

Genital mechanics in some neotropical pholcid spiders (Araneae: Pholcidae), with implications for systematics

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Abstract

Genital mechanics are studied in five species from three genera of neotropical pholcid spiders. The study focuses on the function of a pointed and upward projecting ('pup') apophysis on the male pedipalpal femur: it engages an indentation in the genital bulb during copulation. This character is geographically restricted to spiders in Central and North America and the West Indies and is considered a key character of the monophyletic 'Modisimus group'. This includes the genera *Modisimus* Simon, 1893, *Psilochorus* Simon, 1893, *Bryantina* Brignoli, 1985, *Anopsicus* Chamberlin & Ivie, 1938, and some species now misplaced in *Coryssocnemis* Simon, 1893 and *Blechroscelis* Simon, 1893. Evidence for the polyphyly of the following genera is presented: *Psilochorus*, *Coryssocnemis*, and *Blechroscelis*. Some notes on the reproductive biology of the species studied are briefly presented.

Key words: genital mechanics, functional morphology, Araneae, Pholcidae, systematics

INTRODUCTION

Pholcid spiders have traditionally been considered one of the most homogeneous spider families, with characters offering little variation for classification (Simon, 1893; Mello-Leitão, 1918; Gerhardt, 1933). It is thus no wonder that the existing classifications which are largely based on Simon (1893) are decidedly phenetic and unnatural. Most attention has been directed to eye-patterns and sizes, but the usefulness of these characters is probably very limited (Brignoli, 1972a, 1973; Timm, 1976; Deeleman-Reinhold, 1986; Huber, 1996). Recent research has focused on the relatively complex genitalia, and on their functioning during copulation (Huber, 1994, 1995, In press a, b; Huber & Eberhard, 1997). This has resulted in the proposal of two monophyletic groups of genera: the 'Pholcus group' of 11 Old World genera (Huber, 1995), and the 'Old World group' of about 25 predominantly Old World genera (Huber, In press b). The present paper is the first to delimit a monophyletic group of genera (the name 'Modisimus group' is proposed) in the New World, where the taxonomic situation is exceedingly chaotic (Brignoli, 1972a, b, 1973, 1981). New data about genital morphology and functioning are combined with published data on geographic distribution to argue for changes in pholcid systematics.

The present study focuses on genital morphology and functioning, and on biogeographic data. However, since the biology of neotropical pholcids is as poorly studied as their systematics, data on courtship, copulation, egg production, and other aspects are briefly presented. While these rather anecdotal data are not directly related to the central topic, they complement a series of recent studies that have revealed an astounding diversity in the reproductive behaviour within the family (Eberhard & Briceño, 1983, 1985; Eberhard, 1992; Uhl, 1993; Huber, 1994, 1996, 1997, In press a; Uhl, Huber & Rose, 1995; Huber & Eberhard, 1997). Pholcids have thus become the best known haplogyne spider family with respect to reproductive behaviour and genital mechanics.

MATERIALS AND METHODS

Adult and penultimate individuals were collected at the following localities: *Anopsicus zeteki* (Gertsch, 1939) and *Modisimus david* Huber, 1996 in Panama, Prov. Chiriquí, David, under stones (April 1995); *Modisimus* ('*Hedysilus*') *culicinus* (Simon, 1893) in Costa Rica, Prov. San José, Ciudad Universitaria, in a building (Huber, 1996); *Modisimus guatuso* Huber, In press e in Costa Rica, Prov. San José, Bajo La Hondura, in dome-shaped webs in shady shelters near the ground (April to November 1995); '*Coryssocnemis*' *viridescens* Kraus, 1955 (the generic position of this species is unclear, but

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it is probably not congeneric with the type species of *Coryssocnemis* Simon, 1893 – see below) in Nicaragua, Dept. Matagalpa, near Matagalpa, in sheet webs near the ground on the sides of a brook (July 1995); and on Isla de Ometepe, Lago de Nicaragua, in webs in the declivity of a hollow way (July 1995). The identity of this last species was confirmed by examination of the types (SMF 8554, 8557-8, 8794 – for abbreviations of museums, see ‘Acknowledgements’). Vouchers of each species are deposited at the Escuela de Biología, Universidad de Costa Rica, and at the American Museum of Natural History, New York (1 male and 1 female each).

In addition, I have seen the types of the following species (listed are only those that are relevant for the present paper): *Modisimus glaucus* Simon, 1893 (MNHN); *M. culicinus* (Simon, 1893) (MNHN); *M. globosus* Schmidt, 1971 (SMF); *M. cornutus* Kraus, 1955 (SMF); *M. dilutus* Gertsch, 1941 (AMNH); *M. inornatus* Cambridge, 1895 (BMNH); *M. maculatipes* Cambridge, 1895 (BMNH); *M. propinquus* Cambridge, 1896 (BMNH); *M. pulchellus* Banks, 1929 (MCZ); *M. texanus* Banks, 1906 (MCZ); *Anopsicus chiriqui* Gertsch, 1982 (MCZ); *A. concinnus* Gertsch, 1982 (AMNH); *A. facetus* Gertsch, 1982 (AMNH); *A. turrialba* Gertsch, 1982 (MCZ); *Coryssocnemis callaica* Simon, 1893 (MNHN); *C. uncata* Simon, 1893 (MNHN); *C. altiventer* (Keyserling, 1891); *C. furcula* F. P.-Cambridge, 1902; *C. togata* (Keyserling, 1891); *Blechnoscelis annulipes* (Keyserling, 1877) (BMNH); *B. coerulea* (Keyserling, 1891) (BMNH); *B. cyaneotaeniata* (Keyserling, 1891) (BMNH); *B. modesta* Banks, 1929 (MCZ); *B. serripes* Simon, 1893 (MNHN); *Psilochorus lemniscatus* Simon, 1894 (MNHN); *P. nigrifrons* Simon, 1894 (MNHN); *P. cyaneomaculatus* (Keyserling, 1891); *Bryantina coxana* (Bryant, 1940) (MCZ); *B. incerta* (Bryant, 1940) (MCZ).

Non-type material of the following species was also studied (listed are again only those that are relevant to the present study): *Psilochorus pullulus* (Hentz, 1850) (MNHN); *P. simoni* (Berland, 1911) (in author’s collection); *Psilochorus* spp. from Australia; *Modisimus* sp. A from Eberhard & Briceño, 1985 (MCZ).

The spiders collected alive were kept in the laboratory in plastic containers of different sizes (5-8 cm diameter; 1-10 cm high) that were filled at the bottom with a mixture of activated carbon and alabaster. They were fed *Drosophila* flies.

Courtship and copulation was observed with a dissecting microscope. One to three pairs of each species were freeze-fixed during copulation with liquid nitrogen and the clasped genitalia were then embedded in epoxy resin and serially sectioned (1 µm) with an ultramicrotome (for details of method see Huber, 1993). The following numbers refer to pairs that were observed until the end of copulation (first number), and pairs that were freeze-fixed (second number): *A. zeteki* (2, 3); *M. culicinus* (3, 3); *M. david* (0, 1); *M. guatuso* (4, 2); ‘*C.*’ *viridescens* (4, 3).

RESULTS

Anopsicus zeteki

Genital morphology and mechanics. Figure 1 gives a pair in copulatory position in order to facilitate the interpretation of Figs 2 and 3. The ground plan of pholcid genitalia has been described in detail (Uhl, 1994; Uhl *et al.*, 1995; Huber, 1994, 1995). Only three points need to be emphasized with respect to *A. zeteki*: (1) the presence of a distal apophysis on the male pedipalpal femur (arrow in Fig. 2B) which will be proposed below as one of the key characters supporting the monophyly of the ‘*Modisimus* group’; (2) the presence of a sclerotized apophysis on the bulb (Fig. 2A, B) – this does not contain the sperm duct and is therefore no embolus (the sperm duct opens near the basis of the apophysis with the opening hidden by membraneous structures); (3) the procurus (Fig. 2B) is accompanied by an unsclerotized outgrowth that is characteristically shaped (Fig. 7A). A high degree of sexual dimorphism occurs in the chelicerae: those of the male are equipped with relatively huge apophyses, directed straight forwards and bent downwards at the tip, forming a small hook (Fig. 3). Those of the female are unmodified, as in all known pholcid females.

The female genitalia are simple, without apophyses or indentations externally, with the typical pair of pore plates dorsally in the uterus externus (Fig. 7B), a transverse membraneous fold ventrally (Fig. 3B, where the bulbal apophysis is inserted), and a simple ‘valve’ connecting to the oviduct.

During copulation, both pedipalps were used simultaneously and symmetrically (Fig. 3). Only the procuri and the distal parts of the bulbs were inserted into the female. The procuri were inserted up to the simple ‘valve’ that separates the copulatory chamber (uterus externus) from the oviduct. The apophysis of the bulb was hooked into the ventral, membraneous fold of the copulatory chamber. Outside the female the pedipalp was stabilized in the copulatory position in three ways (Fig. 3A): the trochanter was squeezed between chelicera and pedipalpal coxa; the femur was pressed against the lateral side of the pedipalpal coxa, and held by the ‘coxal apophysis’; and the distal apophysis of the femur was hooked into an indentation of the bulb. Also, the male chelicerae contacted the female. The fangs were pressed against the female genitalic area, apparently opposing the pressure of the procuri. The long frontal apophyses were directed to the female pedicel but their hooks did not engage a female structure (this situation may be an artifact).

Courtship, copulation, and other aspects. From seven copulations obtained in the laboratory, two were observed until the end, three pairs were freeze-fixed, and two pairs separated as they were disturbed by the observer. All females had been collected as adults in the field and were probably not virgin. Male courtship was conspicuous and consisted of leg tapping, brief

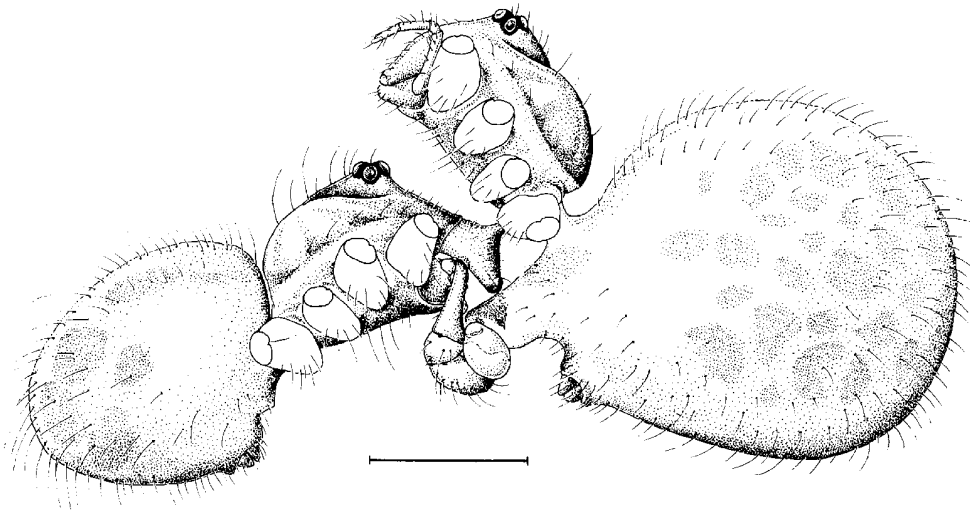


Fig. 1. Copulatory position of *A. zeteki* (legs removed); male on left side. The spiders copulate upside down, but are shown inverted to facilitate comparison with the figure on genital mechanics (Fig. 3). Scale line: 0.5 mm.

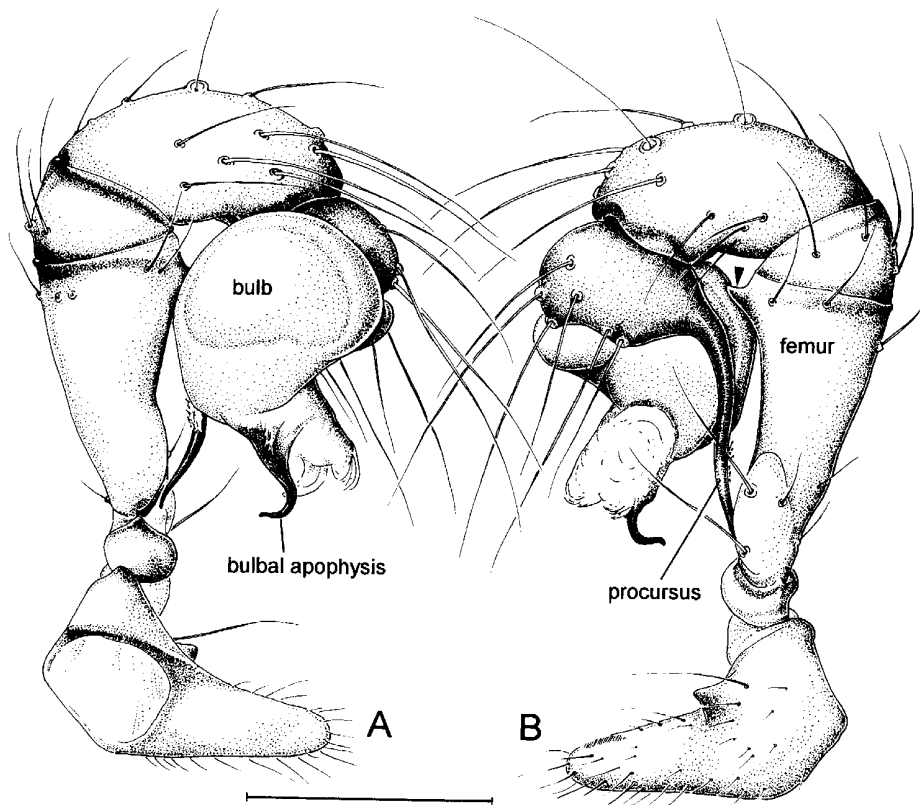


Fig. 2. Left male pedipalp of *A. zeteki*, in prolateral (A) and retrolateral (B) view. Scale line: 0.2 mm. Arrow points to 'pup' apophysis.

vibrations of the entire body, and occasional abdomen bobbing. In one case, both spiders intensely built (repaired?) the web during this period, in two others only the male and only the female, respectively, engaged in this activity. For weaving, the fourth legs were always moved simultaneously (the tips away from and towards the spinnerets). In these cases, courtship lasted 12, 15

and 32 min, whereas courtship without weaving lasted only 5, 6, 6, and 9 min. Before genitalic insertion, males rotated their pedipalps 180° and quickly approached the females. Only in one case did the male need two attempts before succeeding with insertion. In four pairs, copulation started without any struggle or obvious exchange of tactile or vibratory signals, in two there was

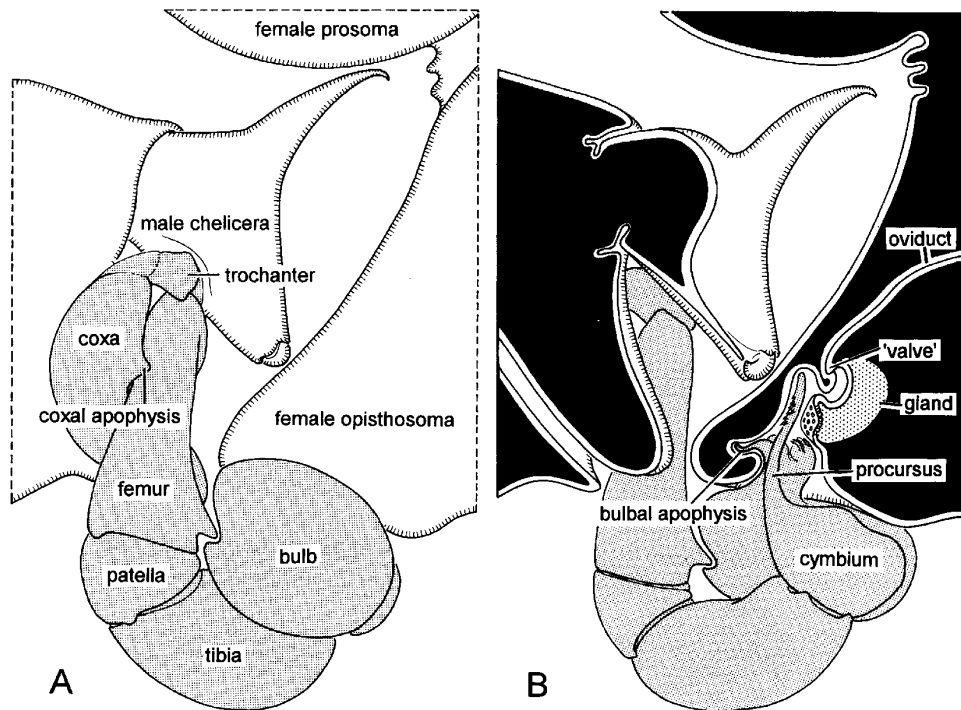


Fig. 3. Schematic representation of copulatory mechanics in *A. zeteki*. In (A) the right palp is viewed from the right side (cf. Fig. 1), in (B) the left palp is seen from the midline of the animals.

intense leg fidgeting for a few seconds, in one the male slightly tapped the female legs before calming down. The copulatory position corresponded to von Helversen's (1976) 'position of web spiders' (Fig. 1). Copulation duration was 13 and 22.5 min, respectively. During copulation, the tips of the male legs 1-3 usually contacted the respective female legs, but sometimes the tips were very close but not touching. Males rhythmically moved their pedipalps and abdomens during copulation. Pedipalps were simultaneously moved in a lateral direction which resulted in a partial withdrawal of the inserted procursi (see below). The initial frequency of these movements was one in 2 s, later it slowed down to about one in 4 s. About 2 min before the end of copulation, movements suddenly almost stopped, with about one slight movement every 10 s, and then resumed high frequency (about one per s) for some seconds in the last minute. This was only observed in the two pairs that were not interrupted. Abdomen movements consisted of short bursts of about 2-4 dorso-ventral flexions at the pedicel. Most of the time they were highly rhythmical, with about one burst every 15 s. Copulation was apparently ended by the male, and both spiders rapidly calmed down after a short period of unrest and renewed male courtship.

Egg production was studied in five females that had been collected as adults in the field and were kept in the laboratory for up to 10 months, without copulation. One of them produced a total of 9 fertile egg-sacs in this period, the others produced 8, 6, 5 and 1. From the

resulting 29 egg-sacs, one 'disappeared', i.e. was probably eaten by the female. An average of 13.4 spiderlings emerged from each of the other egg-sacs (4-24; $N = 28$). Spiderlings hatched after an average of 17.8 days (15-21; $N = 26$), and new egg-sacs were produced after an average of 7.8 days (3-22; $N = 24$).

As expected from the large percentage of time females spent carrying an egg-sac (about 70%, calculated from the numbers in the previous paragraph), they had no problems in attacking prey with an egg-sac in their chelicerae. Rarely did they suspend it before attacking, but usually they attacked the fly and wrapped it with the hind legs, then suspended the egg-sac and returned to the fly to feed on it. Wrapping was either by simultaneous movements as mentioned above or by alternative movements of the fourth legs.

This species was never seen oscillating in the 'typical pholcid manner' when disturbed. Instead, the spiders swiftly ran away and hid in crevices or under objects providing a shelter.

'*Coryssocnemis*' *viridescens*

Genital morphology and mechanics. As in *A. zeteki*, males have an apophysis (though much more prominent) distally on the pedipalpal femur (Fig. 4B), and another one on the bulb (Fig. 4A; this was misinterpreted as an embolus in the original description). Again, the sperm duct opens near the basis of the bulbal

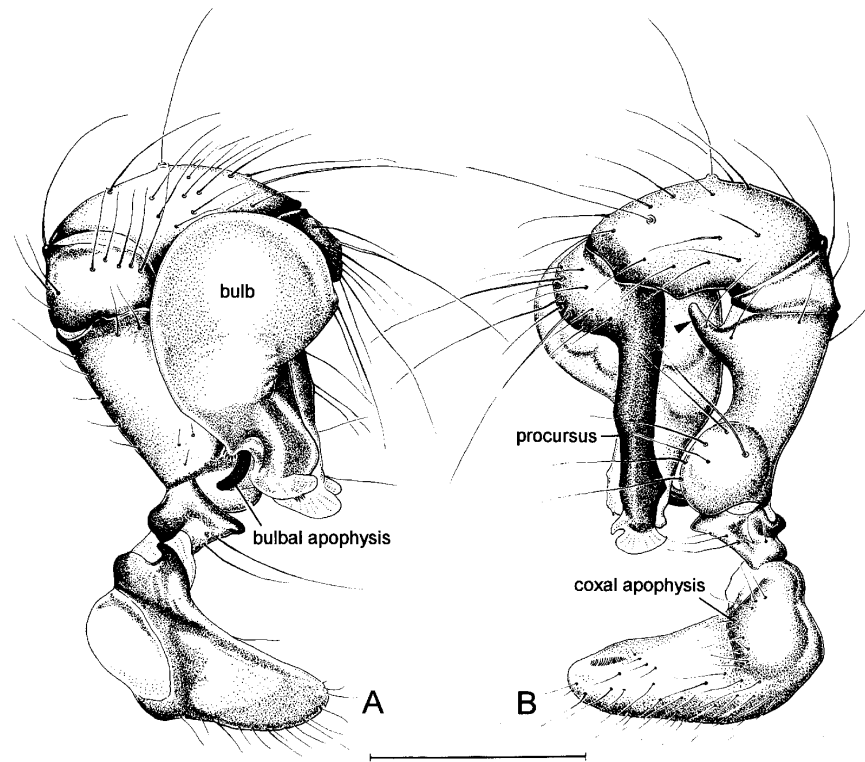


Fig. 4. Left male pedipalp of '*C.*' *viridescens*, in prolateral (A) and retrolateral (B) views. Scale line: 0.4 mm. Arrow points to 'pup' apophysis.

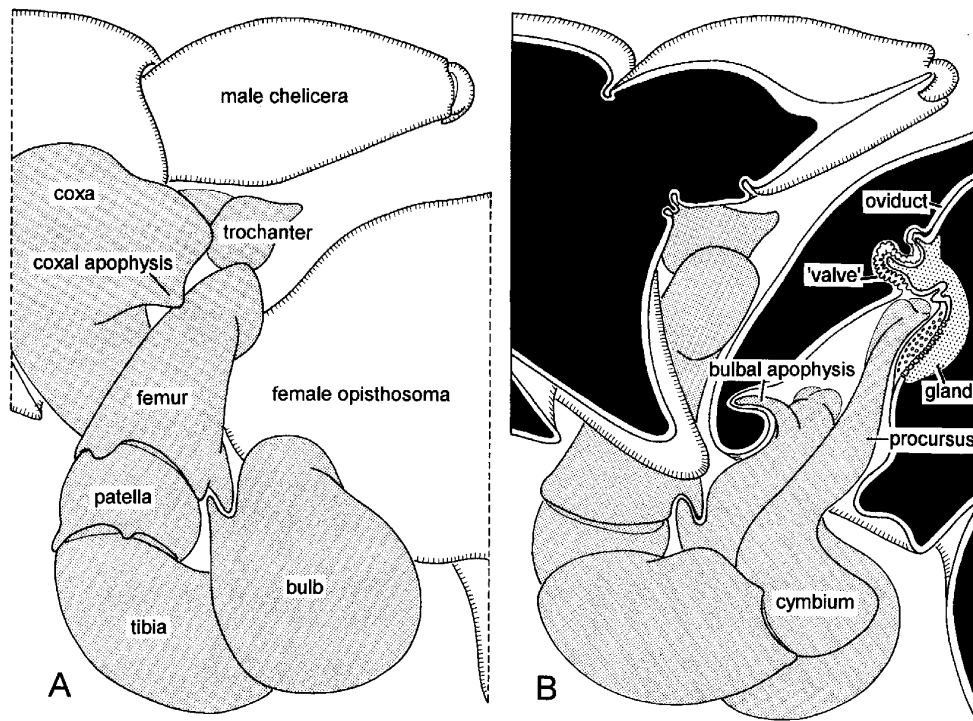


Fig. 5. Schematic representation of copulatory mechanics in '*C.*' *viridescens*. In (A) the right palp is viewed from the right side (cf. Fig. 1), in (B) the left palp is seen from the midline of the animals.

apophysis. The procurus is a simple rod with some membraneous fringes distally (Figs 4B, 7C). The male chelicerae of this species are unmodified, which is rare in pholcids, but explained by their unusual position during copulation (see below).

The female genitalia are marked externally by a large sclerotized plate (Fig. 7D). Internally the uterus externus is equipped with large pore plates (Fig. 7D) and a ventral membraneous fold as in *A. zeteki*. The 'valve' to the oviduct has a unique morphology, different from any other pholcid 'valve' studied so far (Fig. 5B; Huber, *In press b*).

Most details of genital mechanics corresponded exactly to the situation in *A. zeteki* (Fig. 5): simultaneous and symmetrical use of both pedipalps; insertion of only the procuri and the distal parts of the bulbs; positions of the procuri and the bulbal apophyses within the female; engagement of the femur apophyses with indentations in the bulbs. The major difference concerns the position of the male chelicerae which were lifted about 90° from their natural position and pressed against the large female 'epigynum' with their posterior sides. As a result of this, the trochanters were not locked between chelicerae and pedipalpal coxae.

Courtship, copulation, and other aspects. From seven copulations obtained in the laboratory, four were observed until the end, three pairs were freeze-fixed. Three of the females had moulted in captivity and were virgin. Male courtship was almost non-existent, but the males slowly, apparently 'cautiously' approached the female, slightly tapping with the anterior legs, and started copulation within 1-3 min (in one case 10 min). As in *A. zeteki*, males rotated their pedipalps 180° before inserting them into the female. In three cases the males needed two attempts before succeeding with insertion. In another pair, the male failed three times and was then wrapped and preyed upon by the female. Another male managed to insert his genitalia for a few seconds, but then fell victim to the female. However, in one pair the male failed once, and then succeeded because the female positioned herself in a way compensating the misalignment of the male. The most conspicuous movements during copulation were caused by the females: they simultaneously raised all femora of one side, then those of the other side, giving the body a slight, rhythmic lateral swing. Males performed rhythmic movements with their pedipalps. These were simultaneously moved in a lateral direction, but details of the movement were difficult to ascertain because of the female movements. The initial frequency of the male palpal movements was one in 2-3 s, later it slowed down to about one in 4 s. Males also performed irregular up and down movements with their abdomens. Copulation duration was 13 min with a virgin female, 10.5, 15, and a few seconds, respectively, with non-virgin females. No qualitative differences were observed between copulations with virgin and non-virgin females. In three of the four pairs, copulation was apparently ended by the male jumping away, and the spiders rapidly calmed down.

Egg production was studied in 11 females. Nine

females that had been collected as adults in the field were kept in the laboratory for up to 10 months, without copulation. Two more were collected as penultimate instars, were allowed to copulate after the final moult and were then kept for 10 months. No female produced more than three fertile egg-sacs. Four females produced a fourth egg-sac, but no spiderlings emerged from these. From the 24 fertile egg-sacs, an average of 23 spiderlings emerged (9-47). Spiderlings hatched after an average of 21.6 days (17-30; N = 17), and new egg-sacs were produced after an average of 33.4 days (9-68; N = 18).

As in *A. zeteki*, females holding an egg-sac with their chelicerae readily attacked prey. The sequence was the same as in *A. zeteki*. When the female was given a second fly after the first had been wrapped, she attacked again and acted with the fly in her chelicerae like before with the egg-sac.

Several individuals from Matagalpa had mites (unidentified) attached to their cuticle. Most of these spiders died after a few weeks in captivity. In one immature female I removed the mite to save her, but the female never moulted to maturity although she lived another 8 months (usually the penultimate instar in pholcids lasts about 1-2 months).

When disturbed, the spiders performed oscillating movements with their whole bodies, with high frequency but low amplitude.

Females of this species are equipped with a 'stridulation' apparatus of 'type a' (Legendre, 1963), where a pair of sclerotized plates on the opisthosoma act against a pair of sclerotized cones on the prosoma (dorsally). To my knowledge, this type of stridulatory apparatus is only known in certain *Anopsicus* and *Crossopriza* females among pholcids (Millot, 1946; Gertsch, 1982 – a similar but unpaired organ exists in some other pholcid genera). The context in which this structure is used is not known in any of these species.

Modisimus culicinus

Details on mating behaviour, genital morphology, egg-sac production, prey capture and other notes on the natural history of this spider have been presented elsewhere (Huber, 1996, 1997). Most details of genital mechanics (Fig. 6) again correspond exactly to the situation in *A. zeteki* and '*C. viridescens*': simultaneous and symmetrical use of both pedipalps; insertion of only the procuri and the distal parts of the bulbs; positions of the procuri and the bulbal apophyses within the female (Fig. 6B); engagement of the femur apophyses with indentations in the bulbs. Unlike the situation in the above species, the chelicerae are pressed against the female with their frontal sides which are equipped with a pair of apophyses. The trochanters have small apophyses that are locked at the rear side of the chelicerae. A speciality of *M. culicinus* is the contact of a lobe on the male front with the female mouth. This is no locking mechanism but a case of gustatorial courtship (Huber, 1997).

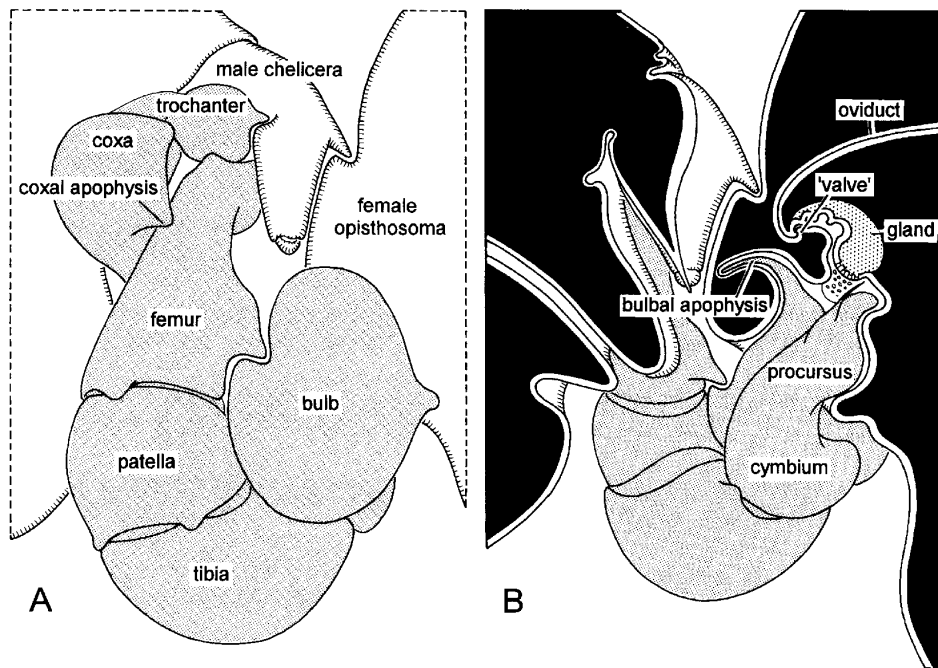


Fig. 6. Schematic representation of copulatory mechanics in *M. culicinus*. In (A) the right palp is viewed from the right side (c.f. Fig. 1), in (B) the left palp is seen from the midline of the animals.

Modisimus david and *Modisimus guatuso*

Genital mechanics in these species was very similar to *M. culicinus*. The armature of the male chelicerae differs (those of *M. david* are unmodified – see figures in Huber, 1996; those of *M. guatuso* are equipped with spines, i.e. strong modified hairs – figured in Huber, In press *e*), but the chelicerae of both species were pressed against the female with their frontal sides as in *M. culicinus*. The bulbal apophysis in *M. guatuso* was not inserted into a ventral pouch in the female but was simply pressed against the ventral cuticle of the uterus externus which is sclerotized and flat. The side of the bulbal apophysis that contacts the female in this way is provided with many small cuticular denticles. Both species lack the type of gustatorial courtship described in *M. culicinus*.

DISCUSSION

Structure and function of the femur apophysis in pholcids

Many genera of both Old and New World pholcids have representatives with apophyses or bulges on the male pedipalpal femora. Figure 8 shows a selection of forms. Only in two species (apart from those in the present paper) has the function of this protrusion been studied: in *Psilochorus simoni*, the apophysis (Fig. 8A) serves exactly the same function as in the species treated in the present paper (Huber, 1994): it engages an indentation on the genital bulb. In *Pholcus phalan-*

gioides, the simple bulge (Fig. 8Q) has no obvious function during copulation but appears to stabilize the palp at rest (Uhl *et al.*, 1995). Three other pholcids whose genital mechanics have been studied lack any protrusion of the femur (*Holocnemus pluchei* – Huber, 1995; *Physocyclus globosus* – Huber & Eberhard, 1997; *Metagonia rica* – Huber, In press *a*). From Fig. 8, it is evident that there is one group of apophyses that is distinguished from all others by its form (Fig. 8A-I); this will here be called a ‘pup’ (pointed and upward projecting) apophysis. All the species treated in this paper and *Psilochorus simoni* have ‘pup’ apophyses. The form of the structure is explained by its function of engaging an indentation of the bulb during copulation. The ultimate function of this engagement was not established, but might have to do with the stabilization of the rotating genital bulb during copulation.

Geographic distribution of pholcids with ‘pup’ apophyses

From taxonomic literature the geographic distribution of the character ‘pup’ apophysis was established. Each square in Fig. 9 gives the type locality of a species with a ‘pup’ apophysis. It might be objected that this is a poor representation of the geographic range of a species, but about 80% of the species included are only known from the type locality or nearby localities anyway. Figure 9 shows that the character ‘pup’ apophysis is restricted to Central America, the U.S.A., and the West Indies. It might be argued further that the South American fauna is too poorly known to discuss the geographic distribu-

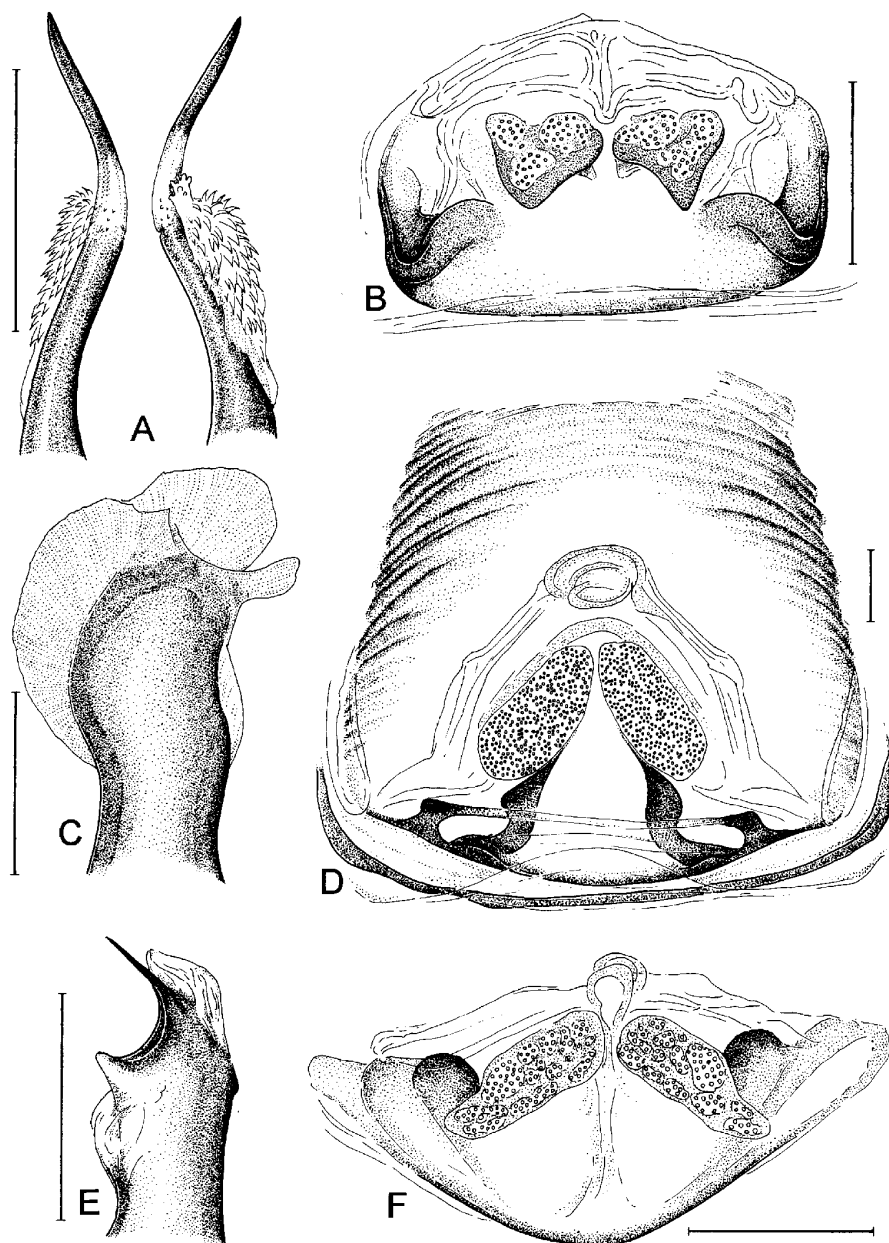


Fig. 7. Tips of the male procrursi, and internal female genitalia viewed from dorsally (after KOH treatment) of *A. zeteki* (A, B), '*C. viridescens*' (C, D), and *M. culicinus* (E, F). Scale lines: 0.1 mm.

tion of the character. However, Figs 10-13 make the trend clear: of the 21 South American species of the respective genera for which the femur was adequately illustrated, none has a 'pup' apophysis; of 96 North and Central American and West Indian species with adequate illustrations available, 88 have a 'pup' apophysis.

Implications for pholcid systematics

A. The monophyly of the 'Modisimus group'

It is here proposed that the limited geographic distribu-

tion of the character 'pup' apophysis is best explained by assuming monophyly for the respective group of genera, herewith called '*Modisimus* group'. This group includes the following genera (synonyms in parentheses): *Modisimus* Simon, 1893 (*Hedypsilus* Simon, 1893; *Modisimops* Mello-Leitão, 1946); *Psilochorus* Simon, 1893; *Anopsicus* Chamberlin & Ivie, 1938 (*Ninetella* Bryant, 1940; *Pholcophorina* Gertsch, 1939); *Bryantina* Brignoli, 1985. Apart from these it includes part of what are now the probably polyphyletic (see below) genera *Coryssocnemis* Simon, 1893 and *Blechoscelis* Simon, 1893. The monophyly of the '*Modisimus* group' contradicts previous classifications of Pholcidae: both Simon's (1893) 'Blechosceleae' and Mello-Leitão's

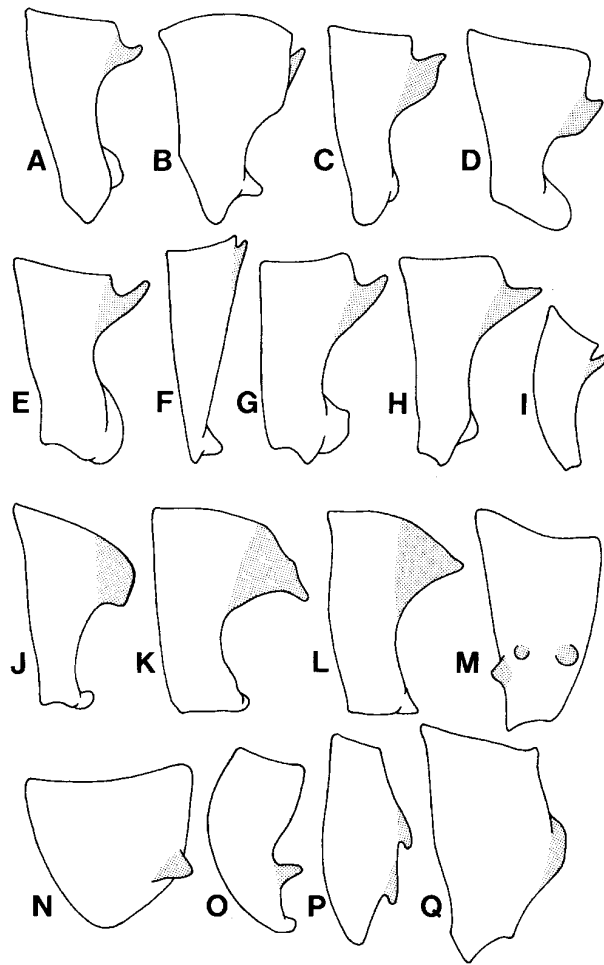


Fig. 8. Different morphologies of male pedipalpal femora in pholcids; apophyses shaded. A-I shows the type of apophysis that is here called 'pup' (pointed and upward projecting) apophysis and that only occurs in North America, Central America and the West Indies; J-Q presents the widest possible range of femur apophyses in other genera. (A) *Psilochorus simoni*; (B) *Psilochorus lemniscatus*; (C) *Modisimus guatuso*; (D) *Modisimus culicinus*; (E) '*Coryssocnemis*' *viridescens*; (F) '*Coryssocnemis*' *pecki*; (G) *Anopsicus chiriQUI*; (H) *Bryantina coxana*; (I) '*Blechnoscelis*' *modesta*; (J) *Litoporus aerius*; (K) *Coryssocnemis callaica*; (L) *Mecolaesthus longissimus*; (M) *Leptopholcus dalei*; (N) *Metagonia uvita*; (O) '*Psilochorus*' *wunderlichii*; (P) *Calapnita vermiformis*; (Q) *Pholcus phalangioides*. From Huber, 1994 (A); Huber, In press c (B, J, K, L); Huber, In press e (C); Huber, 1996 (D); Gertsch, 1971 (F); Huber, In press d (G); Huber, unpubl. data (H); Banks, 1929 (I); Huber, In press a (M, N); Deeleman-Reinhold, 1994 (O); Deeleman-Reinhold, 1986 (P); Uhl *et al.*, 1995 (Q). Drawn at different scales.

(1946) 'Ninetidinae' and 'Blechnosceleae' include part of the genera of the '*Modisimus* group' together with other genera. These classifications were not explicitly proposed as biological ones and merit only a limited heuristic value.

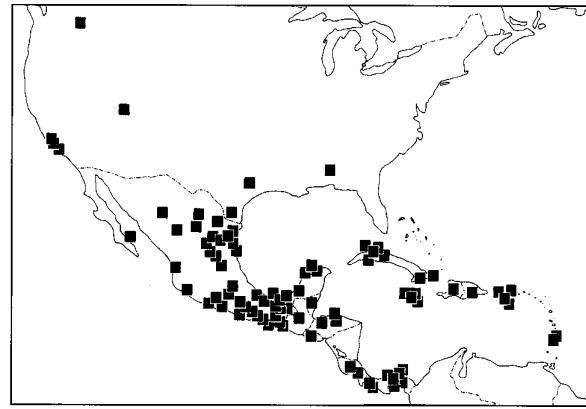


Fig. 9. Geographic distribution of the character 'pup' apophysis. Each square stands for the type locality of one species in which the description clearly shows a 'pup' apophysis on the male palpal femur. Synanthropic species are excluded. Note that there is so far no convincing record of a species with 'pup' apophysis from South America.

B. Evidence for the polyphyly of *Psilochorus*, *Coryssocnemis*, and *Blechnoscelis*

Psilochorus. This genus presently includes species from all of America (Fig. 10) and from Australia (the type *P. pullulus* is North American). No autapomorphy is known for the genus; instead, it is weakly defined by a set of characters that are also shared by other genera (Simon, 1893; Comstock, 1967; Gertsch, 1971; Brignoli, 1973). There is evidence that the Australian species are not 'real' *Psilochorus*: apart from lacking a 'pup' apophysis they have an elaborate valve in the internal female genitalia which places them closer to other Old World genera (Huber, In press b). Deeleman-Reinhold (1994) has suggested a close relationship of Australian *Psilochorus* to the East Asian genera *Holocneminus* and *Trichocyclus*, based on the sculpture of the carapace and the structure of the bulb-embolus complex. Defence behaviour and web structure in the Australian '*Psilochorus*' *sphaeroides* rather resemble those of *Pholcus phalangioides* (whirling in space webs – Jackson, 1992; Jackson, Rowe & Campbell, 1992) than those of the American *Psilochorus simoni* (running away on attached webs or on the ground – Huber, 1994). More problematic are the South American representatives. Eleven species have been described. From these, four (*minimum*; *coeruleiventris*; *bruneocyanus*; *sectus*) are only known from the female, which does not allow any conclusions. In another three species (*dasyops*; *marcuzzii*; *browningi*), the males are known but the existing descriptions do not provide sufficient information about the pedipalpal femur. The remaining four species (*nigridentis*; *fluminensis*; *cyaneomaculatus*; *taperae* – all from Brazil) lack a 'pup' apophysis on the femur and are thus probably not 'real' *Psilochorus*. Additional evidence for the exclusively North American distribution of *Psilochorus* comes from a study of the pholcid fauna of Costa Rica (Huber, In press d) in which not a single *Psilochorus*

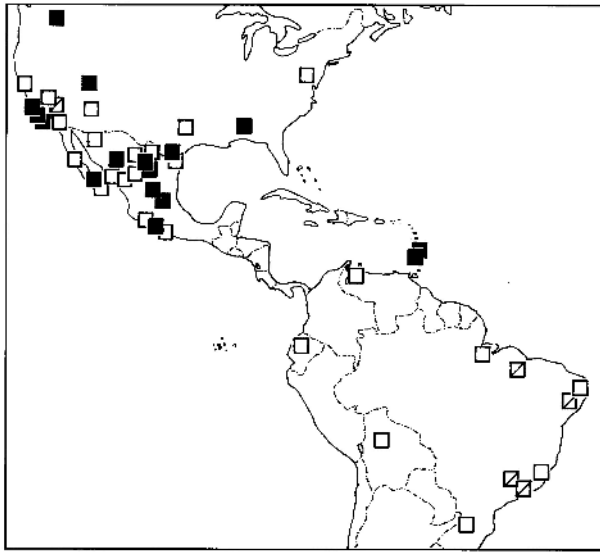


Fig. 10. Geographic distribution of the genus *Psilochorus* (the apparently misplaced Australian species and the synanthropic *P. simoni* are excluded). Each square stands for the type locality of one species. Full squares: species with 'pup' apophysis (including the type species); empty squares: species of which only the female is known or where the male palpal femur has not been adequately illustrated; crossed squares: species that lack a 'pup' apophysis and that are probably misplaced.

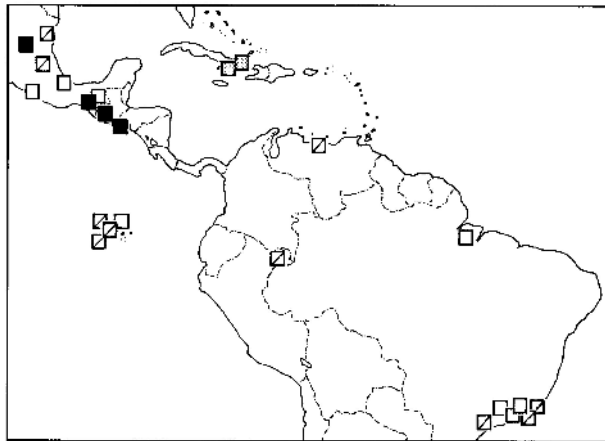


Fig. 11. Geographic distribution of the genera *Coryssocnemis* and *Bryantina*. Each square stands for the type locality of one species. Full squares: '*Coryssocnemis*' species with 'pup' apophysis, thus probably misplaced; empty squares: species of which only the female is known or where the male palpal femur has not been adequately illustrated; crossed squares: species that lack a 'pup' apophysis (including the type species); grey squares: the two *Bryantina* species that both have a 'pup' apophysis.

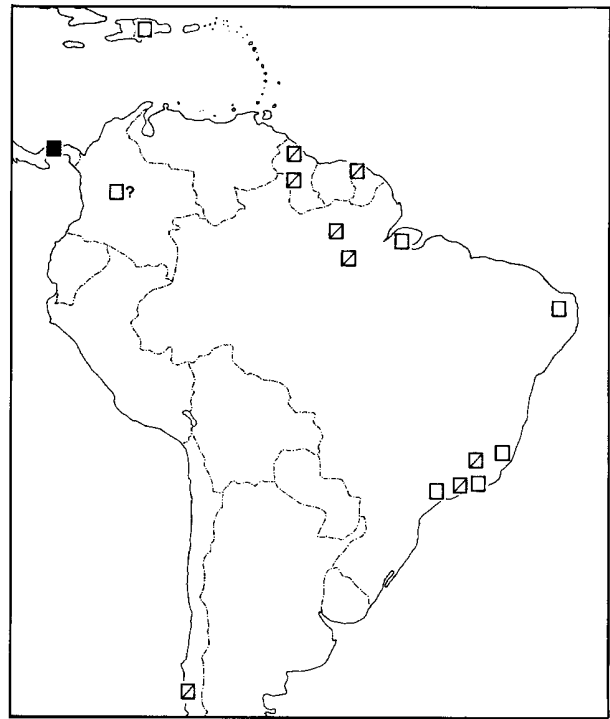


Fig. 12. Geographic distribution of the genus *Blechroscelis*. Each square stands for the type locality of one species. Full square: '*Blechroscelis modesta*' with 'pup' apophysis, thus probably misplaced; empty squares: species of which only the female is known or where the male palpal femur has not been adequately illustrated (including the type species which is accompanied by a question-mark because its type locality is unclear); crossed squares: species that lack a 'pup' apophysis.

species has been found. The two West Indian species (*nigrifrons*; *lemniscatus* – from St. Vincent) have been redescribed recently (Huber, In press c), and belong to the '*Modisimus* group', but they are quite different from North American *Psilochorus*: they are large spiders with elongate abdomens, whereas North American species are small and have globular abdomens. The South American records of *Psilochorus* in purely faunistic studies (such as that of Manhart, 1994 in Peru) need to be reconsidered (the pholcid material of that study is lost, however – C. Manhart, pers. comm.).

Coryssocnemis. The geographic range of this genus presently covers all of America from Mexico to Brazil (Fig. 11) (the type *C. callaica* is from Venezuela). The genus is very heterogeneous, and no autapomorphy is known for it. Both Gertsch (1971) and Brignoli (1981) have expressed doubt on the existing limits. Thirteen species have been described from South America. From these, five (*insularis*; *altiventer*; *paraensis*; *lepidoptera*; *occulta*) are only known from the female. The other eight, including the type species (*callaica*; *uncata*; *conica*; *banksi*; *togata*; *discolor*; *floreana*; *jarmila*), lack a 'pup' apophysis. From the nine Central American species, three (*placida*; *faceta*; *simoni*) are only known from females; two species (*iviei*; *clara*) lack a femur apophysis;

and four species (*pecki*; *furcula*; *abernathi*; *viridescens*) have a 'pup' apophysis and are therefore probably not 'real' *Coryssocnemis*.

Blechroscelis. This is an almost exclusively South American genus (Fig. 12), which is also poorly defined and heterogeneous, and has been considered "often misinterpreted" by Brignoli (1981). In eight South American species the descriptions are sufficient to say that they have no 'pup' apophysis. The only Central American species (*modesta* – from Panama) has a 'pup' apophysis and is therefore probably not congeneric with the South American representatives. Whether the Panamanian or the South American species are 'real' *Blechroscelis* cannot be decided because the type species (*annulipes*) is only known from the female, and its origin is not clear (Santa Fé de Bogotá in Colombia is maybe only the place where it was purchased – see Levi, 1964). Finally, also the single West Indian representative (*serripes*) is only known from the female and might not be congeneric with the type species.

C. Notes on the genera *Modisimus* and *Anopsisus*

The genus *Modisimus* is species-rich in Central America and the West Indies (Fig. 13). It is believed to occur also in South America, but this needs revision. Five species have been described from South America; from these, *M. culicinus* (found at several South American localities) is a synanthropic, pantropic species (therefore not represented in Fig. 13) and may have originated from Central America; *M. exlineae* (from Peru) and *M. solus* (from the Galapagos Islands) are only known from the females; *M. globosus* (from Colombia) is probably a 'real' *Modisimus* (redescription in Huber, 1996), but it arrived in Hamburg, Germany, with a shipment of bananas from Colombia (Schmidt, 1971), which is not a reliable indication about its origin; and *M. ('Hedypsilus') modicus* (from the Galapagos Islands) apparently has no 'pup' apophysis (see fig. 27 in Gertsch & Peck, 1992). Finally, the Colombian species treated as "*Modisimus* sp. A" in the study of Eberhard & Briceño (1985) lacks a 'pup' apophysis (Huber, unpubl. data) and is thus also probably not a 'real' *Modisimus*.

The genus *Anopsisus* is very species-rich in Central America, Cuba and Jamaica (Gertsch, 1982) (Fig. 14). One species was recorded from Trinidad (*A. arima*) but is known from the female only. Another species (*A. banksi*) was found on the Galapagos Islands, but it lacks a femur apophysis (see fig. 51 in Gertsch & Peck, 1992) and is probably misplaced.

D. Misplaced species

As mentioned above, the aim of this paper is the delimitation of the '*Modisimus* group' against other pholcids. I neither attempt to treat the taxonomic status of the genera within the group (some are hardly defined by any autapomorphies), nor decide on the generic status of

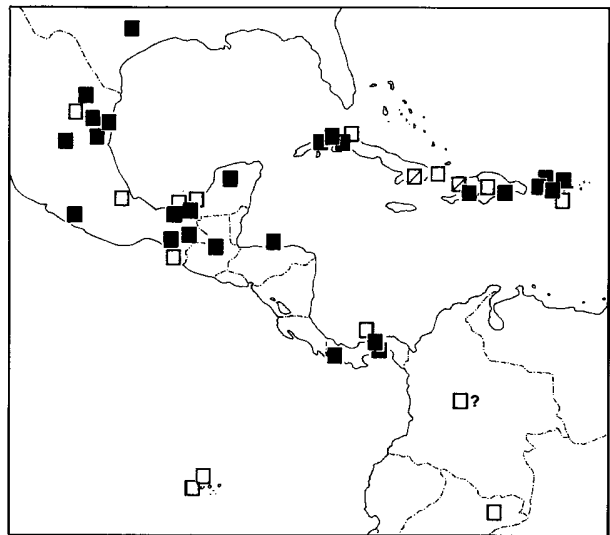


Fig. 13. Geographic distribution of the genus *Modisimus* (the synanthropic *M. culicinus* is excluded). Each square stands for the type locality of one species. Full squares: species with 'pup' apophysis (including the type species); empty squares: species of which only the female is known or where the male palpal femur has not been adequately illustrated; crossed squares: species that lack a 'pup' apophysis and that are probably misplaced. The question mark refers to the uncertain type locality of *M. globosus* Schmidt, 1971.

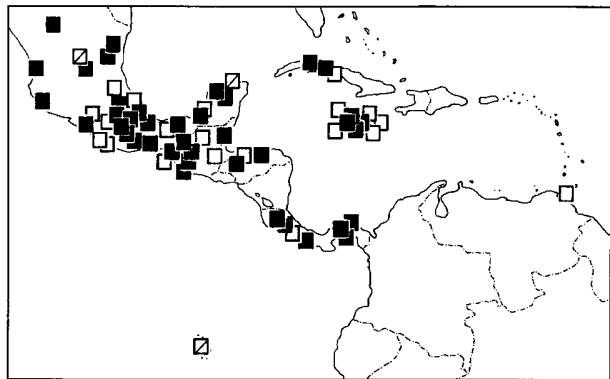


Fig. 14. Geographic distribution of the genus *Anopsisus*. Each square stands for the type locality of one species. Full squares: species with 'pup' apophysis (including the type species); empty squares: species of which only the female is known or where the male palpal femur has not been adequately illustrated; crossed squares: species that lack a 'pup' apophysis and that are probably misplaced.

apparently misplaced species. The actual act of transferring misplaced species to other genera is not considered useful at the present state of knowledge. Instead, I propose to mark apparently misplaced species with quotation marks and to keep them in their traditional genera until a convincing solution is found for their placement. This includes: non-American and South American '*Psilochorus*'; '*Coryssocnemis*' *pecki*, *furcula*, *abernathi* and *viridescens*; '*Blechroscelis*' *modesta*; '*Anopsisus*' *banksi*.

Implications for the usefulness of some characters in pholcid systematics

The species treated in the present study were partly selected to represent the largest possible range of morphological and ecological characters. When the previously studied *Psilochorus simoni* (see Huber, 1994) is included, the following character states are represented: eight vs. six eyes; attached vs. free dome-shaped web; short vs. long-legged; deep vs. shallow thoracic groove; small vs. large overall size; globular vs. oval abdomen; unmodified male chelicerae vs. chelicerae with horns vs. chelicerae with modified hairs; with vs. without eye turret; six eyes in two triads vs. in one group. All of these character states can be found repeatedly in other, distantly related pholcid genera, and may be less informative for the reconstruction of intergeneric relationships than genital characters that reflect a complex coupling or stabilizing mechanism.

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REFERENCES

- Banks, N. (1929). Spiders from Panama. *Bull. Mus. Comp. Zool.* **69**(3): 51-96.
- Brignoli, P. M. (1972a). Sur quelques araignées cavernicoles d'Argentine, Uruguay, Brésil et Venezuela récoltées par le Dr. P. Strinati (Arachnida, Araneae). *Rev. Suisse Zool.* **79**(1): 361-385.
- Brignoli, P. M. (1972b). Some cavernicolous spiders from Mexico (Araneae). *Quad. Accad. Naz. Lincei* **171**(1): 129-155.
- Brignoli, P. M. (1973). Notes on spiders, mainly cave dwelling, of Southern Mexico and Guatemala (Araneae). *Quad. Accad. Naz. Lincei* **171**: 195-238.
- Brignoli, P. M. (1981). Studies on the Pholcidae, I. Notes on the genera *Artema* and *Physocyclus* (Araneae). *Bull. Am. Mus. Nat. Hist.* **170**(1): 90-100.
- Comstock, J. H. (1967). The spider book (reprinted). Ithaca, N.Y.: Cornell University Press.
- Deeleman-Reinhold, C. L. (1986). Studies on tropical Pholcidae II. Redescription of *Micromerys gracilis* Bradley and *Calapnita vermiformis* Simon (Araneae, Pholcidae) and description of some related new species. *Mem. Qd Mus.* **22**(5): 205-224.
- Deeleman-Reinhold, C. L. (1994). Redescription of *Holocnemius multiguttatus* Simon and description of two new species of pholcid spiders from Australia (Arachnida: Araneae: Pholcidae). *Beitr. Araneol.* **4**: 31-11.
- Eberhard, W. G. (1992). Notes on the ecology and behaviour of *Physocyclus globosus* (Araneae, Pholcidae). *Bull. Br. Arachnol. Soc.* **9**(2): 38-42.
- Eberhard, W. G. & Briceño, R. D. (1983). Chivalry in pholcid spiders. *Behav. Ecol. Sociobiol.* **13**: 189-195.
- Eberhard, W. G. & Briceño, R. D. (1985). Behavior and ecology of four species of *Modisimus* and *Blechnoscelis* (Araneae, Pholcidae). *Rev. Arachnol.* **6**(1): 29-36.
- Gerhardt, U. (1933). Neue Untersuchungen zur Sexualbiologie der Spinnen, insbesondere an Arten der Mittelmeerländer und der Tropen. *Z. Morph. Ökol. Tiere* **27**: 1-75.
- Gertsch, W. J. (1971). A report on some Mexican cave spiders. *Assoc. Mex. Cave Stud., Bull.* **4**: 47-111.
- Gertsch, W. J. (1982). The spider genera *Pholcophora* and *Anopsis* (Araneae, Pholcidae) in North America, Central America and the West Indies. *Assoc. Mex. Cave Stud., Bull.* **8**: 95-144.
- Gertsch, W. J. & Peck, S. B. (1992). The pholcid spiders of the Galápagos Islands, Ecuador (Araneae: Pholcidae). *Can. J. Zool.* **70**: 1185-1199.
- Helversen, O. von. (1976). Gedanken zur Evolution der Paarungstellung bei den Spinnen (Arachnida: Araneae). *Ent. germ.* **3**(1/2): 13-28.
- Huber, B. A. (1993). Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). *Can. J. Zool.* **71**: 2437-2447.
- Huber, B. A. (1994). Genital morphology, copulatory mechanism and reproductive biology in *Psilochorus simoni* (Berland, 1911) (Pholcidae; Araneae). *Neth. J. Zool.* **44**(1-2): 85-99.
- Huber, B. A. (1995). Copulatory mechanism in *Holocnemus pluchei* and *Pholcus opilionoides*, with notes on male cheliceral apophyses and stridulatory organs in Pholcidae (Araneae). *Acta zool. (Stockh.)* **76**: 291-300.
- Huber, B. A. (1996). On the distinction between *Modisimus* and *Hedypsilus* (Araneae, Pholcidae), with notes on behaviour and natural history. *Zool. Scr.* **25**: 233-240.
- Huber, B. A. (1997). Evidence for gustatorial courtship in a haplogyne spider (*Hedypsilus culicinus*; Pholcidae). *Neth. J. Zool.* **47**(1): 95-98.
- Huber, B. A. (In press a). On American 'Micromerys' and *Metagonia* (Araneae, Pholcidae), with notes on natural history and genital mechanics. *Zool. Scr.*
- Huber, B. A. (In press b). On the 'valve' in the genitalia of female pholcids (Pholcidae, Araneae). *Bull. Br. Arachnol. Soc.*
- Huber, B. A. (In press c). Redescriptions of Eugène Simon's neotropical pholcids (Araneae: Pholcidae). *Zoosystema*.
- Huber, B. A. (In press d). The pholcid spiders of Costa Rica (Araneae; Pholcidae). *Rev. Biol. Trop.*
- Huber, B. A. (In press e). Notes on the neotropical spider genus *Modisimus* (Pholcidae, Araneae), with descriptions of thirteen new species from Costa Rica and neighboring countries. *J. Arachnol.*
- Huber, B. A. & Eberhard, W. G. (1997). Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). *Can. J. Zool.* **74**: 905-918.
- Jackson, R. R. (1992). Predator-prey interactions between web-invading jumping spiders and two species of tropical web-building pholcid spiders, *Psilochorus sphaeroides* and *Smeringopus pallidus*. *J. Zool. (Lond.)* **227**: 531-536.
- Jackson, R. R., Rowe, R. J. & Campbell, G. E. (1992). Anti-predator defences of *Psilochorus sphaeroides* and *Smeringopus pallidus* (Araneae, Pholcidae), tropical web-building spiders. *J. Zool. (Lond.)* **228**: 227-232.
- Legendre, R. (1963). L'audition et l'émission de sons chez les Aranéides. *Ann. Biol.* **2**: 371-390.

- Levi, H. W. (1964). Nineteenth century South American araneology. *Pap. Avulsos Zool. (São Paulo)* **16**(1): 9-19.
- Manhart, C. (1994). Spiders on bark in a tropical rainforest (Panguana, Peru). *Stud. Neotrop. Fauna Environ.* **29**(1): 49-53.
- Mello-Leitão, C. de (1918). Scytodidas e pholcidas do Brasil. *Rev. Mus. Paul. N.S.* **10**: 88-144.
- Mello-Leitão, C. de (1946). Notas sobre os filistatidae e pholcidae. *An. Acad. Bras. Cienc.* **18**(1): 39-83.
- Millot, J. (1946). Les pholcides de Madagascar (Aranéides). *Mém. Mus. Natl Hist. Nat. N.S.* **22**(3): 127-158.
- Schmidt, G. (1971). Mit Bananen eingeschleppte Spinnen. *Zool. Beitr.* **17**: 387-433.
- Simon, E. (1893). *Histoire naturelle des araignées* **1**(2). 2nd edn. Paris.
- Timm, H. (1976). Die Bedeutung von Genitalstrukturen für die Klärung systematischer Fragen bei Zitterspinnen (Arachnida: Araneae: Pholcidae). *Ent. germ.* **3**(1/2): 69-76.
- Uhl, G. (1993). Mating behaviour and female sperm storage in *Pholcus phalangioides* (Fuesslin) (Araneae). *Mem. Queensl. Mus.* **33**(2): 667-674.
- Uhl, G. (1994). Genital morphology and sperm storage in *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). *Acta zool. (Stockh.)* **75**: 1-12.
- Uhl, G., Huber, B. A. & Rose, W. (1995). Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). *Bull. Br. Arachmol. Soc.* **10**(1): 1-9.