

Exaggerated female genitalia in two new spider species (Araneae: Pholcidae), with comments on genital evolution by female choice versus antagonistic coevolution

BERNHARD A. HUBER, ANTONIO D. BRESCOVIT, and CRISTINA A. RHEIMS

Insect Syst. Evol. Huber, B. A. *et al.*: Exaggerated female genitalia in two new spider species (Araneae: Pholcidae), with comments on genital evolution by female choice versus antagonistic coevolution. *Insect Syst. Evol.* 36: 285-292. Copenhagen, September, 2005. ISSN 1399-560X.



Two new species are described that are remarkable in having exaggerated female genitalia: *Mesabolivar samatiaguassu* sp. n. and *M. cuarassu* sp. n.. Comparative evidence as well as size measurements of male and female structures suggest that the exaggerated female external genitalia correlate functionally with elongated male cheliceral apophyses. These morphological findings are discussed in the light of competing models of genital evolution. Luring mating acts, female cooperative behaviour and morphology, as well as the probable costs associated with the female structures argue against the antagonistic coevolution model and favour sexual selection by cryptic female choice.

B. A. Huber, Zoological Research Institute and Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany (b.huber.zfmk@uni-bonn.de)

A. D. Brescovit, and C. A. Rheims, Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brasil, 1500, CEP 05503-900, São Paulo, SP, Brazil and Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil (adbre@terra.com.br, cris.rheims@butantan.gov.br)

Introduction

Pholcids are unusual among spiders by showing a functional correlation between the male chelicerae and the female external genitalia ('epigynum'). At the onset of copulation, the male contacts the epigynum with his sexually modified chelicerae, and during copulation parts of the female genitalia are firmly locked between male chelicerae and palps. This correlation has been shown both by direct observations (Huber 1995, 1997, 1998a, 2002, Huber & Eberhard 1997, Uhl & al. 1995) and by comparative analyses (Kraus 1984, Huber 1999, 2003b). Comparative analyses are possible in cases where the female offers specific pockets or cavities for specific male apophyses (Fig. 1). Such cooperative structures have evolved several times convergently within the family (Huber 2000, 2003a, b).

In several species, male and female morphologies seem to reflect arms races. Evolutionary changes in female morphology are mirrored in corresponding changes in male morphology, often resulting in exaggerated male cheliceral traits. In some cases this does not seem to involve any sig-

nificant cost to the female, as for example when the only change in females is the position of a pair of pockets on the epigynum (compare Figs 1A and 1B; see also Huber 2000: fig. 638, 2003a: fig. 87). For males, in contrast, a simple shift of the female pockets may select for exaggerated apophyses whose length reflects their need to reach the female pockets (Fig. 1A, B; see also Huber 2000: fig. 631, Huber 2003a: fig. 93, Huber 2003b: fig. 100). In some species of the genus *Mesabolivar*, the arms race appears to result in considerable costs for the female too. In these cases, access to an unpaired female pocket is made difficult by a pair of female humps, forcing the male to develop correspondingly long cheliceral apophyses (Fig. 1C, D; Huber 2000).

The present paper describes two closely related new species in which this latter scenario is realized to an extreme degree. The data are discussed in the light of the recent debate on genital evolution by female choice versus antagonistic coevolution (review in Eberhard 2004).

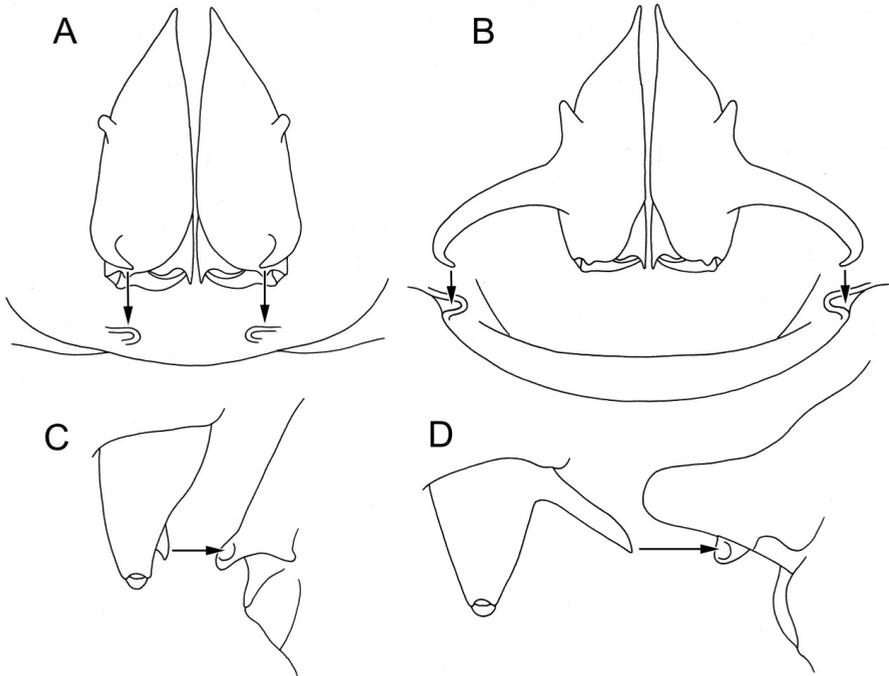


Fig. 1. Male-female coevolution between male chelicerae and female external genitalia in pholcids. Note that in the upper scenario (A, B) a presumably low cost shift of the female pockets results in exaggeration of the male trait. In the lower scenario (C, D), both male and female morphologies may become exaggerated. Drawings simplified from an unpublished manuscript on East Asian '*Belisana*' (A, B), and from Huber (2000) (C: *Mesabolivar cyaneotaeniatu*s; D: *Mesabolivar junin*).

Taxonomy

Style of descriptions is as in Huber (2000). Measurements are in mm, except for eyes which are in μm with a measurement error of about $5\mu\text{m}$. Material is deposited in the collections of the Instituto Butantan, São Paulo (IBSP), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP) and Zoological Research Institute and Museum Alexander Koenig, Bonn (ZFMK).

Genus *Mesabolivar* González-Sponga, 1998

Mesabolivar samatiaguassu sp. n.

(Fig. 2A-C, 3, 4)

Type material. - Male holotype (IBSP 25755), 4♂ 7♀ paratypes from Estação Ecológica Juréia Itatins (24°33'S, 47°13'W), pitfall traps, Peruíbe, São Paulo, Brazil; April 26-May 3, 1999 (A. D. Brescovit, C. A. Rheims, R. Pinto da Rocha, D. Candiani, H. Japyassú, L. Mestre). Paratypes deposited in IBSP (25174, 25551, 25623, 25735, 25745, 25753), ZFMK (1♂1♀) and MZSP (1♂1♀).

Etymology. - The species name is a noun in apposition taken from the Tupi-Guarani Indian language, derived from terms for large (guassú) and vulva (samatiá), referring to the female genitalia.

Diagnosis. - Easily distinguished from most congeners by the exaggerated epigynum (Figs. 2B, C, 3D, 4A), from *M. cuarassu* by the shapes of epigynum, male cheliceral apophyses (Fig. 3C), and procurus (Fig. 3B).

Description. - Male (holotype): Total length 2.36 (2.50 with clypeus), carapace width 1.02. Leg 1: 25.4 (6.1 + 0.4 + 6.5 + 11.1 + 1.3), tibia 2: 4.1, tibia 3: 3.1, tibia 4: 5.2. Tibia 1 L/d: 73. Habitus as in Figure 2A. Carapace light brown, margins and ocular area slightly darker, median line black, sternum and legs light ochre, abdomen greenish-grey with dark bluish spots (unlike photographed male!). Ocular area distinctly elevated, thoracic furrow distinct; distance PME-PME 60 μm ; diameter PME 115 μm ; distance PME-ALE 80 μm ; diameter AME 45 μm , distance AME-AME 20 μm .

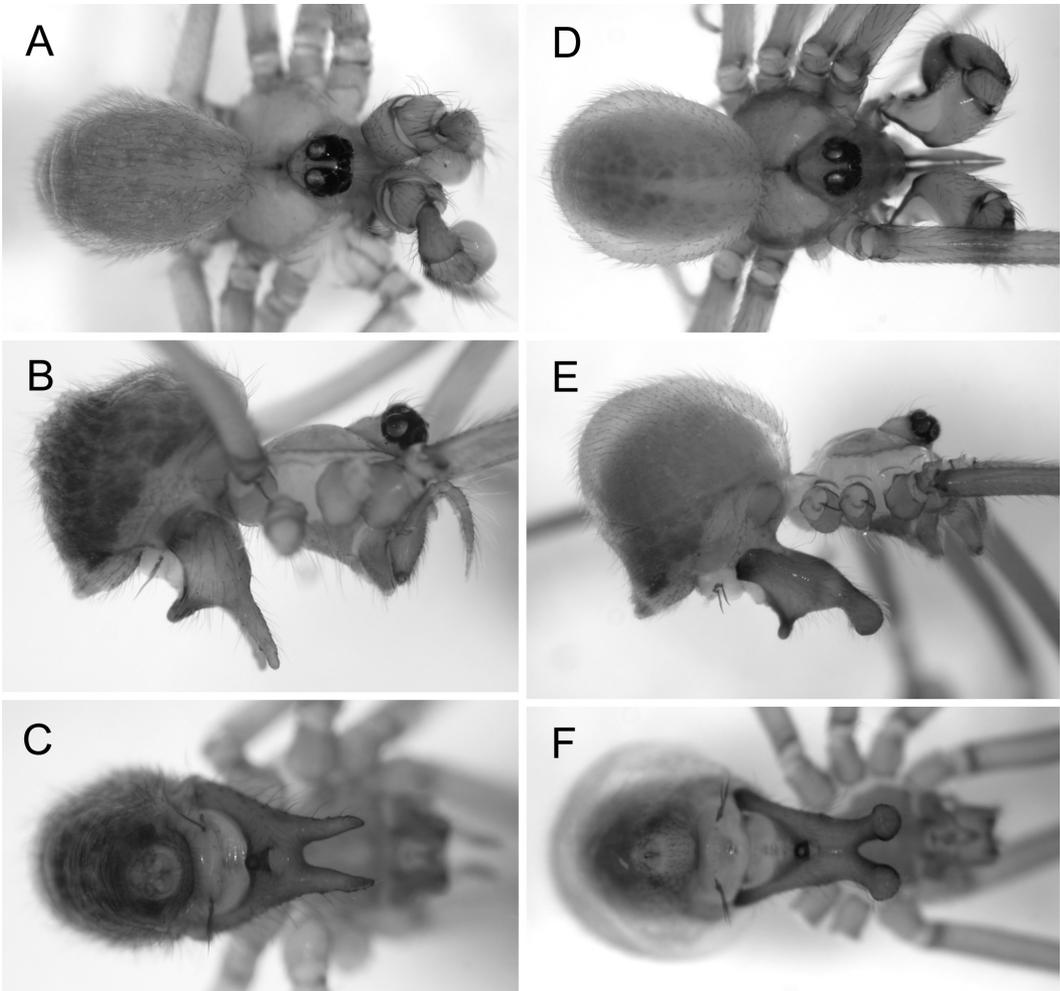


Fig. 2. A-C. *Mesabolivar samatiaguassu*, male dorsal view (A), female lateral (B) and ventral (C) views. D-F. *Mesabolivar cuarassu*, male dorsal view (D), female lateral (E) and ventral (F) views.

Clypeus unmodified. Sternum wider than long (0.77/0.53), unmodified. Chelicerae as in Fig. 3C, with pair of long frontal apophyses close together (~0.44 long when measured from the probable area on contact with the female epigynal apophyses; see asterisk in Fig. 3C). Palps as in Figs 3A, B; coxa with retrolateral apophysis, trochanter with rounded ventral projection, femur very large, femur-patella joints moved towards prolateral side, procurus large but relatively simple, partly covered with small cuticular spines (Fig. 4D), bulb with embolar division and long transparent projection (Figs. 3A, 4E). Retrolateral trichobothrium of

tibia 1 at 5%; legs densely covered with short hairs, without spines and curved hairs, few vertical hairs; tarsus 1 with over 20 pseudosegments, quite distinct distally.

Variation (paratypes): Dark spots on the abdomen variably distinct. Tibia 1: 5.9-6.3 (N = 4, mean: 6.1). Shapes of genitalia and chelicerae virtually identical in paratypes; cheliceral apophysis length: 0.44-0.45 (N = 4).

Female (paratypes): In general similar to male. Tibia 1: 3.4-3.9 (N = 4, mean: 3.59). Female external genitalia strongly protruding (Fig. 2B) with median pocket and pair of pointed projections

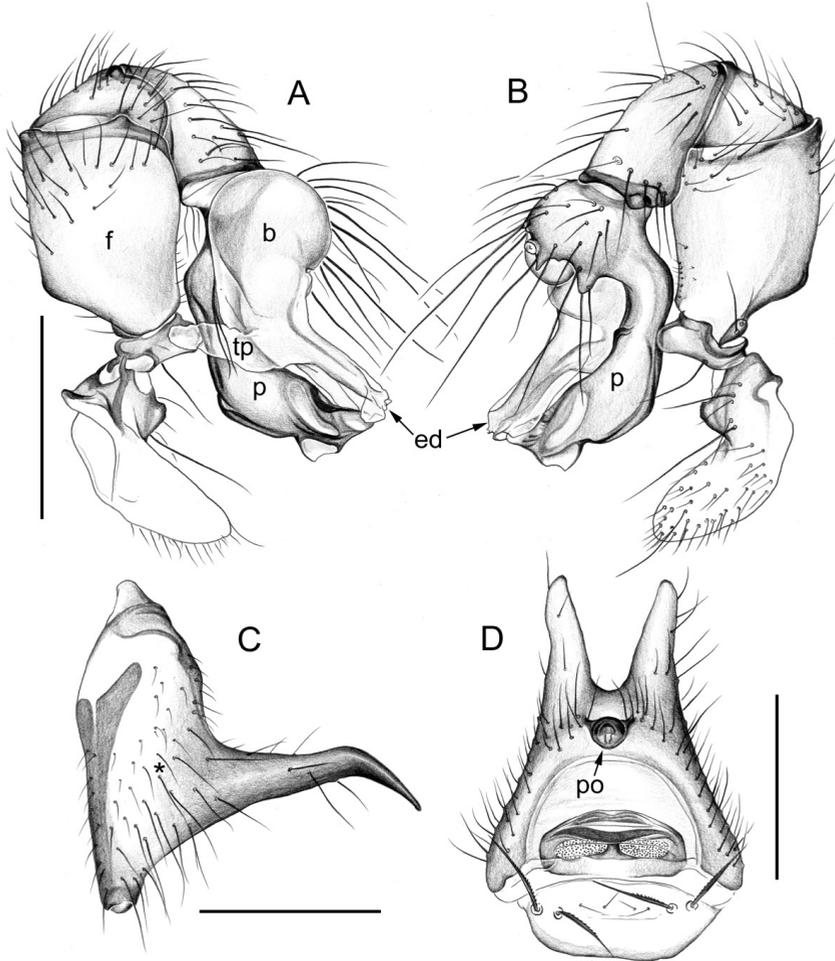


Fig. 3. *Mesabolivar samatiaguassu*. A, B. Left male palp in prolateral (A) and retrolateral (B) views. C. Male chelicera, lateral view; asterisk marks area supposedly contacted by the female epigynal apophyses (derived from the distance between the epigynal apophyses). D. Cleared epigynum, ventral (slightly posterior) view. Abbreviations: b, bulb; ed, embolar division; f, femur; p, procurcus; po, pocket; tp, transparent projection. Scale lines: 0.5 mm (A,B,D), 0.3 mm (C).

(Figs. 3D, 4A, B), with two pairs of strong serrated hairs on membranous area behind gonopore. Distance from bottom of pocket to tip of apophysis: 0.44-0.48 (N = 6, mean: 0.45). Internal genitalia of usual size, with pair of pore plates (Fig. 3D). ALS with only two spigots each, PMS apparently with only one spigot each (Fig. 4C). Abdominal cuticle on both sides of epigynum distinctively sculptured (Fig. 4F).

Distribution. - Known only from type locality.

Material examined. - Only types above.

Mesabolivar cuarassu sp. n.

(Figs 2D-F, 5)

Type material. - Male holotype (IBSP 41167) and 1♂ 5♀ paratypes from Ilha da Queimada Grande (24°30'S, 46°40.5'W), 200 m a.s.l., pitfall traps and manual collecting, Itanhaém, São Paulo, Brazil; April 28-May 1, 2003 (Equipe BIOTA). Paratypes deposited in IBSP (41166, 41168, 43744) and ZFMK (1♂1♀).

Etymology. - The species name is a noun in apposition taken from the Tupi-Guarani Indian language, derived from terms for large (assú) and vulva (cuara), referring to the female genitalia.

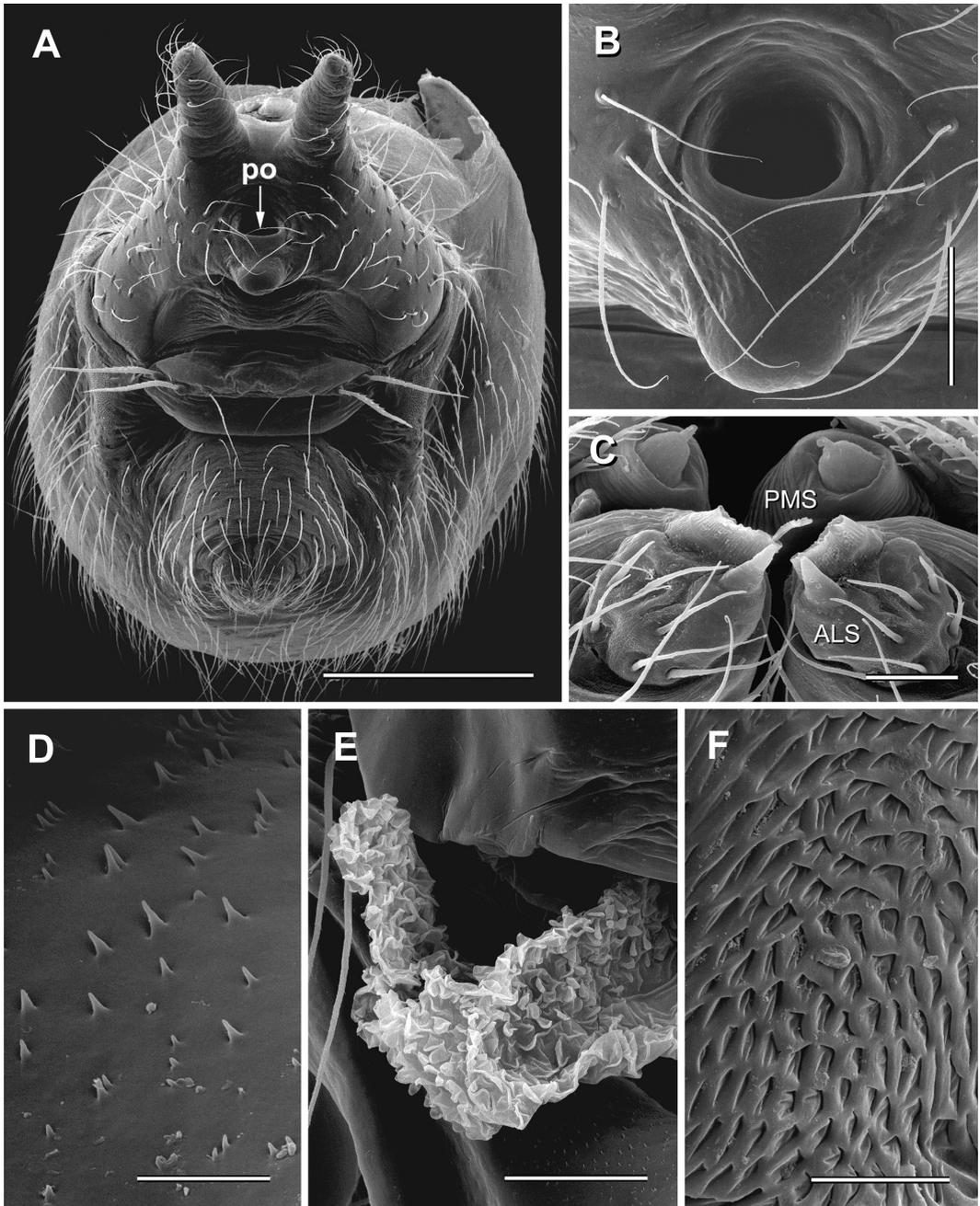


Fig. 4. *Mesabolivar samatiaguassu*. A. Female abdomen, ventral view (po: pocket). B. Median pocket on epigynum. C. Female anterior lateral (ALS) and posterior median spinnerets (PMS). D. Cuticular spines on procurus. E. Transparent projection of male genital bulb. F. Distinctively sculptured abdominal cuticle lateral of epigynum. Scale lines: 500 μm (A), 100 μm (B), 60 μm (E), 20 μm (C,F), 10 μm (D).

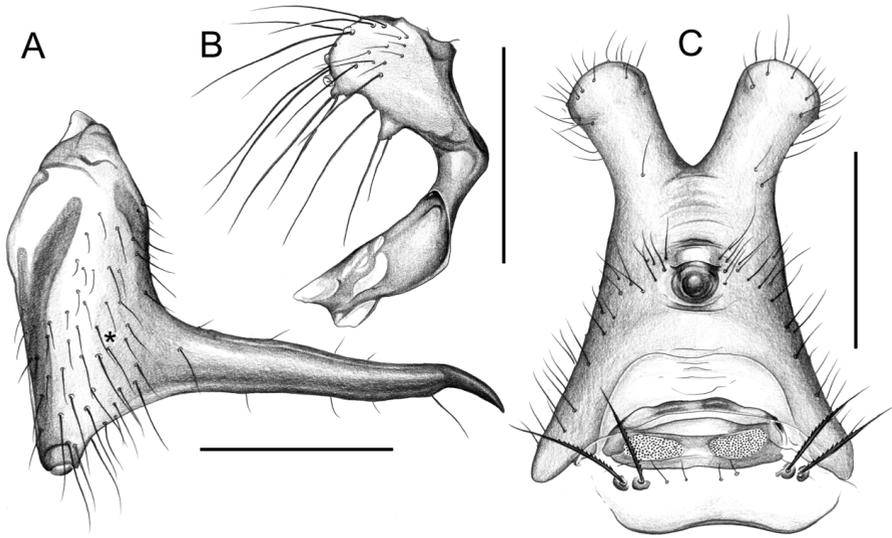


Fig. 5. *Mesabolivar cuarassu*. A. Male chelicera, lateral view; asterisk marks area supposedly contacted by the female epigynal apophyses (derived from the distance between the epigynal apophyses). B. Left procurus, retrolateral view. C. Cleared epigynum, ventral (slightly posterior) view. Same magnifications as in Fig. 3. Scale lines: 0.3 mm (A), 0.5 mm (B, C).

Diagnosis. - Easily distinguished from most congeners by the exaggerated epigynum (Figs. 2E, F, 5C), from *M. samatiaguassu* by the shapes of epigynum, male cheliceral apophyses (Fig. 5A), and procurus (Fig. 5B).

Description. - Male (holotype): Total length 2.13 (2.33 with clypeus), carapace width 1.03. Leg 1: 19.1 (4.7 + 0.4 + 5.0 + 8.4 + 1.3), tibia 2: 3.1, tibia 3: 2.4, tibia 4: 3.9. Tibia 1 L/d: 54. Habitus as in Figure 2D. Carapace light brown, margins and ocular area slightly darker, median line black, sternum light brown, legs ochre to light brown, abdomen greenish-grey with dark bluish spots except ventrally. Ocular area distinctly elevated, thoracic furrow distinct; distance PME-PME 90 μ m; diameter PME 100 μ m; distance PME-ALE 55 μ m; diameter AME 40 μ m, distance AME-AME 25 μ m. Clypeus unmodified. Sternum wider than long (0.77/0.57), unmodified. Chelicerae as in Fig. 5A, with pair of long frontal apophyses (0.62 long) close together (Fig. 2D). Palps very similar to *M. samatiaguassu* (cf. Figs. 3A, B), slightly larger, proximal segments identical in shape, only procurus slightly different (Fig. 5B), bulb as in *M. samatiaguassu*, with long transparent projection. Retrolateral trichobothrium of tibia 1 at 7%; legs densely covered with short hairs, without spines

and curved hairs, few vertical hairs; tarsus 1 with ~25 quite distinct pseudosegments.

Variation (paratype): Tibia 1 in other male: 4.4. Shapes of genitalia and chelicerae virtually identical; cheliceral apophysis length: 0.62.

Female (paratypes): In general similar to male. Tibia 1: 3.4-3.6 (N = 3). Female external genitalia protruding with median pocket and pair of rounded projections (Figs. 2E, F, 5C). Distance from bottom of pocket to tip of apophysis: 0.60-0.66 (N = 3, mean: 0.64). Internal genitalia of usual size, with pair of pore plates (Fig. 5C).

Distribution. - Known only from type locality. *Mesabolivar cuarassu* is probably the first endemic arachnid to be described from the Queimada Grande Island. Intensive collecting on the adjacent mainland has only brought about the closely related *M. samatiaguassu* (see above). This island, located off the coast of São Paulo (for locality description see Duarte, Puerto & Franco 1995), is known for a number of endemic species, especially the well known and dangerous 'jararaca-ilhoa' snake [*Bothrops insularis* (Amaral, 1921)]. In addition, the island fauna also includes two endemic diplopods (Schubart 1949), two chilopods (Büchlerl 1949) and one anuran frog (Lutz & Lutz 1939).

Material examined. - Only types above.

Discussion

A. Male-female coevolution. - We have made no direct observations of copulation in the species studied, but the sizes of male and female structures as well as comparative and observational evidence from other pholcid spiders strongly argue for a functional correlation between male cheliceral apophyses and female epigynal projections and pocket. First, the lengths of male cheliceral apophyses (about 0.44 and 0.62 respectively) correspond tightly with the length of the female epigynal projections (about 0.45 and 0.64 respectively). The same correlation extends to other species of the genus (Huber 2000). Second, all direct observations of copulation in pholcids have found a functional correlation between male chelicerae and female epigynum (Huber 1995, 1997, 1998a, 2002, Huber & Eberhard 1997, Uhl & al. 1995). Third, large comparative data sets clearly demonstrate this same functional correlation in genera that have never been the object of behavioural studies (Kraus 1984, Huber 2003b, unpubl. data on *Belisana* Thorell). Thus we strongly suspect that the male cheliceral apophyses in the species above are inserted into the epigynal pockets, and that the length of the male apophyses is directly linked to the length of the female epigynal projections.

B. Female choice versus antagonistic coevolution. - A current debate revolves around the issue of genital evolution being driven by female choice or antagonistic coevolution (review in Eberhard 2004). According to the female choice hypothesis (Eberhard 1985), female rejection of certain males results in indirect payoffs via superior offspring. In contrast, in antagonistic coevolution envisioned by the 'new arms race' models (*sensu* Eberhard 2004), female rejection results in direct benefits such as increased fecundity (Alexander & al. 1997, Rice & Holland 1999, Gavrillets & al. 2001). The two models generate predictions that may help evaluate the relative importance of both mechanisms in specific cases.

One prediction refers to 'luring' versus 'coercive' mating acts (Alexander & al. 1997). According to the 'new arms race' models, taxa with luring males should have rather simple and uniform genitalia, because females largely control the timing of copulation. Another prediction refers to the design of female structures employed in sexual interactions with males. The female choice model predicts neutral structures or cooperative struc-

tures that aid the male rather than 'aggressive' female resistance structures that hinder access (Eberhard 1997). The female morphology of the two species described above seems to fit both models: the female offers a cooperative structure to the male (a median pocket), but makes access to it difficult (by a pair of projections). In spiders in general, males typically lure rather than coerce females to mate, and female cooperation is usually (always?) a prerequisite for successful genital coupling (Huber 1998b). This suggests that the female barriers in the species above are not a means to reject coercive males and avoid costs associated with copulation. We propose that the female barriers are better explained by female choice, as filters that favour those males that are able to develop exaggerated apophyses that overcome the barrier.

C. The cost of female choice. - It is interesting to note that female choice in these species seems to involve a considerable cost to the female, at least in terms of material. If female choice is indeed responsible for this female morphology, then this is indirect evidence for the benefit females must derive from choosing among males. In theory, females must be under selection to minimize costs associated with choice. In accordance with this prediction, exaggerated female genital morphologies are relatively rare in spiders. Female insemination ducts of certain spiders are also exaggerated, and it has been suggested that these ducts too are involved in female choice (Eberhard 1996).

In contrast, exaggerated genitalia are common in male pholcids: spectacular examples are the procurus of *Kaliana yuruani* Huber, the cheliceral fang apophyses in *Chibchea mayna* Huber, the clypeus projections in *Metagonia furcata* Huber, the elongated palps of *Panjange* spp., and the enlarged male palpal femora of many species, e.g. *Trichocyclus pustulatus* Deeleman-Reinhold (Deeleman-Reinhold & Deeleman 1983, Huber 2000, 2001). In all these cases, female morphology is 'normal', i.e. there is no indication for increased costs as compared with the closest known relatives. The question of why *Mesabolivar* females instead resort to a costly mechanism of female choice remains to be answered.

Acknowledgements

We thank Rafael P. Indicatti and Claudio A. Ribeiro de Sousa for help with the field work, O. A. V. Marques for

supplying bibliography on the Ilha da Queimada Grande's biodiversity, and Nikolaj Scharff for helpful criticism of a previous draft. This study was supported by CNPq (ADB) and FAPESP (99/05446-8; 02/11277-9). This study is part of the BIOTA/FAPESP – The Biodiversity Virtual Institute Program (www.biotasp.org.br).

References

- Alexander, R. D., Marshall, D. C. & Cooley, J. R. (1997) Evolutionary perspectives on insect mating. Pp. 4-31 in Choe, J. C. & Crespi, B. J.: *The Evolution of Mating Systems in Insects and Arachnids*. ix + 387 pp. Cambridge Univ. Press, Cambridge, UK.
- Bücherl, W. (1949) Chilopoda das Ilhas da Queimada Grande e Pequena. *Memorias do Instituto Butantan* 21: 1-8.
- Deeleman-Reinhold, C. L. & Deeleman, P. R. (1983) Studies on tropical Pholcidae I. *Panjange*, a new genus of Indo-Australian leaf- and rock-dwelling pholcid spiders (Araneae). *Zoologische Mededelingen* 57: 121-130.
- Duarte, M. R., Puerto, G. & Franco, F. L. (1995) A biological survey of the pitviper *Bothrops insularis* Amaral (Serpentes, Viperidae): an endemic and threatened offshore island snake of Southeastern Brazil. *Studies on Neotropical Fauna and Environment* 30: 1-13.
- Eberhard, W. G. (1985) *Sexual Selection and Animal Genitalia*. 244 pp. Harvard Univ. Press, Cambridge, Massachusetts.
- Eberhard, W. G. (1996) *Female Control: Sexual Selection by Cryptic Female Choice*. 501 pp. Princeton Univ. Press, Princeton, NJ.
- Eberhard, W. G. (1997) Sexual selection by cryptic female choice in insects and arachnids. Pp. 32-56 in Choe, J. C. & Crespi, B. J.: *The Evolution of Mating Systems in Insects and Arachnids*. ix + 387 pp. Cambridge Univ. Press, Cambridge, UK.
- Eberhard, W. G. (2004) Male-female conflict and genitalia: failure to confirm predictions in insects and spiders. *Biological Reviews* 79: 121-186.
- Gavrillets, S., Arnqvist, G. & Friberg, U. (2001) The evolution of female mate choice by sexual conflict. *Proceedings of the Royal Society London B* 268: 531-539.
- 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. (1997) On American 'Micromerys' and *Metagonia* (Araneae, Pholcidae), with notes on natural history and genital mechanics. *Zoologica Scripta* 25: 341-363.
- Huber, B. A. (1998a) Genital mechanics in some neotropical pholcid spiders (Araneae: Pholcidae), with implications for systematics. *Journal of Zoology, London* 244: 587-599.
- Huber, B. A. (1998b) Spider reproductive behaviour: a review of Gerhardt's work from 1911-1933, with implications for sexual selection. *Bulletin of the British arachnological Society* 11: 81-91.
- Huber, B. A. (1999) Sexual selection in pholcid spiders (Araneae, Pholcidae): artful chelicerae and forceful genitalia. *Journal of Arachnology* 27: 135-141.
- 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* (Araneae: Pholcidae). *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* Milot (Pholcidae, Araneae). *Zoological Journal of the Linnean Society* 137: 261-318.
- Huber, B. A. (2003b) Southern African pholcid spiders: revision and cladistic analysis of *Quantana* 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. & Eberhard, W. G. (1997) Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). *Canadian Journal of Zoology* 74: 905-918.
- Kraus, O. (1984) Male spider genitalia: evolutionary changes in structure and function. *Verhandlungen des naturwissenschaftlichen Vereins Hamburg (NF)* 27: 373-382.
- Lutz, A. & Lutz, B. (1939) New Hylidae from Brazil. *Anais d'Academia Brasileira das Ciencias* 11: 67-89.
- Rice, W. R. & Holland, B. (1999) Reply to comments on the chase-away model of sexual selection. *Evolution* 53: 302-306.
- Schubart, O. (1949) Os diplópodos de algumas ilhas do litoral paulista. *Memorias do Instituto Butantan* 21: 203-254.
- Uhl, G., Huber, B. A. & Rose, W. (1995) Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). *Bulletin of the British arachnological Society* 10: 1-9.

Accepted for publication July 2004