes considerably smaller, with PME between and slightly behind the AME (see Petrunkevitch 1922: Fig. 19). Petrunkevitch did not consider that taphonomic processes may have may have caused these specimens to be preserved in a manner requiring a careful interpretation of the eye arrangement. Re-examination of the type species demonstrated that what Petrunkevitch considered to be the anterior eyes are actually the posterior eyes and vice versa. Although currently considered a valid family, these spiders are actually lycosoids; a revision is in preparation.

Family PROTHERIDIIDAE Wunderlich, 2004

(Fig. 8)

Age: Tertiary (Eocene)

Current status: Valid, but warrants independent assessment (original publication not peer-reviewed)

Species currently included: *Praetheridion fleissneri* Wunderlich, 2004* (Fig. 8), BA (holotype male PCJW F42/BB/AR/PRO); *Protheridion bitterfeldensis* Wunderlich, 2004, BA (Bitterfeld) (holotype male PCJW F250/BB/AR/PRO); *P. detritus* Wunderlich, 2004, BA (holotype male PCJW F44/BB/AR/PRO); *P. obscurum* Wunderlich, 2004, BA (holotype male PCJW F252/BB/AR/PRO); *P. punctatum* Wunderlich, 2004, BA (holotype male PCJW F251/BB/AR/PRO); *P. tibialis* Wunderlich, 2004*, BA (holotype male PCJW F38/BB/AR/PRO).

Remarks: Wunderlich (2004: 1134) was unsure of the correct systematic placement of this family but suggested it might be most closely related to Theridiidae, based on leg autotomy (coxa–trochanter), palpal structure and the presence of a tarsal comb on leg 4.

Family SPATIATORIDAE Petrunkevitch, 1942

Age: Tertiary (Eocene)

Current status: Valid

Species currently included: *Spatiator praeceps* Petrunkevitch, 1942*, BA (holotype female NHM In. 18760 [Klebs 518, no. 3761], an additional male NHM In. 18761 [Klebs 519, no. 3764]).

Species no longer included: *Adorator brevipes* Petrunkevitch, 1942, BA (holotype male NHM In. 18716 [Klebs 474, No. 13455]); *A. samlandicus* Petrunkevitch, 1942, BA (holotype male NHM In. 18144) (=Zodariidae).

Remarks: Wunderlich (1984) placed Spatiatorini as a tribe in Palpimanidae *s.l.* Stenochilinae, but Wunderlich (1986: 21) considered it a valid family and provided a revised diagnosis. Spatiatorids are easily identifiable by the following combination of characters: carapace long with a distinctly raised caput, cheliceral peg teeth, spineless legs and spatulate setae on the tarsi and metatarsi of legs 1 and 2. However, these characters are widespread in Palpimanoidea and a formal diagnosis based on distinct apomorphies is warranted. Wunderlich (2004: 767) proposed that this family was most closely related to the New Zealand family Huttoniidae which had a

broader distribution in the past, evident from fossils in Cretaceous Canadian amber (Penney, Selden 2006). The genus *Adorator* was misplaced in Spatiatoridae because of the presence of leg spines and the lack of spatulate setae, and based on pedipalp structure it belongs in Zodariidae (Wunderlich 2004: 1592).

Concluding Remarks

To date, twenty strictly fossil spider families (including Archaeidae which was originally described as a fossil family) have been described and the expectation is that more await discovery and description. Of these families, one (Archaeidae) had extant species discovered subsequently and it is not unreasonable to expect that a similar situation may occur again, highlighting the need for neontologists to consider palaeontological data when describing new higher taxa because they may already be known 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 the discovery of new material may demonstrate that *Juraraneus* belongs in Araneidae.

The majority of strictly fossil spider families described from the Cenozoic, were established primarily by Petrunkevitch, who often based his new taxa on juvenile specimens. This is the case for the families Adjutoridae, Arthrodictynidae, Inceptoridae and Insecutoridae and the type specimens require formal systematic scrutiny before the validity of these families (including their proposed synonymies) can be determined. Ephalmatoridae and Spatiatoridae, also established by Petrunkevitch have been revised by Wunderlich (1986, 2004) and are currently considered valid, although the systematic affinities of the former are unclear. The families Baltsuccinidae and Protheridiidae were recently described by Wunderlich (2004) and have not yet been critically assessed. The following fossil families have been synonymized with extant taxa: Acrometidae = Synotaxidae, Mithraeidae = Uloboridae, Mizaliidae = Oecobiidae; and recent unpublished data have shown that Parattidae are lycosoid spiders.

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Съставяне дърво на живота – филогения на паяците: преглед на изцяло фосилните семейства

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(Резюме)

“Assembling the Tree of Life (AToL): Phylogeny of Spiders” е амбициозна, шестгодишна програма, целяща изясняването на филогенията на паяците чрез съставяне на родословно дърво, включващо всички известни семейства. За осъществяването на проекта е изготвена таблица, съдържаща морфологични, молекулярни, поведенчески и палеонтологични данни. Тъй като досега фосилните паяци не са били разглеждани в съвременните систематични каталози, настоящата статия прави преглед на описаните до момента от фосилната летопис 20 семейства. От тях, семейство Archaeidae е наскоро открито с рецентен представител, а Acrometidae, Adjutoridae, Arthrodictynidae, Mithraeidae и Mizaliidae са синонимизирани със съвременни семейства. Според авторите валидни таксони са: Permarachnidae, Juraraneidae, Lagonomegopidae, Baltsuccinidae, Ephalmatoridae, Insecutoridae, Protheridiidae, Spatiatoridae, а Arthrolycosidae, Arthromygalidae, Pyritaraneidae, Inceptoridae, Parattidae трябва да бъдат преразгледани. Нито един от фосилните видове, причислени към семейство Archaeometidae не е паяк.