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The smaller arachnid orders: diversity, descriptions and distributions from Linnaeus to the present (1758 to 2007)*

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Abstract

Carolus Linnaeus' contribution to the study of the smaller arachnid orders was modest with the description of four taxa: the pseudoscorpions *Acarus cancroides* and *A. scorpioides*, the whip scorpion *Phalangium caudatum*, and the whip spider *P. reniforme*. Since then, more than 5,100 species have been named in eight orders by a plethora of researchers. Trends in species descriptions over time are explored; the presence of different accumulation curves for some orders is thought to be due to advances in the study of morphology combined with a greater focus on collecting small arachnids in tropical ecoregions. Pseudoscorpion species richness is examined against log-transformed area data for all countries of the world. Anomalies, such as the poor representation of pseudoscorpion diversity in some large countries such as China, appear to be due to a low number of active researchers.

Key words: Arachnida, Opilioacariformes, Ricinulei, Palpigradi, Uropygi, Amblypygi, Schizomida, Solifugae, Pseudoscorpiones, richness, systematics

Introduction

The starting point of zoological nomenclature commenced with the 10th edition of *Systema Naturae* by Carolus Linnaeus published in 1758. The only work deemed to have preceded this publication was by his contemporary Carl A. Clerck who named many Swedish spiders (Clerck 1758). Despite several arachnological works claiming the date of this publication as 1757, the International Commission for Zoological Nomenclature has

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determined the actual date of publication of both Linnaeus (1758) and Clerck (1758) to be 1 January 1758 (Article 3, International Commission on Zoological Nomenclature 1999). The great methodological breakthrough in Linnaeus's work was the consistent use of a binominal nomenclatorial system utilizing a combination of a generic name and a species name allowing biologists to communicate in a universal manner. This innovative system has remained unchanged for nearly 250 years.

Linnaeus (1758) grouped all animals into six classes: Mammalia, Aves, Amphibia, Pisces, Insecta and Vermes. The Insecta were further divided into seven orders: Coleoptera, Hæmiptera, Lepidoptera, Neuroptera, Hymenoptera, Diptera and Aptera. The Aptera—which contained all of the taxa now grouped in the Arachnida, along with Crustacea, Myriapoda and some wingless hexapods, consisted of 14 genera: *Lepisma* (silverfish), *Podura* (springtails), *Termes* (termites), *Pediculus* (lice), *Pulex* (fleas), *Acarus* (mites), *Phalangium* (harvestmen), *Aranea* (spiders), *Scorpio* (scorpions), *Cancer* (crabs), *Monoculus* (copepods), *Oniscus* (woodlice), *Scolopendra* (centipedes) and *Julus* (millipedes). Nowadays, each of these genera represent much higher taxonomic ranks, including independent orders and classes of arthropods.

The Arachnida are one of the longest-surviving and diverse groups of organisms. Their fossil record dates back to the Palaeozoic, and several extant orders are represented as fossils from the Devonian or Silurian (e.g. Dunlop 1997; e.g. Selden 1993; Selden and Dunlop 1998; Selden *et al.* 1991; Shear 1991; Shear *et al.* 1989), predating numerous other extant clades of living organisms. In this short dissertation, I wish to concentrate on a small fraction of the arachnids originally placed by Linnaeus within the genera *Acarus* and *Phalangium* as a way of exploring patterns of discovery in the smaller arachnid orders, including the orders Opilioacariformes, Ricinulei, Palpigradi, Uropygi, Amblypygi, Schizomida, Solifugae, Pseudoscorpiones (Harvey 2002b). This will commence by examining the four species named by Linnaeus, then by updating the data on species richness presented by Harvey (2002b) for these eight orders. Finally I wish to explore the numbers of pseudoscorpions (the most diverse taxon considered within the smaller arachnid orders) found in different regions of the world, and the prospects for more complete documentation of these animals on a global scale.

The Linnaean Legacy

Pseudoscorpions (Order Pseudoscorpiones)

Of the 31 species of *Acarus* treated by Linnaeus (1758), two were pseudoscorpions, *A. cancroides* Linnaeus, 1758 from Europe and *A. scorpioides* Linnaeus, 1758 from America, and both are easily recognized as pseudoscorpions by Linnaeus' clear description of the pedipalps. A third pseudoscorpion, *Phalangium acaroides*, was added by Linnaeus (1767), but this represents a superfluous replacement name for *A. scorpioides* as it is seemingly based upon the same specimens, thus making *P. acaroides* a junior objective synonym of *A. scorpioides*. In that publication he transferred the pseudoscorpions to the genus *Phalangium* Linnaeus, 1758. The three species epithets employed by Linnaeus clearly demonstrate the unusual morphological qualities of these small arachnids—*cancroides* meaning crab-like, *scorpioides* meaning scorpion-like, and *acaroides* meaning mite-like. The description of *A. cancroides* was given as "A[carus]. antennis cheliformibus, abdomine ovato depresso"; i.e. an *Acarus* with chelate pedipalps and a flat, ovate abdomen. *Acarus scorpioides* was described as "A[carus]. antennis cheliformibus, abdomine cylindrico, capite appendiculato"; i.e. an *Acarus* with chelate pedipalps, cylindrical abdomen and head appendages (probably referring to the chelicerae). *Phalangium acaroides* was from tropical America ("America calidiore") and described as "P[halangium]. Abdomine cylindrico, chelis laevibus, capite appendiculato"; i.e. a species of *Phalangium* with a cylindrical abdomen, smooth pedipalps and head appendages.

These descriptions are not particularly illuminating and, to my knowledge, no modern worker has examined in detail any surviving type material that might exist. The modern diagnoses of these species are probably based upon historical convention rather than any detailed knowledge of the original specimens.

Acarus cancroides was swiftly transferred to a separate genus, *Chelifer* Geoffroy, 1762 (Geoffroy 1762) where it has remained ever since. Ironically, Geoffroy's work was deemed to not be a valid publication due to the inconsistent use of binominal nomenclature, and the name *Chelifer* was only validated by the International Commission on Zoological Nomenclature (1989) following an application to conserve the name of this classical pseudoscorpion.

For many years, *Chelifer* was one of only a handful of pseudoscorpion genera, and for the next 100 years only five additional genus-group taxa were named: *Obisium* Illiger, 1798 (now a synonym of *Chelifer*); *Chthonius* C.L. Koch, 1843; *Chelifer (Chelanops)* Gervais, 1849 (now a valid genus); *Cheiridium* Menge, 1855; and *Chernes* Menge, 1855. Between 1804 and 1937, over 250 pseudoscorpion species were named within the genus *Chelifer* but all have since been transferred to other genera. Indeed, in its current conformation (e.g. Beier 1932; Chamberlin 1932), *Chelifer* contains only a single species, *C. cancroides* – which is found in most regions of the world, presumably inadvertently introduced by humans.

Acarus scorpioides was recorded from "America" by Linnaeus (1758), but the location was altered, probably without good reason, to Suriname by Hagen (1867). The modern identity of this species was established by Beier (1948) who transferred it to the genus *Cordylochernes*. Like *Chelifer cancroides*, the identity of *C. scorpioides* has not been tested through the examination of any type specimens. However, such examination cannot reconcile the genetic variation found within populations currently referred to *C. scorpioides* by Zeh and Zeh (1994a) who found significant differences in behavioural cues and spermatophore morphology, and extensive divergence in nine electrophoretic loci and in microsatellite DNA, despite the lack of any significant morphological features, especially in the males which display modifications on some pedipalpal segments.

Since 1992, *Cordylochernes scorpioides* has become one of the most intensely studied arachnids through the work of David and Jeanne Zeh and their collaborators (e.g. Zeh and Zeh 1992a, 1992b, 1994a, 1997, 1999; Zeh *et al.* 1997; Zeh *et al.* 1992; Zeh *et al.* 1994; Zeh 1997; Zeh *et al.* 1998; Zeh and Zeh 1994b, 2006; Zeh *et al.* 2003; Zeh *et al.* 2001).

Whip scorpions (Order Uropygi)

Three species were treated in the genus *Phalangium* by Linnaeus (1758), *P. opilio* Linnaeus, 1758, *P. caudatum* Linnaeus, 1758 and *P. reniforme* Linnaeus, 1758. The harvestman *Phalangium opilio* is common in Europe and North America, and has been found in several other parts of the world such as New Zealand where it has been inadvertently introduced by humans (Forster and Forster 1999). This genus is now included in the arachnid order Opiliones, which contains a vast array of taxa found all over the world (Pinto-da-Rocha *et al.* 2007).

The second species of *Phalangium* described by Linnaeus, *P. caudatum*, was named for the long tail-like structure situated at the terminal end of the opisthosoma, nowadays referred to as the flagellum. The description was incredibly short, "P. chelis ramosis, abdominie mucronato". The distribution was given as "Habitat in India" but this has since been refined to the Indonesian island of Java by Linnaeus (1764, 1767). Linnaeus' specimen of *P. caudatum*, lodged in the Uppsala University, Museum of Evolution (Wallin 1994), was examined by Lönnberg (1897, 1898), thus providing some clue to the identity of this species. This species was subsequently placed in its own genus, *Thelyphonus*, named by Latreille (1802). *Thelyphonus* and its relatives form the modern order Uropygi (sometimes called Thelyphonida), and consist of 108 Recent species placed in 18 genera (Table 1). Whip scorpions have also been found in Carboniferous (*Geralinura* Scudder, 1884 and *Proschizomus* Dunlop and Horrocks, 1997) and Cretaceous deposits (*Mesoproctus* Dunlop, 1998).

Whip spiders (Order Amblypygi)

The third species of *Phalangium* described by Linnaeus (1758), *P. reniforme*, was diagnosed as "P. antennis corpore longioribus, thorace reniformi" and occurred in "America". The specific epithet referred to the reniform carapace, a feature found in most amblypygids (Weygoldt 2000). The type specimen of *P. reniforme*, lodged in the Uppsala University, Museum of Evolution, was also examined by Lönnberg (1897, 1898) who suggested that the specimen should be regarded as the type, rather than any specimens associated with the literature references that were cited by Linnaeus.

The identity of *P. reniforme* vacillated for decades, sometimes referring to a Central American species, and at other times referring to an Asian species. Over the years *P. reniforme* has been referred to the genera *Tarantula* Fabricius, 1793, *Phrynus* Lamarck, 1801 and *Damon* C.L. Koch, 1850, before being designated the type species of the new genus *Phrynichus* Karsch, 1879 by Karsch (1879) who suggested that the species was found in Sri Lanka. Even though the original type specimen of *P. reniforme* was lodged in Uppsala University, Museum of Evolution (Wallin 1994), Weygoldt (1998, 2002) preferred to use the binomen *Phrynichus ceylonicus* (C.L. Koch, 1843) for this species, claiming that the name *P. reniforme* was hopelessly compromised by inaccurate usage for over two centuries. This decision was later ratified by the International Commission on Zoological Nomenclature (2004).

TABLE 1. Numbers of valid Recent families, genera and species of the smaller arachnid orders.

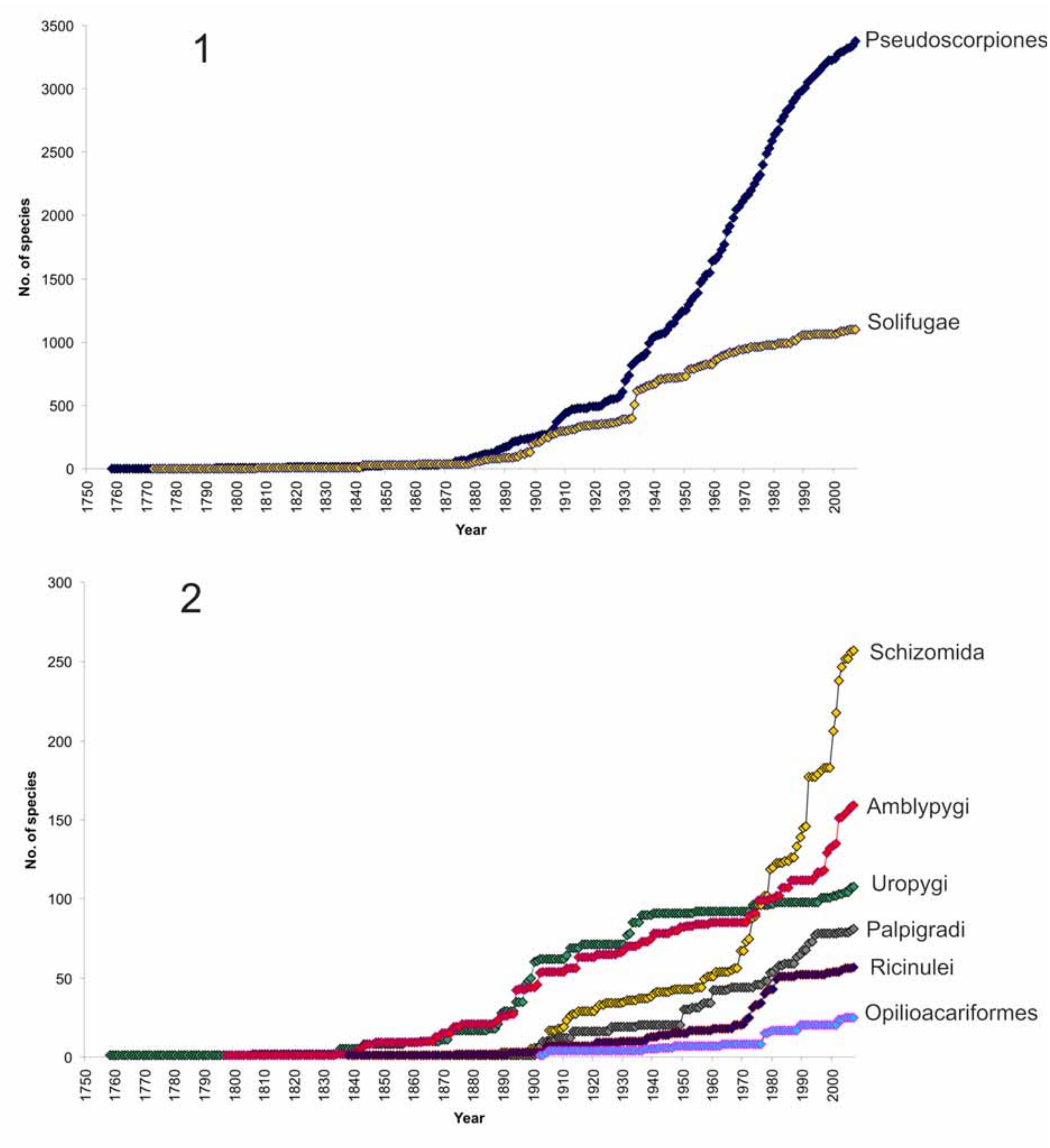
	Families	Genera	Species
Opilioacariformes	1	8	24
Ricinulei	1	3	58
Palpigradi	2	6	82
Uropygi	1	18	108
Amblypygi	5	17	158
Schizomida	2	46	258
Solifugae	12	141	1,100
Pseudoscorpiones	25	439	3,380
TOTAL	49	678	5,168

Diversity of the smaller arachnid orders

Since the pioneering, but extremely limited, publications of Linnaeus (1758, 1767) which produced four valid species, the known diversity of the smaller arachnid orders has increased such that there are now over 5,000 recognized species (Table 1). The smaller arachnid orders were recently documented by Harvey (2002b) who recorded the number of valid taxa (families, genera, species and subspecies) and plotted the naming of new taxa (genera and species) over time. These data have been updated for the intervening seven years (the original data set was valid until December 2000), and the number of valid families, genera and species (valid until September 2007) is outlined in Table 1. The description of novel taxa plotted over time shows a somewhat steady increase in the numbers of new taxa (Figures 1, 2). Several different trends, however, are apparent within the eight orders.

The description of new species of pseudoscorpions has continued on a fairly steady trend since the 1940s (Figure 1), although a slight rate reduction was apparent after the passing in 1979 of Max Beier of the Naturhistorisches Museums, Wien, whose prolific output resulted in the description of more than 1,200 pseudoscorpion species of which 1,180 are currently listed as valid species. This phenomenal publication rate represented in the description of 36% of the currently recognized species (Figure 4). The next most productive describers of pseudoscorpion species, V. Mahnert (278 species), W.B. Muchmore (271 species), J.C. Chamberlin (179 species), C.C. Hoff (125 species), B.P.M. Ćurčić (112 species), E. Ellingsen (81 species), M.S. Harvey (80 species), and V. Redikorzev (65 species), have contributed 34% of the total diversity, and all other workers have described 30% of the fauna. Typical of many scientific disciplines, none of these authors worked in the developing world—all were based in Europe, U.S.A. or Australia—despite the vast majority of pseudoscorpion species occurring outside of these three areas.

The rate of description of solifuge species (Order Solifugae, Figure 1) has barely altered since 2000. Harvey (2002b) noted the rapid rise of named species during the 1930's due to the prolific output of C.F. Roewer (1932, 1933, 1934) whose taxonomic legacy, while productive, left a barely tenable classification that will take a generation of researchers to unravel.



FIGURES 1–2. Numbers of valid Recent species of the smaller arachnid orders, 1758-2007: 1, Pseudoscorpiones and Solifugae; 2, Schizomida, Amblypgi, Uropygi, Palpigradi, Ricinulei and Opilioacariformes.

Schizomids (Order Schizomida) have undergone a very different taxonomic history from the Pseudoscorpions and Solifugae. Species diversity was poorly represented until the pioneering works of P.M. Brignoli (e.g. Brignoli 1973) and J.M. Rowland and J.R. Reddell (e.g. Rowland and Reddell 1979a, 1979b, 1980, 1981), who found substantial and important taxonomic characters within the female genitalic system enabling the easy recognition of distinct species. These observations, coupled with more detailed collecting in tropical regions of the world, have resulted in a rapid increase in species descriptions since 1970 (Figure 2).

The numbers of known whip spiders (Amblypygi) remained relatively stable during much of the 20th century but a noticeable rise in the description rate can be seen since the 1990's (Figure 2), largely due to the efforts of P. Weygoldt who, with a variety of collaborators, has described 22 new species since 1998.

Whip scorpion (Uropygi) diversity has only increased marginally since the 1930's (Figure 2) and it seems likely that the total diversity of this group is relatively small and will not grow substantially in the future. Nevertheless, 10 species have been named since 1996 (Armas 2000, 2002; Ballesteros and Francke 2006; Haupt 1996, 2004; Haupt and Song 1996; Víquez and Armas 2006, 2007). More importantly, perhaps, has been the recognition of three new genera from central America and the Caribbean region (Víquez and Armas 2005, 2006), raising the number of recognized genera to 18.

The rate of discovery of new palpigrades (Order Palpigradi) has been fairly constant over much of the 20th century, but two marked rate increases are apparent. P. Rémy described 21 new species between 1950 and 1960, and B. Condé named 34 species between 1956 and 1995 (Figure 2). Between them they have named 68% of the recognized palpigrade fauna of the world.

Once considered the rarest and most enigmatic of all arachnids, ricinuleid (Order Ricinulei) diversity remained steady until the middle of the 20th century (Figure 2), with only 18 species named to 1960. The 'golden era' of ricinuleid taxonomy occurred between 1967 and 1982 with 31 species descriptions, and a further six species between 1998 and 2007.

The least diverse living arachnid order, the Opilioacariformes, has had a modest descriptive rate (Figure 2), with a total of 24 species, four of these in a single recent publication (Vázquez and Klompen 2002).

The smaller arachnid orders represent only a small fraction of total arthropod diversity but are still higher than the total number of Recent mammals, of which there are estimated to be some 4,629 species (data obtained from http://earthtrends.wri.org; accessed 24 October 2007). Indeed, the rate of discovery of new species of these eight arachnid orders is somewhat greater than the rate of discovery and description of new mammal species, although they attract far less press coverage than mammals. Whilst new species of the smaller arachnid orders are regularly being described, the descriptive process lags far behind the discovery and recognition of new species, as the rate of description is dependent upon a specialist actively working on the fauna.

Pseudoscorpion species richness

The species richness of pseudoscorpions was assessed using records of named species from individual countries or major principalities of the world, based upon an unpublished database maintained by the author. These data are presented in Table 2, along with land surface area of each country (sourced from The Times Comprehensive Atlas of the World 1999). By plotting species richness against log-transformed land area (Kuntner and Šereg 2002), patterns of recorded diversity could be visually assessed (Figure 4).

The most diverse countries to date, each with over 100 recorded species, are the U.S.A. excluding Hawaii and off-shore territories (402 species), Italy (223 species), Spain including Islas Baleares (but excluding Islas Canarias) (191 species), Brazil (167 species), Australia (165 species), Mexico (160 species), India (141 species), South Africa (134 species), Kenya (131 species), Greece (123 species), France (121 species) and the Democratic Republic of the Congo (101 species). There appear to be a variety of different reasons why each of these countries has such high described diversity.

The fauna of the mainland U.S.A. has been extensively named and studied, principally by J.C. Chamberlin, C.C. Hoff, W.B. Muchmore and their collaborators, who between them have described 291 species representing 72% of the fauna. Of a total named fauna of over 400 species, nearly 150 species from the U.S.A. have been described from caves, the vast majority of which represent highly modified cave-dwelling species with troglomorphic adaptations including depigmentation, loss or reduction of eyes and attenuated appendages.

The European region has a rich tradition of pseudoscorpion research, fostered by prolific authors such as M. Beier, G. Callaini, B.P.M. Ćurčić, R.N. Dimitrijeviæ, G. Gardini, J. Hadži, J. Heurtault, L. Koch, V. Mahnert, E. Simon, M. Vachon, J. Zaragoza and their various collaborators studying and naming the local fauna. The high diversity levels found in the larger Mediterranean countries of Italy, Greece, France and Spain are partly due to more favourable climatic variables, combined with historical factors; most importantly the lack of glaciation during the Pleistocene. In addition, there are high numbers of troglomorphic species from the numerous karst systems that exist in the region.

The Brazilian fauna, currently consisting of 167 species, has been studied by a variety of researchers but 30 species were named by M. Beier between 1930 and 1974, and 67 species have been named by V. Mahnert and his co-workers since 1979. This figure is clearly a small proportion of the total fauna, and numerous new species await discovery and description.

Australian pseudoscorpions have been studied by several specialists, and of the 164 species, 57 were named by M. Beier between 1933 and 1976, and 64 species have been named by M. Harvey and his co-workers since 1981. Like the Brazilian fauna, the Australian pseudoscorpion fauna is much larger than current named species would indicate, and Yeates *et al*. (2004) estimated that 750 species may occur in the region, some of which fit the criteria for short-range endemic taxa as defined by Harvey (2002a).

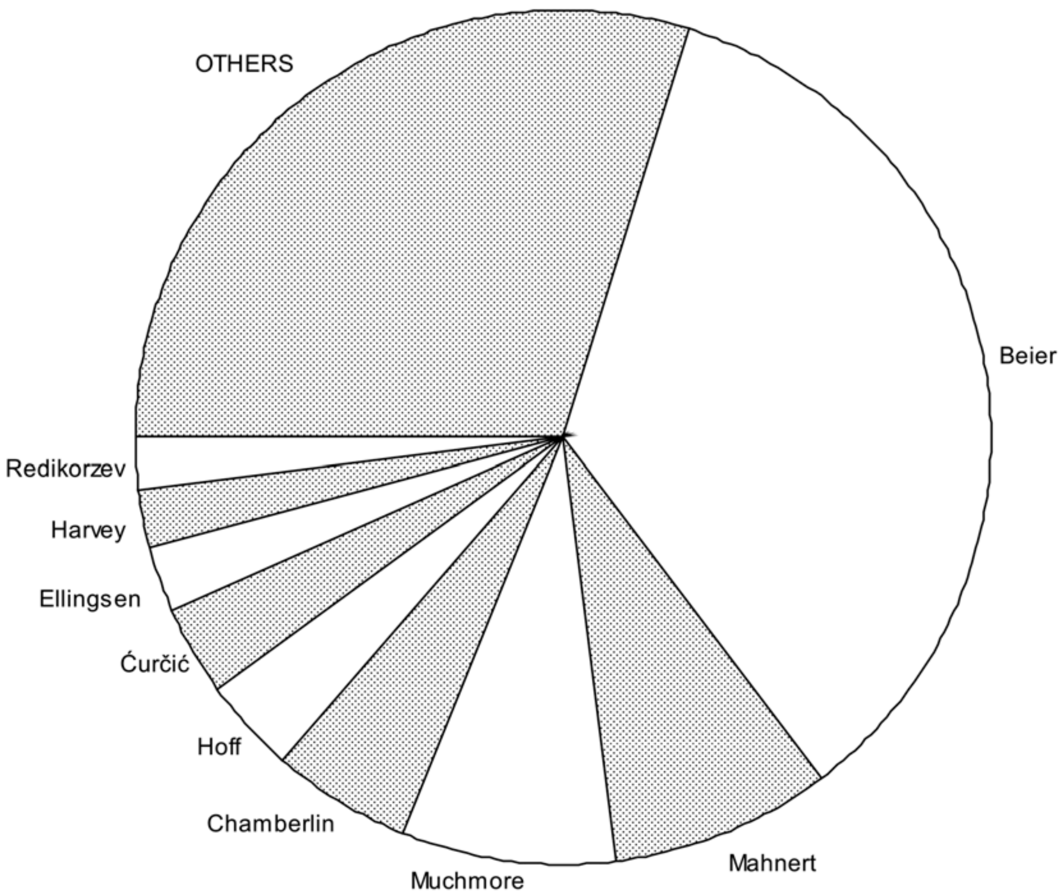


FIGURE 3. Proportion of pseudoscorpion species described by various authors, 1758–2007.

TABLE 2. Numbers of pseudoscorpion species recorded from individual countries, and in some cases separate territories (denoted with *), with land area per region (The Times Comprehensive Atlas of the World 1999).

Region	Country	No. of species	Area (km^2)
AFRICA	Algeria	46	2,381,741
	Angola	6	1,246,700
	Benin	0	112,620
	Botswana	2	581,370
	Burkina Faso	0	274,200
	Burundi	4	27,835
	Cameroon	25	475,442
	Cape Verde	4	4,033
	Central African Republic	3	622,436
	Chad	23	1,284,000
	Comoros	0	719
	Congo, Republic of the...	28	342,000
	Côte d'Ivoire	28	322,463
	Democratic Republic of the Congo	101	2,345,410
	Djibouti	1	23,200
	Egypt	12	1,000,250
	Equatorial Guinea	9	28,051
	Eritrea	2	117,400
	Ethiopia	20	1,133,880
	French Southern and Antarctic Lands*	2	7,781
	Gabon	7	267,667
	Gambia	0	11,295
	Ghana	11	238,537
	Guinea	17	245,857
	Guinea-Bissau	9	36,125
	Îles Glorieuses*	1	5
	Islas Canarias*	47	7,447
	Ilhas Selvagens*	5	3
	Kenya	131	582,646
	Lesotho	9	30,355
	Liberia	2	111,369
	Libyan Arab Jamahiriya	14	1,759,540
	Madagascar	13	587,041
	Madeira*	21	779
	Malawi	6	118,484
	Mali	26	1,240,140
	Mauritania	2	1,030,700

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TABLE 2 (continued)

Region	Country	No. of species	Area (km^2)
	Mauritius	4	2,040
	Mayotte*	1	373
	Morocco	38	446,550
	Mozambique	8	799,380
	Namibia	39	824,292
	Niger	2	1,267,000
	Nigeria	4	923,768
	Réunion*	6	2,551
	Rwanda	7	26,338
	Sao Tome and Principe	9	964
	Senegal	5	196,720
	Seychelles	23	455
	Sierra Leone	2	71,740
	Somalia	21	637,657
	South Africa	134	1,219,090
	St Helena*	13	121
	Sudan	13	2,505,813
	Swaziland	0	17,364
	Togo	5	56,785
	Tunisia	25	164,150
	Uganda	29	241,038
	United Republic of Tanzania	52	945,087
	Zambia	3	752,614
	Zimbabwe	27	390,759
ASIA	Afghanistan	32	652,225
	Armenia	19	29,800
	Azerbaijan	49	86,600
	Bahrain	0	691
	Bangladesh	2	143,998
	Bhutan	11	46,620
	British Indian Ocean Territory*	1	60
	Brunei Darussalam	0	5,765
	Cambodia	15	181,000
	China	50	9,584,492
	Democratic People's Republic of Korea	0	120,538
	Georgia	46	69,700
	India	141	3,065,027
	Indonesia	81	1,919,445

...... continued

TABLE 2 (continued)

Region	Country	No. of species	Area (km²)
	Iran, Islamic Republic of...	39	1,648,000
	Iraq	2	438,317
	Israel	39	20,770
	Japan	66	377,727
	Jordan	2	89,206
	Kazakhstan	25	2,717,300
	Kuwait	1	17,818
	Kyrgyzstan	24	198,500
	Lao People's Democratic Republic	9	236,800
	Lebanon	10	10,452
	Malaysia	35	332,965
	Maldives	1	298
	Mongolia	23	1,565,000
	Myanmar	14	676,577
	Nepal	37	147,181
	Oman	83	309,500
	Pakistan	30	803,940
	Philippines	41	300,000
	Qatar	0	11,437
	Republic of Korea	17	99,274
	Saudi Arabia	16	2,200,000
	Singapore	4	639
	Sri Lanka	43	65,610
	Syrian Arab Republic	9	185,180
	Tajikistan	18	143,100
	Thailand	44	513,115
	Timor-Leste	0	14,874
	Turkey	88	779,452
	Turkmenistan	26	488,100
	United Arab Emirates	0	83,600
	Uzbekistan	26	447,400
	Viet Nam	60	329,565
	Yemen	26	527,968
EUROPE	Albania	16	28,748
	Andorra	1	465
	Austria	69	83,855
	Belarus	0	207,600
	Belgium	23	30,520

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TABLE 2 (continued)

Region	Country	No. of species	Area (km²)
	Bosnia and Herzegovina	51	51,130
	Bulgaria	51	110,994
	Croatia	99	56,538
	Cyprus	12	9,251
	Czech Republic	37	788,864
	Denmark	19	43,075
	Estonia	2	45,200
	Finland	16	338,145
	France	121	543,965
	Germany	49	357,028
	Greece	123	131,957
	Hungary	40	93,030
	Iceland	2	102,820
	Ireland	17	70,282
	Italy	223	301,245
	Latvia	11	63,700
	Liechtenstein	0	160
	Lithuania	0	65,200
	Luxembourg	2	2,586
	The former Yugoslav Republic of Macedonia	43	25,713
	Malta	23	316
	Moldova	4	33,700
	Monaco	0	2
	Netherlands	0	41,526
	Norway	16	323,878
	Poland	38	312,683
	Portugal (mainland)	36	88,940
	Portugal (Azores)*	10	2,300
	Romania	70	237,500
	San Marino	0	61
	Slovakia	38	49,035
	Slovenia	31	20,251
	Spain (mainland, Islas Baleares)	191	504,782
	Sweden	21	449,964
	Switzerland	40	41,293
	Ukraine	21	603,700
	United Kingdom of Great Britain and Northern Ireland	28	244,082
	Yugoslavia (Montenegro & Serbia)	91	120,173

...... *continued*

TABLE 2 (continued)

Region	Country	No. of species	Area (km²)
EUROPE/ASIA	Russian Federation	32	17,075,400
NORTH AMERICA	Antigua and Barbuda	1	442
	Bahamas	4	13,939
	Barbados	1	430
	Belize	10	22,965
	Bermuda*	1	54
	Canada	24	9,970,610
	Cayman Islands*	8	259
	Costa Rica	23	51,100
	Cuba	27	110,860
	Dominica	1	750
	Dominican Republic	26	48,442
	El Salvador	10	21,041
	Grenada	3	378
	Guadeloupe*	8	1,780
	Guatemala	17	108,890
	Haiti	3	27,750
	Honduras	0	112,088
	Jamaica	31	10,991
	Martinique*	5	1,079
	Mexico	160	1,972,545
	Netherlands Antilles*	14	800
	Nicaragua	2	130,000
	Panama	15	77,082
	Puerto Rico*	18	9,104
	Saint Kitts and Nevis	1	261
	Saint Lucia	0	616
	Saint Vincent and the Grenadines	9	389
	Trinidad and Tobago	15	5,130
	U.K. Virgin Islands*	2	153
	United States of America (mainland)	402	9,809,378
	U.S. Virgin Islands*	12	352
OCEANIA	American Samoa	1	197
	Australia	165	7,682,395
	Cook Islands*	1	293
	Fiji	3	18,330
	French Polynesia*	4	3,265
	Guam*	5	541

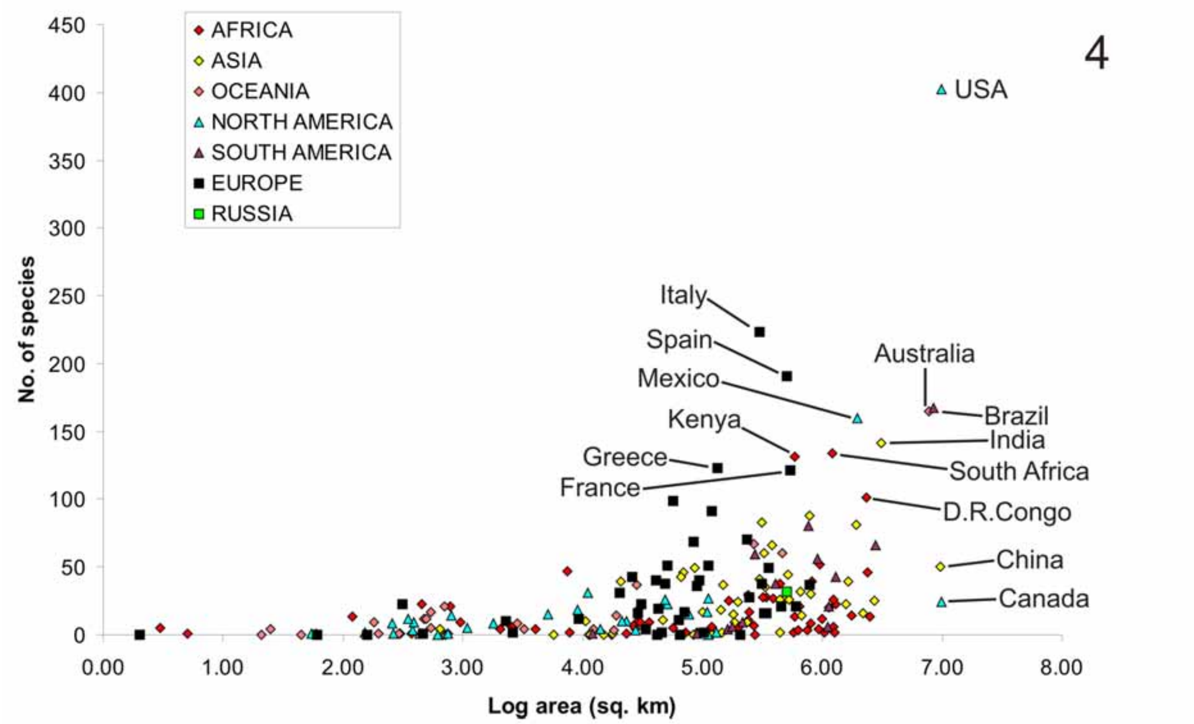
...... continued

TABLE 2 (continued)

Region	Country	No. of species	Area (km^2)
	Hawaii*	17	
	Kiribati	0	717
	Marshall Islands	9	181
	Micronesia, Federated States of...	21	701
	Nauru	0	21
	New Caledonia*	14	19,058
	New Zealand	67	270,534
	Northern Mariana Islands*	12	477
	Palau	12	497
	Papua New Guinea	60	462,840
	Pitcairn Islands*	0	45
	Samoa	8	2,831
	Solomon Islands	37	28,370
	Tonga	1	748
	Tuvalu	4	25
	Vanuatu	4	12,190
SOUTH AMERICA	Argentina	66	2,766,889
	Bolivia	6	1,098,581
	Brazil	167	8,547,379
	Chile	80	756,945
	Colombia	21	1,141,748
	Ecuador	59	272,045
	Falkland Islands*	1	12,170
	French Guiana*	1	90,000
	Guyana	9	214,969
	Paraguay	38	406,752
	Peru	43	1,285,216
	Suriname	4	163,820
	Uruguay	6	176,215
	Venezuela	56	912,050

The Mexican pseudoscorpion fauna consists of 160 species, of which 33 were named by J.C. Chamberlin between 1921 and 1947, and 55 by W.B. Muchmore and his collaborators between 1969 and 1998. Only 29 Mexican species are also found in the U.S.A., most of which are found near the contiguous border shared by these two countries.

The Indian fauna of 141 species is the most diverse within the Asian region, with 33 species named by M. Beier between 1930 and 1978, and 53 species by V.A. Murthy (mostly with T.N. Ananthakrishnan) between 1960 and 1977. The synopsis published by Murthy and Ananthakrishnan (Murthy and Ananthakrishnan 1977) is a useful guide to the pseudoscorpion fauna of the region.



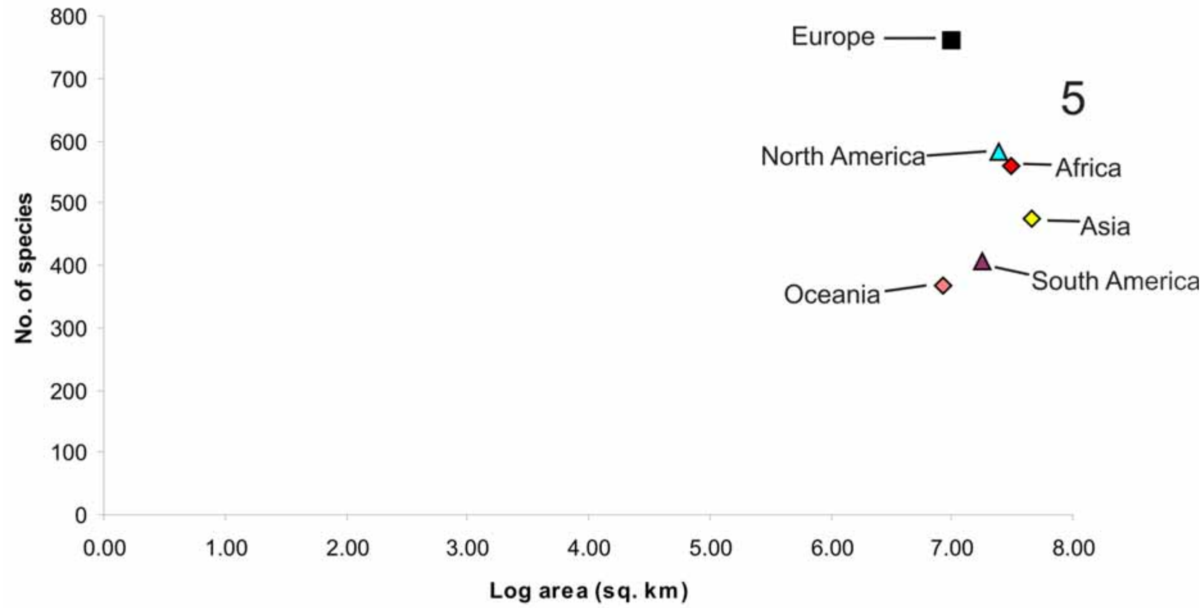


FIGURE 4. Pseudoscorpion species diversity plotted against log country area.
FIGURE 5. Pseudoscorpion species diversity plotted against log continental area.

Only three African countries have more than 100 species currently recorded. The South African fauna of 134 species has been mostly described by M. Beier who named 74 species between 1931 and 1970 and A. Tullgren with 24 species mostly described in three papers published in 1907 and 1908. The 131 species recorded from Kenya were described by M. Beier with 56 species between 1932 and 1967, and V. Mahnert with 51 species between 1981 and 1988. The fauna of the Democratic Republic of Congo (formerly Zaire) of 101 species was largely named by M. Beier with 77 species between 1932 and 1979, based upon collections made by various Belgian expeditions to the region.

The remaining countries possess fewer than 100 species, with many large countries having only a handful of recorded species. For example, eight countries of over 1,000,000 km^2 have fewer than 20 recorded species, including Mauritania (2 species), Niger (2 species), Angola (6 species), Bolivia (6 species), Egypt (12 species), Libya (14 species), Sudan (13 species) and Saudi Arabia (16 species). These data points are situated near the bottom-right section of Figure 4. In comparison, the vast majority of countries lying within the upper-left region of the data points, i.e. those with high species richness per land area, are mostly from Europe. It can be expected that with further taxonomic research in other regions of the world, many countries will approach or even surpass the European values. Notable is the recorded diversity of the five largest countries of the world. As discussed previously, the U.S.A. is relatively well-known with 402 species, followed by Australia and Brazil with 165 and 167 species, respectively. China and Canada, on the other hand have only 50 and 24 species, respectively. The low value for Canada is easily explained by its high latitudinal position and inhospitable climate for pseudoscorpions. The vast ice-sheets of North America that covered all of Canada during the Pleistocene (Williams *et al.* 1998) undoubtedly destroyed the pre-Pleistocene fauna and the entire fauna is the result of post-Pleistocene migration. The presence of only a single species endemic to Canada (*Syarinus palmeni* Kaisila, 1964 from Newfoundland) reinforces this observation. China, on the other hand, is poorly represented (see Schawaller 1995; see Mahnert 2003) despite its enormous land area, large latitudinal and altitudinal range and high ecological diversity.

Similar conclusions can be drawn when compiling the species diversity data for the six major geographical regions inhabited by pseudoscorpions (Table 3, Figure 5). The greatest recorded diversity occurs in Europe with 760 species, followed by North America with 583 species, Africa with 559 species, Asia with 476 species, South America with 405 species and Oceania with 367 species. European and North American diversity is primarily concentrated in the southern areas that were relatively unaffected by Pleistocene glaciation events (Williams *et al.* 1998), but the pseudoscorpion faunae of Asia, Africa, South America and Oceania are obviously understudied in comparison with the northern regions.

TABLE 3. Pseudoscorpion diversity for each major geographic region, with land area (The Times Comprehensive Atlas of the World 1999) and fitted least-squares values.

Region	No. of species	Area (km^2)	Regression value (R^2)
AFRICA	559	30,343,578	0.09
ASIA	476	45,036,492	0.27
EUROPE	760	9,908,599	0.16
NORTH AMERICA	583	24,680,331	0.31
OCEANIA	367	8,504,256	0.63
SOUTH AMERICA	405	17,815,420	0.53

Summary

Despite the landmark achievement of Carolus Linnaeus in formulating the binominal system of nomenclature, his descriptions can be hardly regarded as helpful, and descriptive standards have improved dramatically over the past 250 years. It is somewhat lamentable that up until the mid-20th century the descriptions of many species of the smaller arachnid orders provided very few taxonomic illustrations. That trend has fortunately passed with modern descriptions often providing numerous line drawings, photographs or scanning electron micrographs to more fully document the morphology of the taxa in question.

The rate of publication of new species of the smaller arachnid orders varies between the different orders. The smallest orders have marked rate increases when specialist taxonomists become interested in a particular taxon (e.g. Ricinulei, Palpigradi) or when methodological advances occur (e.g. Schizomida). However, there does not appear to be a true asymptote being approached for any of the orders, except perhaps for the Solifugae (Figure 1) and Uropygi (Figure 2), although in the case of Solifugae this may simply represent a lack of taxonomists currently working on these extraordinary animals.

Of course, naming a species cannot be considered as the pinnacle of a taxonomic career. Some of the best taxonomic descriptions have been presented as parts of revisionary systematic papers, and some of the least informative taxonomic descriptions have been those of new species. Nevertheless, the data presented in this paper allow for trends to be observed and regional gaps in our knowledge to be assessed through analyses highlighting regions of low species richness (Figure 4).

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