

Phylogeny and classification of Pholcidae (Araneae): an update

Bernhard A. Huber: Alexander Koenig Research Museum of Zoology, Adenauerallee 160, 53113 Bonn, Germany.

E-mail: b.huber.zfmk@uni-bonn.de

Abstract. For over 100 years, Eugène Simon's system of pholcid classification has been used with only minor modifications. Phylogenetic research over the last decade has shown that some fundamental changes are necessary if the formal system is to reflect putative evolutionary relationships. Based on cladistic analyses of morphological and molecular data and on qualitative character assessment, the family is here divided into five subfamilies: Ninetinae, Arteminae, Modisiminae, Smeringopinae, and Pholcinae. All currently valid genera are placed in a cladogram. Even though the evidence supporting some of the nodes and assignments is weak, the cladogram generates numerous testable hypotheses and provides an improved framework for the mapping of 'new' characters like those from sperm ultrastructure and chromosome analysis.

Keywords: Ninetinae, Arteminae, Modisiminae, Smeringopinae, Pholcinae

When Simon (1893) presented the first classification of Pholcidae, he did so in the Linnaean tradition, with similarity as the main grouping criterion. His system (Table 1) proved to be useful as a means to organize information, and for over 100 years it was used with only minor modifications. New genera were added, some genera were shifted to other groups, and some of Simon's groups were merged, but judging from our current view of pholcid phylogeny, the two major updates by Petrunkevitch (1928) and Mello-Leitão (1946) were quite obviously based on a poorer understanding of the family than Simon's original system (a view already expressed by Brignoli 1972a, 1972b, 1980).

The first phylogenetic analysis of the family (in Huber 2000) indicated that some of Simon's groups were very likely not monophyletic, but for several reasons I hesitated to present a new formal system because: 1) some of the major clades did not seem well supported (e.g., ninetines, holocnemines); 2) the taxon sample of some major groups was inadequate (especially true for Old World taxa); and 3) forthcoming projects were likely to result in further changes to our understanding of pholcid phylogeny. I thus decided to use provisional, informal names such as "ninetines", "holocnemines", "New World clade", and "pholcines" rather than formal subfamily names (Huber 2000).

Since 2000, several further phylogenetic analyses have been published, using both morphological and molecular data (Astrin et al. 2007; Bruvo-Madarić et al. 2005; Huber 2001, 2003a, 2003b, 2003c, 2005a, 2005b, 2007). Even though many of the same reasons that prevented me from publishing a formal system in 2000 could still be invoked, it appears justified to present the systematic *status quo* after a decade of phylogenetic work on the family Pholcidae. Some major clades now appear well supported and likely to be stable, and most genera can be placed with some confidence into one of these groups. The current paper is thus an attempt to summarize, update, and formalize the subfamily-level classification of the Pholcidae. However, the system below is a working hypothesis, and ongoing projects justify the hope that it will not last as long as Simon's.

METHODS

The phylogenetic hypothesis presented below is mainly derived from two sources: 1) cladistic analyses of the entire

family or of subgroups of Pholcidae (Astrin et al. 2007; Bruvo-Madarić et al. 2005; Huber 2000, 2001, 2003a, 2003b, 2003c, 2005a, 2005b, 2007; Huber in press on *Pholcus* Walckenaer 1805 and close relatives); and 2) qualitative assessment of particular characters (e.g., tarsus 4 comb-hairs: Huber & Fleckenstein 2008). Since the aim is to present a hypothesis for the placement of all named genera, a supertree or supermatrix approach was not feasible; too many genera have never been included in any cladistic analysis, and some genera are extremely poorly known (e.g., some monotypic Venezuelan genera recently described by González-Sponga 1998, 2003, 2009). As a result, no meaningful branch support values can be given that are comparable across the entire tree. Instead, the support for each node is presented and discussed separately, using admittedly subjective and qualitative judgments, though in a manner that is hopefully transparent and traceable.

The subfamily names presented below are mostly taken from Simon's (1893) system, even though Simon recognized only two subfamilies: Ninetidinae and Pholcinae (Table 1). However, the latter subfamily was divided into seven subgroups, and four of these family-group names are here elevated to subfamily rank. Thus, the Pholcinae as delimited herein is much narrower in scope than Simon's Pholcinae, but it is also very different to his Pholceae. The same is true of most other subfamilies. Only Ninetinae are fully congruent in both systems, but this is simply due to the fact that Simon's (1893) Ninetidinae was monotypic.

CLASSIFICATION

Family Pholcidae C.L. Koch 1850

The monophyly of Pholcidae has never been seriously questioned, and a good number of characters are both synapomorphic and useful for easy diagnosis (Huber 2000). The male pedipalp is usually heavily modified, including even the proximal segments (Figs. 3–7). A process of the palpal tarsus (the 'procurus') occurs in almost all species (p in Figs. 3–7). The male chelicerae are also usually modified (Fig. 2), and these modifications are functionally related to modifications of the female external genitalia (Huber 1994,

Table 1.—Eugène Simon's (1893) scheme of classification for the Pholcidae. * *Blechnoscelis* has been synonymized with *Priscula* (Huber 2000); *Hedypsilus* has been synonymized with *Modisimus* (Huber 1996b).

Higher taxa	Included genera
Pholcidae	
Ninetidinae	<i>Ninetis</i> Simon 1890
Pholcinae	
Artemeae	<i>Artema</i> Walckenaer 1837
Pholceae	<i>Physocyclus</i> Simon 1893, <i>Pholcus</i> Walckenaer 1805, <i>Holocnemus</i> Simon 1875, <i>Spermophora</i> Hentz 1841, <i>Metagonia</i> Simon 1893
Leptopholceae	<i>Leptopholcus</i> Simon 1893, <i>Micromerys</i> Bradley 1877
Smeringopodeae	<i>Smeringopus</i> Simon 1890, <i>Uthina</i> Simon 1893, <i>Crossopriza</i> Simon 1893
Prisculeae	<i>Priscula</i> Simon 1893
Blechnosceleae	<i>Mecolaesthus</i> Simon 1893, <i>Psilochorus</i> Simon 1893, <i>Coryssocnemis</i> Simon 1893, <i>Blechnoscelis</i> Simon 1893*, <i>Litoporus</i> Simon 1893, <i>Systemita</i> Simon 1893
Modisimeae	<i>Modisimus</i> Simon 1893, <i>Hedypsilus</i> Simon 1893*

1995, 1997a, 1998, 2002). The latter are often sculptured and more or less sclerotised externally, resulting in an epigynum that has evolved independently of the entelegyne epigynum (and that is functionally related to the male chelicerae rather than to the male pedipalp as in Entelegynae). Other putative synapomorphies are the high clypeus (Figs. 8, 9), the arrangement of eyes (two triads separate from the anterior median eyes – the latter may be absent; Figs. 8–11), three trichobothria on the leg tibiae, tarsal pseudosegments, comb-hairs on the fourth tarsi (Figs. 12, 13), and egg sacs carried by females with their chelicerae.

Subfamily Ninetinae Simon 1890

Type genus.—*Ninetis* Simon 1890 (by monotypy).

Ninetinae: Simon 1890:93.

Ninetidinae: Simon 1893:486. Even though this is the grammatically correct spelling, the elided original form is in prevailing use and is maintained in accordance with Article 29.3.1.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999).

The monophyly of Ninetinae is supported by two putative morphological synapomorphies (Huber 2000): a narrow opening of the capsulate tarsal organ (compare Figs. 17 and 18) and a relatively distal position of the retrolateral trichobothrium on the leg tibiae (beyond 45% of tibia length). The compact ocular area with the anterior median eyes in a very high position (sometimes even above the anterior lateral eyes; Fig. 9) might be a further synapomorphy. Short legs (male tibia 1 only up to 2.5 × carapace width) are typical for ninetines, but this is possibly the plesiomorphic pholcid condition. Molecular data have so far supported the monophyly of ninetines, but the sample of both taxa (three species) and genes is still inadequate (Astrin et al. 2007). Ninetines may indeed be sister to all other pholcids (as implied

in Simon's 1893 system), but phylogenetic support for the latter clade (clade 1a in Fig. 1) is weak and ambiguous: a wide sternum and long legs may be morphological synapomorphies; molecular support is also weak (Bruvo-Madarić et al. 2005; Astrin et al. 2007).

Within ninetines, the genera in clade 2a share a long spine-like process on the male palpal bulb (Huber 2000: figs. 321, 335); the genera in clade 2b share reduced epiandrous spigots and an exposed tarsal organ (a character combination reminiscent of Modisiminae: Figs. 19, 22; Huber 2000; Huber & El Hennawy 2007); the genera in clade 2c share a large dorsal flap on the procurus (Huber 2000: figs. 374, 383); the genera in clade 2d share a long procurus with characteristic proximal course (Huber 2000: figs. 353, 360); the genera in clade 2e share a simplified (or even reduced) procurus (Huber 2000: figs. 437, 454, 466). The significance of frontal humps on the male sternum is dubious; they occur in various Ninetinae but also in Modisiminae (Huber 2000).

Ninetinae currently includes 42 species in 16 genera. These numbers suggest relatively high genus-level diversity but a lack of major radiations. Most ninetines are tiny spiders that live close to the ground, in plant debris and under rocks. They are largely restricted to semiarid regions (Huber & Brescovit 2003), but almost nothing is known about their biology. The highest diversity occurs in the New World (Fig. 24), with only *Ninetis* and *Nita* widespread in Africa and the Middle East. The Malaysian *Mystes* Bristowe 1938 is a dubious monotypic genus based on a single female specimen. *Aucana kaala* Huber 2000 from New Caledonia is the only representative of the genus outside Chile.

Composition: *Aucana* Huber 2000; *Chisosa* Huber 2000; *Enetea* Huber 2000; *Galapa* Huber 2000; *Gertschiola* Brignoli 1981; *Guaranita* Huber 2000; *Ibotyporanga* Mello-Leitão 1944; *Kambiwa* Huber 2000; *Mystes* Bristowe 1938; *Nerudia* Huber 2000; *Ninetis* Simon 1890; *Nita* Huber & El Hennawy 2007; *Papiamenta* Huber 2000; *Pholcophora* Banks 1896; *Serratorchus* Wunderlich 1988; *Tolteca* Huber 2000.

Subfamily Arteminae Simon 1893

Type genus.—*Artema* Walckenaer 1837 (by monotypy).

Artemeae: Simon 1893:463.

The only known morphological synapomorphy of Arteminae is a pair of distinctive structures on the male procurus: a dorsal apophysis and a ventral pocket (Fig. 6). In *Physocyclus globosus* (Taczanowski 1874), the function of these structures has been studied in some detail: during copulation, the apophysis of one procurus is lodged in the pocket of the other procurus, resulting in asymmetric insertion of the procuri (Huber & Eberhard 1997). Molecular data also tend to group the three artemine genera sequenced so far (Bruvo-Madarić et al. 2005; Astrin et al. 2007). Arteminae may be sister to Modisiminae (clade 1b in Fig. 1), but this relationship was only supported by a combined analysis of molecular and morphological data in Bruvo-Madarić et al. (2005). The reduction of epiandrous spigots and molecular data suggest that the two genera in clade 3a are more closely related to each other than both are to *Artema* (Huber 2001; Bruvo-Madarić et al. 2005).

Arteminae currently includes 64 species in 5 genera, with the large majority of species in the genera *Physocyclus* Simon 1893

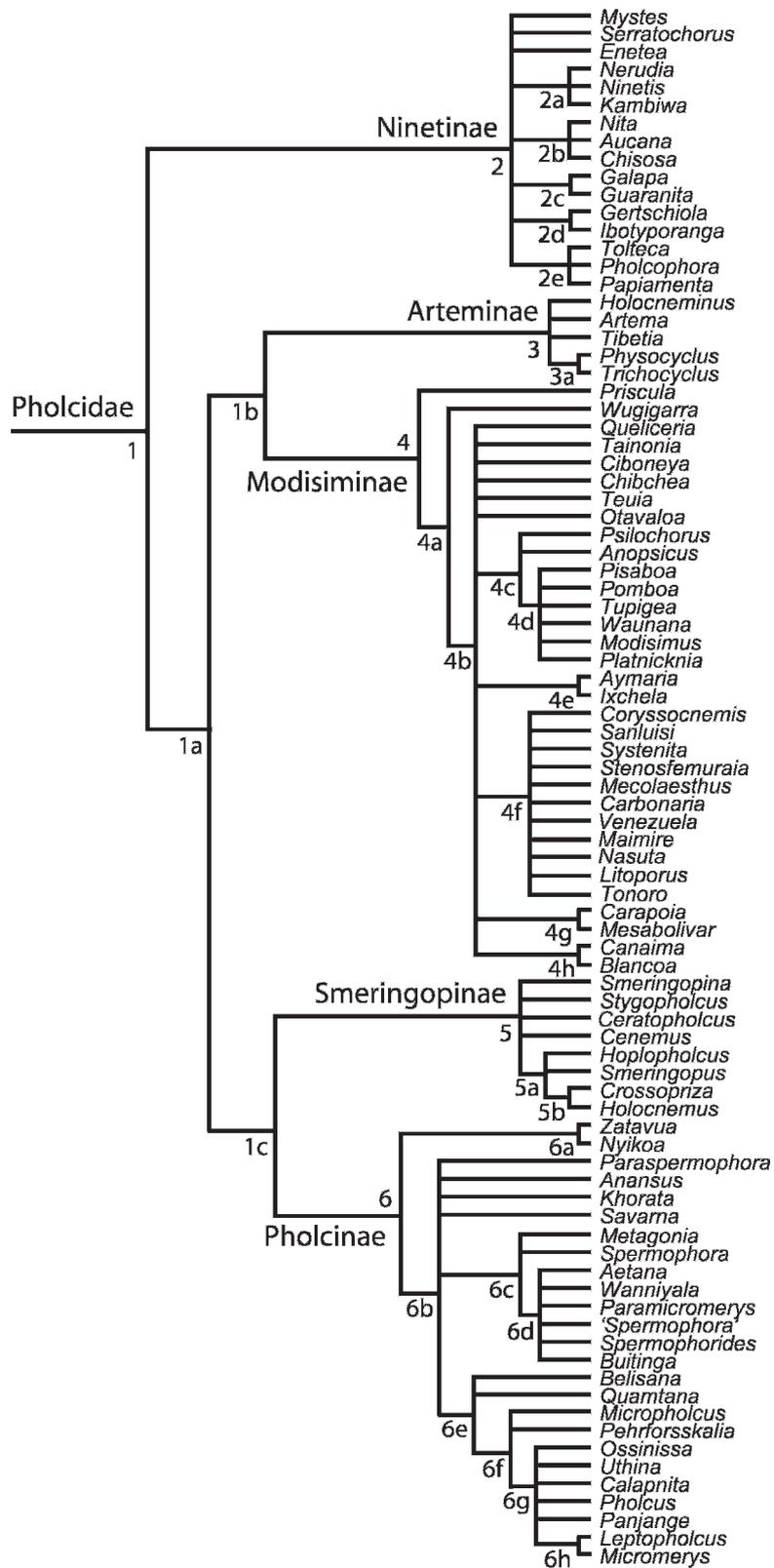
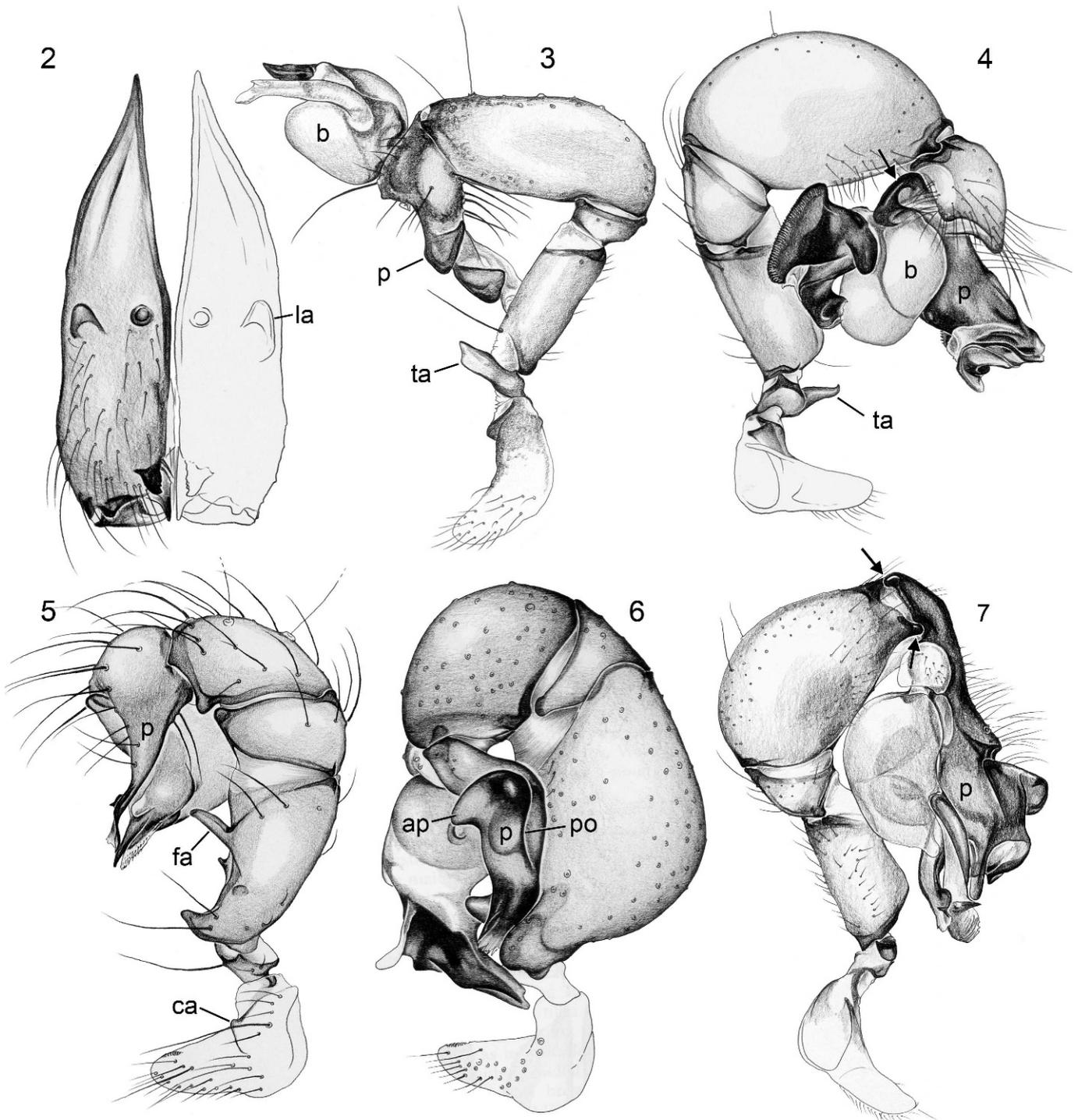


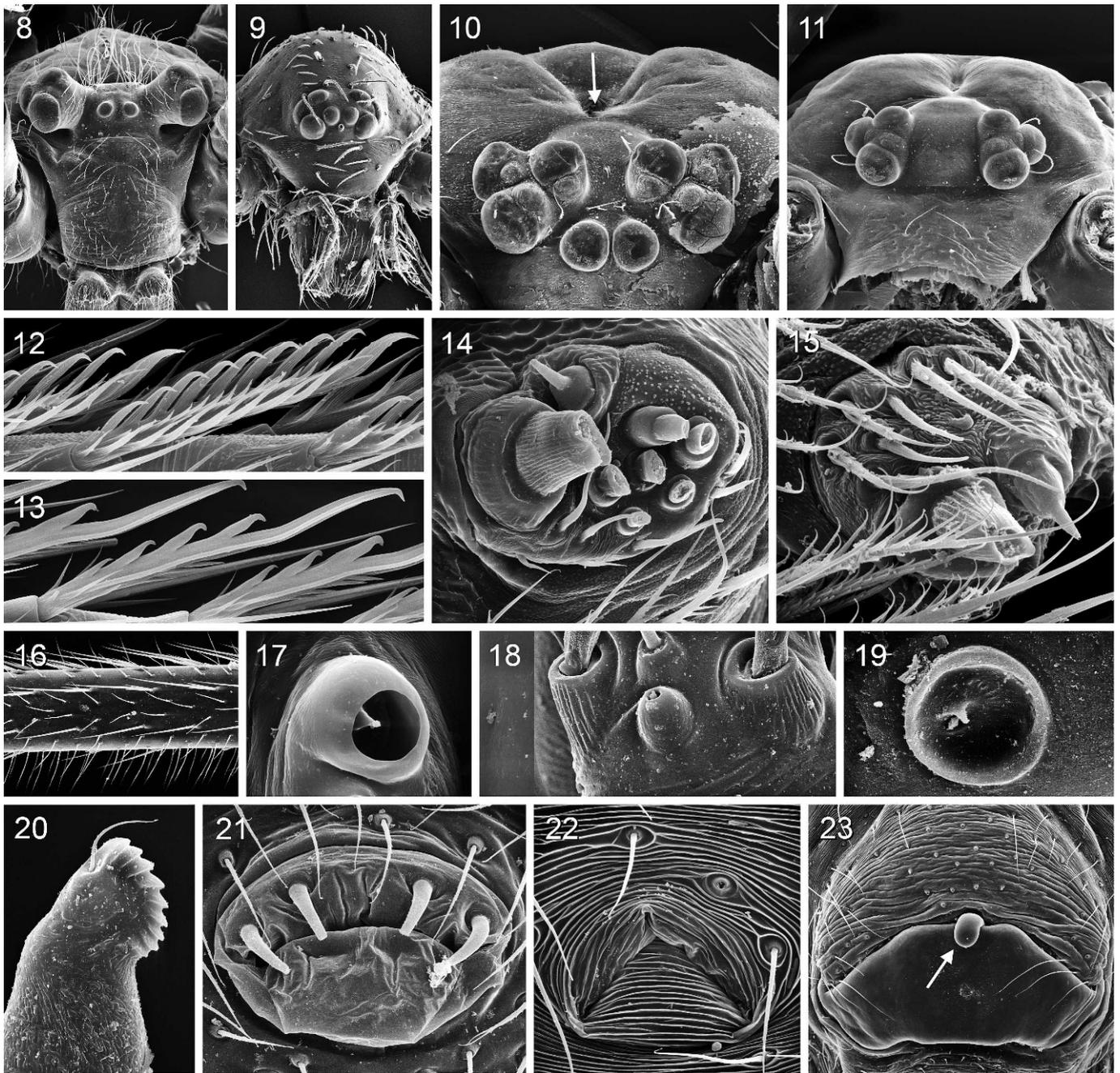
Figure 1.—Proposed cladogram for the family Pholcidae, with all currently valid genera included. Numbered nodes are discussed in the text.



Figures 2–7.—Chelicerae and pedipalps, illustrating important pholcid characters (p: procurus; ta: trochanter apophysis). 2. Male chelicerae with frontal and lateral apophyses (la) (*Pholcus quinquenotatus*). 3. Pedipalp with dorsal attachment of bulb (b) to tarsus (*Buitinga kadogo*). 4. Pedipalp with distinct sclerite (arrow) between tarsus and bulb (b) (*Pholcus quinquenotatus*). 5. Pedipalp with coxa apophysis (ca) and pointed and upward projecting femoral apophysis (fa) (*Tupigea penedo*). 6. Pedipalp with procurus provided with dorsal apophysis (ap) and ventral pocket (po) (*Trichocyclus arawari*). 7. Pedipalp with shifted tibia-tarsus joints (arrows; compare with Fig. 4) (*Zatavua zanahary*). From Huber 2001, 2003a, 2003b, in press, Huber & Rheims 2011.

and *Trichocyclus* Simon 1908. Most Arteminae are relatively large spiders with long, strong legs and high globose abdomens. Just like Ninetinae, they often occur in rather dry regions, sometimes even in deserts, like the Australian

Trichocyclus. The biology of the pantropical *Physocyclus globosus* and its close relative *P. dugesi* Simon 1893 has been studied in some detail (Eberhard 1992a; Eberhard et al. 1993; Huber 1996a; Huber & Eberhard 1997; Peretti et al. 2006).



Figures 8–23.—Scanning electron micrographs illustrating important pholcid characters. 8, 9. Prosomata, frontal views, showing eye arrangement and high clypeus (8, *Pholcus bourgini*; 9, *Ninetis subtilissima*). 10. Ocular area and thoracic pit (arrow) in *Crossopriza cylindrogaster*. 11. Ocular area of *Tupigea teresopolis*, showing reduction of anterior median eyes. 12, 13. Comb-hairs on the fourth tarsi, complex (12) and simple (13) types (12, *Belisana ketambe*; 13, *Pholcus chattoni*). 14, 15. Anterior lateral spinnerets, with complete (14) and reduced (15) set of spigots (14, *Pholcus lamperti*; 15, *Calapnita saluang*). 16. Vertical hairs in high density on the femur of *Modisimus palvet*. 17–19. Palpal tarsal organs, ‘normal’ capsulate type (17), ninetnine type with small opening (18), and exposed type (19) (17, *Belisana hornigai*; 18, *Ninetis subtilissima*; 19, *Tainonia serripes*). 20. Serrated tip of male palpal trochanter apophysis (*Leptopholcus debakkeri*). 21, 22. Male gonopores, with and without epiandrous spigots (21, *Leptopholcus gracilis*; 22, *Tupigea angelim*). 23. Epigynum with knob-like structure (arrow) (*Pholcus kwangumi*). From Huber 2005a, 2009, in press, Huber & Rheims 2011, Huber et al. 2010, Huber & van Harten 2001.

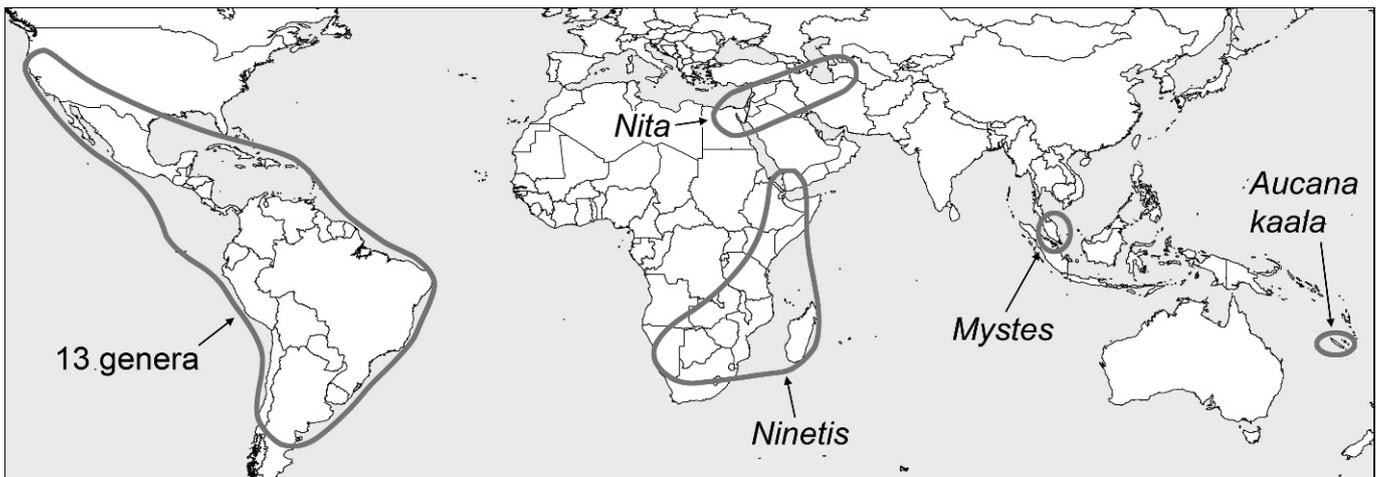


Figure 24.—Known distribution of Ninetinae.

Physocyclus is the only New World genus in Arteminae; the other genera occur in Asia and Australia (Fig. 25). With the exception of two pantropical, synanthropic species (*P. globosus*, *Artema atlanta* Walckenaer 1837) Arteminae seems to be absent from South America and Africa.

Composition: *Artema* Walckenaer 1837; *Holocneminus* Berland 1942; *Physocyclus* Simon 1893; *Tibetia* Zhang, Zhu & Song 2006; *Trichocyclus* Simon 1908.

Subfamily Modisiminae Simon 1893

Type genus.—*Modisimus* Simon 1893 (by subsequent designation—herein).

Modisimeae: Simon 1893:484.

“New World clade”: Huber 2000:36.

The monophyly of Modisiminae *sensu stricto* (clade 4b in Fig. 1) is well supported by the presence of a retrolateral apophysis on the male palpal coxa (Fig. 5) that stabilizes the palp in its rotated position at the onset of copulation (Huber

1998, 2000) and by the reduction of epiandrous spigots (compare Figs. 21 and 22). Molecular data also support the monophyly of this core group of genera (Bruvo-Madarić et al. 2005; Astrin et al. 2007). The Australian *Wugigarra* Huber 2001 shares with taxa in clade 4b the reduction of piriform gland spigots on the anterior lateral spinnerets (as shown in Fig. 15 for a representative of Pholcinae; Huber 2001), but its phylogenetic position is dubious. Species of *Wugigarra* share with Arteminae the distinctive procurus modifications mentioned above (cf. Fig. 6); molecular data are not yet available for *Wugigarra*. *Priscula* Simon 1893 shares with *Wugigarra* and Modisiminae *sensu stricto* an exposed tarsal organ (Fig. 19) and a large distance between the anterior lateral and posterior median eyes ($> 0.55 \times$ diameter of posterior median eyes). Molecular data have either suggested a weak affinity of *Priscula* to Modisiminae *sensu stricto* or an unresolved basal position (Astrin et al. 2007).

Relationships within Modisiminae have proven difficult to resolve. Some genera (clade 4c; the “*Modisimus* group” *sensu* Huber 1998) share a distinctively shaped apophysis on the

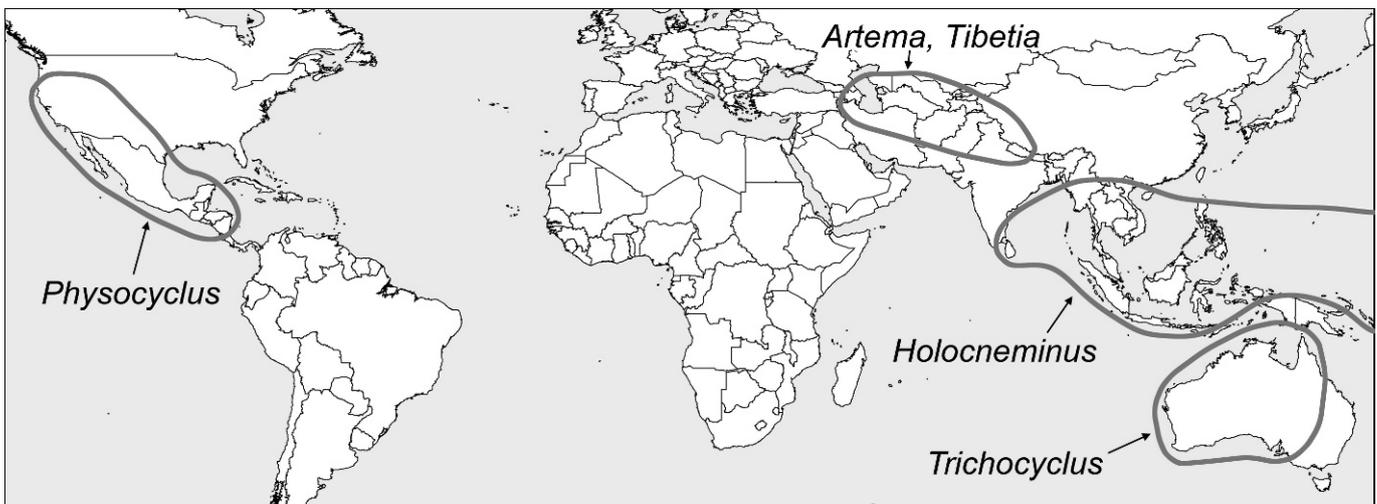


Figure 25.—Known distribution of Arteminae. The synanthropic *Physocyclus globosus* and *Artema atlanta* have pantropical distributions and are excluded. *Holocneminus piritarsis* Berland 1942 is widely distributed in the Pacific, probably as a result of human transport. The South American *Physocyclus viridis* Mello-Leitão 1940 is considered misplaced.

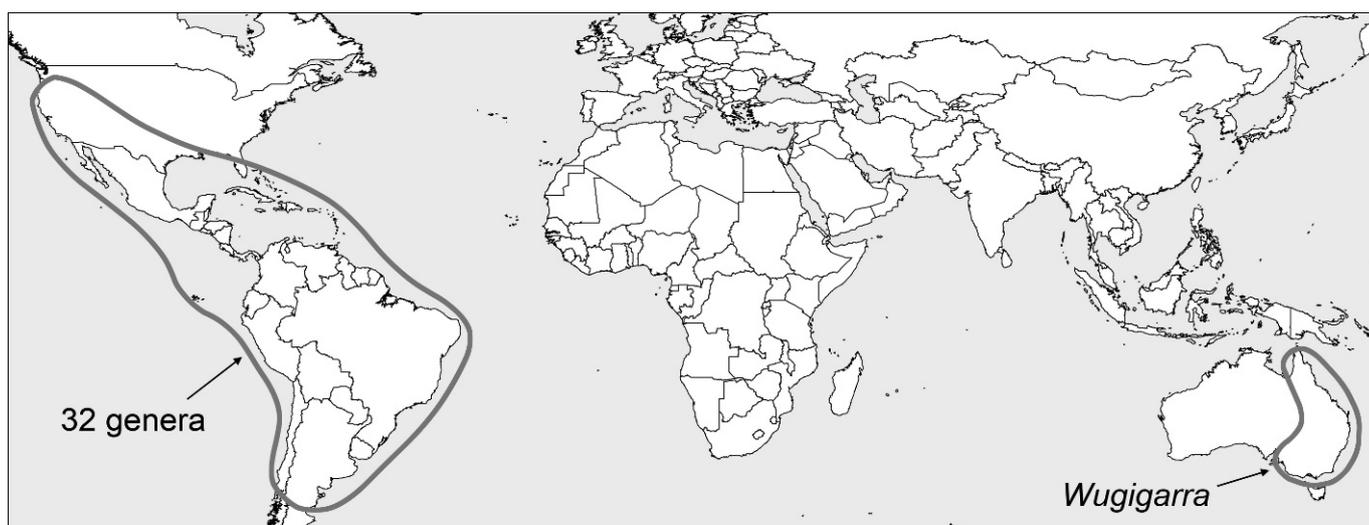


Figure 26.—Known distribution of Modisiminae. The synanthropic *Modisimus culicinus* (pantropical) and *Psilochorus simoni* (introduced to Europe and New Zealand) are excluded.

male palpal femur (pointed and upward projecting) (Fig. 5; Huber 1998, 2000), but molecular data have so far not supported the monophyly of this taxon (Huber & Astrin 2009). Within this clade, some genera (clade 4d) share short vertical hairs in high density on the male leg tibiae and/or femora (Fig. 16; Huber 2000). Such hairs also occur in the two genera in clade 4h, a group that is otherwise only supported by superficial similarity (as are taxa in clade 4e). Clade 4f includes mostly Venezuelan genera that share an apophysis on the male palpal femur that is directed towards proximal (or away from the femur at a right angle; Huber 2000: figs. 989, 1016, 1066). The morphological and ecological diversity within this group is remarkable and explains the considerable number of genera described by Simon (1893) after his expedition to Venezuela in 1887–1888 (Levi 1964). Recently, the situation in this clade has been complicated further by the description of numerous monotypic genera by González-Sponga (1998, 2003, 2009). Finally, a close relationship between the genera in clade 4g is suggested by molecular data (Astrin et al. 2007).

Modisiminae currently includes 402 species in 33 genera. It is one of the two largest subfamilies of Pholcidae, with several very species-rich genera (e.g., *Anopsicus* Chamberlin & Ivie 1938, *Psilochorus* Simon 1893, *Modisimus*, *Mesabolivar* González-Sponga 1998) and many undescribed species. Modisiminae are the typical pholcids of the humid Neotropics, where they occupy a wide variety of microhabitats from leaf litter to tree canopies. The ecological variety is paralleled by a wide range of body forms, from tiny leaf- and litter-dwelling forms to some of the largest pholcids with leg spans of over 15 cm (Huber & Astrin 2009). Basic biological data and some details about sexual behavior have been studied in a number of species (Briceño 1985; Eberhard 1992b; Eberhard & Briceño 1983, 1985; Fürst & Blandenier 1993; Huber 1994, 1996b, 1997b, 1998, 2005c). With the exception of the dubious *Wugigarra* (see above) and two synanthropic species (*Modisimus culicinus* [Simon 1893]; *Psilochorus simoni* [Berland 1911]), Modisiminae is restricted to the New World (Fig. 26).

Composition: *Anopsicus* Chamberlin & Ivie 1938; *Aymaria* Huber 2000; *Blancoa* Huber 2000; *Canaima* Huber 2000; *Carapoia* González-Sponga 1998; *Carbonaria* González-Sponga 2009; *Chibchea* Huber 2000; *Ciboneya* Pérez 2001; *Coryssocnemis* Simon 1893; *Ixchela* Huber 2000; *Litoporus* Simon 1893; *Maimire* González-Sponga 2009; *Mecolaesthus* Simon 1893; *Mesabolivar* González-Sponga 1998; *Modisimus* Simon 1893; *Nasuta* González-Sponga 2009; *Otavaloa* Huber 2000; *Pisaboa* Huber 2000; *Platnicknia* Özdikmen & Demir 2009; *Pomboia* Huber 2000; *Priscula* Simon 1893; *Psilochorus* Simon 1893; *Queliceria* González-Sponga 2003; *Sanluisi* González-Sponga 2003; *Stenosfemuraia* González-Sponga 1998; *Systenita* Simon 1893; *Tainonia* Huber 2000; *Teuia* Huber 2000; *Tonoro* González-Sponga 2009; *Tupigea* Huber 2000; *Venezuela* Koçak & Kemal 2008; *Waunana* Huber 2000; *Wugigarra* Huber 2001.

Subfamily Smeringopinae Simon 1893

Type genus.—*Smeringopus* Simon 1890 (by subsequent designation—herein).

Smeringopodeae Simon 1893:474.

“*Holocnemus*-group”: Timm 1976:70.

The monophyly of Smeringopinae is weakly supported by the presence of a large thoracic pit on the carapace (Fig. 10; rather than a narrow furrow or an evenly domed carapace as in Figs. 8, 9, 11). Molecular data have partly supported the monophyly of the taxa sequenced (Bruvo-Madarić et al. 2005), and partly they have suggested rather obscure relationships, casting doubt on the sequences or on the usefulness of the molecular markers more than on the relationships suggested by morphology (e.g., the position of *Holocnemus* among Ninetinae in Astrin et al. 2007). Molecular data have consistently tended to suggest a close relationship between Smeringopinae and Pholcinae (clade 1c in Fig. 1), and such a relationship is also supported by the distribution of comb-hairs on the fourth tarsus (over the entire tarsus length rather than restricted to the tarsus tip; Huber & Fleckenstein 2008).

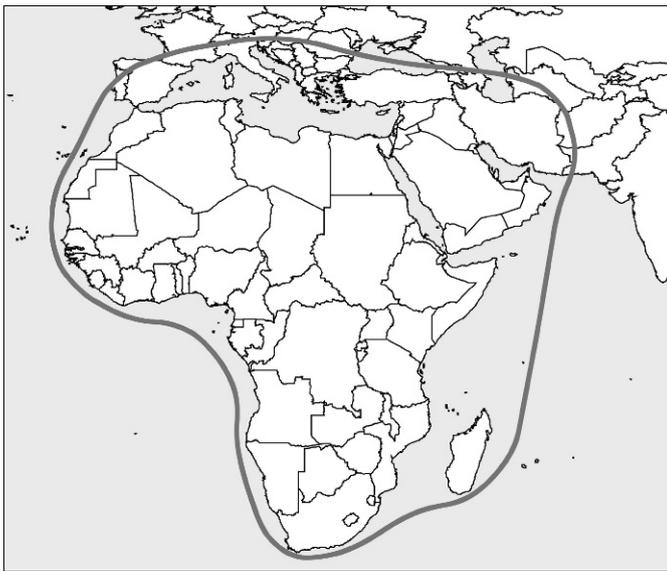


Figure 27.—Known distribution of Smeringopinae. The synanthropic *Crossopriza lyoni*, *Smeringopus pallidus* and *Holocnemus pluchei* have worldwide distributions and are excluded.

Within Smeringopinae, some genera (clade 5a) share web ornaments made of numerous small silk balls (not all individuals within a species make these silk balls, but the exact conditions under which web ornaments are built are controversial: Hajer & Řeháková 2003; Japyassú & Macagnan 2004; B.A. Huber unpubl. observ.), and within this group the genera in clade 5b share spotted legs.

With 56 species in eight genera, Smeringopinae is a rather small subfamily, and *Smeringopus* is currently the only genus with more than ten named species. Like Ninetinae and Arteminae, Smeringopinae are often found in rather arid regions. Three species are widespread synanthropes (*Smeringopus pallidus* [Blackwall 1858], *Crossopriza lyoni* [Blackwall 1867], *Holocnemus pluchei* [Scopoli 1763]), and most of what we know about the biology of Smeringopinae relates to one of these three species (Jackson 1992a, 1992b; Jackson et al. 1992, 1993; Huber 1995; Jakob 1991, 1994, 2004; Jakob & Dingle 1990; Blanchong et al. 1995; Kaster & Jakob 1997; Sedey & Jakob 1998; Johnson & Jakob 1999; Jakob et al. 2000; Strickman et al. 1997; Calbacho-Rosa et al. 2010; - for other species see Senglet 2001; Hajer & Řeháková 2003; Huber 2009). The original distribution of the subfamily is Africa, the Mediterranean, and the Middle East (Fig. 27).

Composition: *Cenemus* Saaristo 2001; *Ceratopholcus* Spassky 1934; *Crossopriza* Simon 1893; *Holocnemus* Simon 1875; *Hoplopholcus* Kulczyński 1908; *Smeringopina* Kraus 1957; *Smeringopus* Simon 1890; *Stygopholcus* Kratochvíl 1932.

Subfamily Pholcinae C.L. Koch 1850

Type genus.—*Pholcus* Walckenaer 1805 (by monotypy).

Pholcidae: C. L. Koch 1850:31 (International Code of Zoological Nomenclature, Article 36: Principle of Coordination; International Commission on Zoological Nomenclature 1999).

“*Pholcus*-group”: Huber 1995:298.

The monophyly of Pholcinae is well supported by morphological and molecular data. Male chelicerae usually are provided with a pair of proximal lateral apophyses (Fig. 2). In addition, the tarsal comb hairs are reduced to a single ventral row (Huber & Fleckenstein 2008: figs. 19, 30). Molecular data are available for only a limited number of genera, but so far the results are largely congruent with those from morphology (Bruvo-Madarić et al. 2005; Astrin et al. 2007). All Pholcinae except *Zatavua* Huber 2003 and *Nyikoa* Huber 2007 (clade 6b in Fig. 1) share an apophysis on the male palpal trochanter (Figs. 3, 4) that interacts with the proximal lateral cheliceral apophysis during copulation (Huber 1995, 2003a). *Zatavua* and *Nyikoa* (clade 6a) share a peculiar shift of the male palpal tibia-tarsus joints (the retrolateral joint is moved towards dorsal, the prolateral joint toward ventral, so that both joints are visible in prolateral view: Fig. 7) (Huber 2007). Members of a large group of genera including *Spermophora* Hentz 1841 and *Metagonia* Simon 1893 (clade 6c) share a dorsal (rather than prolateral) attachment of the bulb to the tarsus (Fig. 3). Within this group, five genera and African ‘*Spermophora*’ (clade 6d) share the reduction of piriform gland spigots on the anterior lateral spinnerets (compare Figs. 14 and 15; Huber 2003a, b, 2005b). Another major group (clade 6e) shares a strong and large sclerite connecting the genital bulb to the tarsus (Fig. 4; Huber 2003c). Within this group, *Pholcus* and its closest relatives (clade 6f) are characterized by simplified tarsus 4 comb-hairs (Fig. 13; Huber & Fleckenstein 2008) and a knob-like structure on the epigynum (Fig. 23). Relationships within this group are difficult to resolve (Huber in press), but *Leptopholcus* Simon 1893 and *Micromerys* Bradley 1877 (clade 6h) are very likely close relatives (in agreement with Simon 1893, but contrary to Timm 1976). They share a derived male cheliceral armature (lateral apophyses very distally and no frontal modification) and a serrated tip of the palpal trochanter apophysis (Fig. 20; Huber in press).

With currently 548 species in 24 genera, Pholcinae is the most species-rich subfamily within the Pholcidae, including the largest genus (*Pholcus*, currently 174 species) and several other species-rich genera (e.g., *Metagonia* and *Belisana* Thorell 1898). In a sense, Pholcinae is the Old World counterpart to Modisiminae, with highest diversity in the humid tropics and subtropics and a large variety of body forms reflecting adaptation to different microhabitats. A large body of literature deals with the biology of the cosmopolitan *Pholcus phalangioides* (Fuesslin 1775) (e.g., Kirchner 1986; Jackson & Brassington 1987; Kirchner & Opderbeck 1990; Uhl 1993, 1996, 1998; Uhl et al. 1995, 2004; Schäfer & Uhl 2002; Schaefer & Uhl 2003; Japyassú & Macagnan 2004; Schäfer et al. 2008), but little is known about the biology of other species (Deeleman-Reinhold 1986; Huber 1997a, 2002; Senglet 2001, 2008; Huber & Wunderlich 2006; Huber & Schütte 2009; Chen & Li 2005a, 2005b; Chen et al. 2008; Xiao et al. 2009, 2010). Most genera are restricted to the Old World, with the notable exception of the New World endemic *Metagonia* and a few relict species currently assigned to *Pholcus* and *Leptopholcus* (Huber 2000, in press; Huber et al. 2005) (Fig. 28). Some synanthropic species have attained worldwide distributions or extended their ranges to another continent (*Pholcus phalangioides*, *Spermophora*

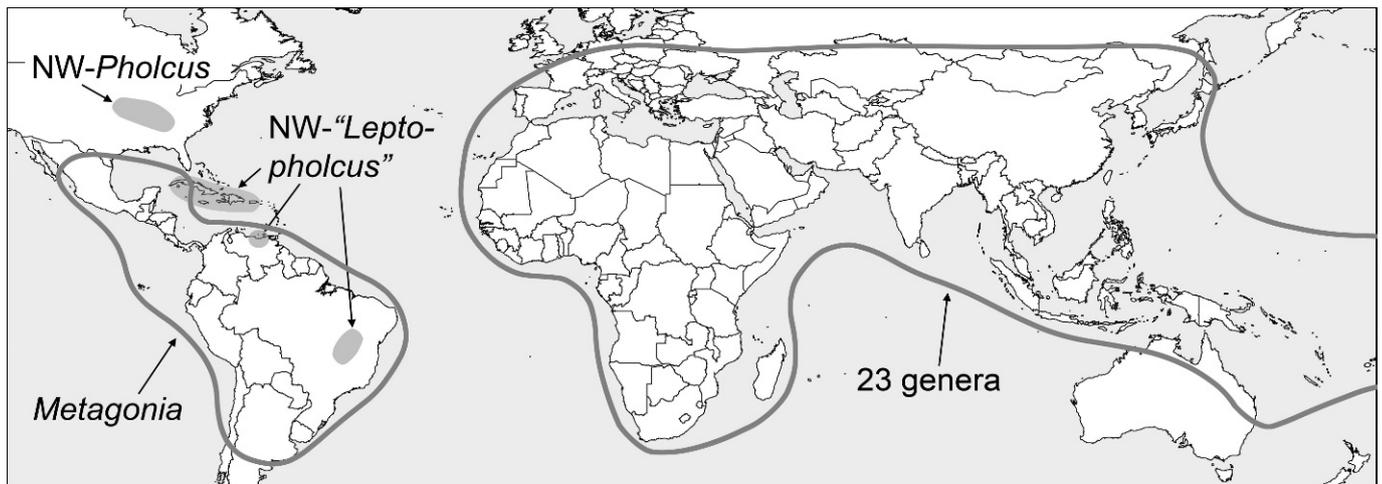


Figure 28.—Known distribution of Pholcinae. The synanthropic *Pholcus phalangioides* and *Spermophora senoculata* (both cosmopolitan), *Micropholcus fauroti* (pantropical) and *Pholcus manueli* (introduced to North America) are excluded.

senoculata [Dugès 1836], *Micropholcus fauroti* [Simon 1887], *Pholcus manueli* Gertsch 1937).

Composition: *Aetana* Huber 2005; *Anansus* Huber 2007; *Belisana* Thorell 1898; *Buitinga* Huber 2003; *Calpnita* Simon 1892; *Khorata* Huber 2005; *Leptopholcus* Simon 1893; *Metagonia* Simon 1893; *Micromerys* Bradley 1877; *Micropholcus* Deeleman-Reinhold & Prinsen 1987; *Nyikoa* Huber 2007; *Ossinissa* Dimitrov & Ribera 2005; *Panjange* Deeleman-Reinhold & Deeleman 1983; *Paramicromerys* Millot 1946; *Paraspermophora* Wunderlich 2004; *Pehrforsskalia* Deeleman-Reinhold & van Harten 2001; *Pholcus* Walckenaer 1805; *Quamtana* Huber 2003; *Savarna* Huber 2005; *Spermophora* Hentz 1841; *Spermophorides* Wunderlich 1992; *Uthina* Simon 1893; *Wanniyala* Huber & Benjamin 2005; *Zatavua* Huber 2003.

DISCUSSION AND OUTLOOK

The numerous large polytomies in the cladogram in Fig. 1 show that many nodes within the Pholcidae remain unresolved. In addition, some nodes are weakly supported and are in need of further study. At the level of subfamilies, generic composition may change in several cases: Ninetinae may not contain clade 2b (i.e., *Aucana*, *Nita*, *Chisosa*); Arteminae may contain *Wugigarra* and be paraphyletic with respect to Modisiminae; and Smeringopinae may be paraphyletic with respect to Pholcinae.

Similar problems occur at the level of genera, and some terminal taxa as presented in Fig. 1 may not even be monophyletic. This is especially true of the genera *Belisana* (Huber 2005), *Quamtana* Huber 2003 (Huber 2003c), *Mesabolivar* and *Mecolaesthus* Simon 1893 (Huber 2000), *Spermophora* (Huber 2005b), *Leptopholcus* and *Pholcus* (Huber in press).

At the level of species, many hundreds of taxa remain undescribed, and the species numbers above may not even reflect relative species richness. For example, a recent revision of the genus *Belisana* has elevated species numbers from two to 64 (Huber 2005a). Other genera that are known to contain a large number of undescribed species are *Metagonia*, *Mesabolivar*, *Modisimus*, *Smeringopina*, and *Pholcus*.

Many hypotheses can be derived from the cladogram in Fig. 1, and some can be easily tested as material becomes available. For example, the cladogram predicts several

characters for the genus *Tonoro* González-Sponga 2009, none of which is mentioned in the original description: 1) exposed tarsal organ; 2) complex comb-hairs restricted to a patch near the tip of tarsus 4; 3) reduced piriform gland spigots on the anterior lateral spinnerets; 4) reduced epiandrous spigots; 5) presence of a male palpal coxa apophysis; and 6) a ventral male palpal femoral apophysis that is not directed distally.

At a phylogenetic level, a large scale analysis of molecular data will most likely be necessary to further resolve pholcid relationships and to advance pholcid systematics significantly. Even though some results from recent molecular work appear dubious, most relationships suggested are either congruent with morphological data or suggest reasonable alternatives. The unexplored potential of traditional morphological characters seems very limited in the Pholcidae, but sperm ultrastructure and chromosome morphology are among the non-molecular characters most promising to contribute to our understanding of pholcid phylogeny (Michalik & Uhl 2005; Michalik et al. 2005; Michalik & Huber 2006; Oliveira et al. 2007; Ramalho et al. 2008; J. Kral pers. comm.).

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LITERATURE CITED

- Astrin, J.J., B. Misof & B.A. Huber. 2007. The pitfalls of exaggeration: molecular and morphological evidence suggests *Kaliana* is a synonym of *Mesabolivar* (Araneae: Pholcidae). *Zootaxa* 1646: 17–30.
- Blanchong, J.A., M.S. Summerfield, M.A. Popson & E.M. Jakob. 1995. Chivalry in pholcid spiders revisited. *Journal of Arachnology* 23:165–170.
- Briceno, R.D. 1985. Sticky balls in webs of the spider *Modisimus* sp. (Araneae, Pholcidae). *Journal of Arachnology* 13:267–269.
- Brignoli, P.M. 1972a. Sur quelques araignées cavernicoles d'Argentine, Uruguay, Brésil et Venezuela récoltées par le Dr. P. Strinati (Arachnida, Araneae). *Revue Suisse de Zoologie* 79:361–385.
- Brignoli, P.M. 1972b. Some cavernicolous spiders from Mexico (Araneae). *Quaderni dell'Accademia Nazionale dei Lincei* 171: 129–155.

- Brignoli, P.M. 1980. Sur le genre *Leptopholcus* Simon, 1893 (Araneae, Pholcidae). *Revue Zoologique Africaine* 94:649–655.
- Bruvo-Madarić, B., B.A. Huber, A. Steinacher & G. Pass. 2005. Phylogeny of pholcid spiders (Araneae: Pholcidae): combined analysis using morphology and molecules. *Molecular Phylogenetics and Evolution* 37:661–673.
- Calbacho-Rosa, L., A. Córdoba-Aguilar & A.V. Peretti. 2010. Occurrence and duration of post-copulatory mate guarding in a spider with last sperm precedence. *Behaviour* 147:1267–1283.
- Chen, H., W. Chen & S. Li. 2008. Leg autotomy in *Pholcus beijingensis* (Araneae: Pholcidae). *Acta Zoologica Sinica* 54: 998–1004.
- Chen, H. & S. Li. 2005a. The reproductive behaviour of *Pholcus beijingensis*. *Chinese Journal of Zoology* 40:14–20.
- Chen, H. & S. Li. 2005b. Time allocation of costly behavior in group-living spider *Pholcus affinis*. *Chinese Journal of Zoology* 40:21–27.
- Deeleman-Reinhold, C.L. 1986. Leaf-dwelling Pholcidae in Indo-Australian rain forests. Pp. 45–48. *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..
- Eberhard, W.G. 1992a. Notes on the ecology and behaviour of *Physocyclus globosus* (Araneae, Pholcidae). *Bulletin of the British Arachnological Society* 9:38–42.
- Eberhard, W.G. 1992b. Web construction by *Modisimus* sp. (Araneae, Pholcidae). *Journal of Arachnology* 20:25–34.
- Eberhard, W.G. & R.D. Briceño. 1983. Chivalry in pholcid spiders. *Behavioral Ecology and Sociobiology* 13:189–195.
- Eberhard, W.G. & R.D. Briceño. 1985. Behavior and ecology of four species of *Modisimus* and *Blechnroschelis* (Araneae, Pholcidae). *Revue Arachnologique* 6:29–36.
- Eberhard, W.G., S. Guzmán-Gómez & K.M. Catley. 1993. Correlation between spermathecal morphology and mating systems in spiders. *Biological Journal of the Linnean Society* 50:197–209.
- Fürst, P.-A. & G. Blandenier. 1993. *Psilochorus simoni* (Berland, 1911) (Araneae, Pholcidae): Découvertes de nouvelles stations suisses et discussion de son écologie. *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 116:75–85.
- González-Sponga, M.A. 1998. Arácnidos de Venezuela. Cuatro nuevos géneros y cuatro nuevas especies de la familia Pholcidae Koch, 1850 (Araneae). *Memoria, Sociedad de Ciencias Naturales, La Salle* 57(148):17–31.
- González-Sponga, M.A. 2003. Arácnidos de Venezuela. Cuatro géneros y cuatro especies nuevas de la familia Pholcidae. *Memoria de la Fundación La Salle de Ciencias Naturales* 155:91–104.
- González-Sponga, M.A. 2009. Arácnidos de Venezuela. Cuatro nuevos géneros y cinco especies nuevas de la familia Pholcidae (Araneae). *Anartia* 21:1–16.
- Hajer, J. & D. Řeháková. 2003. Spotted dome-shaped webs of the pholcids *Crossopriza* sp. and *Holocnemus plucheii* (Araneae: Pholcidae). *Bulletin of the British Arachnological Society* 12:345–354.
- Huber, B.A. 1994. Genital morphology, copulatory mechanism and reproductive biology in *Psilochorus simoni* (Berland, 1911) (Pholcidae; Araneae). *Netherlands Journal of Zoology* 44: 85–99.
- Huber, B.A. 1995. Copulatory mechanism in *Holocnemus plucheii* and *Pholcus opilionoides*, with notes on male cheliceral apophyses and stridulatory organs in Pholcidae (Araneae). *Acta Zoologica (Stockholm)* 76:291–300.
- Huber, B.A. 1996a. Genitalia, fluctuating asymmetry, and patterns of sexual selection in *Physocyclus globosus* (Araneae: Pholcidae). *Revue Suisse de Zoologie, Supplement* 1996:289–294.
- Huber, B.A. 1996b. On the distinction between *Modisimus* and *Hedypsilus* (Araneae, Pholcidae), with notes on behavior and natural history. *Zoologica Scripta* 25:233–240.
- Huber, B.A. 1997a. On American ‘*Micromerys*’ and *Metagonia* (Araneae, Pholcidae), with notes on natural history and genital mechanics. *Zoologica Scripta* 25:341–363.
- Huber, B.A. 1997b. Evidence for gustatorial courtship in a haplogyne spider (*Hedypsilus culicinus*: Pholcidae: Araneae). *Netherlands Journal of Zoology* 47:95–98.
- Huber, B.A. 1998. Genital mechanics in some neotropical pholcid spiders (Araneae: Pholcidae), with implications for systematics. *Journal of Zoology, London* 244:587–599.
- Huber, B.A. 2000. New World pholcid spiders (Araneae: Pholcidae): a revision at generic level. *Bulletin of the American Museum of Natural History* 254:1–348.
- Huber, B.A. 2001. The pholcids of Australia (Araneae; Pholcidae): taxonomy, biogeography, and relationships. *Bulletin of the American Museum of Natural History* 260:1–144.
- Huber, B.A. 2002. Functional morphology of the genitalia in the spider *Spermophora senoculata* (Pholcidae, Araneae). *Zoologischer Anzeiger* 241:105–116.
- Huber, B.A. 2003a. Cladistic analysis of Malagasy pholcid spiders reveals generic level endemism: Revision of *Zatavua* n. gen. and *Paramicromerys* Millot (Pholcidae, Araneae). *Zoological Journal of the Linnean Society* 137:261–318.
- Huber, B.A. 2003b. High species diversity in one of the dominant groups of spiders in East African montane forests (Araneae: Pholcidae: *Buitinga* n. gen., *Spermophora* Hentz). *Zoological Journal of the Linnean Society* 137:555–619.
- Huber, B.A. 2003c. Southern African pholcid spiders: revision and cladistic analysis of *Quamtana* n. gen. and *Spermophora* Hentz (Araneae: Pholcidae), with notes on male-female covariation. *Zoological Journal of the Linnean Society* 139:477–527.
- Huber, B.A. 2005a. High species diversity, male-female coevolution, and metaphyly in Southeast Asian pholcid spiders: the case of *Belisana* Thorell 1898 (Araneae, Pholcidae). *Zoologica* 155:1–126.
- Huber, B.A. 2005b. Revision of the genus *Spermophora* Hentz in Southeast Asia and on the Pacific Islands, with descriptions of three new genera (Araneae: Pholcidae). *Zoologische Mededelingen* 79–2(4):61–172.
- Huber, B.A. 2005c. Evidence for directional selection on male abdomen size in *Mecolaesthus longissimus* (Araneae, Pholcidae). *Journal of Arachnology* 33:573–581.
- Huber, B.A. 2007. Two new genera of small, six-eyed pholcid spiders from West Africa, and first record of *Spermophorides* for mainland Africa (Araneae: Pholcidae). *Zootaxa* 1635:23–43.
- Huber, B.A. 2009. Life on leaves: leaf-dwelling pholcids of Guinea, with emphasis on *Crossopriza cylindrogaster*, a spider with inverted resting position, pseudo-eyes, lampshade web, and tetrahedral egg-sac (Araneae: Pholcidae). *Journal of Natural History* 43:2491–2523.
- Huber, B.A. In press. Revision and cladistic analysis of *Pholcus* and closely related taxa (Araneae, Pholcidae). *Bonner Zoologische Monographien*.
- Huber, B.A. & J.J. Astrin. 2009. Increased sampling blurs morphological and molecular species limits: revision of the Hispaniolan endemic spider genus *Tainonia* (Araneae: Pholcidae). *Invertebrate Systematics* 23:281–300.
- Huber, B.A. & A.D. Brescovit. 2003. *Ibotyporanga* Mello-Leitão: tropical spiders in Brazilian semi-arid habitats (Araneae: Pholcidae). *Insect Systematics and Evolution* 34:15–20.
- Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). *Canadian Journal of Zoology* 74:905–918.
- Huber, B.A. & H. El Hennawy. 2007. On Old World ninetine spiders (Araneae: Pholcidae), with a new genus and species and the first record for Madagascar. *Zootaxa* 1635:45–53.
- Huber, B.A., N. Fischer & J.J. Astrin. 2010. High level of endemism in Haiti’s last remaining forests: a revision of *Modisimus* (Araneae: Pholcidae) on Hispaniola, using morphology and molecules. *Zoological Journal of the Linnean Society* 158:244–299.

- Huber, B.A. & N. Fleckenstein. 2008. Comb-hairs on the fourth tarsi in pholcid spiders (Araneae, Pholcidae). *Journal of Arachnology* 36:232–240.
- Huber, B.A., A. Pérez G. & R.L.C. Baptista. 2005. *Leptopholcus* (Araneae: Pholcidae) in continental America: rare relicts in low precipitation areas. *Bonner Zoologische Beiträge* 53:99–107.
- Huber, B.A. & C.A. Rheims. 2011. Diversity and endemism of pholcid spiders in Brazil's Atlantic Forest, with descriptions of four new species of the Atlantic Forest endemic genus *Tupigea* (Araneae: Pholcidae). *Journal of Natural History* 45:275–301.
- Huber, B.A. & A. Schütte. 2009. Preliminary notes on leaf-dwelling *Metagonia* spiders (Araneae: Pholcidae) in the Esquinas Rainforest near La Gamba, Costa Rica: leaf preference, mimesis, and web structure. *Contributions to Natural History (Bern)* 12:681–697.
- Huber, B.A. & A. van Harten. 2001. *Ninetis subtilissima* Simon, 1890 (Araneae: Pholcidae): Redescription and SEM ultrastructure. *American Museum Novitates* 3336:1–7.
- Huber, B.A. & J. Wunderlich. 2006. Fossil and extant species of the genus *Leptopholcus* in the Dominican Republic, with the first case of egg-parasitism in pholcid spiders (Araneae: Pholcidae). *Journal of Natural History* 40:2341–2360.
- International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, Fourth edition. International Trust for Zoological Nomenclature, London.
- Jackson, R.R. 1992a. Predator-prey interactions between web-invading jumping spiders and two species of tropical web-building pholcid spiders, *Psilochorus sphaeroides* and *Smeringopus pallidus*. *Journal of Zoology, London* 227:531–536.
- Jackson, R.R. 1992b. Predator-prey interactions between web-invading jumping spiders and a web-building spider, *Holocnemus pluchei* (Araneae, Pholcidae). *Journal of Zoology, London* 228: 589–594.
- Jackson, R.R. & R.J. Brassington. 1987. The biology of *Pholcus phalangioides* (Araneae, Pholcidae): predatory versatility, araneophagy and aggressive mimicry. *Journal of Zoology, London* 211:227–238.
- Jackson, R.R., E.M. Jakob, M.B. Willey & G.E. Campbell. 1993. Anti-predator defences of a web-building spider, *Holocnemus pluchei* (Araneae, Pholcidae). *Journal of Zoology, London* 229: 347–352.
- Jackson, R.R., R.J. Rowe & G.E. Campbell. 1992. Anti-predator defences of *Psilochorus sphaeroides* and *Smeringopus pallidus* (Araneae, Pholcidae), tropical web-building spiders. *Journal of Zoology, London* 228:227–232.
- Jakob, E.M. 1991. Costs and benefits of group living for pholcid spiderlings: losing food, saving silk. *Animal Behaviour* 41:711–722.
- Jakob, E.M. 1994. Contests over prey by group-living pholcids (*Holocnemus pluchei*). *Journal of Arachnology* 22:39–45.
- Jakob, E.M. 2004. Individual decisions and group dynamics: why pholcid spiders join and leave groups. *Animal Behaviour* 68:9–20.
- Jakob, E.M., J.A. Blanchong, M.A. Popson, K.A. Sedey & M.S. Summerfield. 2000. Ontogenetic shifts in the cost of living in groups: focal observations of a pholcid spider (*Holocnemus pluchei*). *American Midland Naturalist* 143:405–413.
- Jakob, E.M. & H. Dingle. 1990. Food level and life history characteristics in a pholcid spider (*Holocnemus pluchei*). *Psyche* 97:95–110.
- Japyassú, H.F. & C.R. Macagnan. 2004. Fishing for prey: the evolution of a new predatory tactic among spiders (Araneae, Pholcidae). *Revista de Etología* 6:79–94.
- Johnson, S.A. & E.M. Jakob. 1999. Leg autotomy in a spider has minimal costs in competitive ability and development. *Animal Behaviour* 57:957–965.
- Kaster, J.L. & E.M. Jakob. 1997. Last-male sperm priority in a haplogyne spider (Araneae: Pholcidae): correlations between female morphology and patterns of sperm usage. *Annals of the Entomological Society of America* 90:254–259.
- Kirchner, W. 1986. Das Netz der Zitterspinne (*Pholcus phalangioides* Fuesslin) (Araneae: Pholcidae). *Zoologischer Anzeiger* 216:151–169.
- Kirchner, W. & M. Opperbeck. 1990. Beuteerwerb, Giftwirkung und Nahrungsaufnahme bei der Zitterspinne *Pholcus phalangioides* (Araneae, Pholcidae). *Abhandlungen des Naturwissenschaftlichen Vereins Hamburg (NF)* 31/32:15–45.
- Koch, C.L. 1850. Übersicht des Arachnidensystems. Nürnberg 5: 1–77.
- Levi, H.W. 1964. Nineteenth century South American araneology. *Papéis avulsos do Departamento de Zoologia* 16:9–19.
- Mello-Leitão, C. de. 1946. Notas sobre os Filistatidae e Pholcidae. *Anais da Academia Brasileira de Ciências* 18:39–83.
- Michalik, P., R. Dallai, F. Giusti, D. Mercati & G. Alberti. 2005. Spermatozoa and spermiogenesis of *Holocnemus pluchei* (Scopoli, 1763) (Pholcidae, Araneae). *Tissue and Cell* 37:489–497.
- Michalik, P. & B.A. Huber. 2006. Spermiogenesis in *Psilochorus simoni* (Berland, 1911) (Pholcidae, Araneae): evidence for considerable within-family variation in sperm structure and development. *Zoology* 109:14–25.
- Michalik, P. & G. Uhl. 2005. The male genital system of the cellar spider *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae, Araneae): development of spermatozoa and seminal secretion. *Frontiers in Zoology* 2:12.
- Oliveira, R.M., A.C. de Jesus, A.D. Brescovit & D.M. Cella. 2007. Chromosomes of *Crossopriza lyoni* (Blackwall 1867), intraindividual numerical chromosome variation in *Physocylus globosus* (Taczanowski 1874), and the distribution pattern of NORs (Araneomorphae, Halogynae, Pholcidae). *Journal of Arachnology* 35:293–306.
- Peretti, A., W.G. Eberhard & R.D. Briceño. 2006. Copulatory dialogue: female spiders sing during copulation to influence male genitalic movements. *Animal Behaviour* 72:413–421.
- Petrunkévitch, A. 1928. *Systema araneorum*. Transactions of the Connecticut Academy of Arts and Sciences 29:1–270.
- Ramalho, M.O., D. Araujo, M.C. Schneider, A.D. Brescovit & D.M. Cella. 2008. *Mesabolivar brasiliensis* (Moenkhaus 1898) and *Mesabolivar cyaneotaeniatus* (Keyserling 1891) (Araneomorphae, Pholcidae): close relationship reinforced by cytogenetic analyses. *Journal of Arachnology* 36:453–456.
- Schaefer, D. & G. Uhl. 2003. Male competition over access to females in a spider with last-male sperm priority. *Ethology* 109:385–400.
- Schäfer, M., B. Misof & G. Uhl. 2008. Effects of body size of both sexes and female mating history on male mating behaviour and paternity success in a spider. *Animal Behaviour* 76:75–86.
- Schäfer, M. & G. Uhl. 2002. Determinants of male paternity in the cellar spider *Pholcus phalangioides* (Araneae: Pholcidae): the role of male and female mating behaviour. *Behavioral Ecology and Sociobiology* 51:368–377.
- Sedey, K.A. & E.M. Jakob. 1998. A description of an unusual dome web occupied by egg-laying *Holocnemus pluchei* (Araneae, Pholcidae). *Journal of Arachnology* 26:385–388.
- Senglet, A. 2001. Copulatory mechanisms in *Hoplopholcus*, *Stygopholcus* (revalidated), *Pholcus*, *Spermophora* and *Spermophoridae* (Araneae, Pholcidae), with additional faunistic and taxonomic data. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 74:43–67.
- Senglet, A. 2008. New species of *Pholcus* and *Spermophora* (Pholcidae, Araneae) from Iran and Afghanistan, with notes on mating mechanisms. *Revue Suisse de Zoologie* 115:355–376.
- Simon, E. 1890. Étude sur les arachnides de l'Yemen. *Annales de la Société Entomologique de France* 6:77–124.
- Simon, E. 1893. *Histoire Naturelle des Araignées*. 2nd edition Volume 1(2):256–488. Librairie Encyclopédique de Roret, Paris.
- Strickman, D., R. Sithiprasasna & D. Southard. 1997. Bionomics of the spider, *Crossopriza lyoni* (Araneae, Pholcidae), a predator of Dengue vectors in Thailand. *Journal of Arachnology* 25:194–201.

- Timm, H. 1976. Die Bedeutung von Genitalstrukturen für die Klärung systematischer Fragen bei Zitterspinnen (Arachnida: Araneae: Pholcidae). *Entomologica Germanica* 3:69–76.
- Uhl, G. 1993. Mating behaviour and female sperm storage in *Pholcus phalangioides* (Fuesslin) (Araneae). *Memoirs of the Queensland Museum* 33:667–674.
- Uhl, G. 1996. Sperm storage secretion of female cellar spiders (*Pholcus phalangioides*; Araneae): a gel-electrophoretic analysis. *Journal of Zoology, London* 240:153–161.
- Uhl, G. 1998. Mating behaviour in the cellar spider, *Pholcus phalangioides*, indicates sperm mixing. *Animal Behaviour* 56:1155–1159.
- Uhl, G., B.A. Huber & W. Rose. 1995. Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). *Bulletin of the British Arachnological Society* 10:1–9.
- Uhl, G., S. Schmitt, M.A. Schäfer & W. Blanckenhorn. 2004. Food and sex specific growth strategies in a spider. *Evolutionary Ecology Research* 4:523–540.
- Xiao, Y., J. Zhang & S. Li. 2009. A two-component female-produced pheromone of the spider *Pholcus beijingensis*. *Journal of Chemical Ecology* 35:769–778.
- Xiao, Y., J. Zhang & S. Li. 2010. Male-specific (Z)-9-tricosene stimulates female mating behaviour in the spider *Pholcus beijingensis*. *Proceedings of the Royal Society B, Biological Sciences* 277:3009–3018.

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