

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/232692671>

The neglected cousins: What do we know about the smaller Arachnid orders?

Article in *Journal of Arachnology* · January 2009

DOI: 10.1636/0161-8202(2002)030[0357:TNCWDW]2.0.CO;2

CITATIONS

78

READS

395

1 author:



[Mark Stephen Harvey](#)

Western Australian Museum

443 PUBLICATIONS 6,492 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Diversity and systematics of schizomids from the Pilbara Region, Western Australia [View project](#)



Fauna Europaea [View project](#)

THE NEGLECTED COUSINS: WHAT DO WE KNOW ABOUT THE SMALLER ARACHNID ORDERS?

Mark S. Harvey: Department of Terrestrial Invertebrates, Western Australian Museum, Francis St, Perth, Western Australia 6000, Australia. E-mail: mark.harvey@museum.wa.gov.au

ABSTRACT. An overview of the systematics of smaller arachnid orders (Opilioacariformes, Ricinulei, Palpigradi, Uropygi, Amblypygi, Schizomida, Solifugae and Pseudoscorpiones) is provided, along with data on numbers of recognized families, genera and species for each group. The micro-diverse orders, Opilioacariformes (1 family, 9 genera, 19 species), Ricinulei (1 family, 3 genera, 55 species), Palpigradi (2 families, 6 genera, 78 species), Uropygi (1 family, 16 genera, 103 species), Amblypygi (5 families, 17 genera, 136 species) and Schizomida (2 families, 34 genera, 205 species), are amongst the smallest of all terrestrial arthropod orders. The meso-diverse orders, Solifugae (12 families, 140 genera, 1,087 species) and Pseudoscorpiones (24 families, 425 genera, 3,239 species)—along with the Scorpiones (1,279 species) and Opiliones (c. 6,000 species) which are not dealt with in this contribution—are dwarfed by the three mega-diverse arachnid orders, Araneae (c. 36,000 species), Parasitiformes and Acariformes (with a combined total of c. 48,000).

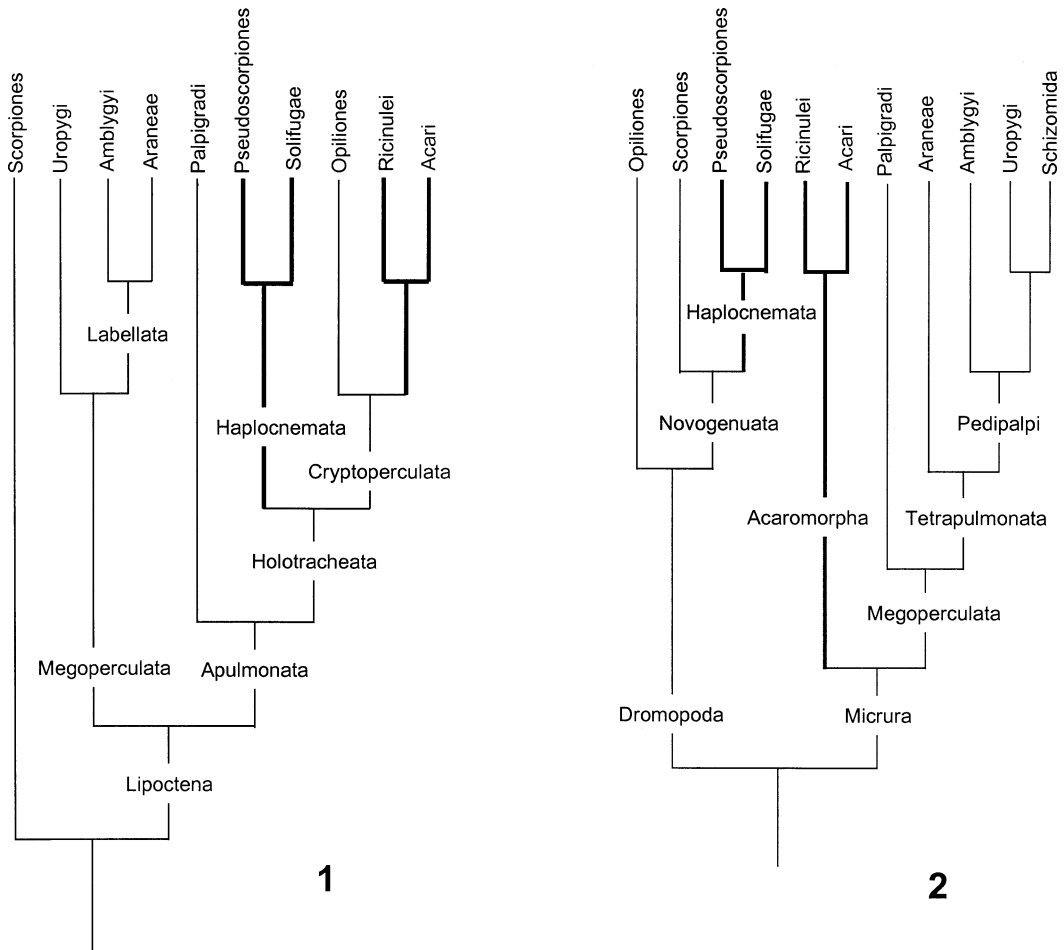
Keywords: Arachnida, Opilioacariformes, Ricinulei, Palpigradi, Uropygi, Amblypygi, Schizomida, Solifugae, Pseudoscorpiones, diversity, systematics

The Arachnida are a conspicuous and dominant animal group. They have diversified into virtually every terrestrial environment, with a few freshwater and marine representatives. Most are predators, but some are phytophages and others are obligate parasites of animals or plants. Adults range in size from 250 μ m mites to the plate-sized tarantulas. Arachnids include some of the most poisonous animals on Earth—some spiders and scorpions are capable of quickly killing an adult human—and many evoke fear and loathing in human cultures. Some mites and ticks are vectors for debilitating diseases, which cause immeasurable suffering to many humans. Most, however, are harmless to humans and are rarely seen by non-biologists.

Arachnida are traditionally ranked as an arthropod class within the subphylum Chelicerata, alongside pycnogonids, xiphosurans, eurypterids and some other minor extinct taxa. The number of orders recognized within the Arachnida has changed over time and between researchers. The current consensus of 10 non-acarine orders seems to be holding firm, but the number of recognized acarine orders varies from one to nine. For the purposes of this study, I follow Halliday (1998) who treat-

ed three orders, Opilioacariformes, Parasitiformes and Acariformes. Thus, a total of 13 orders are recognized here. While the taxonomic rank assigned to particular monophyletic groups of organisms is immaterial to most systematists (in sharp contrast to the consternation shown by some other sections of the biological community) the relationships between these taxa are of much more interest. Indeed, arachnids have been the subject of several recent phylogenetic treatments, including morphological and molecular data-sets (Kraus 1976; Shultz 1989, 1990; Weygoldt 1998a; Weygoldt & Paulus 1979a, 1979b; Wheeler & Hayashi 1998). Results obtained from these studies are not, however, uniform, and considerable differences exist in hypothesized relationships between orders (Figs. 1, 2).

Arachnids have a long ancestry. At least three Recent orders appeared in the fossil record during the Silurian or Devonian, and most of the remaining extant orders appeared by the Carboniferous (Selden 1993). Scorpions possess the longest lineage and have been found in Upper Silurian marine sediments. Morphological evidence suggests that Silurian scorpions were all aquatic. Trigonotarbid also



Figures 1–2.—Cladograms depicting relationships between Recent arachnid orders presented by (1) Weygoldt & Paulus (1979b) and (2) Shultz (1990). Note the differences in the positions of Scorpiones, Palpigradi and Opiliones, among others. The only concordant clades are highlighted with bold lines.

appeared by the Upper Silurian but, like the later Haptopoda and Phalangiotarbida, disappeared by the end of the Carboniferous. The Silurian trigonotarbid, *Palaeotarbus jerami* (Dunlop 1996), is the first unequivocal evidence of terrestrialization in Arachnida (Dunlop 1996a), which was followed by several acariform mites (Norton et al. 1988) and a pseudoscorpion (Schawaller et al. 1991) in the late Devonian. Somewhat surprisingly, many of these Devonian species are remarkably similar to Recent species. The Carboniferous represents the earliest records for the Solifugae, Opiliones, Ricinulei, Amblypygi, Uropygi and Araneae, but the first Schizomida, Parasitiformes, and the first unequivocal Pal-

pigradi did not appear until the Tertiary. Fossil Opilioacariformes are not yet known.

ARACHNID DIVERSITY

The 13 arachnid orders can be divided into three groups—mega-diverse, meso-diverse and micro-diverse—based purely upon the numbers of described species. The three mega-diverse orders—Araneae (spiders), Parasitiformes and Acariformes (mites and ticks)—possess the bulk of arachnid diversity, with some 88% of described species (Fig. 3). This large proportion will continue to increase as further taxa are described—indeed, revisions of individual mite or spider groups sometimes contain more new species than the

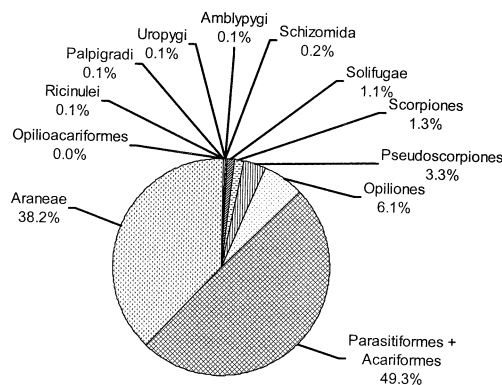


Figure 3.—Chart depicting proportion of described, valid arachnid species showing the numerical dominance of the Araneae and the two major orders of Acari, Parasitiformes and Acariformes.

entire number of species in one of the other arachnid orders. Spiders now total 37,296 described species (Platnick 2001), and the Acari (Opilioacariformes + Parasitiformes + Acariformes) are estimated to include some 48,200 described species (Halliday et al. 2000). This rich diversity is accompanied by varied morphological and ecological traits.

The four meso-diverse orders—Opiliones, Pseudoscorpiones, Scorpiones and Solifugae—possess more than 1,000 named species, but do not, and will not, approach the levels of diversity seen in the Araneae or Acari. The Opiliones are the most diverse with an estimated 6,000 described species (J.C. Cokendolpher, pers. comm.). Pseudoscorpiones con-

tain 3,239 described species, with the Scorpiones (Fet et al. 2000) and Solifugae possessing 1,279 and 1,087 described species, respectively.

The micro-diverse orders—Schizomida, Amblypygi, Uropygi, Palpigradi, Ricinulei and Opilioacariformes—include some of the most geographically restricted arthropod orders, with none currently possessing more than 210 described species.

The total level of arachnid diversity is hard to assess, as there are still considerable taxonomic impediments to be overcome, mostly in the form of vast numbers of undescribed taxa awaiting description. The current figure of approximately 97,000 described species (Table 1) is likely to represent a small proportion of the total diversity. Continued funding for taxonomic research, particularly in tropical and southern temperate regions, is of paramount importance if we are to attempt to reasonably assess the total global diversity of these fascinating creatures. Many are undoubtedly being lost through extinction as habitat destruction and modification continues to play a significant role in shaping the destiny of many arachnids.

In this paper I have restricted my discussion to those taxa for which I have compiled sufficient data and for which I have sufficient knowledge to make some observations which may prove to be of interest to readers. I have chosen to concentrate on the “smaller” orders as they are often neglected in deference to the

Table 1. Arachnid orders with numbers of valid Recent described taxa to December 2000. Figures in italics are estimates only.

Order	Families	Genera	Species	Authority
Opilioacariformes	1	9	20	this paper
Ricinulei	1	3	55	this paper
Palpigradi	2	6	78	this paper
Uropygi	1	16	106	this paper
Amblypygi	5	17	136	this paper
Schizomida	2	34	205	this paper
Solifugae	12	141	1,087	this paper
Scorpiones	16	155	1,279	Fet et al. (2000)
Pseudoscorpiones	24	425	3,239	Harvey (1991); this paper
Opiliones	25	500	6,000	J.C. Cokendolpher, pers. comm.
Araneae	106	3,450	37,296	Platnick (2001)
Parasitiformes + Acariformes	350–422	3,300–4,000	48,181	Adis & Harvey (2000), Halliday et al. (2000)
TOTAL	545–617	8,055–8,755	97,682	

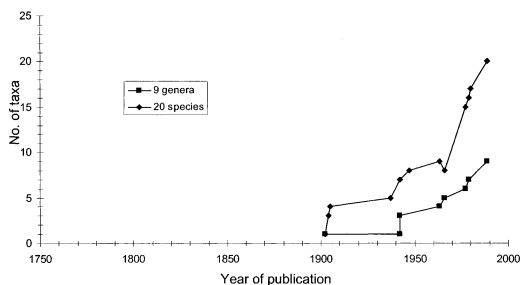


Figure 4.—Numbers of valid Recent opilioacariform genera and species.

three dominant arachnid orders mentioned above. Similar data on two other meso-diverse orders, Scorpiones and Opiliones, have not been compiled.

Despite their modest levels of diversity, there have been several recent breakthroughs in our understanding of the relationships within some of these smaller orders that may prove of interest to a wider audience. I treat the orders in sequence from least to most species-rich.

METHODS

The graphs presented below (Figs. 4–7, 9, 11, 12, 14) were produced from a primary database that I maintain as part of my systematic research and cataloguing activities. This database is current to December 2000. The date of description of a new taxon, in this case genus or species, was transferred to an Excel 2000 spreadsheet to produce the cumulative plots. I also included taxa that are currently treated as junior synonyms, but deleted one taxonomic unit when the taxon's name was judged to have been first placed in synonymy. This provided an estimate of the number of taxa recognized at any one time, although species which were treated as synonyms for part of their "life" but are currently recognized as valid have been treated as having never been synonymized. Homonyms were treated from the year they were first described and not by the date in which they were first given a replacement name.

OPILIOACARIFORMES

The smallest arachnid order, the Opilioacariformes—sometimes termed the Notostigmata or Opilioacarida—was first discovered by With (1902) who briefly described *Opilioacarus segmentatus* With 1902 from Alge-

ria. That was quickly followed by a fully illustrated description of *O. segmentatus* (which was erroneously placed in the new genus *Eucarus*) and the description of *Eucarus italicus* With 1904 from Sicily and *E. arabicus* With 1904 from Aden (With 1904). Since then, 17 additional species have been described, one of which was placed in the synonymy of another. Of these descriptions, most notable were those of Hammen (1966, 1968, 1969, 1971, 1977) and Coineau & Hammen (1979) who had commenced a series of papers on the morphology and taxonomy of the group in which a new generic classification and a phylogenetic analysis was proposed.

The Opilioacariformes consists of a single family, Opilioacaridae, and the 20 named species are currently placed in nine genera (Fig. 4), the majority of which have been described during the past 30 years. They possess uniform morphology but two genera, *Paracarus* Chamberlin & Mulaik 1942 from Kirghizia and *Siamacarus* Leclerc 1989 from Thailand, possess three pairs of lateral eyes (Hammen 1968; Leclerc 1989). The remaining taxa possess only two pairs. Harvey (1996) presented a cladogram of opilioacarid genera, based upon an unpublished cladistic analysis, which suggested that *Paracarus* and *Siamacarus* were the sister-group to the remaining genera. Important publications about opilioacariforms include Chamberlin & Mulaik (1942), Grandjean (1936), Hammen (1966, 1968, 1969, 1971, 1977), Leclerc (1989), Juvara-Bals & Baltac (1977) and With (1904).

RICINULEI

Ricinuleids have often been described as "living fossils" (Selden 1986)—a fitting appellation given their bizarre appearance and gait—but in many respects they are highly modified arachnids with a number of autapomorphies, including a peculiar pre-carapaceal structure, the cucullus, a characteristic mode of sperm transfer and modified pedipalps.

The first Recent ricinuleid species, *Cryptostemma westermanni* Guérin-Méneville 1838 from west Africa, was described by Guérin-Méneville (1838) who attributed the animal to the order Opiliones. A second genus and species, *Cryptocellus foedus* Westwood 1874 was described from Amazonia. Further species have since been described from tropical Africa and America. Ironically, the first

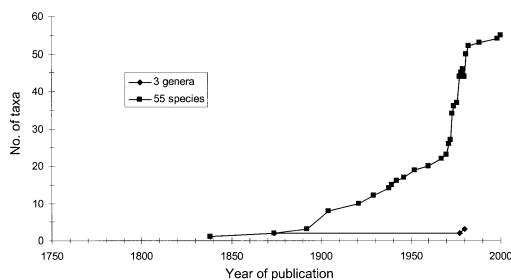


Figure 5.—Numbers of valid Recent ricinuleid genera and species. Note the rapid increase of new species since 1970.

species nowadays attributed to the order, *Curculioides ansticii* Buckland (along with *C. prestvicii* Buckland, which is now regarded as a member of the extinct tetrapulmonate order Trigonotarbita), was described in 1837, a year prior to the discovery of living forms. As the name attests, Buckland (1837) erroneously considered that the fossils, from the fossil-rich Carboniferous British Coal Measures, were insects and it was many years before it was discovered that they were in fact arachnids.

Selden (1992) divided the Ricinulei into two suborders: the Neoricinulei for the Recent species of Ricinoididae, and the Palaeoricinulei for the 15 Carboniferous species placed in the Curculioididae and Poliocheridae. The Recent taxa are currently assigned to three genera: *Ricinoides* Ewing 1929 from west and central Africa, and *Cryptocellus* Westwood 1874 and *Pseudocellus* Platnick 1980 from the Americas.

Relationships among the three Recent genera are uncertain, as there are no unambiguous characters which serve to place one genus closer to another. Of the 55 species currently recognized, 37 have been described since 1960 (Fig. 5), and although some are found only in caves, the vast majority are from rainforest habitats. Many species are only known from a single locality, and some may possess naturally small distributions. This places them at risk of extinction through clearing of primary rainforest and similar habitats, especially in West Africa.

Although ricinuleids possess a suite of peculiar features, the most extraordinary is their mode of sperm transfer, which is facilitated by an elaborate copulatory apparatus on the third leg of the male. This structure rivals the morphological complexity of the modified pedi-

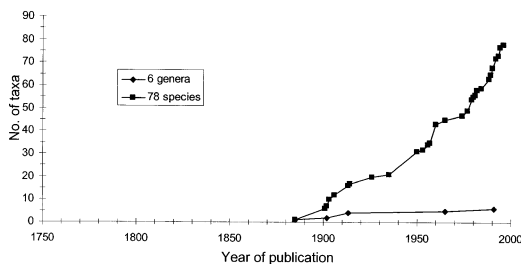


Figure 6.—Numbers of valid Recent palpigrade genera and species. Note the steady increase in described species in the latter part of the 20th century.

palpal tarsus of male spiders which is used for the same purpose. Like the spider pedipalp, the ricinuleid third leg offers numerous species-specific features that are very important taxonomically.

The literature on ricinuleids is not extensive, but important papers include Hansen & Sørensen (1904), Mitchell (1970), Pittard & Mitchell (1972), Tuxen (1974), Platnick & Paz (1979), Platnick (1980), Platnick & Shadab (1981), Legg (1976) and Selden (1992). The Ricinulei are usually placed as the sister-group to the Acari (Shultz 1990; Weygoldt & Paulus 1979b), but Dunlop (1996b) suggested that they represent the sister-group of the Trigonotarbita within the Tetrapulmonata.

PALPIGRADI

Palpigrades are probably the most enigmatic of all of the arachnid orders. They are extremely small and fragile creatures, with a long multi-segmented flagellum that is frequently broken off during collection or from handling preserved specimens. Their relationships are obfuscated by a suite of reductional apomorphies, but they have been either placed within the Tetrapulmonata (e.g. Shultz 1990; Weygoldt & Paulus 1979b) or as a sister-group to the mite order Actinotrichida (Hammen 1982).

The first palpigrade, *Koenenia mirabilis* Grassi & Calandruccio 1885, was described from specimens collected in Sicily, and ascribed to the "Microteliphonida", a name that was promptly changed to Palpigradi by Thorell (1888). The majority of the 78 Recent species have been described since 1950 (Fig. 6) by P. Rémy and B. Condé (see Condé 1996). The order is divided into two families, Eukoeneiidae and Prokoeneiidae. The Euko-

eneniidae comprises four genera with the vast majority of species placed in *Eukoenenia* Börner 1901. The Prokoeneniidae consists of seven species in two genera. The differences between palpigrade genera were summarized by Condé (1996), but there has been no explicit examination of their relationships.

The two fossil species attributed to the Palpigradi add little to our understanding of the group. *Paleokoenenia* Rowland & Sissom 1980, with the sole species *P. mordax* Rowland & Sissom 1980, is from onyx marble in Arizona, suspected to be from the Pliocene (Rowland & Sissom 1980), and is currently not assigned to any family. *Sternarthron* Haase 1890, with *S. zitteli* Haase 1890, is from the Jurassic of Germany, and with a total length of 15 mm (Haase 1890), is substantially larger than any other palpigrade. However, it is probably misplaced within the Palpigradi and may not even be an arachnid (Selden 1993).

The most important contributions to the taxonomy and classification of the order have been made by B. Condé, which were summarized in Condé (1996). Other important references include Hansen & Sörensen (1897), Hansen (1901) and Rowland & Sissom (1980).

UROPYGI

Whip-scorpions are imposing, robust tropical predators with enlarged raptorial pedipalps and a multi-segmented elongate post-pygidium. Like schizomids, they possess anal glands that they use to accurately spray a chemical cocktail to deter predators (Eisner et al. 1961).

Linnaeus (1758) was the first to describe a whip-scorpion, based upon a specimen from "India"—by which he probably referred to the entire east Indies—which he named *Phalangium caudatum* Linnaeus 1758. Linnaeus's use of the generic name *Phalangium* Linnaeus 1758 was quite different to that employed by later biologists, as he included several different arachnids nowadays placed in separate orders. The distinguished invertebratologist P.A. Latreille (1802) was amongst the first to dismember *Phalangium*, and his name *Thelyphonus* Latreille 1802 was the first to be applied solely to a whip-scorpion. Uropygid species were slowly added to the group by 19th century workers, including A.G. Butler, T.

Thorell, R.I. Pocock and K. Kraepelin. F.H. Gravely seems to have been the first uropygid taxonomist with first-hand knowledge of live whip-scorpions which he studied while based at the Indian Museum in Calcutta.

Rowland & Cooke (1973) provided a useful synopsis of the order, including a key to genera and a checklist of species. They also presented a novel classification that included the division of the group into two families, Thelyphonidae and Hypoconidae. Weygoldt (1979) suggested that the existence of two families was not supported by the available data, and Haupt & Song (1996) formally reduced the Hypoconidae to a subfamily as there was little support for a monophyletic Hypoconidae. Dunlop & Horrocks (1996) suggested that the "hypoconids" may be the sister-group to the Schizomida + *Proschizomus* Dunlop & Horrocks 1996, but the character polarities they utilized were regarded as uncertain and many features of *Proschizomus* were not observable in the fossilized material.

Several uropygid genera appear to be unsupported by any apomorphic character states and are clearly paraphyletic. The most glaring example is *Thelyphonus* which is characterized by a series of plesiomorphies. Further research into this, the oldest uropygid genus, would be most welcome to clearly understand the evolutionary relationships of these fascinating animals.

Some 103 whip-scorpion species are currently recognized and placed in 16 genera. Two genera, *Thelyphonus* and *Hypoconus* Thorell 1888, account for nearly half of the species diversity of the order, with some 31 and 19 species, respectively. Nearly two-thirds of the species currently recognized were collected and described over 100 years ago, and the past century has produced only about 40 new species (Fig. 7). Significantly, six of the 16 recognized genera were described in this same interval—all of which contain only one or two species. The validity of many of these taxa has not been rigorously tested, and I suspect that some will eventually prove to be synonyms of older genera once the relationships of whip-scorpions are fully investigated.

The uropygid genera have some level of geographical discreteness, with three major areas of occupancy: the Americas, West Africa and Australasia. The American fauna con-

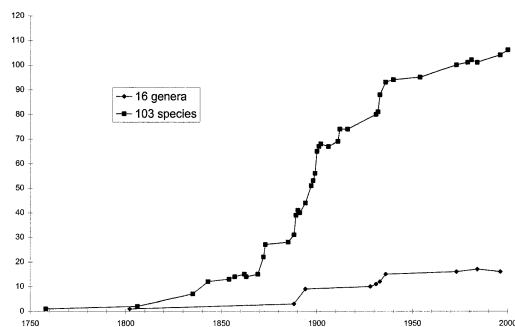


Figure 7.—Numbers of valid Recent uropygid genera and species. Note the rapid increase in described species during the latter part of the 19th century.

sists of three genera and 17 species, *Mastigoproctus* Pocock 1894 (14 species, southern U.S.A. to Brazil), *Thelyphonellus* Pocock 1894 (two species, Brazil, Surinam and Guyana) and *Amauromastigon* Mello-Leitão 1931 (one species, Brazil). The sole West African species, *Etiennius africanus* (Hentschel 1984), is found in Gambia and Senegal. The Australasian fauna, by far the most diverse, ranges from India to Fiji, and comprises 85 species in 13 genera (*Abaliella* Strand 1928, *Chajnus* Speijer 1936, *Ginosigma* Speijer 1936, *Glyptogluteus* Rowland 1973, *Hypoctonus*, *Labochirus* Pocock 1894, *Mastigoproctus*, *Mimoscorpius* Pocock 1894, *Minbosius* Speijer 1933, *Tetrabalius* Thorell 1888, *Thelyphonus*, *Typopeltis* Pocock 1894 and *Uroproctus* Pocock 1894).

Fossil uropygids have been described from Europe and North America, in the Carboniferous genera *Geralinura* Scudder 1884 and *Proschizomus*, the Cretaceous *Mesoproctus* Dunlop 1998 and a species of *Thelyphonus* from the Miocene.

Important papers on the taxonomy of the Uropygi include Kraepelin (1897), Gravely (1916), Millot (1949), Rowland & Cooke (1973) and Dunlop & Horrocks (1996). Although the Uropygi are firmly placed as the sister-group of the Schizomida (which are sometimes included as a suborder of the Uropygi), the systematic position of Uropygi + Schizomida varies. They were treated as the sister-group to the Amblypygi + Araneae by Weygoldt & Paulus (1979b), and as the sister-group to Amblypygi by Shultz (1990), with the entire Pedipalpi (Amblypygi + Schizom-

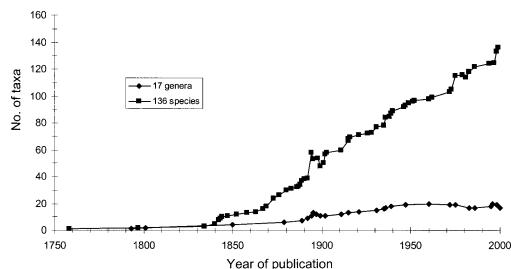


Figure 8.—Numbers of valid Recent amblypygid genera and species. Note the steady increase in new species since the 1880's and the differences in taxonomic opinion between rival taxonomists in the 1890's, when numerous species were synonymized by Kraepelin (1895; 1899a).

ida + Uropygi) as the sister-group to the Araneae. As mentioned above, Dunlop & Horrocks (1996) presented a different scenario.

AMBLYPYGI

Amblypygi—commonly known as whip-spiders—are flattened creatures with multi-segmented, extremely long front legs that act as tactile organs. Whip-spiders are primarily restricted to the tropics where they most commonly occur in rainforests. Several troglotic and trogliphilic species are known (Weygoldt 1994), some of which display typical cave-dwelling facies with loss of pigmentation, elongate appendages, and the reduction or loss of eyes.

The first amblypygid, *Phalangium reniforme* Linnaeus 1758, was based upon a specimen from "America." Only a few further species were named until the middle of the 19th century, when many species and genera were described by A.G. Butler, K. Kraepelin, R.I. Pocock and others. The fluctuating numbers of species recognized in the 1890's (Fig. 8) was largely based upon the large number of synonymies instituted by Kraepelin (1895, 1899a). Many of these synonymies have not been supported by later workers (e.g. Quintero 1981) and much revisionary work is needed to untangle the calamitous taxonomic state of some genera. Despite the legacy left by Kraepelin's synonymies, new species have been consistently described over the past 100 years, and the current total of 136 described species will surely continue to climb as further genera are examined in detail.

Weygoldt (1996a) presented a detailed cla-

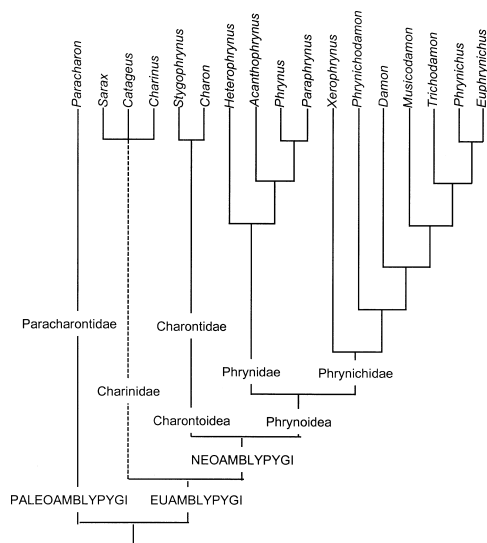


Figure 9.—Relationships between the Recent genera of Amblypygi, redrawn from Weygoldt (1996a, 1996b).

distic analysis of amblypygid genera and proposed a new classification that encompassed five families divided between two suborders, Paleoamblypygi and Euamblypygi. The Paleoamblypygi are represented by a single curious species, *Paracharon caecus* Hansen 1921 (Paracharontidae), which was taken from a termite nest in Guinea-Bissau (Hansen 1921). Its position as the sister-group to the remaining Recent amblypygids (Weygoldt 1996a, and Fig. 9) makes it the only monotypic arachnid suborder in existence, and its isolated and archaic nature is highlighted by a suspected relationship with the four known Carboniferous species (Weygoldt 1996a).

Euamblypygi are represented by four families with varying distributions. The Charinidae is the most widespread family and occurs in most tropical regions of the world; it consists of one circum-tropical genus (*Charinus* Simon 1892), and two genera restricted to south-east Asia (*Catageus* Thorell 1889 and *Sarax* Simon 1892). Weygoldt (1996a) was unable to establish a monophyletic origin for the Charinidae, and further work is needed to determine the species relationships. The Charontidae (*Charon* Karsch 1879 and *Stygophrynus* Kraepelin 1895) are endemic to Australasia, ranging from Burma to the Solomon Islands and northern Australia. The Phrynichidae are found in Africa to south-east Asia

(*Damon* C.L. Koch 1850, *Euphrynichus* Weygoldt 1995, *Muscodamon* Fage 1939, *Phrynichodamon* Weygoldt 1996, *Phrynichus* Karsch 1879 and *Xerophrynus* Weygoldt 1996), with a single outlying genus in Brazil (*Trichodamon* Mello-Leitão 1935). The Phrynidae (*Acanthophrynus* Kraepelin 1899, *Heterophrynus* Pocock 1894, *Paraphrynus* Moreno 1940 and *Phrynus* Lamarck 1801) range from the southern U.S.A. to northern Brazil, although the recent discovery of a member of the genus *Phrynus* from Indonesia (Harvey 2002) raises the prospect of a much wider distribution pattern for the family.

Important papers on amblypygid systematics and taxonomy include Kraepelin (1895), Mullinex (1975), Quintero (1981, 1986), Simon (1892) and Weygoldt (1996a, 1998b, 1999a, 1999b). A comprehensive review of amblypygid morphology, behavior and systematics was recently provided by Weygoldt (2000). The Amblypygi are usually regarded as the sister-group to the Uropygi + Schizomida, thus forming the taxon Pedipalpi (e.g. Shultz 1990), but Weygoldt & Paulus (1979b) placed them as the sister-group to the Araneae.

SCHIZOMIDA

The first Schizomida were described by O. P.-Cambridge (1872) from specimens collected in Sri Lanka. They are small creatures—generally less than 5 mm—with long, tactile anterior legs, and the ability to move very rapidly over short distances. They generally occur in rainforest leaf litter although many species have been described from caves. Others have been accidentally transported with humans, appearing in hot-houses and other environments with constant high humidity. Schizomids possess a peculiar form of sexual dimorphism in which the flagellum of the male is enlarged into a bulbous, unsegmented structure, whereas the segmented female flagellum is unexpanded. Cambridge's (1872) description of the Sri Lankan material treated the male and female specimens as different species—appropriately termed *Nyctalops crassicaudatus* O.P.-Cambridge 1872 and *N. tenuicaudatus* O.P.-Cambridge 1872—until the error was detected. It has since been established that the male flagellum is gripped by the female during courtship (Sturm 1958) and

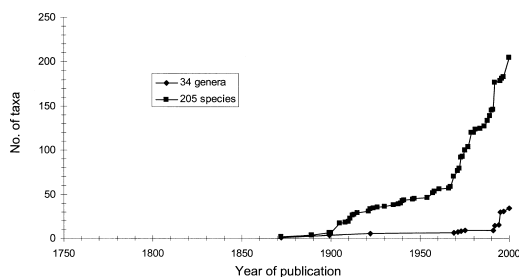


Figure 10.—Numbers of valid Recent schizomid genera and species. Note the rapid increase of new species since 1970, and new genera since 1990.

presumably serves a role in species recognition.

Schizomids are a reasonably uniform group in which, until recently, only a handful of genera and species were known. Until the mid-1980's the majority of species were placed in either *Schizomus* Cook 1899 or *Trithyreus* Kraepelin 1899, but redescrptions of the type species of each genus by Reddell & Cokendolpher (1984, 1991), allowed for a more reasonable taxonomic break-up of the order. Harvey (1992a) revised the Australian fauna and dispensed with the notion that the majority of schizomids could be included in a few genera, as the level of variation, particularly of the female genitalia, was found to be a useful and significant tool in separating distinct groups of species into genera. Reddell & Cokendolpher (1995) revised the world fauna, described a further 15 genera and removed several older names from synonymy. Additional genera have since been described by Reddell, Cokendolpher, Harvey and their co-workers. To date there are 34 genera of schizomids placed in two families, Protoschizomidae and Hubbardiidae. Twenty-three of these genera have been described since 1990 (Fig. 10) and many more are to be expected once the Asian and African faunas, which have not yet been studied in detail, are considered. Over 180 species have been described, 72% of these since 1960. I expect that over 500 species will eventually be recognized world-wide, as the discovery of new taxa in the Australasian region alone (Harvey, unpublished data) continues. Indeed, since my 1992 revision in which 26 species were recognized (Harvey 1992a), a further 45 new species have been detected, and every new sample seems to contain further species (Harvey 2000, 2001). Cokendolpher & Red-

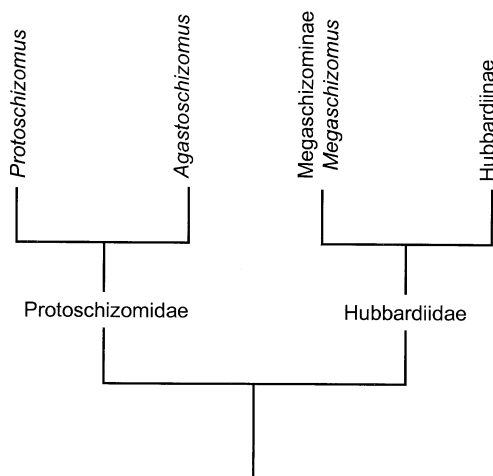


Fig. 11.—Relationships amongst the Schizomida, redrawn from Cokendolpher & Reddell (1992).

dell (1992) presented a cladistic analysis of the Schizomida (Fig. 11), and showed that both families are monophyletic. The fossil record is scant, with three Tertiary genera placed in either the Hubbardiidae (*Calcoschizomus* Pierce 1951 and *Onychothelyphonus* Pierce 1950) or Calcitronidae (*Calcitro* Petrunkevitch 1945). Little can be deduced from the morphology of these Tertiary species, as the preservation is generally poor, and any comparison with modern representatives is extremely difficult.

The Schizomida are strongly confirmed as the sister-group of the Uropygi, but Uropygi + Schizomida are either treated as the sister-group to the Amblypygi (Shultz 1990) or as the sister-group to the Amblypygi + Araneae (e.g., Weygoldt & Paulus 1979b). Important papers on the systematics of schizomids are Hansen & Sørensen (1905), Lawrence (1969), Rowland & Reddell (1979a, 1979b, 1980, 1981), Harvey (1992a), Cokendolpher & Reddell (1992) and Reddell & Cokendolpher (1995).

SOLIFUGAE

The Solifugae, sometimes called sun-spiders, wind-scorpions or camel-spiders, are some of the most spectacular arachnids and are equipped with large, powerful, two-segmented chelicerae. Adults range in size from 1–7 cm. They can be easily distinguished from other arachnids by the presence of malloleoli (racquet organs), the peculiar, stalked

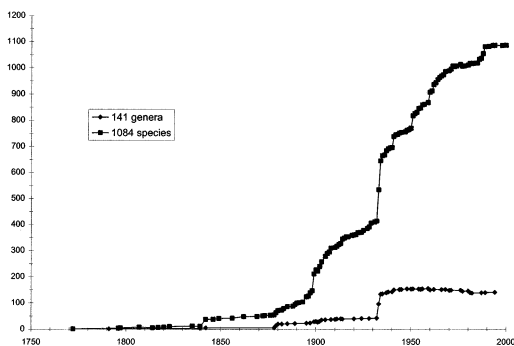


Figure 12.—Numbers of valid Recent solifuge genera and species. Note the marked increase in described genera and species during the 1930's, which was largely the work of one worker, C.F. Roewer.

structures situated on the ventral surfaces of leg IV.

Although solpugids were known to pre-Linnean scholars, the first solpugid was officially described as *Phalangium araneoides* Pallas 1772. Lichtenstein (1796) and Lichtenstein & Herbst (1797) added four new species that were placed in the first genus dedicated to the group, *Solpuga* Lichtenstein 1796. Early attempts at producing a classification of the order were attempted by C.L. Koch (1842), Simon (1879) and Kraepelin (1899b), but the modern classification was established by Roewer (1932, 1933, 1934) who instigated a new classification and described numerous new genera and species (Fig. 12). Roewer's reliance upon a small set of character systems to distinguish between genera or subfamilies has been critically challenged by numerous workers (e.g. see Muma 1976) and it is clear that the current classification is severely flawed at many levels. Much work must be undertaken to even begin to sort out the confusion. The only regional fauna which is in relatively good condition is that of the New World, where Roewer had little impact, and where later researchers such as Muma and Brookhart (e.g. Brookhart & Muma 1981, 1987; Muma 1951, 1970, 1971; Muma & Brookhart 1988) and Maury (e.g. Maury 1982, 1985, 1987) have been able to formulate a worthwhile classification based upon a synthesis of many characters.

Solifugae currently consists of 12 families, 141 genera and 1,084 species (Table 1). No attempt has been made to group the 12 fam-

ilies into superfamilies and the current classification is a flat structure devoid of any phylogenetic signal. The Rhagodidae seem to stand apart from the remaining Solifugae in a number of ways and Roewer (1934) depicted them as separate from other families. However, the systematic position of this family has not been empirically tested, and a phylogenetic study of the Solifugae would allow testing of morphological and behavioral traits.

Three species have been described from fossils, and each is placed in a monotypic genus: *Protosolpuga carbonaria* Petrunkevitch 1913 (Protosolpugidae) from the Pennsylvanian (Carboniferous) of Mazon Creek, U.S.A., *Haplodontus proterus* Poinar and Santiago-Blay 1989 (Ammotrechidae) from Miocene-Eocene Dominican Amber and *Cratosolpuga wunderlichi* Selden 1996 (Ceromidae) from the Aptian (Lower Cretaceous) of Brazil.

The Solifugae are commonly accepted as the sister-group to the Pseudoscorpiones, and both are placed in the clade Haplocnemata (e.g. Shultz 1990; Weygoldt & Paulus 1979b).

Important publications include Simon (1879), Kraepelin (1899b), Roewer (1932, 1933, 1934), Birula (1938), Muma (1951, 1976), Lawrence (1955), Selden & Shear (1996) and Punzo (1998).

PSEUDOSCORPIONES

Pseudoscorpions are small predatory arachnids, which superficially resemble scorpions, but that lack the elongate metasoma (tail) and telson (sting) characteristic of the latter group. The resemblance is mostly due to the enlarged pedipalps that in both groups are modified with the tarsus inserted ventrally under the tibia to form a chelate appendage. Adults range from less than 1 mm to 1 cm in length.

The first pseudoscorpions were described by Linnaeus (1758) who named *Acarus cancroides* Linnaeus 1758 from Europe and *Acarus scorpoides* Linnaeus 1758 from Surinam—ironically the three names he used linked the group to mites (*Acarus* Linnaeus 1758), crabs (*cancroides*) and scorpions (*scorpoides*), indicating a distinct uncertainty of their relationships! Geoffroy (1762) quickly realized that *A. cancroides* was misplaced among the mites and erected the inaugural generic name, *Chelifer* Geoffroy 1762.

All pseudoscorpions were placed in a single family until 1892 when the young Italian bi-

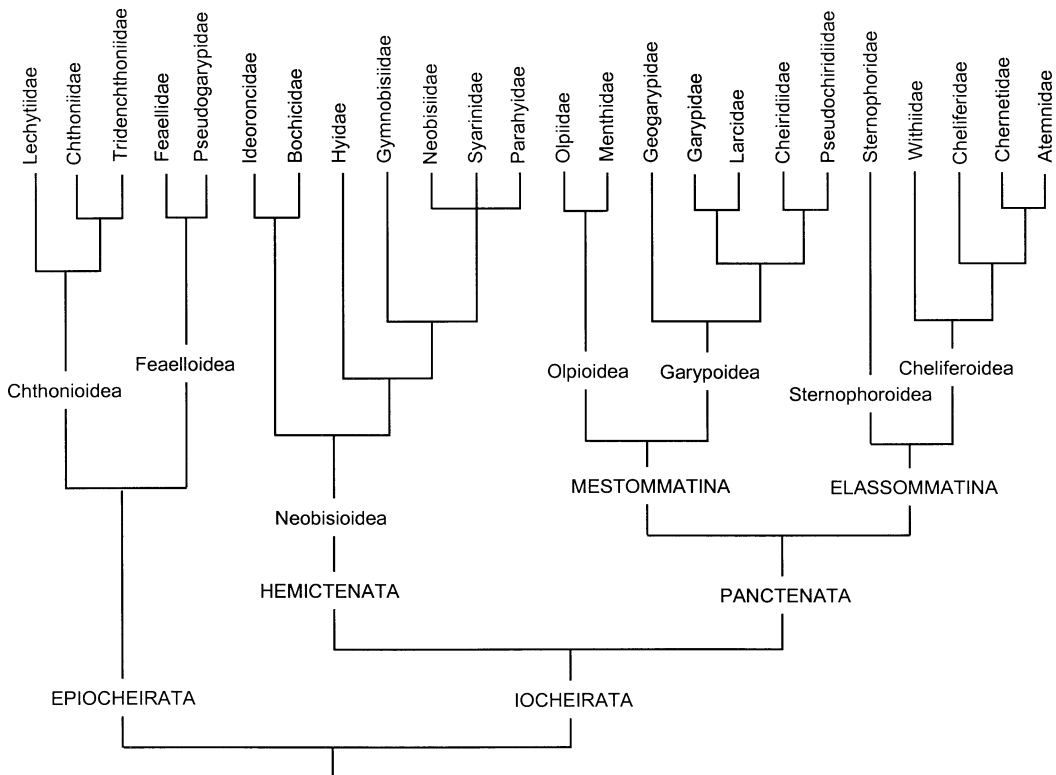


Figure 13.—Relationships amongst the Pseudoscorpiones, redrawn from Harvey (1992b).

ologist L. Balzan produced a novel classification in which the order was divided into two suborders—Hemictenodactyli and Panctenodactyli—and four families (Balzan 1892). Chamberlin (1929, 1930, 1931) produced a different classification that remained largely unchanged for over 60 years, despite minor modifications by Beier (1932a, b) and others. Harvey (1992b) provided the first comprehensive cladistic treatment of the order (Fig. 13) and recognized two suborders—Epiocheirata

and Iocheirata—each based on several autapomorphic characters. These include the presence (Iocheirata) or absence (Epiocheirata) of a venom apparatus in the chelal fingers, and the presence (Epiocheirata) or absence (Iocheirata) of the accessory trichobothrium *xs* and coxal spines. Among several changes to the previous classifications, Harvey (1992b) transferred the Cheiridiidae and Pseudochiridiidae, which until then had been combined with the Sternophoridae in the Cheiridioidea (e.g. Chamberlin 1931), to the Garypoidea. Judson (2000) has recently questioned the position of these two families and reinstated the Cheiridioidea for the Cheiridiidae and Pseudochiridiidae.

Over 3,200 species in 425 genera are currently recognized and the discovery of new species and genera continues unabated (Fig. 14), even in well-studied areas such as North America. The number of Recent families currently stand at 24 (Harvey 1992b), but the systematic position of several unusual groups currently included within other families may expand this number.

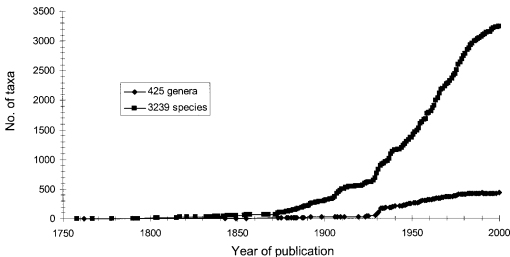


Figure 14.—Numbers of valid Recent pseudoscorpion genera and species. Note the steady increase in described species since the 1930's.

Until recently, the fossil record solely consisted of Tertiary species embedded in amber from the Baltic, Caribbean or Burma, with most species placed in Recent genera. The discovery of Cretaceous pseudoscorpions (Schawaller 1991; Whalley 1980) and most importantly, the description of *Dracochela deprehendor* Schawaller, Shear & Bonamo 1991 from the Devonian of New York, has firmly established that the order is an ancient clade that moved into terrestrial environments some time prior to 380 MBP. Harvey (1992b) treated *Dracochela* Schawaller, Shear & Bonamo 1991 as a member of the suborder Epiocheirata, although certain morphological features are not sufficiently preserved or visible on the specimens to enable the placement within the group to be tested with certainty. Important publications include Chamberlin (1931), Beier (1932a, 1932b), Muchmore (1990), and Harvey (1991, 1992b).

DISCUSSION

The somewhat provocative title of this paper is not intended to scorn those arachnologists who focus upon the mega-diverse groups. Indeed, the challenges faced in documenting and understanding the enormous diversity of the Acari and Araneae (Halliday et al. 2000; Platnick 1999) far outweigh the problems faced by researchers dealing with the smaller arachnid orders. Nevertheless there is still much to be gained from a more coordinated and detailed examination of the phylogeny and diversity of the other orders. New species are constantly being found in most groups, new characters are being discovered which are helping to refine and challenge previous classifications and the use of cladistic methodology has produced some testable phylogenetic hypotheses. Although some orders have been the subject of detailed phylogenetic analysis (i.e., Amblypygi, Schizomida and Pseudoscorpiones), others have yet to be examined empirically, and none have been the subject of combined molecular and morphological treatments such as that recently conducted for Opiliones (Shultz & Regier 2001). Such studies are needed to further test the monophyly of purported groups within each order and to provide a judicious phylogenetic framework within which other scientific disciplines can operate.

ACKNOWLEDGMENTS

I am extremely grateful to Petra Sierwald for inviting me to speak at the XIV International Congress of Arachnology, Chicago, thus compelling me to collate the data presented here, and to Ansie Dippenaar-Schoeman for inviting me to present an update at the XV International Congress of Arachnology, Badplaas. I also wish to thank my many friends and colleagues who have kindly provided me with literature, both old and new, which has allowed the compilation of these data-sets. The manuscript was critically reviewed by Bill Humphreys, Andy Austin and an anonymous referee, to whom I am indebted for their comments.

LITERATURE CITED

- Adis, J. & M.S. Harvey. 2000. How many Arachnida and Myriapoda are there world-wide and in Amazonia? Studies on Neotropical Fauna and Environment 35:129–141.
- Balzan, L. 1892. Voyage de M. E. Simon au Venezuela (Décembre 1887—Avril 1888). Arachnides. Chernetes (Pseudoscorpiones). Annales de la Société Entomologique de France 60:497–552.
- Beier, M. 1932a. Pseudoscorpionidea I. Subord. Chthoniinea et Neobisiinea. Tierreich 57:i–xx, 1–258.
- Beier, M. 1932b. Pseudoscorpionidea II. Subord. C. Cheliferinea. Tierreich 58:i–xxi, 1–294.
- Birula, A. 1938. Arachnides, Ordo Solifuga. Pp. i–vii, 1–173. Vol. 1(3). L'Académie des Sciences de l'URSS, Moscow, Leningrad. (in Russian)
- Brookhart, J.O. & M.H. Muma. 1981. The *pallipes* species-group of *Eremobates* Banks (Solpugida: Arachnida) in the United States. Florida Entomologist 64:283–308.
- Brookhart, J.O. & M.H. Muma. 1987. *Arenotherus*, a New Genus of Eremobatidae (Solpugida), in the United States. Privately published by the authors.
- Buckland, W. 1837. Geology and Minerology Considered with Reference to Natural Theology. Vol. 2. William Pickering, London.
- Chamberlin, J.C. 1929. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. Part I. The Heterosphyronida (Chthoniidae) (Arachnida-Chelonethida). Annals and Magazine of Natural History (10) 4:50–80.
- Chamberlin, J.C. 1930. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. Part II. The Diplosphyronida (Arachnida-Chelonethida). Annals and Magazine of Natural History (10) 5:1–48, 585–620.

- Chamberlin, J.C. 1931. The arachnid order Chelonethida. Stanford University Publications, Biological Sciences 7(1):1–284.
- Chamberlin, R.V. & S. Mulaik. 1942. On a new family in the Notostigmata. Proceedings of the Biological Society of Washington 55:125–132.
- Coineau, Y. & L. van der Hammen. 1979. The post-embryonic development of Opilioacarida, with notes on new taxa and on a general model for the evolution. Pp. 437–441. In Proceedings of the 4th International Congress of Acarology, 1974. (E. Piffel ed.). Akadémiai Kiadó, Budapest.
- Cokendolpher, J.C. & J.R. Reddell. 1992. Revision of the Protoschizomidae (Arachnida: Schizomida) with notes on the phylogeny of the order. Texas Memorial Museum, Speleological Monographs 3:31–74.
- Condé, B. 1996. Les Palpigrades, 1885–1995: acquisitions et lacunes. Revue Suisse de Zoologie, hors série 1:87–106.
- Dunlop, J.A. 1996a. A trigonotarbid arachnid from the Upper Silurian of Shropshire. Palaeontology 39:605–614.
- Dunlop, J.A. 1996b. Evidence for a sister group relationship between Ricinulei and Trigonotarbida. Bulletin of the British Arachnological Society 10:193–204.
- Dunlop, J.A. & C.A. Horrocks. 1996. A new Upper Carboniferous whip scorpion (Arachnida: Uropygi: Thelyphonida) with a revision of the British Carboniferous Uropygi. Zoologischer Anzeiger 234:293–306.
- Eisner, T., J. Meinwald, A. Monro & R. Ghent. 1961. Defense mechanisms of arthropods—I. The composition and function of the spray of the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida: Pedipalpida). Journal of Insect Physiology 6:272–298.
- Fet, V., W.D. Sissom, G. Lowe & M.E. Braunwalder. 2000. Catalogue of the Scorpions of the World (1758–1998). New York Entomological Society, New York.
- Geoffroy, E.L. 1762. Histoire Abrégée des Insectes qui se Trouvent aux Environs de Paris; dans Laquelle ces Animaux sont Rangés Suivant un Ordre Méthodique. Vol. 2. Durand, Paris.
- Grandjean, F. 1936. Un acariens synthétique: *Opilioacarus segmentatus* With. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 27:413–444.
- Grassi, B. & S. Calandruccio. 1885. Intorno ad un nuovo Aracnide Artrogastro (*Koenenia mirabilis* [sic]) che crediamo rappresentante d'un nuovo ordine (Microteliphonida). Naturalista Siciliano 4:127–133, 162–168.
- Gravely, F.H. 1916. The evolution and distribution of the Indo-Australian Thelyphonidae, with notes on the distinctive characters of various species. Records of the Indian Museum 12:59–85.
- Guérin-Ménéville, F.E. 1838. Note sur l'*Acanthodon* et sur le *Cryptostemma*, nouveaux genres d'Arachnides. Revue Zoologique 1:10–14.
- Haase, E. 1890. Beiträge zur Kenntniss der fossilen Arachniden. Zeitschrift der Deutschen Geologischen Gesellschaft 42:629–657.
- Halliday, R.B. 1998. Mites of Australia, a Checklist and Bibliography. CSIRO Publishing, Melbourne.
- Halliday, R.B., B.M. O'Connor & A.S. Baker. 2000. Global diversity of mites. Pp. 192–203. In Nature and Human Society—the Quest for a Sustainable World. (P. H. Raven ed.). National Academy Press, Washington D.C.
- Hansen, H.J. 1901. On six species of *Koenenia*, with remarks on the order Palpigradi. Entomologisk Tidskrift 22:193–240.
- Hansen, H.J. 1921. The Pedipalpi, Ricinulei, and Opiliones (exc. Op. Laniatores) collected by Mr. Leonardo Fea in tropical West Africa and adjacent islands. Pp. 1–55. In Studies on Arthropoda. Vol. 1. Gyldendalske Boghandel, København.
- Hansen, H.J. & W. Sørensen. 1897. The order Palpigradi Thor. (*Koenenia mirabilis* Grassi) and its relationship to the other Arachnida. Entomologisk Tidskrift 18:223–240.
- Hansen, H.J. & W. Sørensen. 1905. The Tartarides, a tribe of the order Pedipalpi. Arkiv för Zoologi 2(8):1–78.
- Hansen, H.J. & W. Sørensen. 1904. On Two Orders of Arachnida. Cambridge University Press, Cambridge.
- Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester University Press, Manchester.
- Harvey, M.S. 1992a. The Schizomida (Chelicerata) of Australia. Invertebrate Taxonomy 6:77–129.
- Harvey, M.S. 1992b. The phylogeny and systematics of the Pseudoscorpionida (Chelicerata: Arachnida). Invertebrate Taxonomy 6:1373–1435.
- Harvey, M.S. 1996. Small arachnids and their value in Gondwanan biogeographic studies. Pp. 155–162. In Gondwanan Heritage: Past, Present and Future of the Western Australian Biota. (S. D. Hopper, J. A. Chappill, M. S. Harvey & A. S. George eds). Surrey Beatty & Sons, Chipping Norton.
- Harvey, M.S. 2000. A review of the Australian schizomid genus *Notozomus* (Hubbardiidae). Memoirs of the Queensland Museum 46:161–174.
- Harvey, M.S. 2001. New cave-dwelling schizomids (Schizomida: Hubbardiidae) from Australia. Records of the Western Australian Museum, Supplement 64:171–185.
- Harvey, M.S. 2002. The first Old World species of

- Phrynidae (Amblypygi): *Phrynus exsul* from Indonesia. Journal of Arachnology. In press.
- Haupt, J. & D. Song. 1996. Revision of East Asian whip scorpions (Arachnida Uropygi Thelyphonida). I. China and Japan. Arthropoda Selecta 5: 43–52.
- Judson, M.L.I. 2000. *Electrobisium acutum* Cockerell, a cheiridiid pseudoscorpion from Burmese amber, with remarks on the validity of the Cheiridioidea (Arachnida, Chelonethi). Bulletin of the Natural History Museum, Geology 56:79–83.
- Juvara-Bal, I. & M. Baltac. 1977. Deux nouvelles espèces d'*Opilioacarus* (Acarina: Opilioacarida) de Cuba. Pp. 169–184. In Résultats des Expéditions Biospéologiques Cubano-Roumaines à Cuba. (T. Orghidan, A. Núñez Jiménez, V. Decou, S. Negrea & N. V. Bayés eds). Vol. 2. Editura Academiei Republicii Socialiste România, Bucuresti.
- Koch, C.L. 1842. Systematische Uebersicht über die familie der Galeoden. Archiv für Naturgeschichte 8:350–356.
- Kraepelin, K. 1895. Revision der Tarantuliden Fabr. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 13(3):3–53.
- Kraepelin, K. 1897. Revision der Uropygi Thor. (Thelyphonidae auct.). Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben vom Naturwissenschaftlichen Verein in Hamburg 15:1–58.
- Kraepelin, K. 1899a. Scorpiones und Pedipalpi. Tierreich 8:i–xviii,1–265.
- Kraepelin, K. 1899b. Zur Systematik der Solifugen. Mitteilungen aus dem Naturhistorischen Museum in Hamburg 16:195–258.
- Kraus, O. 1976. Zur phylogenetischen Stellung und Evolution der Chelicerata. Entomologica Germanica 3:1–12.
- Latreille, P.A. 1802. Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes. Vol. 3. F. Dufart, Paris.
- Lawrence, R.F. 1955. Solifugae, scorpions and Pedipalpi, with checklists and keys to South African families, genera and species. Pp. 152–262. In South African Animal Life. Results of the Lund Expedition in 1950–1951. Vol. 1. Almquist and Wiksell, Stockholm.
- Lawrence, R.F. 1969. The Uropygi (Arachnida: Schizomida) of the Ethiopian region. Journal of Natural History 3:217–260.
- Leclerc, P. 1989. Considerations paleobiogeographiques a propos la decouverte en Thaïlande d'*Opilioacariens* nouveaux (Acari—Notostigmata). Compte Rendu des Seances, Société de Biogéographie, Paris 65:162–174.
- Legg, G. 1976. The external morphology of a new species of ricinuleid (Arachnida) from Sierra Leone. Zoological Journal of the Linnean Society 59:1–58.
- Lichtenstein, A.A.H. 1796. Catalogus Musei Zoologici Ditiissimi Hamburgi, d. III. Februar. 1796 Auctionis Lege Distrahendi. Sectio Tertia. Continens Insecta. Schniebes, Hamburg.
- Lichtenstein, A.A.H. & J.F.W. Herbst. 1797. Naturgeschichte der Insekten-Gattungen *Solpuga* und *Phalangium*.. In Natursystem der Ungeflügelten Insekten. (J. F. W. Herbst ed.). Vol. 1. G.A. Lange, Berlin.
- Linnaeus, C. 1758. Systema naturae. Vol. 1. L. Salvii, Holmiae.
- Maury, E.A. 1982. Solifugos de Colombia y Venezuela (Solifugae, Ammotrechidae). Journal of Arachnology 10:123–143.
- Maury, E.A. 1985. Nota sobre los géneros *Namibesia* y *Syndaesia* (Solifugae, Daesiidae). Aracnologia 4:1–6.
- Maury, E.A. 1987. Consideraciones sobre algunos solifugos de Chile (Solifugae: Ammotrechidae, Daesiidae). Revista de la Sociedad Entomológica Argentina 44:419–432.
- Millot, J. 1949. Ordre des Uropyges. Pp. 533–562. In Traité de Zoologie. (P.-P. Grassé ed.). Vol. 6. Masson, Paris.
- Mitchell, R.W. 1970. Population size and dispersion and species associations of a Mexican cavernicole ricinuleid. Ciencia, México 27:63–74.
- Muchmore, W.B. 1990. Pseudoscorpionida. Pp. 503–527. In Soil Biology Guide. (D. L. Dindal ed.). John Wiley and Sons, New York.
- Mullinex, C.L. 1975. Revision of *Paraphrynus* Moreno (Amblypygida: Phrynidae) for North America and the Antilles. Occasional Papers of the California Academy of Sciences 116:1–80.
- Muma, M.H. 1951. The arachnid order Solpugida in the United States. Bulletin of the American Museum of Natural History 97:35–141.
- Muma, M.H. 1970. A synoptic review of North American, Central American, and West Indian Solpugida (Arthropoda: Arachnida). Arthropods of Florida and Neighboring Land Areas 5:1–62.
- Muma, M.H. 1971. The solpugids (Arachnida, Solpugida) of Chile, with descriptions of a new family, new genera, and new species. American Museum Novitates 2476:1–23.
- Muma, M.H. 1976. A review of solpugid families with an annotated list of western hemisphere solpugids. Publication of the Office of Research, Western New Mexico University, Silver City 2: 1–33.
- Muma, M.H. & J. Brookhart. 1988. The *Eremobates palpisetulosus* Species-Group (Solpugida: Eremobatidae) in the United States. Cherry Creek School District, Englewood.
- Norton, R.A., P.M. Bonamo, J.D. Grierson & W.A. Shear. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. Journal of Paleontology 62:259–269.

- Pallas, P.S. 1772. *Spicilegium Zoologicum*. Vol. 1(9). Gottl. August. Lange, Berolini.
- Pickard-Cambridge, O. 1872. On a new family and genus and two new species of Thelyphonidea. *Annals and Magazine of Natural History* (4) 10: 409–413.
- Pittard, K. & R.W. Mitchell. 1972. Comparative morphology of the life stages of *Cryptocellus pellaesi* (Arachnida, Ricinulei). Graduate Studies, Texas Tech University 1:1–78.
- Platnick, N.I. 1980. On the phylogeny of Ricinulei. Pp. 349–353. *In* Verhandlungen des 8. Internationalen Arachnologen-Kongress, Wien. (J. Gruber ed.). H. Egermann, Wien.
- Platnick, N.I. 1999. Dimensions of biodiversity: targeting megadiverse groups. Pp. 33–52. *In* The Living Planet in Crisis: Biodiversity Science and Policy. (J. Cracraft & F. T. Grifo eds). Columbia University Press, New York.
- Platnick, N.I. 2001. The World Spider Catalog, Version 2.0. American Museum of Natural History, New York at <http://research.amnh.org/entomology/spiders/catalog81-87/index.html>.
- Platnick, N.I. & N. Paz S. 1979. On the *Cryptocellus magnus* group (Arachnida, Ricinulei). *American Museum Novitates* 2677:1–9.
- Platnick, N.I. & M.U. Shadab. 1981. On the *Cryptocellus centralis* group (Arachnida, Ricinulei). *Bulletin of the American Museum of Natural History* 170:18–22.
- Punzo, F. 1998. *The Biology of Camel-Spiders* (Arachnida, Solifugae). Kluwer Academic Publishers, Boston.
- Quintero, D., Jr. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). *Journal of Arachnology* 9:117–166.
- Quintero, D., Jr. 1986. Revision de la clasificación de Amblypygidos pulvinados: creación de subordenes, una nueva familia y un nuevo género con tres nuevas especies (Arachnida: Amblypygi). Pp. 203–212. *In* Proceedings of the Ninth International Congress of Arachnology, Panama 1983. (W. G. Eberhard, Y. D. Lubin & B. C. Robinson eds). Smithsonian Institution Press, Washington D.C.
- Reddell, J.R. & J.C. Cokendolpher. 1984. Redescription of *Trithyreus grassii* (Arachnida: Schizomida: Schizomidae). *Oriental Insects* 18:43–52.
- Reddell, J.R. & J.C. Cokendolpher. 1991. Redescription of *Schizomus crassicaudatus* (Pickard-Cambridge) and diagnoses of *Hubbardia* Cook, *Stenochrus* Chamberlin, and *Sotanostenochrus* new genus, with description of a new species of *Hubbardia* from California (Arachnida: Schizomida: Hubbardiidae). *Pearce Sellards Series* 47:1–24.
- Reddell, J.R. & J.C. Cokendolpher. 1995. Catalogue, bibliography, and generic revision of the order Schizomida (Arachnida). *Texas Memorial Museum, Speleological Monographs* 4:1–170.
- Roewer, C.F. 1932. Solifugae, Palpigradi. Pp. 1–160. *In* Klassen und Ordnungen des Tierreichs. 5: Arthropoda. IV: Arachnoidea. (H. G. Bronns ed.). Vol. 5(IV)(4)(1). Akademische Verlagsgesellschaft M.B.H., Leipzig.
- Roewer, C.F. 1933. Solifugae, Palpigradi. Pp. 161–480. *In* Klassen und Ordnungen des Tierreichs. 5: Arthropoda. IV: Arachnoidea. (H. G. Bronns ed.). Vol. 5(IV)(4)(2–3). Akademische Verlagsgesellschaft M.B.H., Leipzig.
- Roewer, C.F. 1934. Solifugae, Palpigradi. Pp. 481–723. *In* Klassen und Ordnungen des Tierreichs. 5: Arthropoda. IV: Arachnoidea. (H. G. Bronns ed.). Vol. 5(IV)(4)(4–5). Akademische Verlagsgesellschaft M.B.H., Leipzig.
- Rowland, J.M. & J.A.L. Cooke. 1973. Systematics of the arachnid order Uropygida (= Thelyphonida). *Journal of Arachnology* 1:55–71.
- Rowland, J.M. & J.R. Reddell. 1979a. The order Schizomida (Arachnida) in the New World. I. Protoschizomidae and *dumitrescoae* group (Schizomidae: *Schizomus*). *Journal of Arachnology* 6: 161–196.
- Rowland, J.M. & J.R. Reddell. 1979b. The order Schizomida (Arachnida) in the New World. II. *Simonis* and *brasiliensis* groups (Schizomidae: *Schizomus*). *Journal of Arachnology* 7:89–119.
- Rowland, J.M. & J.R. Reddell. 1980. The order Schizomida (Arachnida) in the New World. III. *Mexicanus* and *pecki* groups (Schizomidae: *Schizomus*). *Journal of Arachnology* 8:1–34.
- Rowland, J.M. & J.R. Reddell. 1981. The order Schizomida (Arachnida) in the New World. IV. *Goonightorum* and *briggsi* groups (Schizomidae: *Schizomus*). *Journal of Arachnology* 9:19–46.
- Rowland, J.M. & W.D. Sissom. 1980. Report on a fossil palpigrade from the Tertiary of Arizona, and a review of the morphology and systematics of the order (Arachnida). *Journal of Arachnology* 8:69–86.
- Schawaller, W. 1991. The first Mesozoic pseudoscorpion, from Cretaceous Canadian amber. *Paleontology* 34:971–976.
- Schawaller, W., W.A. Shear & P.M. Bonamo. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). *American Museum Novitates* 3009:1–24.
- Selden, P.A. 1986. Ricinuleids—living fossils? Pp. 425. *In* Actas X Congreso Internacional de Arachnologia, Jaca. (J. A. Barrientos ed.). Vol. 1.
- Selden, P.A. 1992. Revision of the fossil ricinuleids. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 83:595–634.
- Selden, P.A. 1993. Fossil arachnids—recent advances and future prospects. *Memoirs of the Queensland Museum* 33:389–400.
- Selden, P.A. & W.A. Shear. 1996. The first Meso-

- zoic Solifugae (Arachnida), from the Cretaceous of Brazil, and a redescription of Palaeozoic Solifuge. *Palaeontology* 39:583–604.
- Shultz, J.W. 1989. Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. *Zoological Journal of the Linnean Society* 97:1–56.
- Shultz, J.W. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6:1–38.
- Shultz, J.W. & J.C. Regier. 2001. Phylogenetic analysis of Phalangida (Arachnida, Opiliones) using two nuclear protein-encoding genes supports monophyly of Palpatores. *Journal of Arachnology* 29:189–200.
- Simon, E. 1879. Essai d'une classification des Galéodes, remarques synonymiques et description d'espèces nouvelles ou mal connues. *Annales de la Société Entomologique de France* (5) 9:93–154.
- Simon, E. 1892. Arachnides des îles Philippines. *Annales de la Société Entomologique de France* 61:35–52.
- Sturm, H. 1958. Indirekte Spermatophorenübertragung bei dem Geisselskorpion *Trithyreus sturmi* Kraus (Schizomidae, Pedipalpi). *Naturwissenschaften* 45:142–143.
- Thorell, T. 1888. Pedipalpi e Scorpioni dell'Arcipelago Malese conservati nel Museo Civico di Storia Naturale di Genova. *Annali del Museo Civico di Storia Naturale di Genova* 26:327–428.
- Tuxen, S.L. 1974. The African genus *Ricinoides* (Arachnida, Ricinulei). *Journal of Arachnology* 1:85–106.
- van der Hammen, L. 1966. Studies on Opilioacarida (Arachnida). I. Description of *Opilioacarus texanus* (Chamberlin and Mulaik) and revised classification of the genera. *Zoologische Verhandlungen* 86:1–80.
- van der Hammen, L. 1968. Studies on Opilioacarida (Arachnida). II. Redescription of *Paracarus hexophthalmus* (Redikorzev). *Zoologische Mededelingen* 43:57–76.
- van der Hammen, L. 1969. Studies on Opilioacarida (Arachnida). III. *Opilioacarus platensis* Silvestri and *Adenacarus arabicus* (With). *Zoologische Mededelingen* 44:113–131.
- van der Hammen, L. 1971. La phylogénèse des Opilioacarides, et leur affinités avec les autres Acariens. *Acarologia* 12:465–473.
- van der Hammen, L. 1977. Studies on Opilioacarida (Arachnida). IV. The genera *Panchaetes* Naudo and *Salfacarus*, gen. nov. *Zoologische Mededelingen* 51:43–78.
- van der Hammen, L. 1982. Comparative studies in Chelicerata II. Epimerata (Palpigradi and Actinotrichidia). *Zoologische Verhandlungen* 196:1–70.
- Westwood, J.O. 1874. *Thesaurus Entomologicus Oxoniensis*. Clarendon Press, Oxford.
- Weygoldt, P. 1979. *Thelyphonellus ruschii* n. sp. und die taxonomische Stellung von *Thelyphonellus* Pocock 1894 (Arachnida: Uropygi: Thelyphonida). *Senckenbergiana Biologica* 60:109–114.
- Weygoldt, P. 1994. Amblypygi. Pp. 241–247. In *Encyclopaedia Biospeologica*. (C. Juberthie & V. Decu eds). Vol. 1. Société de Biospéologie, Moulis and Bucarest.
- Weygoldt, P. 1996a. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). *Journal of Zoological Systematics and Evolution Research* 34:185–202.
- Weygoldt, P. 1996b. The relationships of the south east African whip spiders *Hemiphrynus machadoi* Fage, 1951 and *Phrynichus scullyi* Purcell, 1901: introduction of the new generic names *Xerophrynus* and *Phrynichodamon* (Chelicerata: Amblypygi). *Zoologischer Anzeiger* 235:117–130.
- Weygoldt, P. 1998a. Evolution and systematics of the Chelicerata. *Experimental and Applied Acarology* 22:63–79.
- Weygoldt, P. 1998b. Revision of the species of *Phrynichus* Karsch, 1879 and *Euphrynichus* Weygoldt, 1995 (Chelicerata, Amblypygi). *Zoologica, Stuttgart* 147:1–65.
- Weygoldt, P. 1999a. Revision of the genus *Damon* C.L. Koch, 1850 (Chelicerata: Amblypygi: Phrynichidae). *Zoologica, Stuttgart* 150:1–45.
- Weygoldt, P. 1999b. Spermatophores and the evolution of female genitalia in whip spiders (Chelicerata, Amblypygi). *Journal of Arachnology* 27:103–116.
- Weygoldt, P. & H.F. Paulus. 1979a. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. I. Morphologische Untersuchungen. *Zeitschrift für die Zoologische Systematik und Evolutionforschung* 17:85–116.
- Weygoldt, P. & H.F. Paulus. 1979b. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. II. Cladogramme und die Entfaltung der Chelicerata. *Zeitschrift für die Zoologische Systematik und Evolutionforschung* 17:177–200.
- Whalley, P.E.S. 1980. Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon. *Bulletin of the British Museum of Natural History (Geology)* 33:157–164.
- Wheeler, W.C. & C.Y. Hayashi. 1998. The phylogeny of the extant chelicerate orders. *Cladistics* 14:173–192.
- With, C.J. 1902. A new acaride *Opilioacarus segmentatus*. *Compte Rendu du Congrès des Naturalistes et Médecins du Nord*:4–5.
- With, C.J. 1904. The Notostigmata, a new suborder of Acari. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* 1904:137–191.

Manuscript received 13 August 2001, revised 9 April 2002.