

## On the “valve” in the genitalia of female pholcids (Pholcidae, Araneae)

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### Summary

The morphology of the “valve”, a chitinous structure between the uterus externus and the uterus internus, is described in 29 species from about 25 genera and used as a taxonomic character. A highly developed, morphologically complex valve is probably synapomorphic for the “Old World” group of pholcids which comprises about 25 Old World genera, the New World genus *Physocyclus*, and at least one, probably undescribed, South American genus. Of the eight genera that have been thought to occur in both the Old and the New World (not counting synanthropic cosmopolitan species), only *Leptopholcus* is supported by valve structure and male genitalic characters. *Micromerys* is restricted to the Old World, *Psilochorus* is restricted to the New World. The New World records of the following genera are called into question and need confirmation (except anthropophilous species): *Crossopriza*, *Myrmidonella*, *Ninetis*, *Pholcus*, *Spermophora*.

### Introduction

In his pioneer works on South American spiders, Keyserling (1877, 1887, 1891) recognised only two pholcid genera: *Pholcus* Walckenaer and *Spermophora* Hentz. Both of these were also known from the Old World. Later, Simon (1893) created several new genera for New World species, and he, together with Moenkhaus (1898), transferred most of Keyserling's species to newly established genera. In the century since then, this separation between Old World and New World genera has been widely followed, but today several genera persist that supposedly occur on both sides of the Atlantic (without considering synanthropic cosmopolitan species): *Crossopriza* Simon, *Leptopholcus* Simon, *Micromerys* Bradley, *Myrmidonella* Berland, *Ninetis* Simon, *Pholcus*, *Psilochorus* Simon, and *Spermophora*.

Brignoli (1981) proposed a preliminary separation of pholcids into a group “better (or exclusively) represented in the Old World”, and one “which seems to be limited to the New World (with few exceptions)”. One of the characters supporting his view was the presence and degree of development of a “sclerotized arch” in the female internal genitalia (“always evident” in the “Old World” group, “transformed” or “reduced” in the “New World” group). These arches correspond to the “valve” (“Verschluss”) of Wiehle (1933), which is a structure that seems to close the entrance from the ectodermal uterus externus into the mesodermal uterus internus (Fig. 1). The only detailed account of the

morphology of this structure has been published by Uhl (1994) for *Pholcus phalangioides* (Fuesslin).

The present paper examines the morphology of this “valve” in 29 species from about 25 genera, and discusses the evidence for the separation of pholcids into a “New World” group and an “Old World” group.

### Material and methods

Table 1 presents a list of the pholcid species studied. The following species were also studied, as outgroups: *Ochyrocera* sp. (Ochyroceratidae), and *Scytodes* sp. (Scytodidae), both from Costa Rica, San Antonio de Escazú, October 1995 (W. G. Eberhard). Female genitalia were embedded in epoxy resin (ERL 4206) and serially sectioned (1 µm, sagittal sections) with an ultramicrotome (Reichert Ultracut S), using a diamond knife. The sections were stained with methylene blue (1%) in an aqueous borax solution (1%).

An index was developed to reflect the “strength” or degree of development of the female “valve”: the absolute area of the “valve” in a sagittal (about median) section was multiplied by the number of ridges (see Fig. 2G, where the “ridges” are numbered), and — to correct for the size of the spider — divided by the product of prosoma length and prosoma width. The result was multiplied by 10<sup>3</sup> in order to obtain easily comparable numbers (Table 1):

$$I_{(f)} = 10^3 \times \frac{\text{“valve” area} \times n \text{ ridges}}{\text{pros. length} \times \text{pros. width}}$$

To test for a possible correlation between female valve and male genitalic strength, a corresponding male index was calculated: the product of diameter of pedipalpal femur and tibia was divided by the product of prosoma width and prosoma length and multiplied by 10<sup>3</sup>:

$$I_{(m)} = 10^3 \times \frac{\text{diam. femur} \times \text{diam. tibia}}{\text{pros. length} \times \text{pros. width}}$$

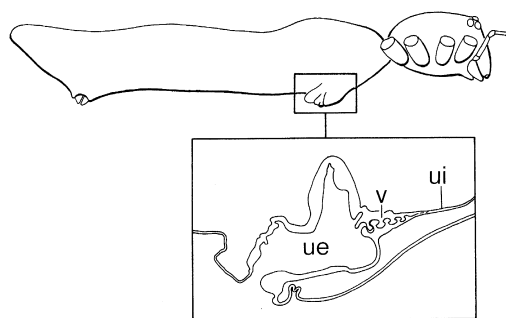


Fig. 1: Female pholcid in side view (*Leptopholcus dalei*, from Huber, 1997a), and sagittal section of the genitalia, showing position of the “valve”. Abbreviations: ue = uterus externus, ui = uterus internus, v = “valve”.

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## Results

### The female “valve”

There was a clear separation into two groups with respect to the morphology and degree of development of the female “valve” that corresponded almost exactly with the geographical distinction between Old and New World. The female index in the “New World” group ranged from 0 to 4, and in the “Old World” group from 11 to 83. This distinction became more obvious when details of morphology that were not incorporated into the index were taken into consideration. Even the weakest valves in the “Old World” group had mushroom-shaped “ridges” (e.g. *Spermophora senoculata* (Dugès), Fig. 2I), whereas the strongest valves in the “New World” group had a smoother outline (e.g. “*Micromerys*” *delicatus* (O.P.-Cambr.), Fig. 3B). Three species

from the New World had typical “Old World” valves: *Physocyclus globosus* (Taczanowski) (Fig. 2P,  $I_{(f)}=47$ ), *Leptopholcus dalei* (Petrunkévitch) (Fig. 2J;  $I_{(f)}=58$ ), and “*Blechnoscelis*” sp. (Fig. 2S,  $I_{(f)}=49$ ). Only one species from the Old World lacked the “Old World” valve: *Ninetis* sp. from Kenya (Fig. 3K,  $I_{(f)}=1$ ).

Within the genus *Psilochorus* both morphologies were present (see discussion of polyphyly of the genus below): while the New World (“real”) *Psilochorus simoni* (Berland) had a female index of 4, and simple morphology (Fig. 3I), the two “*Psilochorus*” species from Australia had female indices of 11 and 14 respectively, and the typical “Old World morphology” (Fig. 2L, M). The same was true in the genus *Micromerys*: the Old World (“real”) *Micromerys* sp. had a strong valve ( $I_{(f)}=58$ , Fig. 2C), whereas the New World “*Micromerys*” *delicatus* (which has been transferred to

Species	Collected in	I(m)	I(f)
<b>“Old World” group</b>			
<i>Pholcus opilionoides</i> (Schrank, 1781)	Austria	117	83
<i>Micromerys</i> sp. <sup>1</sup>	West Irian	70	58
<i>Micropholcus fauroti</i> (Simon, 1887)	Cabo Verde I.	79	41
<i>Uthina</i> sp. <sup>2</sup>	Sumatra	75	40
gen. sp. indet. 1 <sup>3</sup>	Sumatra	70	34
gen. sp. indet. 2 <sup>4</sup>	Bali	107	44
<i>Calapnita vermiformis</i> Simon, 1892	N. Sumatra	116	41
<i>Calapnita phyllicola</i> Deeleman, 1986	Sumatra	85	22
<i>Spermophora senoculata</i> (Dugès, 1836)	Greece	44	11
<i>Spermophora misera</i> Bristowe, 1952	W. Sumatra	50	26
<i>Leptopholcus dalei</i> (Petrunkévitch, 1929)	Puerto Rico	92	58
<i>Holocnemus pluchei</i> (Scopoli, 1763)	Italy	55	37
<i>Crossopriza lyoni</i> (Blackwall, 1867)	Nicaragua <sup>5</sup>	84	40
<i>Smeringopus pallidus</i> (Blackwall, 1858)	Costa Rica <sup>5</sup>	40	13
“ <i>Psilochorus</i> ” sp. 1 <sup>6</sup>	Australia	73	14
“ <i>Psilochorus</i> ” sp. 2 <sup>7</sup>	Australia	63	11
<i>Holocnemus multiguttatus</i> (Simon, 1905)	Indonesia	177	68
<i>Physocyclus globosus</i> (Taczanowski, 1873)	Costa Rica <sup>5</sup>	95	47
“ <i>Blechnoscelis</i> ” sp. <sup>8</sup>	Colombia	109	49
<b>“New World” group</b>			
<i>Metagonia rica</i> Gertsch, 1986	Costa Rica	103	1
“ <i>Micromerys</i> ” <i>delicatus</i> O.P.-Cambridge, 1895 <sup>9</sup>	Panama	177	4
“ <i>Coryssocnemis</i> ” <i>viridescens</i> Kraus, 1955 <sup>10</sup>	Nicaragua	23	3
<i>Modisimus</i> sp. <sup>11</sup>	Costa Rica	23	1
<i>Hedyspilus culicinus</i> Simon, 1893 <sup>12</sup>	Costa Rica	37	2
<i>Anopsicus zeteki</i> (Gertsch, 1939)	Panama	34	0
<i>Psilochorus simoni</i> (Berland, 1911)	Austria <sup>5</sup>	25	4
<i>Ninetis</i> sp. 1 <sup>13</sup>	Chile	42	1
<i>Ninetis</i> sp. 2 <sup>14</sup>	Kenya	26	1
“ <i>Coryssocnemis</i> ” <i>furcula</i> F.O.P.-Cambridge, 1902 <sup>15</sup>	Guatemala	34	2

Table 1: Species studied, collection sites, and male and female indices (explanation of indices in text).

<sup>1</sup>Undescribed species from Bagusa, along Mamberano river, SW of Rombekai Lake, 1 October 1982 (Y. Laumonier), in coll. Deeleman. <sup>2</sup>Undescribed species from Kerinci National Park, elev. 800 m, near river, 21–30 July 1988 (S. Djojosedharmo), in coll. Deeleman. <sup>3</sup>Undescribed species, new genus, from Gn. Leuser National Park at Bohorok (S. Djojosedharmo), in coll. Deeleman. <sup>4</sup>Undescribed species, new genus, from Bali, secondary forest litter, January 1990 (S. Djojosedharmo), in coll. Deeleman. <sup>5</sup>Synanthropic species. <sup>6</sup>Undescribed species from 30 km W of Innesfoul: Palmerston N.P., and Mittag Mittag (female), July 1992 (J. Wunderlich). <sup>7</sup>Undescribed species from Magnetic Island, July 1992 (J. Wunderlich). <sup>8</sup>Undescribed species from Meta, 20 km N Rio Muco, “Carimagua”, 175 m, 1978 (W. G. Eberhard), in coll. Escuela de Biología, Universidad de Costa Rica. <sup>9</sup>This species has been transferred to *Metagonia* Simon (Huber, 1997a). <sup>10</sup>This species is not congeneric with the type species, *C. callaica* Simon, but more closely related to the genera *Modisimus*, *Hedyspilus*, *Psilochorus*, *Anopsicus*, *Bryantina* (Huber, in press b). <sup>11</sup>Undescribed species from Prov. Limón, Cahuita, 13–15 June 1995 (B. A. Huber), in author’s collection. <sup>12</sup>The genus *Hedyspilus* Simon has been synonymised with *Modisimus* Simon (Huber, 1996b). <sup>13</sup>Undescribed species, in AMNH. <sup>14</sup>Undescribed species from leaf litter near beach at Kilifi, no date (J. & F. Murphy). <sup>15</sup>This species is not congeneric with the type species, *C. callaica*. For a detailed redescription see Huber, in press c.

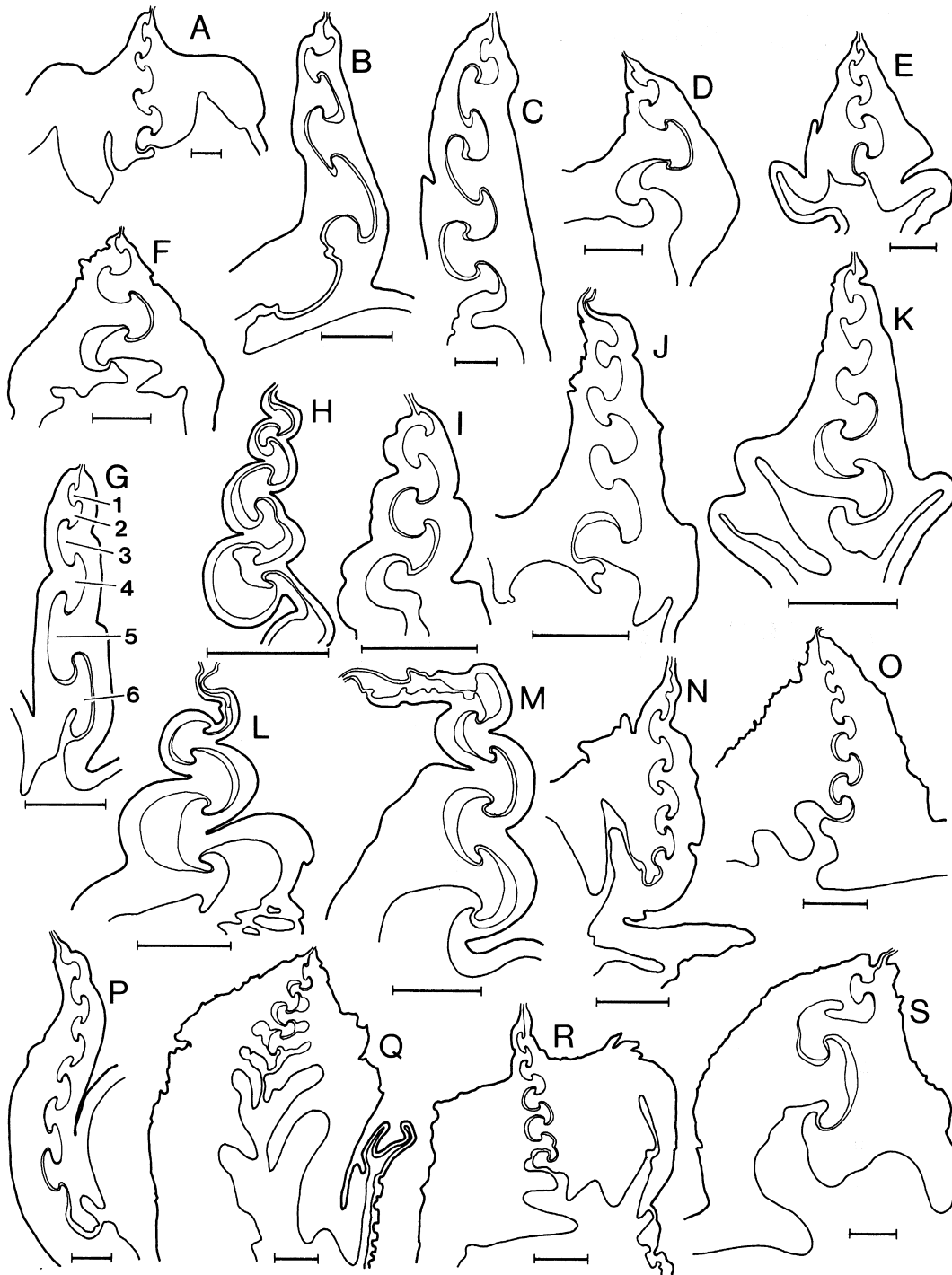


Fig. 2: Valves of representatives of the "Old World" group. The sections shown are close to the median line of the female body. **A** *Pholcus opilionoides* (from Huber, 1995); **B** *Micropholcus fauroti*; **C** *Micromerys* sp.; **D** *Uthina* sp.; **E** gen. sp. from Sumatra; **F** *Calapnita vermiformis*; **G** *Calapnita phyllicola* (valve ridges numbered); **H** *Spermophora misera*; **I** *Spermophora senoculata*; **J** *Leptopholcus dalei*; **K** gen. sp. from Bali; **L** "*Psilochorus*" sp. from Magnetic Island; **M** "*Psilochorus*" sp. from Mittag Mittag; **N** *Smeringopus pallidus*; **O** *Holocnemus pluchei* (from Huber, 1995); **P** *Physocyclus globosus*; **Q** *Holocnemus multiguttatus*; **R** *Crossopriza lyoni*; **S** "*Blechnoscelis*" sp. Scale lines = 30  $\mu$ m.

the New World genus *Metagonia* — Huber, 1997a) had a weak valve ( $I_{(f)}=4$ , Fig. 3B).

Most Old World pholcids had a valve morphology that is here called “*Pholcus* type”, with the “mushrooms” of the dorsal and ventral halves of the valve fitting tightly together (Fig. 2A–G, I–K, N–P, R, S). Three species differed slightly in having more space between the two halves of the valve: *Spermophora misera* Bristowe and “*Psilochorus*” sp. 1 and sp. 2 (Fig. 2H, L, M). In *Holocneminus multiguttatus* (Simon) the “mushrooms” had exceptionally high stalks (Fig. 2Q). New World pholcids showed no consistent morphology. Most had simple “valves” with differences in details (Fig. 3). One species was deviant: “*Coryssocnemis*” *viridescens* Kraus, which had two types of cuticle in a unique pattern (only visible in lateral parts of the “valve”: Fig. 3D).

#### Male strength

Male genitalic strength as defined above ranged from 23 to 177 in the spiders studied. Figure 4 shows the difference between the male of a “weak” species ( $I_{(m)}=14$ ) and a “strong” species ( $I_{(m)}=256$ ), drawn at different scales so that their body sizes match (these particular species were not included in the study because

no females were available for sectioning). There appears to be a general correlation between male strength and development of the female “valve”. Apart from *Metagonia rica* Gertsch and “*Micromerys*” *delicatus*, all the species studied fall close to an imaginary line if the male index is plotted against the female index (Fig. 5). Neither male nor female strength appear to be correlated with overall size (see Fig. 5, where solid squares represent large species, empty squares small species).

#### Discussion

##### *The complex valve: primitive or derived?*

Brignoli (1981) considered simple valves as “transformed” or “reduced”, thereby implying that complex valves are primitive in pholcids. Outgroup comparison suggests the opposite: valves of a comparable type have not been described in any other spider family. Sections of the internal female genitalia of *Ochyrocera* sp. and *Scytodes* sp. confirmed the absence of a valve. Valves have been described (Gertsch, 1958a,b) in Diguettidae and Plectreuridae (which were together proposed as sister group of Pholcidae — Coddington & Levi, 1991), but their morphology corresponds to that of a simple “New World” valve rather than to the complex valves of

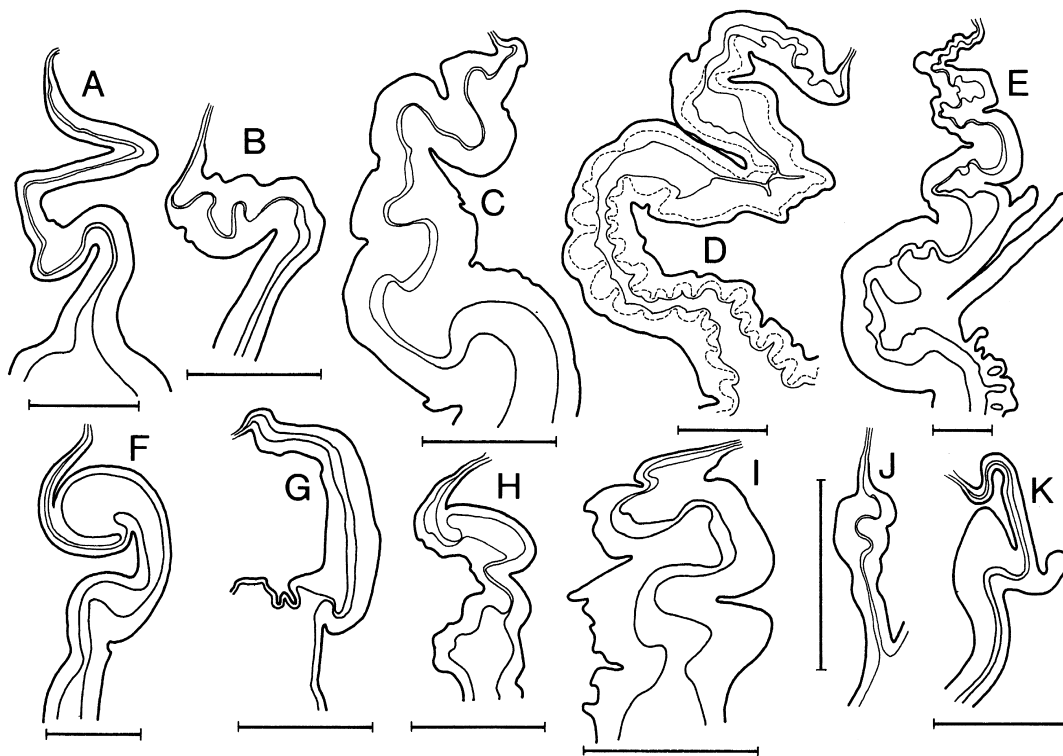


Fig. 3: Valves of representatives of the “New World” group. The sections shown are close to the median line of the female body, except D, which gives a more lateral section in addition to the median section shown in C. A *Metagonia rica*; B “*Micromerys*” *delicatus*; C–D “*Coryssocnemis*” *viridescens*; E “*Coryssocnemis*” *furcula*; F *Modisimus* sp.; G *Hedyspilus culicinus*; H *Anopsicus zeteki*; I *Psilochorus simoni* (from Huber, 1994); J *Ninetis* sp. from Chile; K *Ninetis* sp. from Kenya. Scale lines = 30  $\mu$ m.

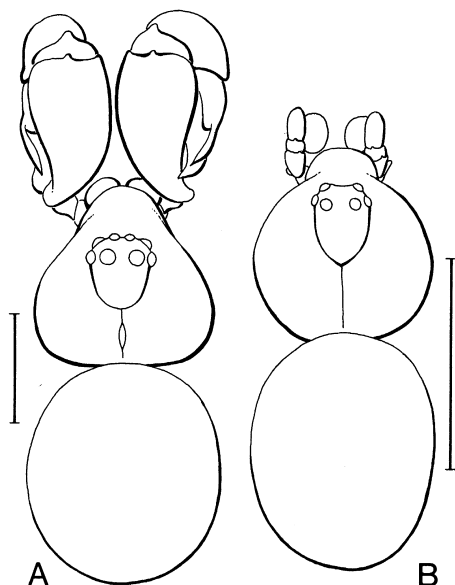


Fig. 4: A "strong" (A) and a "weak" (B) male, demonstrating the significance of the male index. A *Physocyclus dugesi* (from Huber, 1997b), male index=256; B *Anopsicus* sp. n. (from Huber, in press a), male index=14. Scale lines=1 mm.

Old World pholcids. Therefore, the "Old World" group is here tentatively proposed as a monophyletic group, with the presence of a highly developed valve as a synapomorphy (for other possible supporting characters see below). This includes the "Pholcus group" (11 genera — Huber, 1995), the "Holcnemus group" (6 genera — Timm, 1976), the "Trichocyclus group" (new name) as defined by Deeleman-Reinhold (1995) (3 genera), the genera *Artema* Walckenaer and *Physocyclus* Simon, the undescribed "*Blechnoscelis*" sp. included in this study, and probably some other as yet only poorly known genera (*Pholciella* Roewer, *Pholcoides* Roewer, *Mystes* Bristowe). The name "Old World group" is here adopted from Brignoli (1981), but it must be stressed that some New World pholcids are included in this group.

#### Correlation between female valve and male genital vigour

Pholcids apparently are unusual in that male genital vigour may play a significant role during (copulatory) courtship (Huber, 1996a; Huber & Eberhard, 1997). The swollen pedipalpal femora and tibiae of some species are filled with muscle tissue, and these muscles perform the rhythmic movements during copulation described in a variety of species (review in Huber & Eberhard, 1997). Figure 5 suggests a functional correlation between the strength of a male's genitalia and the development of the respective female's valve. The figure also shows that both male genital vigour and development of the female valve are not simply functions of the size of the species: there are both small and large species with

strong males and well developed valves, and small and large species with weak males and poorly developed valves. However, in the absence of any phylogeny of pholcids, which would be a prerequisite for a comparative analysis (Harvey & Pagel, 1991), the significance of the apparent correlation cannot be assessed. Moreover, several studies have failed to demonstrate an obvious change (e.g. opening) of the valve caused by the male genitalia during copulation (Uhl *et al.*, 1995; Huber, 1994, 1995; Huber & Eberhard, 1997).

#### Taxonomic implications

Twenty-seven of the 40 currently recognised pholcid genera are geographically restricted to either the Old or the New World. This section discusses only those genera that are supposed to have representatives both in the Old and the New World. Genera whose only cosmopolitan species are synanthropic are excluded (*Hedyspilus* Simon, *Micropholcus* Deeleman-Reinhold & Prinsen, *Physocyclus*, *Smeringopus* Simon, *Artema*). This leaves the following eight supposedly natural cosmopolitan genera:

*Crossopriza*: This genus is distributed throughout the Old World (type species: *C. pristina* (Simon, 1890) from "S.-Arabia"). Six species have been recorded in America. Of these, *C. sexsignata* Franganillo, 1926 has recently been synonymised with *Artema atlanta* Walckenaer, 1837 (Pérez González, 1996). *Crossopriza pristina* was cited by Franganillo (1926, 1936) from Cuba, but its presence there is doubted (Pérez González, 1996). *Crossopriza lyoni* (Blackwall, 1867), which was recently reported from Florida (Edwards, 1993), is a synanthropic cosmopolitan species. The

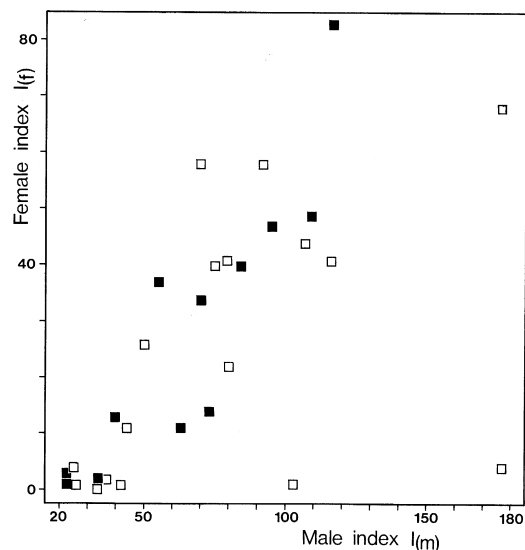


Fig. 5: Scatter diagram, showing the correlation between male strength and development of the female "valve". Each square represents one species (cf. Table 1). Solid squares represent large species (prosoma width >1 mm); empty squares small species (prosoma width <1 mm).

South American *Crossopriza mucronata* Mello-Leitão, 1942 is a synonym of *C. lyoni* (Huber *et al.*, in prep.). The two other South American species (*Crossopriza saltensis* Mello-Leitão, 1941) and *C. brasiliensis* Mello-Leitão, 1935) are apparently correctly placed but may also be synonyms of Old World species.

*Leptopholcus*: This is a largely African and Asian genus (type species: *L. signifer* Simon, 1893 from Zaire), with currently two representatives in America: *L. dalei* (Petrunkévitch, 1929) from Puerto Rico and *L. delicatulus* Franganillo, 1930 from Cuba (the Cuban species was erroneously synonymised with *L. dalei* by Bryant (1940) — Huber & Pérez González, in press). There is strong evidence that the American species are closely related to Old World *Leptopholcus*: the valve is of the "*Pholcus* type", and details of the genital morphology (Huber, 1997a) support their inclusion in the "*Pholcus* group" *sensu* Huber (1995), of which *Leptopholcus* is part. However, the male genitalia of African *Leptopholcus* species appear much closer to *Pholcus* than to *L. dalei* and *L. delicatulus* (compare figures in Brignoli, 1980; Uhl *et al.*, 1995; Huber, 1997a). Therefore, the American *Leptopholcus* species might well belong to another or a new genus within the "*Pholcus* group".

*Micromerys*: Currently this genus comprises only a few Australian species (Deeleman-Reinhold, 1986b) (type species: *M. gracilis* Bradley, 1877 from Australia), and three American representatives. The congenity of the American species has been doubted previously (Brignoli, 1980; Deeleman-Reinhold, 1986a,b), and two of them (*M. delicatus* and *M. conicus* Simon) have been transferred to the New World genus *Metagonia* on the basis of male genitalic morphology (Huber, 1997a). The present data on female morphology strongly support this transfer. The third American species (*M. occidentalis* (Mello-Leitão, 1929)) was described only from the female, and the description reveals nothing about its relationship.

*Myrmidonella*: This genus currently consists of only two species, both of which are known only from the female. The type species is *M. minuta* Berland, 1919 (from E. Africa), and the American representative is *M. anomala* (Mello-Leitão, 1918). The description of the latter is totally inadequate, without figures, and does not allow any conclusions.

*Ninetis*: This is another genus of which only two species have been described: the type species, *N. subtilissima* Simon, 1890 from "SW-Arabia", and *N. neotropica* Kraus, 1957 from Brazil. The principal character defining this genus (the absence of thoracic grooves) is probably plesiomorphic. Brignoli (1981) considered the American species as "either introduced or misplaced". It is worth stressing that the Kenyan *Ninetis* sp. from the present study was the only Old World species that lacked the "Old World valve". This is in agreement with the traditional notion that *Ninetis* might be a primitive genus within pholcids, but further study of these tiny and almost unknown spiders is urgently needed.

*Pholcus*: This genus is very species-rich and widely distributed in the Old World, but most of its American

representatives have been transferred to various New World genera: of the 31 *Pholcus* species described from America, only four are left. Two of these are anthropophilous: *P. phalangioides* and *P. opilionoides* (Schränk). *Pholcus muralicola* Maughan & Fitch, 1976 was considered as "probably misplaced" by Brignoli (1983). Finally, *P. dubiomaculatus* Mello-Leitão, 1918 is probably a real *Pholcus*, but the author failed to provide any characters that would distinguish it from either of the anthropophilous species mentioned above.

*Psilochorus*: This is a species-rich genus in America (type species *P. pullulus* (Hentz, 1850) from USA), and with three described and some undescribed representatives in Australia and New Guinea (Deeleman-Reinhold, 1995). The presence of an elaborate valve in Australian representatives clearly moves these closer to other Old World genera than to American *Psilochorus*. Moreover, American *Psilochorus* species share with other New World genera (*Modisimus* Simon, *Hedyspilus*, *Anopsicus* Chamberlin & Ivie, *Bryantina* Brignoli, *Coryssocnemis* Simon in part) details of male genitalic morphology that are not present in Australian species (Huber, in press b). In sum, there is strong evidence that *Psilochorus* is a pure American genus (with one synanthropic species in Europe: *P. simoni* (Berland, 1911) — Fürst & Blandinier, 1993), and the Australian representatives need to be transferred to a new or another genus.

*Spermophora*: This genus is distributed throughout the Old World (type species: *S. senoculata* (Dugès, 1836), holarctic). Of the ten species described from the New World, most have been transferred or synonymised, and only three are left: *S. senoculata* which is synanthropic, and *S. unicolor* Keyserling, 1891 and *S. maculata* Keyserling, 1891 from Brazil. The last two species are known only from the female, and the descriptions offer no characters that would distinguish the species from representatives of the American genus *Metagonia*. More than two decades ago, Brignoli (1974) proposed the absence of "true" *Spermophora* in the Americas.

In conclusion, of the eight supposedly cosmopolitan pholcid genera, two are certainly not cosmopolitan (*Micromerys*, *Psilochorus*), five are insufficiently known and all their American representatives may be introduced or misplaced (*Crossopriza*, *Myrmidonella*, *Ninetis*, *Pholcus*, *Spermophora*), and only *Leptopholcus* might really be a cosmopolitan genus.

#### The position of *Physocyclus*

The phylogenetic position of the genus *Physocyclus* is of special interest because it was considered to be the only pholcid genus in the New World that has close affinities to an Old World genus (to *Artema*: Brignoli, 1981). However, Brignoli stated only that "[*Physocyclus*] is evidently related to *Artema*" (1981: 94) and "judging by the structure of the male pedipalp and of the chelicerae, *Artema* is closely related to *Physocyclus*" (1981: 92), but he presented no synapomorphies.

The valve (Fig. 2P) clearly shows that *P. globosus* is a representative of the “Old World” group, thus making *Physocyclus* the only named genus of that group (so far) that occurs exclusively in the New World (with most of the 26 known species occurring in Mexico, some species with doubtful taxonomic position in South America and *P. globosus* as the only pantropical species). (*Blechnoscelis* Simon might be a second New World genus belonging to the “Old World” group, but the genus is poorly known (the type species is known only from the female, and the type locality is uncertain), and the “*Blechnoscelis*” sp. sectioned for this study may not be congeneric with the type species.)

Judging from the method of locking of the rotated pedipalp on the chelicerae, *Physocyclus* is not part of the “*Pholcus* group”, which is characterised by a pair of lateral cheliceral apophyses which couple with apophyses on the palpal trochanters during copulation (Huber, 1995). *Physocyclus globosus* shows the plesiomorphic condition of locking the pedipalp behind the chelicerae (Huber & Eberhard, 1997). It is also not part of the “*Holocnemus* group” *sensu* Timm (1976) or the “*Trichocyclus* group” as presented by Deebleman-Reinhold (1995). Among the remaining six genera (most of which are very poorly known), *Artema* is probably the closest relative. *Pholciella* and *Pholcoides* are only known from Afghanistan, *Mystes* from SE Asia, *Myrmidonella* from E. Africa, and *Ninetis* from “SW-Arabia” (for discussion of neotropical species see above). Thus, although a synapomorphy between *Physocyclus* and a sister group remains to be found, Brignoli’s statement on the close relationship between *Physocyclus* and *Artema* mentioned above remains unrefuted. These two genera might be close to the “*Holocnemus* group” *sensu* Timm (1976), but so far the only character known to support this view is the deep round pit on the carapace behind the eyes (C. L. Deebleman-Reinhold, pers. comm.).

#### Open questions

From a taxonomic-systematic point of view, this study does not include some genera that might have significantly improved or reduced the power of the argument but of which I was not able to obtain material for sectioning. Among the most interesting ones are the American genera *Blechnoscelis*, *Litoporus* Simon, *Coryssocnemis*, *Pholcophora* Banks, and “*Priscula*” Simon (synonymised with *Physocyclus* by Brignoli (1981) but maybe a valid genus — Huber, 1997b). Geographically, future research should concentrate more on South American and African representatives.

From a functional point of view the most puzzling open question is how females (especially of the “Old World” group) manage to get their relatively huge eggs through the valve. Muscles are attached to the structure (Uhl, 1994; pers. obs.) but it is hard to imagine how these could unzip a well-developed valve of the “*Pholcus*-type”.

Finally, it is worth stressing that the “valve” was only one of five characters used by Brignoli (1981) to support

a distinction between an “Old World” group and a “New World” group. Brignoli presented the character states defining each group in a very superficial way (bulb “relatively complicated” versus “simpler”, procursus “larger” versus “smaller”, male chelicerae “more transformed” in one group than in the other, abdomen “more or less rounded” versus “elongated, oval, or sausage-shaped”), but the general conclusion might have been based on his profound knowledge of the family, making a detailed reinvestigation into each of the characters a promising field for further research.

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