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On the New World spiders previously misplaced in *Leptopholcus*: molecular and morphological analyses and descriptions of four new species (Araneae : Pholcidae)

Bernhard A. Huber[A,E], *Leonardo S. Carvalho*[B,C] *and Suresh P. Benjamin*[A,D]

[A]Alexander Koenig Research Museum of Zoology, Adenauerallee 160, 53113 Bonn, Germany.
[B]Universidade Federal do Piauí, Campus Amílcar Ferreira Sobral – CAFS, BR 343, KM 3.5, Bairro Meladão, CEP 64800-000, Floriano, PI, Brazil.
[C]Programa de Pós-Graduação em Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil.
[D]Institute of Fundamental Studies, Hantana Road, Kandy 20000, Sri Lanka.
[E]Corresponding author. Email: b.huber@zfmk.de

Abstract. The generic placement of New World pholcids assigned to the genus *Leptopholcus* Simon, 1893 has long been questioned and recent molecular data have shown that Caribbean (Hispaniolan) representatives are more closely related to the Old World genus *Micropholcus* Deeleman-Reinhold & Prinsen, 1987 than to 'true' African *Leptopholcus* (Dimitrov, Astrin and Huber 2013, *Cladistics* 29: 132–146). Here we provide new molecular (16S, 18S, 28S, COI, H3, WNT1) and morphological data about Caribbean (Cuban, Puerto Rican) and South American (Brazilian) representatives, supporting the sister-group relationship with *Micropholcus* and suggesting a monophyletic New World clade that in turn consists of a Caribbean and a South American clade. The ten New World species previously assigned to *Leptopholcus* are thus transferred to *Micropholcus* for which an emended diagnosis is provided: *M. baoruco* (Huber, 2006), comb. nov.; *M. brazlandia* (Huber, Pérez & Baptista, 2005), comb. nov.; *M. dalei* (Petrunkevitch, 1929), comb. nov.; *M. delicatulus* (Franganillo, 1930), comb. nov.; *M. evaluna* (Huber, Pérez & Baptista, 2005), comb. nov.; *M. hispaniola* (Huber, 2000), comb. nov.; *M. jamaica* (Huber, 2000), comb. nov.; *M. kiskeya* (Huber & Wunderlich, 2006), comb. nov.; *M. pataxo* (Huber, Pérez & Baptista, 2005), comb. nov.; *M. toma* (Huber, 2006), comb. nov. Four Brazilian species are newly described: *M. piaui*, sp. nov.; *M. piracuruca*, sp. nov.; *M. crato*, sp. nov.; *M. ubajara*, sp. nov. Natural history data are provided for *M. piaui* and *M. ubajara.*

Additional keywords: Brazil, *Micropholcus*, molecular phylogeny, taxonomy.

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Introduction

The genus *Leptopholcus* Simon, 1893 traditionally included pholcids with unusually long and slender abdomens (Figs 1, 2). The African type species *L. signifer* Simon, 1893 and its closest known African and Asian relatives are leaf-dwelling spiders that build barely visible webs closely attached to the undersides of preferably large leaves in tropical and subtropical forests (Huber 2011). They are night-active spiders that spend most of the day with their bodies tightly pressed against the leaf. This position, together with their pale colouration, gives them a very cryptic appearance.

Pholcids with similar general morphology and behaviour but not currently assigned to *Leptopholcus* exist in South-east Asia and Australia. Their relationships have proven difficult to resolve: the genera *Calapnita* Simon, 1892 and *Micromerys* Bradley, 1877 resemble African *Leptopholcus* and belong to the same group of currently ten genera (*Pholcus*-group; Huber 2011), but their affinities with *Leptopholcus* remain unclear. *Calapnita* may eventually turn out to include two distinct genera, while *Micromerys* may be nested within *Leptopholcus* (Huber 2011). A convincing solution for these groups will probably only come by analyses of molecular data, but no representatives of *Calapnita* nor *Micromerys* have ever been sequenced.

In the New World, spiders similar to African *Leptopholcus* (Fig. 1) were originally assigned to *Leptopholcus* (Franganillo 1930, 1931) or *Micromerys* (Petrunkevitch 1929). While *Micromerys* has been shown to be restricted to the Australian continent (Huber 1996, 2001, 2011), *Leptopholcus* has become the default option for new Caribbean and South American species resembling African *Leptopholcus*, more by custom and lack of a more convincing solution than by synapomorphies (Huber 2000; Huber *et al*. 2005; Huber and Wunderlich 2006). The correct assignment of these Caribbean and South American taxa was repeatedly doubted, though never with a formal cladistic analysis (Brignoli 1980; Huber 2000; Huber *et al*. 2005). Two recent phylogenetic analyses have finally provided strong evidence for

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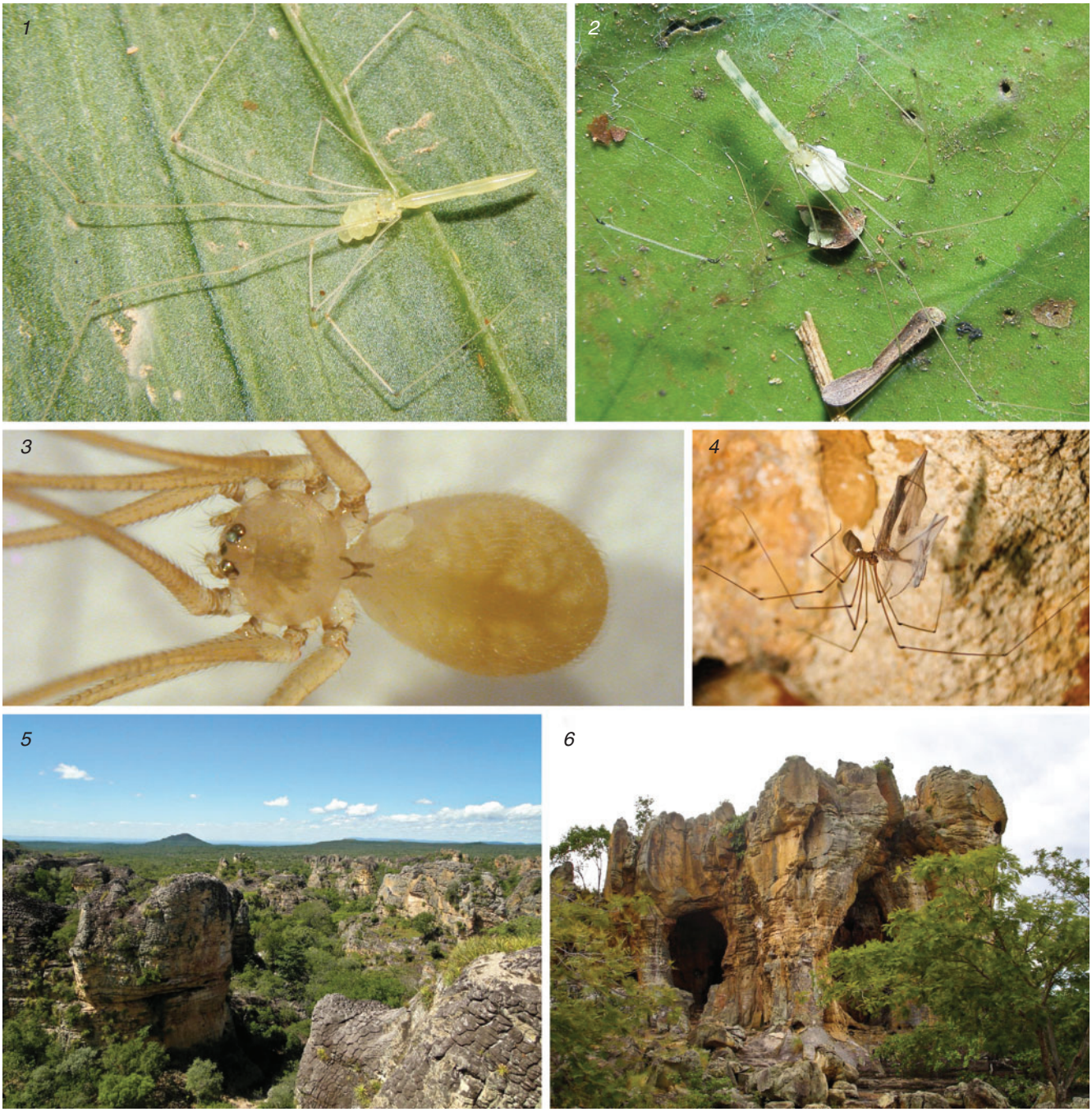


Figs 1–6. Photos of living specimens and type localities. *1*, *Micropholcus delicatulus* from Pico Turquino, Cuba, photo R. Teruel. *2*, *Leptopholcus tipula* from Dieke Forest, Guinea, photo BAH. *3*, *Micropholcus fauroti* from Port-au-Prince, Haiti, photo BAH. *4*, *Micropholcus ubajara* from Gruta do Morcego Branco, Brazil, photo LSC. *5*, Sete Cidades National Park, showing cerrado and gallery forest (type locality of *M. piracuruca*), photo LSC. *6*, Castelo do Piauí, cave and surrounding vegetation (type locality of *M. piaui*), photo LSC.

the polyphyly of Old World and New World *Leptopholcus*, independently based on morphological and molecular data (Huber 2011; Dimitrov *et al*. 2013). However, since both of these analyses included only Caribbean but no South American *Leptopholcus*, formal nomenclatural changes were postponed until SEM and molecular data would become available for South American species. The present paper finally provides these data, suggesting that New World species previously assigned to *Leptopholcus* are monophyletic but misplaced.

Materials and methods

The material studied herein is deposited in the following institutions: Instituto Butantan, São Paulo (IBSP); Museu

Paraense Emilio Goeldi, Belém (MPEG); Museu Nacional, Rio de Janeiro (MNRJ); Universidade Federal de Minas Gerais, Belo Horizonte (UFMG); Universidade Federal do Piauí, Floriano (UFPI); Alexander Koenig Research Museum of Zoology, Bonn (ZFMK). Paratypes of *Micropholcus jacominae* were borrowed from Naturalis Biodiversity Center, Leiden. Abbreviations used in descriptive section: ALE, anterior lateral eyes; ALS, anterior lateral spinnerets; AME, anterior median eyes; L/d, length by diameter; PME, posterior median eyes; PMS, posterior median spinnerets.

Morphological methods and terminology are as in Huber (2011). Measurements are in mm unless otherwise noted; eye measurements are ±5 µm. Drawings were done with a camera lucida on a Leitz Dialux 20 compound microscope. Photographs were taken with a Nikon Coolpix 995 digital camera (2048 × 1536 pixels) mounted on a Nikon SMZ1500 dissecting microscope. For SEM photos, specimens were cleaned ultrasonically, dried in HMDS (Brown 1993), and photographed with a Hitachi S–2460 scanning electron microscope. Cleared epigyna were stained with chlorazol black.

Molecular data were analysed for seven species of New World '*Leptopholcus*', eight species of 'true' Old World *Leptopholcus*, and for twelve species of outgroup taxa (Table 1). Outgroup choice was based on the results in Dimitrov *et al*. (2013). Table 2 gives the collection data of all newly sequenced specimens. Methodology and data analysis follow Dimitrov *et al*. (2013). Genomic DNA was extracted from ethanol-preserved leg tissue or alternatively from whole spiders using the Qiagen DNeasy Tissue Kits (Qiagen, Valencia, CA, USA). The targeted markers (16S, 18S, 28S, COI, H3, WNT1) and primers used were the same as in Dimitrov *et al*. (2013). However, we were unable to amplify the 12S region for any of the targeted taxa using the primers mentioned in Dimitrov *et al*. (2013). Amplification of 16S, 28S and COI was only partially successful (Table 1). In some cases, 28S pseudogenes were amplified and were not included in the analysis.

Polymerase chain reaction (PCR) was carried out in total reaction mixes of 20 µL, including 2 µL of undiluted DNA template, 1.6 µL of each primer (10 pM/µL), 2 µL of 'Q-Solution' and 10 µL of 'Multiplex PCR Master Mix', containing hot start Taq DNA polymerase and buffers. The latter components come with the 'Multiplex PCR' kit from Qiagen. Polymerase chain reaction products were purified using the QIAquick PCR Purification Kit (Qiagen) and sent to Macrogen, Amsterdam, Netherlands for double stranded sequencing.

Multiple sequence alignments were performed with Muscle ver. 3.8.31 (Edgar 2004) under default settings. Parsimony searches were conducted using TNT 1.1 (Goloboff *et al*. 2008). All multistate characters were treated as non-additive (Fitch 1971). In all parsimony analyses, heuristic searches under the 'traditional search' option were performed using 1000 replicates, holding 10 trees per replicate to a maximum of 10 000 trees and using implied weights (*K* 6 to 20; Goloboff 1993). Gaps were treated as missing data. Clade support was assessed by means of symmetric resampling using default settings in TNT (1000 pseudoreplicates with 100 interactions of random addition of taxa and holding 10 trees per interaction).

Maximum likelihood (ML) trees were inferred with RaxML-HPC ver. 7.6.3 (Stamatakis 2006) as implemented on the CIPRES science gateway (Miller *et al*. 2010) using default settings. For the ML searches a GTR+G model of sequence evolution was applied for each partition following the program recommendations. Clade support was estimated with the fast bootstrap algorithm using the GTRCAT model (Stamatakis *et al*. 2008). The following are the specific command line options used to run RaxML (note that some flags may be specific for the CIPRES implementation): raxmlHPC-HYBRID -T 6 -s infile -n result -p 12345 -x 12345 -N 1000-c 25 -m GTRCAT.

Natural history data were collected during four expeditions (by L.S. Carvalho) for populations from two localities: Castelo do Piauí, Piauí (July 2012 and May 2013) and Ubajara, Ceará (September 2012 and May 2013).

Results

Molecular phylogeny

Both analyses resulted in similar topologies. As in the previous study by Dimitrov *et al*. (2013), ML analyses of the DNA sequences studied strongly suggest a close relationship between 'true' Old World *Leptopholcus* and the African endemic genus *Pehrforsskalia* Deeleman-Reinhold & van Harten, 2001 while New World species previously assigned to *Leptopholcus* are more closely related to *Micropholcus fauroti* (Simon, 1887), the type species of *Micropholcus*. Both of these sister-group relationships receive maximum bootstrap support in the ML tree (Fig. 7). In addition, our new data suggest that Caribbean and South American '*Leptopholcus*' are each monophyletic and together are likely monophyletic as well.

However, our maximum parsimony (MP) analysis failed to recover a monophyletic Caribbean + South American '*Leptopholcus*' clade. The recovered Caribbean and South American '*Leptopholcus*' clades both received low support values and formed a polytomy with *Micropholcus fauroti*. The reason for this is not clear, but might be due to the large amount of missing data within the Caribbean and South American '*Leptopholcus*' taxa. As our results from the ML analyses of the combined dataset corroborate the results by Dimitrov *et al*. (2013), we use the ML tree to illustrate our results (Fig. 7).

Morphology

The monophylum including the type species of *Micropholcus* and New World '*Leptopholcus*' is supported by a single but apparently unique character: a distinctively modified hair at the tip of the male palpal trochanter apophysis (Figs 32, 33, 57–59). Most of the 24 genera currently included in Pholcinae share a palpal trochanter apophysis, but only one other genus (*Sihala* Huber, 2011 from Sri Lanka and southern India) shares a similar modified hair at the tip of the apophysis (cf. Huber and Benjamin 2005: figs 3e, f; Huber 2011: fig. 104). For *Micropholcus fauroti*, this hair was first illustrated in Huber (2000: fig. 106); for *M. jacominae* from Yemen it was confirmed by the study of a paratype for the purpose of the present paper. Most or all New World '*Leptopholcus*' also have this modified hair (confirmed by SEM: Huber 2000: fig. 105; Huber and Wunderlich 2006:

figs 4h, 6h, 8d; herein, Figs 32, 33, 57–59; shown in drawings but not confirmed by SEM: Huber *et al*. 2005: figs 15, 20, 25). By contrast, the tip of the trochanter apophysis is serrated in 'true' Old World *Leptopholcus* (Huber 2011), while *Pehrforsskalia* and other Pholcinae genera have a simple unmodified tip.

Taxonomy

Genus ***Micropholcus*** Deeleman-Reinhold & Prinsen, 1987

Micropholcus Deeleman-Reinhold & Prinsen, 1987: 73. Type species: *Pholcus fauroti* Simon, 1887.

Mariguitaia González-Sponga, 2004: 64 (type species: *Mariguitaia divergentis* González-Sponga, 2004); synonymised by Huber (2009).

Diagnosis

Representative of Pholcinae (male chelicerae with proximal lateral projections; male palpal trochanter with ventral to retrolateral apophysis), and of the *Pholcus*-group of genera (tarsus 4 comb-hairs of the simplified type in a single row; Huber and Fleckenstein 2008). Distinguished from close relatives (except from *Sihala*) by distinctive modified hair at tip of male palpal trochanter apophysis (Figs 32, 33, 57–59). *Sihala* is easily distinguished from *Micropholcus* by its massive male palpal femur (much larger than tibia) and the very short and simple procursus (cf. Huber 2011: fig. 104).

Description

Small to medium-size pholcids (total body length ~2–6) with long legs (leg 1 ~20–55; tibia 1 L/d ~50–110), pale colouration with or without dark marks, oval to long cylindrical abdomen. With 6 or 8 eyes, triads widely separated (Figs 9, 11, 28, 29, 55). Carapace without thoracic furrow. Clypeus unmodified. Chelicerae always with distal frontal apophyses provided with 2–5 modified hairs each (Figs 35, 36, 60, 61); usually with proximal lateral apophyses (absent only in *M. crato*, sp. nov.), in Old World species also with proximal frontal apophyses. Palpal trochanter with ventral (or retrolatero-ventral) apophysis with distinctive modified hair at tip (Figs 32, 33, 57–59); procursus with or without ventral 'knee', in Old World species with distinctive dorsal hinged process; tarsal organ capsulate; bulb with strong proximal sclerite (Fig. 17), always with appendix, with or without uncus. Legs without spines and curved hairs, few vertical hairs; prolateral trichobothrium absent on tibia 1, present on other tibiae. Tarsus 4 with single row of comb-hairs (Fig. 56). Gonopore with four epiandrous spigots (rarely five; Figs 34, 62). ALS with 7 or 8 spigots (Figs 37, 63). Epigynum weakly sclerotised, with or without posterior 'knob' (Figs 31, 65).

Distribution

Micropholcus as delimited here is one of only three pholcid genera with indigenous species on both sides of the Atlantic. For the distribution of the two Old World species see Huber (2011: fig. 82). New World taxa are mainly found on the Greater Antilles and in the semiarid corridor between the Amazon and the Atlantic Forest. One species was found in the dry coastal region of Venezuela (Fig. 8).

Composition

Micropholcus now consists of 16 nominal species; two Old World species: *M. fauroti* (Simon, 1887) and *M. jacominae* Deeleman-Reinhold & van Harten, 2001; six extant and one fossil Caribbean species: *M. baoruco* (Huber, 2006), comb. nov.; *M. dalei* (Petrunkevitch, 1929), comb. nov.; *M. delicatulus* (Franganillo, 1930), comb. nov.; *M. hispaniola* (Huber, 2000), comb. nov.; *M. jamaica* (Huber, 2000), comb. nov.; *M. kiskeya* (Huber & Wunderlich, 2006), comb. nov.; *M. toma* (Huber, 2006), comb. nov.; one Venezuelan species: *M. evaluna* (Huber, Pérez & Baptista, 2005), comb. nov.; and six Brazilian species: *M. brazlandia* (Huber, Pérez & Baptista, 2005), comb. nov.; *M. crato*, sp. nov.; *M. pataxo* (Huber, Pérez & Baptista, 2005), comb. nov.; *M. piaui*, sp. nov.; *M. piracuruca*, sp. nov.; *M. ubajara*, sp. nov.

Micropholcus piaui, sp. nov.

(Figs 9–10, 13, 17–37)

Material examined

Holotype. ♂, Brazil, Piauí, Castelo do Piauí, Parque Municipal da Pedra do Castelo (5°12.1′S, 41°41.2′W), 200 m above sea level (a.s.l.), from cave in caatinga/cerrado ecotone, 26.ii.2012 (I.L.F. Magalhães *et al*.), in IBSP (162467).

Non-type material. BRAZIL: *Piauí*: Castelo do Piauí, Parque Municipal da Pedra do Castelo, same data as holotype, 3♂ 4♀ in IBSP (162464–66, 69–72); same data as holotype (L.S. Carvalho), 1♂ 2♀ 1 juv. in pure ethanol, in UFPI (262, 263, 301); same data as holotype, 1♂ 1♀ in pure ethanol, in UFMG (11015–16; ex IBSP 162468, 73); same locality as holotype, 9.viii.2013 (L.S. Carvalho), 1♂, preyed by a conspecific male, in UFPI (599); same locality as holotype, 9.v.2013 (L.S. Carvalho), 1♂ 2♀ in pure ethanol, in UFMG (12813–15). Castelo do Piauí, Furna do Urubu (5°22.4′S, 41°21.5′W), 23.vii.2012 (L.S. Carvalho), 1♂ 1 juv. in pure ethanol, in UFPI (264). Castelo do Piauí, Furna do Baixão do Cajueiro (5°23.3′S, 41°24.1′W), 23.vii.2012 (L.S. Carvalho), 1♂ 1♀ in pure ethanol, in UFPI (265). Castelo do Piauí, Furna da Santinha (5°21.8′S, 41°22.5′W), 23.vii.2012 (L.S. Carvalho), 1♀ in pure ethanol, in UFPI (266).

Assigned tentatively. BRAZIL: *Ceará*: Ubajara, Parque Nacional de Ubajara, Gruta do Morcego Branco (3°49.9′S, 40°54.0′W), 13.v.2013 (L.S. Carvalho), 1♂ in pure ethanol, in UFMG (12819 part). Quixadá, Fazenda Magé (4°56.8′S, 39°01.4′W), 6.v.2012 (I.L.F. Magalhães, L.S. Carvalho), 1♂ 1♀ 1 juv. in pure ethanol, in UFMG (11683), and 1♂ 1♀ in pure ethanol, in IBSP (162684). Pentecoste, Fazenda Experimental Vale do Curu (3°49.3′S, 39°20.8′W), 4.v.2012 (I.L.F. Magalhães, A.J. Santos), 1♂ 1♀ in pure ethanol, in IBSP (163075), and 1♀ in pure ethanol in UFMG (12208).

Diagnosis

Small, six-eyed, pale pholcine with widely curved procursus, easily distinguished from most similar known congeners by long ventral apophysis on male palpal trochanter (Fig. 18; short in *M. brazlandia* and *M. crato*), curved dorsal process of male palpal tarsus (Fig. 17; straight in *M. piracuruca*), simple lateral male cheliceral projections (Fig. 19; absent in *M. crato*; larger and in more frontal position in *M. piracuruca*; indistinguishable in *M. brazlandia*). Females are difficult to distinguish externally (pore plates larger and wider apart than in *M. piracuruca*; pair of distinctive internal sclerites absent in *M. crato*, closer together in *M. brazlandia*).

Table 1. Material analysed, GenBank accession numbers and ID of vouchered DNA
Bold, sequenced for this study; na, no sequences available

Species	GenBank accession numbers							ID of vouchered DNA
	12S	16S	18S	28S	COI	H3	WNT1	
Outgroups								
P0240 *Zatavua analalava*(?)	JX023824	JX023921	JX024027	JX024126	na	na	JX023749	ZFMK-DNA-100433837
P0179 *Nyikoa limbe*	JX023789	JX023879	JX023976	JX024085	JX023564	JX023638	na	ZFMK-DNA-100446423
P0183 *Quamtana* Cam117	JX023793	JX023883	JX023978	JX024086	JX023567	JX023641	JX023731	ZFMK-DNA-100446427
P0272 *Spermophora minotaura*	na	JX023938	JX024048	JX024139	JX023604	JX023702	na	ZFMK-DNA-100433830
P0267 *Buitinga* Uga61	JX023838	JX023934	JX024046	JX024138	na	JX023698	JX023757	ZFMK-DNA-100437896
P0216 *Metagonia furcata*	JX023815	JX023906	JX024004	JX024112	JX023591	JX023667	JX023739	ZFMK-DNA-100446397
P0281 *Pholcus atrigularis*	JX023846	JX023945	JX024057	na	JX023606	na	na	ZFMK-DNA-100437887
P0222 *Pholcus dade*	JX023817	JX023909	JX024010	JX024116	JX023595	na	na	ZFMK-DNA-100446391
P0288 *Pholcus jiuwei*	JX023849	JX023950	JX024063	JX024146	JX023609	JX023714	na	ZFMK-DNA-100437875
P0247 *Pholcus* cf. *jaegeri*	JX023829	JX023924	JX024032	JX024129	JX023603	JX023685	na	ZFMK-DNA-100437916
P0151 *Pehrforsskalia conopyga*	JX023764	JX023857	JX023956	JX024069	JX023549	JX023616	JX023719	ZFMK-DNA-100446462
P0168 *Pehrforsskalia conopyga*	JX023781	JX023870	JX023969	na	JX023559	JX023628	JX023725	ZFMK-DNA-100446445
(Old World) *Leptopholcus*								
P0150 *L. guineensis*	JX023763	JX023856	JX023955	JX024068	JX023548	JX023615	JX023718	ZFMK-DNA-100446463
P0160 *L. gracilis*	JX023773	na	JX023962	JX024076	JX023554	JX023622	na	ZFMK-DNA-100446452
P0220 *L. gracilis*	na	JX023908	JX024008	JX024114	na	JX023671	JX023741	ZFMK-DNA-100446393
P0146 *L. tipula*	na	JX023853	JX023954	JX024067	JX023545	JX023611	JX023716	ZFMK-DNA-100446467
P0192 *L. dschang*	JX023800	JX023886	JX023987	JX024094	na	JX023646	JX023737	ZFMK-DNA-100446421
P0235 L. MRAC 530	na	JX023918	JX024022	JX024123	na	na	JX023746	ZFMK-DNA-100446383
P0260 *L. budongo*	na	na	JX024041	JX024135	na	JX023691	JX023756	ZFMK-DNA-100437914
P0276 *L. guineensis*	JX023845	JX023941	JX024052	JX024141	na	JX023704	na	ZFMK-DNA-100437882
P0279 *L. podophthalmus*	na	na	JX024055	na	na	JX023707	na	ZFMK-DNA-100437885
Old World *Micropholcus*								
P0193 *M. fauroti*	JX023801	JX023887	JX023988	JX024095	JX023574	JX023647	na	ZFMK-DNA-100446420
Caribbean *Micropholcus*								
P0165 *M. hispaniola*	JX023778	na	JX023966	na	JX023558	JX023625	na	ZFMK-DNA-100446457
P0166 *M. baoruco*	JX023779	na	JX023967	na	na	JX023626	na	ZFMK-DNA-100446103
P0167 *M.* sp.	JX023780	na	JX023968	JX024078	na	JX023627	na	ZFMK-DNA-100446446
Lep7 *M. dalei*	na	na	**KF715594**	**KF715612**	**KF715606**	**KF715577**	**KF715601**	ZFMK-DNA-100417581
Lep8 *M. dalei*	na	na	**KF715595**	**KF715613**	**KF715605**	**KF715578**	**KF715602**	ZFMK-DNA-100417582
Lep9 *M. delicatulus*	na	na	**KF715591**	na	na	**KF715579**	**KF715604**	ZFMK-DNA-100417583
Lep10 *M. delicatulus*	na	**KF715618**	**KF715592**	na	na	**KF715576**	**KF715603**	ZFMK-DNA-100417872
Lep11 *M. delicatulus*	na	na	**KF715593**	na	na	**KF715574**	na	ZFMK-DNA-100417866
Lep12 *M. delicatulus*	na	**KF715619**	**KF715596**	**KF715614**	na	**KF715575**	na	ZFMK-DNA-100417884
South American *Micropholcus*								
Lep1 *M. piaui*	na	na	**KF715581**	**KF715609**	na	**KF715570**	na	ZFMK-DNA-100436974
Lep2 *M. piaui*	na	**KF715615**	**KF715588**	**KF715608**	na	**KF715567**	**KF715598**	ZFMK-DNA-100436777
Lep3 *M. piaui*	na	na	**KF715585**	na	na	**KF715569**	**KF715597**	ZFMK-DNA-100437031
Lep4 *M. piaui*	na	**KF715617**	**KF715586**	**KF715607**	na	**KF715571**	**KF715600**	ZFMK-DNA-100436983
Lep5 *M. piaui*	na	**KF715616**	**KF715583**	**KF715610**	na	**KF715568**	**KF715599**	ZFMK-DNA-100436807
Lep6 *M. piaui*	na	na	**KF715582**	na	na	**KF715565**	na	ZFMK-DNA-100436930
Lep13 *M. piaui*	na	na	**KF715587**	na	na	**KF715566**	na	ZFMK-DNA-100436843
Lep14 *M. piaui*	na	na	**KF715584**	**KF715611**	na	**KF715580**	na	ZFMK-DNA-100436853
Lep15 *M. ubajara*	na	na	**KF715589**	na	na	**KF715572**	na	ZFMK-DNA-100437029
Lep16 *M. ubajara*	na	na	**KF715590**	na	na	**KF715573**	na	ZFMK-DNA-100436821

Description

Male (holotype)

Total body length 2.7, carapace width 1.0. Leg 1 missing, tibia 2: 2.9, tibia 3: 1.8, tibia 4: 2.7. Distance PME–PME 265 µm, diameter PME 70 µm, distance PME–ALE 35 µm, AME absent. Carapace ochre-yellow with brown posterior mark; clypeus with pair of indistinct light brown marks below eye triads, sternum whitish; legs ochre-yellow with barely darker patellae and tibia-metatarsus joints; abdomen pale grey with darker spots dorsally and laterally. Habitus as in Figs 9 and 10, ocular area not elevated, each triad on low hump; clypeus unmodified (Fig. 28); no thoracic furrow (Fig. 28). Chelicerae as in Fig. 19, with weakly sclerotised lateral apophyses and distal apophyses provided with two modified hairs each (Figs 35, 36). Palps as in Figs 17 and 18; coxa unmodified; trochanter

Table 2. Species names and collection data of the specimens newly sequenced in this study
For other taxa in Table 1 see Dimitrov *et al*. (2013)

Species	Code	Collection data
M. dalei	Lep7	Puerto Rico: *Rio Grande*: El Yunque, Big Trees Trail (18.309°N, 65.775°W), 145 m, 16–18.vii.2011 (Agnarsson *et al*.) (PR02)
	Lep8	Puerto Rico: *Arecibo*: Mata de Platano (18.414°N, 66.729°W), 150 m, 24–26.vii.2011 (Esposito *et al*.) (PR33)
M. delicatulus	Lep9	Cuba: *Pinar del Río*: Viñales, forest at base of mogote, 'site 1' (22.622°N, 83.737°W), 150 m, on green leaves, 22.iv.2012 (B.A. Huber) (Cub12–189)
	Lep10	Cuba: *Camagüey*: Sierra de Cubitas, Estación Limones-Tuabaquey, forest along trail near station (21.597°N, 77.786°W), 130 m, on green leaves, 11.iv.2012 (B.A. Huber) (Cub12–200)
	Lep11	Cuba: *Guantanamo*: Baracoa, forest along Duaba river (20.332°N, 74.569°W), 60 m, on green leaves, 4.iv.2012 (B.A. Huber) (Cub12–207)
	Lep12	Cuba: *Santiago de Cuba*: Estación Biológica La Platica, forest near brook (20.009°N, 76.894°W), 830 m, 27 and 29.iii.2012 (B.A. Huber) (Cub12–226)
M. piaui	Lep1/Lep2	Brazil: *Piauí*: Castelo do Piauí, Parque Municipal da Pedra do Castelo (5°12.1′S, 41°41.2′W), 200 m, from cave in caatinga, 26.ii.2012 (L.S. Carvalho), in UFPI (262) (Carv01)
	Lep3	Brazil: *Piauí*: Castelo do Piauí, Furna do Urubu (5°22.4′S, 41°21.5′W), 23.vii.2012 (L.S. Carvalho), in UFPI (264) (Carv02)
	Lep4	Brazil: *Piauí*: Castelo do Piauí, Parque Municipal da Pedra do Castelo (5°12.1′S, 41°41.2′W), 200 m, from cave in caatinga, 26.ii.2012 (L.S. Carvalho), in UFPI (263) (Carv03)
	Lep5/Lep6	Brazil: *Piauí*: Castelo do Piauí, Furna do Baixão do Cajueiro (5°23.3′S, 41°24.1′W), 23.vii.2012 (L.S. Carvalho), in UFPI (265) (Carv04)
	Lep13/Lep14	Brazil: *Ceará*: Quixadá, Fazenda Magé (4°56.8′S, 39°01.4′W), 6.v.2012 (I.L.F. Magalhães, L.S. Carvalho), in UFMG (11683) (Carv16)
M. ubajara	Lep15/Lep16	Brazil: *Ceará*: Ubajara, Parque Nacional de Ubajara, Gruta do Morcego Branco (3°50.0′S, 40°54.0′W), 530 m, 4.ix.2012 (L.S. Carvalho), in UFPI (295) (Carv17)

with short conical retrolateral process and long ventral apophysis provided at its tip with distinct modified hair (Figs 32, 33); femur with two small processes proximally (retrolaterally and retrolatero-dorsally); tarsus with rounded and curved dorsal projection and widely curved procursus with distinctive distal elements (Figs 17, 18, 30); bulb with strong proximal sclerite, weakly sclerotised embolus, and sclerotised branched process (putative appendix; Figs 20, 21). Legs apparently without spines, curved hairs, and vertical hairs (most hairs missing). ALS with seven spigots each (cf. female; Fig. 37). Gonopore with four epiandrous spigots (Fig. 34).

Variation

Leg 1 in other male from type locality: 19.4 (5.0 + 0.4 + 5.0 + 8.0 + 1.0); retrolateral trichobothrium on tibia 1 at 5%; tibia 1 L/d: 71; prolateral trichobothrium apparently absent on tibia 1; ~15 pseudosegments on tarsus 1. Tibia 1 in two other males from type locality: 4.6, 5.0. Males from the other localities in Piauí are smaller but have indistinguishable palps (tibia 1: 3.1, 4.2; total body length of smaller male: 2.1). Males from Ceará are assigned tentatively because they have slightly different bulbal processes (Figs 22–25); otherwise, their palps appear indistinguishable. The male from Ubajara is almost identical to the male from Pentecoste but the tip of the bulbal process has two large spikes instead of many small ones (arrow in Fig. 22). Tibiae 1 missing in all males from Ceará.

Female

In general similar to male; eye triads slightly closer together (Fig. 29). Tibia 1 in five females from type locality: 3.7–4.4 (mean 4.1); in three females from Ceará: 3.2–3.6. Epigynum simple, weakly sclerotised plate without 'knob' (Figs 13, 31), internal 'valve' and distinctive pair of sclerites visible through cuticle (internal sclerites poorly visible in females from Ceará). Internal genitalia as in Figs 26 and 27.

Distribution

Known from Piauí and Ceará states (specimens from Ceará assigned tentatively) (Fig. 8).

Natural history

Most of the information presented here was gathered (by L. S. Carvalho) in a single cave in Parque Municipal Pedra do Castelo (the type locality; Fig. 6). On the first expedition to the area (July 2012, dry period) the spiders were observed exclusively in the aphotic zone, in a large oval saloon of ~12 × 10 × 6 m. During the rainy season in May 2013 a few (<15) individuals were observed outside the aphotic zone. Population size within the aphotic zone ranged from 55 to 89 individuals (mean 69) during the four counts performed.

The mean height above the ground at which specimens were found was 82 cm (260 observations; range: 10 to >200 cm). This was significantly higher (U = 1746, p-value (bilateral) < 0.0001) than the sympatric pholcid *Mesabolivar spinulosus* (Mello-Leitão, 1939), which was found at a mean height of only 27 cm (63 observations; range: 10–145 cm), suggesting that the two pholcids occupy different microhabitats within the cave (Fig. 66).

Most individuals (~80%) were observed outside webs, with their bodies pressed against the cave walls. Others were observed

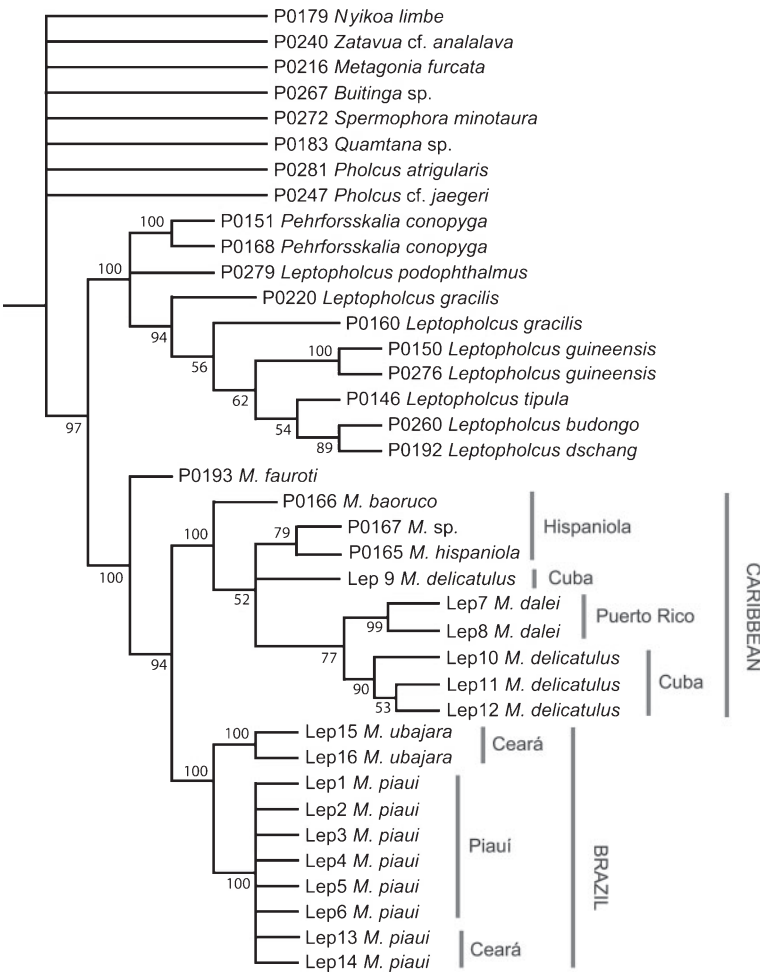


Fig. 7. Maximum likelihood tree (RaxML-HPC); numbers at nodes are levels of bootstrap support. *M.*, *Micropholcus*.

in small indistinct sheet webs (mostly ~4 × 4 cm; up to 10 × 13 cm), with anchoring lines fixed to the walls and its recesses. In one case, a series of five interconnected webs (three females and two males) measured ~60 × 50 cm.

The position of the spiders on the cave walls did not seem to be random: 73% of individuals were observed less than 50 cm from a conspecific, while only 13% were observed more than 100 cm from the next conspecific.

Feeding was observed five times, with two individuals feeding on beetles (Tenebrionidae), two on ants (Formicidae, *Atta* sp. and *Acromyrmex* sp.), and an adult male feeding on a conspecific male (UFPI 599). One couple was observed mating for ~20 min in a typical Pholcidae mating position (cf. Huber 2011: fig. 20). Females with egg sacs were observed at both expeditions (six in July 2012; 24 in May 2013). Egg sacs contained only 3–7 eggs ($N = 4$) and were weakly enveloped with silk lines. Eight male–female pairs (less than 10 cm from each other) were observed in July 2012. Sex ratio (males/females) was 0.59, indicating a female-biased population ($\chi^2 = 11.488$, d.f. = 1, $P = 0.0009$, with Yates correction).

Six types of reactions to disturbance (studied by slightly touching the spiders with forceps) were observed: 'shake' (spider shakes or vibrates its body); 'walk' (spider slowly walks a short distance); 'run' (spider quickly runs a longer distance); 'wall' (spider presses its body tightly against the cave wall); 'jump' (spider actively jumps from the web or the cave wall to the ground); and 'no reaction'. Most specimens showed no reaction (56 observations) or pressed their bodies against the cave walls (50 observations). Different responses dominated in the sympatric *Mesabolivar spinulosus*, where most individuals jumped to the ground, walked in their webs, or shook their bodies (Fig. 68).

Specimens from Pentecoste and Quixadá (assigned tentatively, see above) were not collected from caves but from small sheet webs on the undersides of green leaves near large rock outcrops (I.L.F. Magalhães, pers. comm.). The single male from Ubajara was collected under a small stone near the entrance of the Gruta do Morcego Branco cave, the type-locality of *Micropholcus ubajara*.

Etymology

The species name is a noun in apposition, derived from the type locality.

Fig. 8. Known distribution of *Micropholcus* in the New World (the widespread synanthropic *M. fauroti* is not shown), and detailed map of Brazilian species.

Micropholcus crato, sp. nov.

(Figs 14, 38–42)

Material examined

Holotype. ♂, Brazil, Ceará, Crato, Sitio Fundão (7°14′S, 39°26′W), 4.vi.2003 (N.M. Sierra), in MNRJ.

Non-type material. BRAZIL: *Ceará*: Crato, Sitio Fundão, same data as holotype, 2♀ together with holotype and 1♂ in separate vial, 11.vi.2003, in MNRJ.

Diagnosis

Small, six-eyed, pale pholcine with widely curved procursus, easily distinguished from most similar known congeners by male chelicerae (absence of proximal lateral projections; Fig. 40); from *M. piracuruca* and *M. piaui* also by shorter male palpal trochanter apophysis (Fig. 39); from *M. piracuruca* also by short curved dorsal process on male palpal tarsus (Fig. 38). Females are difficult to distinguish externally (pore plates larger and wider apart than in *M. piracuruca*; no pair of distinctive internal sclerites as in *M. piaui* and *M. brazlandia*).

Description

Male (holotype)

Total body length 2.7, carapace width 0.8. Leg 1 missing, tibia 2: 2.8, tibia 3: 1.8, tibia 4 missing. Distance PME–PME 250 µm, diameter PME 85 µm, distance PME–ALE 35 µm, AME absent. Entire animal very pale, carapace with light brown mark posteriorly, clypeus with indistinct darker marks, abdomen monochromous. Habitus similar to *M. piaui* but abdomen with pointed elongation above spinnerets; ocular area not elevated, each triad on low hump; clypeus unmodified; no thoracic furrow. Chelicerae as in Fig. 40, with pair of distal apophyses provided with two modified hairs each, without proximal modification. Palps as in Figs 38 and 39; coxa unmodified; trochanter with short retrolateral process and relatively short (compared with Brazilian congeners) ventral apophysis; femur with only one small projection (retrolaterally); tarsus with rounded and curved dorsal projection and widely curved procursus with distinctive distal elements; bulb with strong proximal sclerite, weakly sclerotised embolus, and sclerotised bifid process (putative appendix). Legs apparently without spines, curved hairs, and vertical hairs (most hairs missing).

Figs 9–16. Habitus photographs (males in dorsal and lateral views) and female abdomens in ventral views (at different scales). *9*, *10*, *Micropholcus piaui* (UFPI 262); *11*, *12*, *M. ubajara* (UFPI 268); *13*, *M. piaui* (UFPI 262); *14*, *M. crato* (MNRJ); *15*, *M. piracuruca* (MPEG 11543); *16*, *M. ubajara* (UFPI 267).

Variation

Not seen. Leg 1 missing also in second male examined.

Female

In general similar to male. Tibia 1: 2.8 (missing in second female examined). Epigynum simple, weakly sclerotised plate without 'knob', internal 'valve' visible through cuticle (Fig. 14). Internal genitalia as in Figs 41 and 42.

Distribution

Known from type locality in Ceará state only (Fig. 8).

Etymology

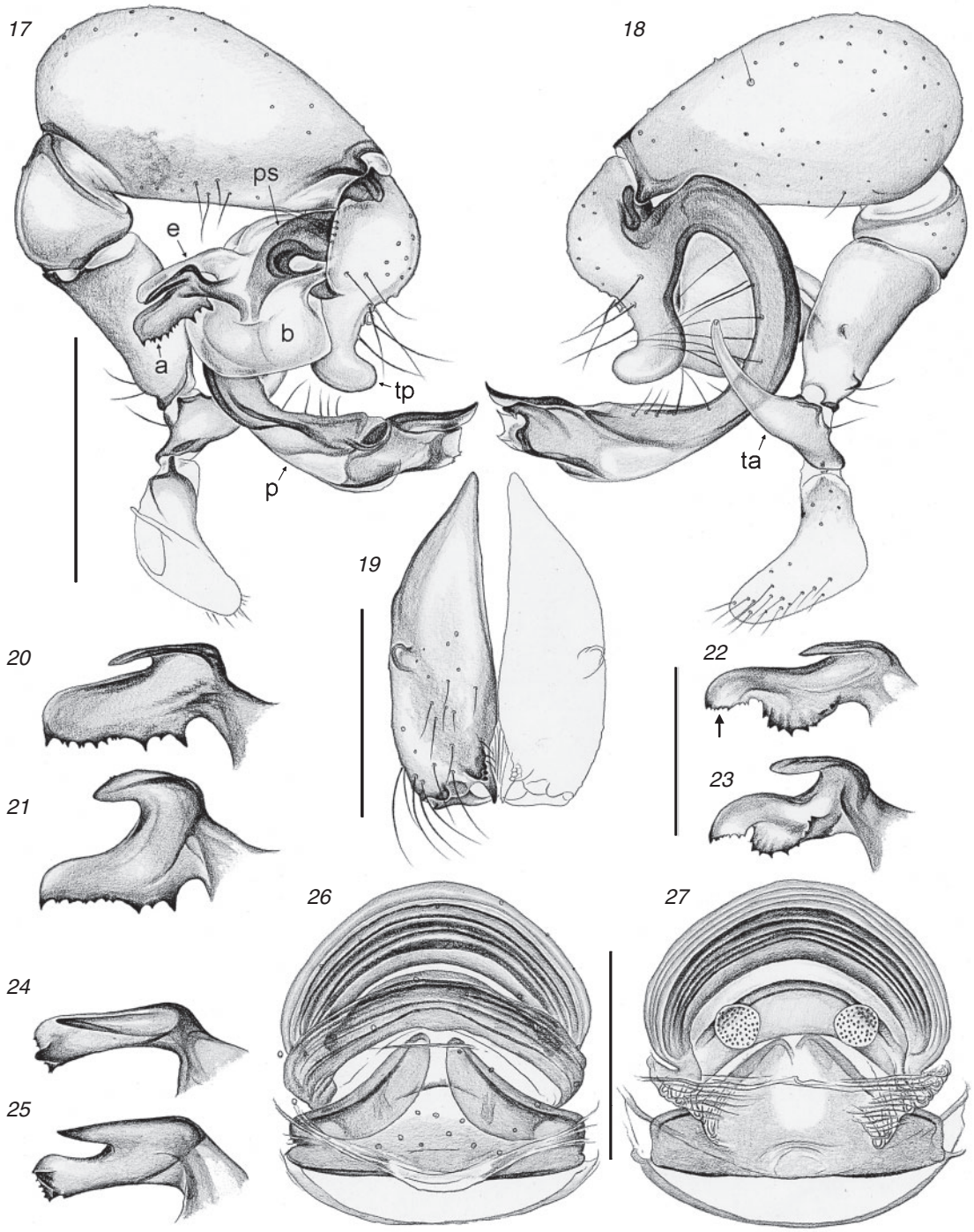
The species name is a noun in apposition, derived from the type locality.

Micropholcus piracuruca, sp. nov.

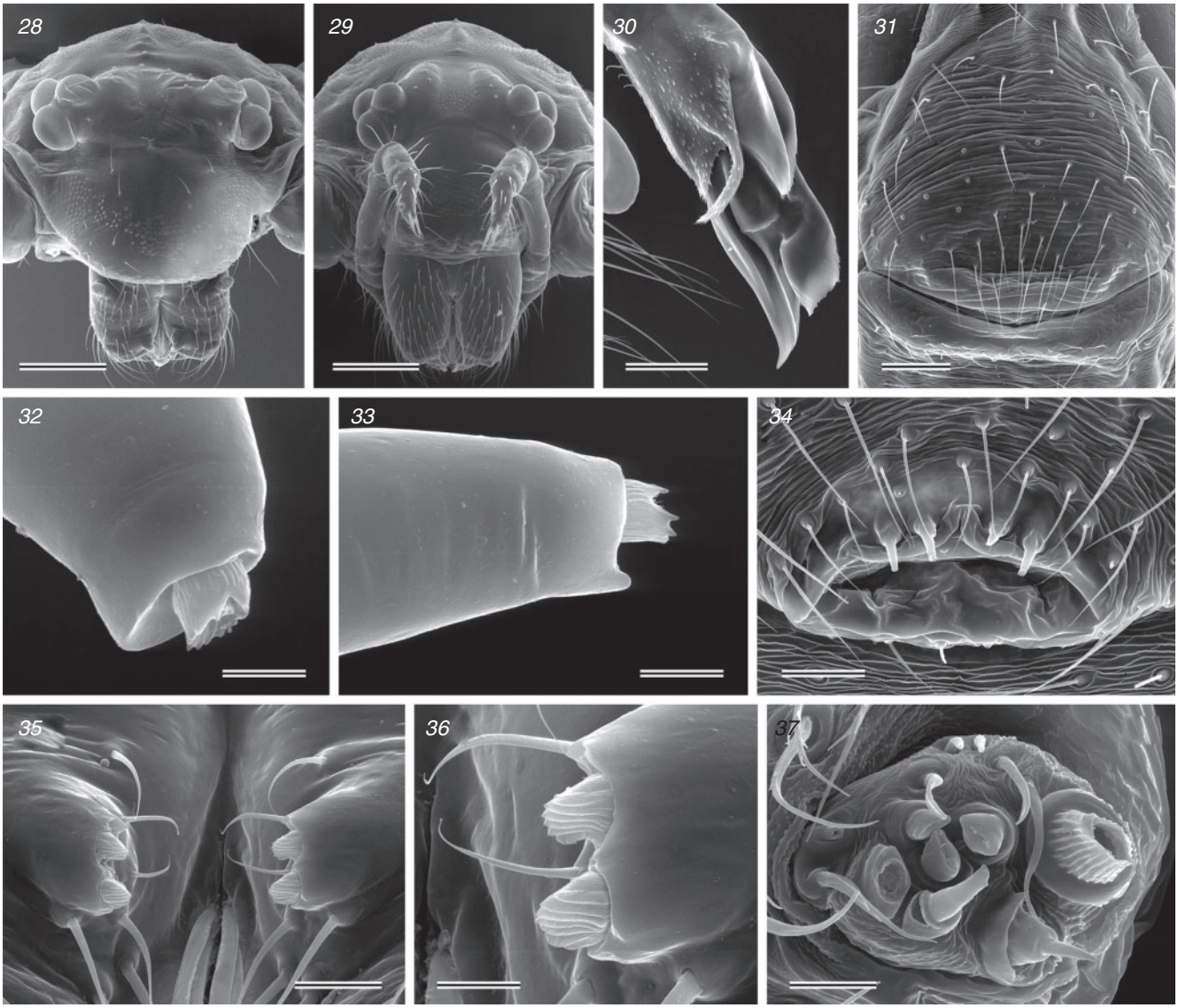
(Figs 15, 43–47)

Material examined

Holotype. ♂, Brazil, Piauí, Brasileira e Piracuruca, Parque Nacional de Sete Cidades (4°05.7′S, 41°43.9′W), 13.xii.2006 (N.F. Lo Man Hung), in MPEG (11541).



Figs 17–27. *Micropholcus piaui. 17*, *18*, Left male palp, prolateral and retrolateral views (IBSP 162467). *19*, Male chelicerae, frontal view (IBSP 162467). *20–25*, Bulbal processes (appendices; all at same scale) in prolateral and slightly dorsal views, males from Castelo do Piauí (20–21; type locality; UFPI 262), Pentecoste (22–23; IBSP 163075; arrow points at detail that differs slightly in male from Ubajara; see text), and Quixadá (24–25; UFMG 11683). *26*, *27*, Cleared female genitalia in ventral and dorsal views (IBSP 162470). Abbreviations: a, appendix; b, bulb; e, embolus; p, procursus; ps, proximal (bulbal) sclerite; ta, trochanter apophysis; tp, tarsal process. Scale bars = 0.2 (*20–25*), 0.3 (*19*, *26*, *27*), 0.5 (*17*, *18*).



Figs 28–37. *Micropholcus piaui* (UFPI 262). *28*, *29*, Male and female prosomata, frontal views. *30*, Tip of right procursus, prolateral view. *31*, Epigynum, ventral view. *32*, *33*, Tip of male palpal trochanter apophysis. *34*, Male gonopore. *35*, *36*, Male distal cheliceral apophyses. *37*, Female anterior lateral spinneret. Scale bars = 6 µm (*32*, *33*); 8 µm (*36*); 10 µm (*37*); 20 µm (*35*); 40 µm (*34*); 80 µm (*30*); 100 µm (*31*); 200 µm (*28*, *29*).

Non-type material. BRAZIL: *Piauí*: Brasileira e Piracuruca, Parque Nacional de Sete Cidades, 2.ii.2007 (E.B.O. Marques), beating tray, gallery forest, 1♂ in ZFMK (Ar 10591); same locality, 4.xii.2006 (D.F. Candiani), 1♀ in MPEG (11542); 20.vi.2007 (F.M. Oliveira-Neto), 1♀ in MPEG (11543); 3.ii.2007 (L.S. Carvalho), nocturnal manual search, gallery forest, 1♀ in ZFMK (Ar 10592).

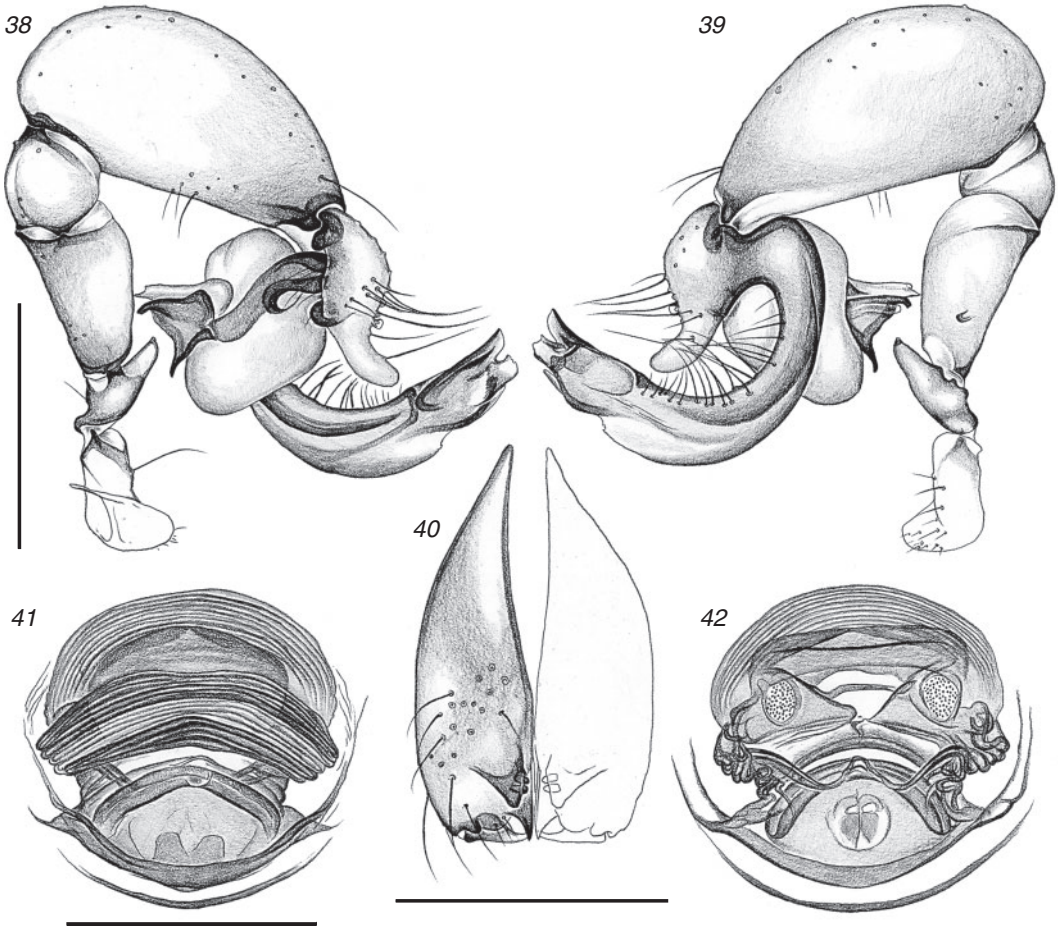
Diagnosis

Small, six-eyed, pale pholcine with widely curved procursus, easily distinguished from most similar known congeners by straight dorsal process on male palpal tarsus (Fig. 43; curved in *M. piaui*, *M. crato* and *M. brazlandia*); also by large lateral male cheliceral projections in unusually frontal position (Fig. 45; absent in *M. crato*; smaller and more lateral in *M. piaui* and *M. brazlandia*); from *M. piaui*, *M. crato* and *M. brazlandia* also by very long male palpal trochanter apophysis (Fig. 44). Females are difficult to distinguish externally (pore plates smaller and closer together than in relatives; posterior border of epigynum distinctively sculptured; Figs 46, 47).

Description

Male (holotype)

Total body length 2.0, carapace width 0.7. Leg 1: 11.8 (3.0 + 0.3 + 3.1 + 4.6 + 0.8), tibia 2: 2.0, tibia 3: 1.3, tibia 4: 1.8. Tibia 1 L/d: 50. Distance PME–PME 230 µm, diameter PME 80 µm, distance PME–ALE 35 µm, AME absent. Prosoma and legs pale ochre-yellow with barely visible darker mark medially on carapace; abdomen pale grey with darker spots dorsally. Habitus as in *M. piaui* (cf. Figs 9, 10), ocular area not elevated, each triad on low hump; clypeus unmodified; no thoracic furrow. Chelicerae as in Fig. 45, with pair of distal



Figs 38–42. *Micropholcus crato*. *38*, *39*, Left male palp, prolateral and retrolateral views (non-type male in MNRJ). *40*, Male chelicerae, frontal view (non-type male in MNRJ). *41*, *42*, Cleared female genitalia in ventral and dorsal views. Scale bars = 0.3 (*40–42*), 0.5 (*38*, *39*).

apophyses each with 2–3 modified hairs, with large proximal projections in unusually frontal position. Palps as in Figs 43 and 44; coxa unmodified; trochanter with short retrolateral process and very long ventral apophysis; femur with two small proximal processes (retrolaterally and retolatero-dorsally); tarsus with distinctive straight dorsal projection and curved procursus with distinctive distal elements; capsulate tarsal organ at basis of dorsal projection; bulb with strong proximal sclerite, weakly sclerotised embolus, and sclerotised process (putative appendix). Legs apparently without spines, curved hairs and vertical hairs (most hairs missing). Trichobothria on tibiae not seen. Tarsus 1 with ~10 pseudosegments.

Variation

Tibia 1 in other male: 4.0; this male without spots on abdomen and with slightly more distinct elongation of abdomen above spinnerets.

Female

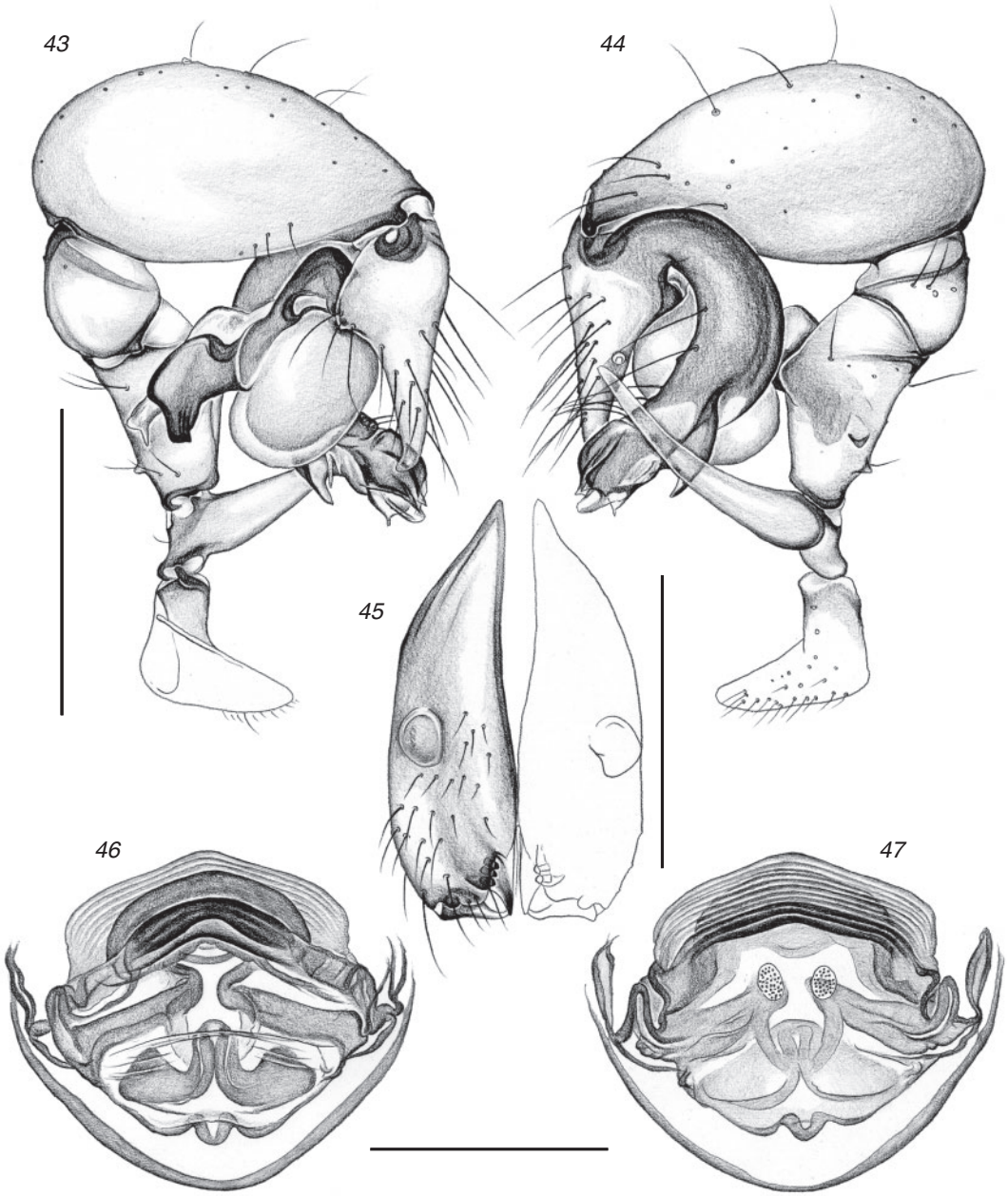
In general similar to male; all females without spots on abdomen and with more distinct pointed elongation of abdomen above spinnerets. Tibia 1: 2.7, 2.9, 3.4. Epigynum simple, weakly sclerotised protruding plate, posterior border indented with indistinct 'knob' (barely visible in dissecting microscope), internal 'valve' visible through cuticle (Fig. 15); internal genitalia as in Figs 46 and 47; pore plates very small and close together.

Distribution

Known from type locality in Piauí state only (Fig. 8).

Natural history

Sete Cidades National Park is covered by a mosaic of phytophysiognomies of the Cerrado biome (Fig. 5). It includes savanna (evergreen broad-leaved sclerophyllous shrubland = 'cerrado *sensu strictu*'; and deciduous subdesert shrubland with succulents = 'cerrado rupestre'), forest (evergreen broad-leaved woodland = 'cerradão'; tropical ombrophilous alluvial occasionally flooded forest = gallery forest; and tropical semi-deciduous dry forest), and grassland (Oliveira *et al*. 2007). During a structured inventory from December 2006 to June 2007 (by L. S. Carvallo) using five



Figs 43–47. *Micropholcus piracuruca*. *43*, *44*, Left male palp, prolateral and retrolateral views (ZFMK Ar 10591). *45*, Male chelicerae, frontal view (ZFMK Ar 10591). *46*, *47*, Cleared female genitalia in ventral and dorsal views (MPEG 11543). Scale bars = 0.3 (*45–47*), 0.5 (*43*, *44*).

collecting methods (beating tray, pit-fall traps, Winkler extractors, sweeping-net and nocturnal manual collecting), five individuals were captured in gallery forest, tropical semi-deciduous dry forest, and cerrado rupestre areas (by beating trays and nocturnal manual collecting).

Etymology

The species name is a noun in apposition, derived from the type locality.

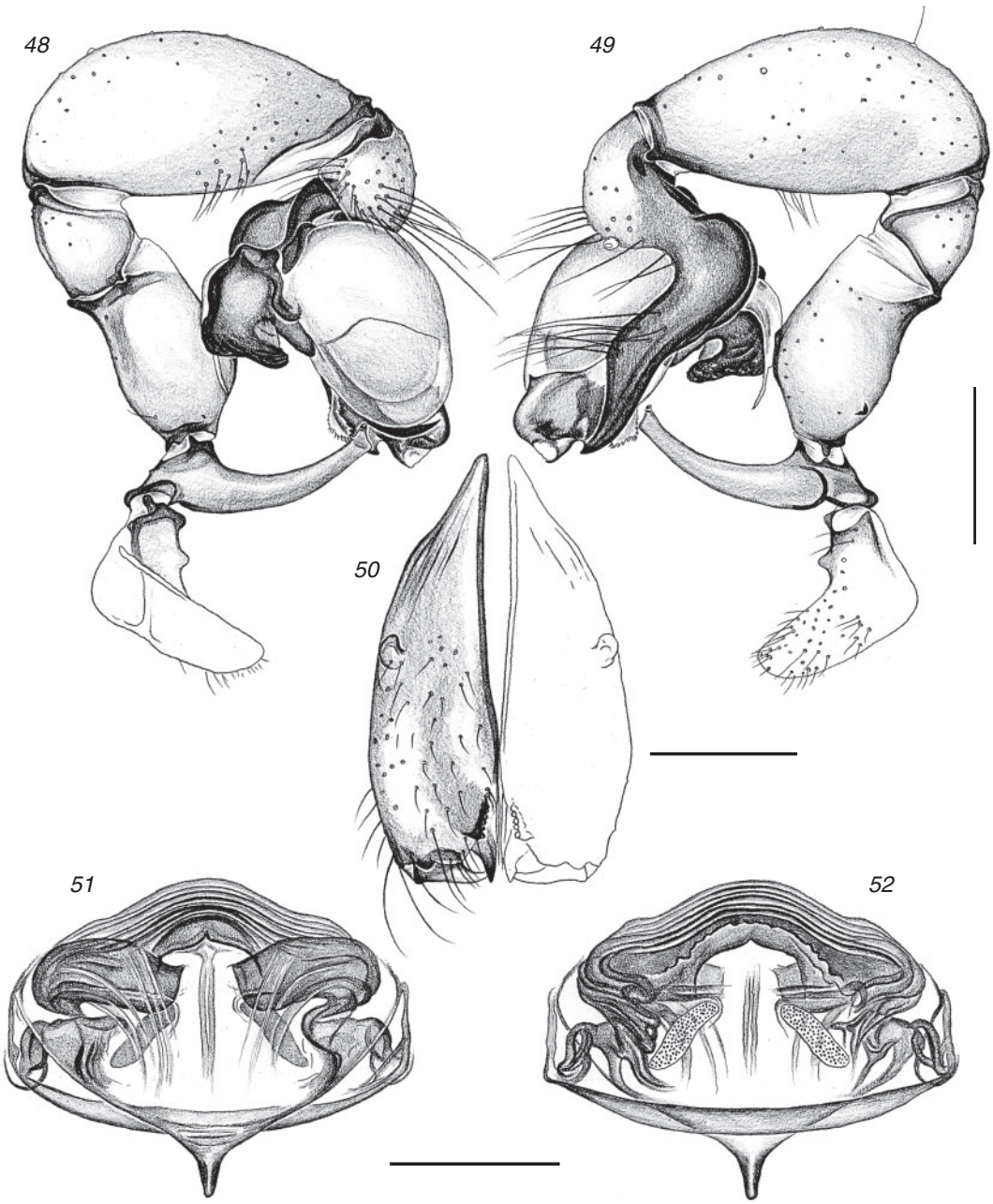
Micropholcus ubajara, sp. nov.

(Figs 4, 11, 12, 16, 48–65)

Material examined

Holotype. ♂, Brazil, Ceará, Ubajara, Parque Nacional de Ubajara, Gruta do Morcego Branco (3°50.0′S, 40°54.0′W), 530 m a.s.l., 22.x.2011 (L. S. Carvalho), in UFPI (267 part).

Non-type material. BRAZIL: *Ceará*: Ubajara, Parque Nacional de Ubajara, Gruta do Morcego Branco, same data as holotype, 15♂ 14♀ 10



Figs 48–52. *Micropholcus ubajara* (UFPI 267). *48*, *49*, Left male palp, prolateral and retrolateral views. *50*, Male chelicerae, frontal view. *51*, *52*, Cleared female genitalia in ventral and dorsal views. Scale bars = 0.3 (*50*), 0.5 (*48*, *49*, *51*, *52*).

juvs in UFPI (267, 268: leg. E. Araújo) and ZFMK (Ar 10593; 2♂ 2♀ separated from UFPI 267); same locality, 4.ix.2012 (L.S. Carvalho), 7♂ 3♀ 6 juvs in pure ethanol, in UFPI (295, 297, 299: 4♂ 1♀ 6 juvs), IBSP (162936; 3♂) and ZFMK (Ar 10594; 2♀ separated from UFPI 295); same locality, 13.v.2013 (L.S. Carvalho), 3♀ 1 juv. in pure ethanol, in UFMG (12816–18, 12819 part).

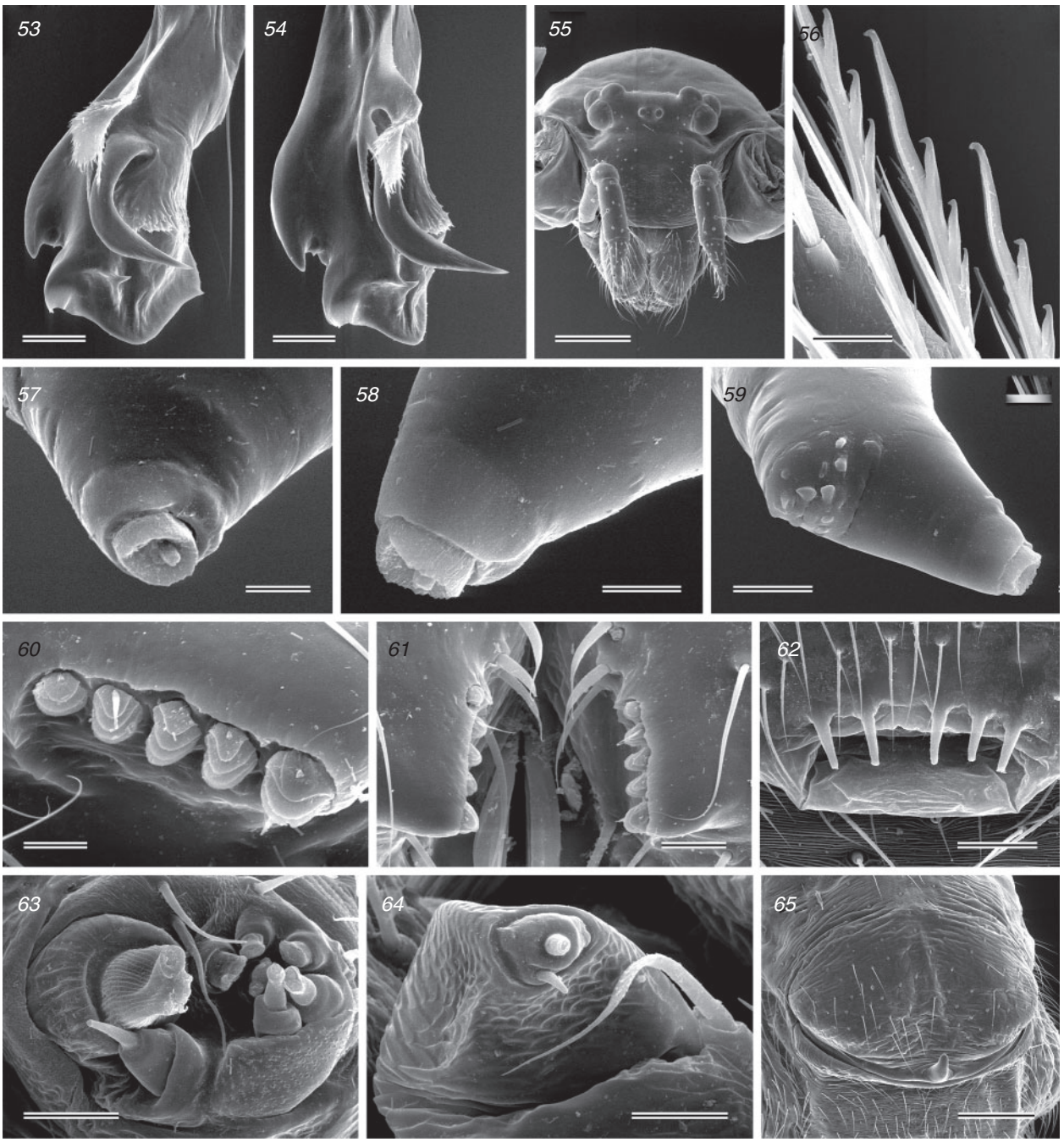
Diagnosis

Medium-size, eight-eyed pholcine, easily distinguished from known congeners by details of male palp (Figs 48, 49; coxa with ventral process; long trochanter apophysis with short subdistal process; shapes of procursus and bulbal process), and by distinctive median process on epigynum (Figs 51, 65); from most Brazilian congeners (except *M. pataxo*) also by presence of AME (Fig. 55).

Description

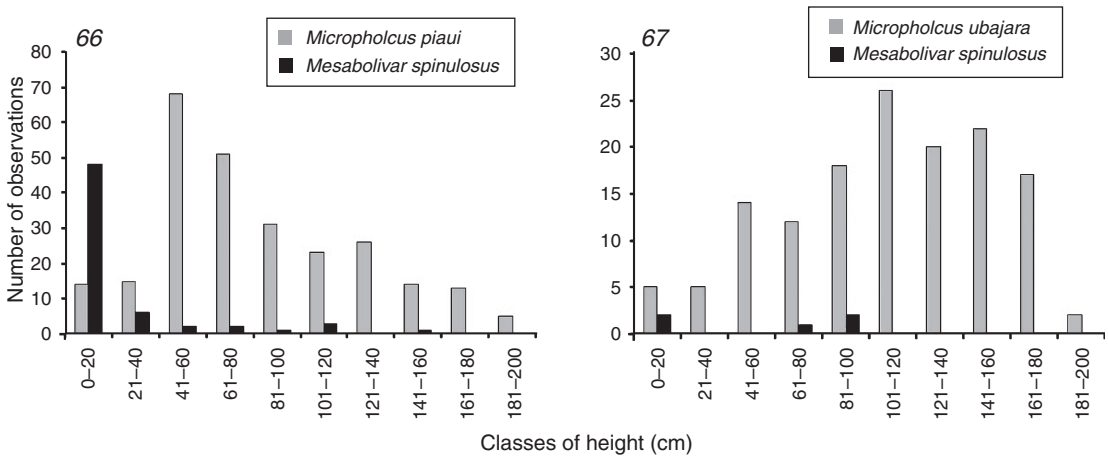
Male (holotype)

Total body length 5.5, carapace width 1.6. Leg 1: 52.5 (12.4 + 0.7 + 12.5 + 25.0 + 1.9), tibia 2: 8.6, tibia 3: 5.3, tibia 4: 7.2. Tibia 1 L/d: 83. Distance PME–PME 480 μm, diameter PME

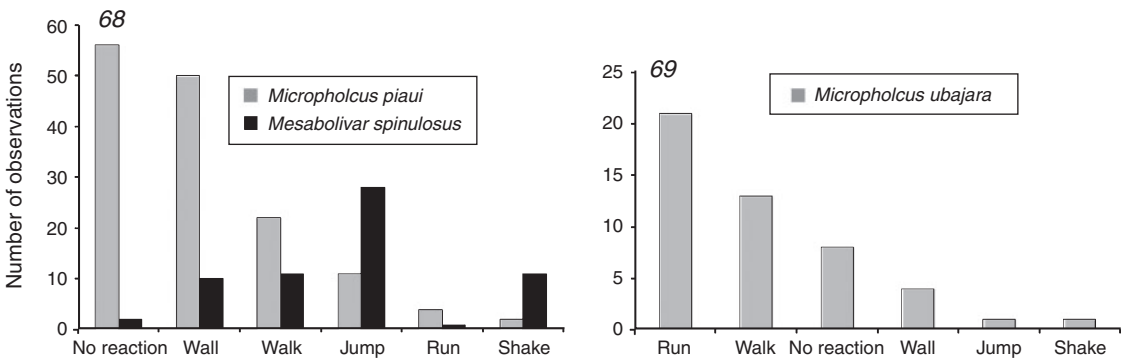


Figs 53–65. *Micropholcus ubajara* (UFPI 267). *53*, *54*, Tip of left procursus, prolateral and slightly ventral views. *55*, Female prosoma, frontal view. *56*, Comb-hairs on female tarsus 4. *57–59*, Tip of male palpal trochanter apophysis. *60*, *61*, Male distal cheliceral apophyses. *62*, Male gonopore. *63*, Male anterior lateral spinneret. *64*, Female posterior median spinneret. *65*, Epigynum. Scale bars = 10 µm (*57*, *58*, *60*); 20 µm (*56*, *59*, *61*, *63*, *64*); 50 µm (*62*); 100 µm (*53*, *54*); 300 µm (*65*); 400 µm (*55*).

135 µm, distance PME–ALE 35 µm, diameter AME 55 µm, distance AME–AME 45 µm. Carapace ochre with large brown median mark, clypeus with pair of brown marks, sternum pale ochre with narrow brown margins, darker medially; legs ochre to light brown, patellae and tibia-metatarsus joints darker; abdomen monochromous pale grey. Habitus as in Figs 11 and 12, ocular area slightly elevated, each triad on low hump directed towards lateral; clypeus unmodified; no thoracic furrow. Chelicerae as in Fig. 50, with small proximal lateral projections and pair of distal apophyses with five modified hairs each (Figs 60, 61). Palps as in Figs 48 and 49; coxa with small ventral process; trochanter with short and wide retrolateral process and very long ventral apophysis with distinct modified hair at tip (Figs 57, 58) and short subdistal process (Fig. 59);



Figs 66–67. Height above the ground at which the Pholcidae species studied were found at: *66*, Parque Municipal da Pedra do Castelo; *67*, and Parque Nacional de Ubajara.



Figs 68–69. Defensive behaviours of the Pholcidae species studied at: *68*, Parque Municipal da Pedra do Castelo; *69*, and Parque Nacional de Ubajara.

femur with two small proximal processes (retrolaterally and retolatero-dorsally); tarsus without dorsal projection, procursus complex distally, prolaterally with distinctive pointed process and membranous flap (Figs 53, 54); bulb with strong proximal sclerite, weakly sclerotised embolus, and bifid sclerotised process (putative appendix). Legs apparently without spines, curved hairs and vertical hairs (most hairs missing). Retrolateral trichobothrium on tibia 1 at 4%; prolateral trichobothrium absent on tibia 1. Tarsus 1 with >15 pseudosegments, distally fairly distinct. ALS with eight spigots each (Fig. 63); PMS with two spigots each (cf. female; Fig. 64). Gonopore with five epiandrous spigots (Fig. 62) (probably an exception from the usual number of four in the specimen studied by SEM).

Variation

Tibia 1 in 18 other males: 10.8–12.8 (mean 11.9).

Female

In general similar to male. Tibia 1 in 13 females: 9.6–12.0 (mean 10.6). Epigynum weakly sclerotised plate with distinctive posterior process (Figs 16, 65). Internal genitalia as in Figs 51 and 52, with pore plates elongate and diverging posteriorly.

Distribution

Known from type locality in Ceará state only (Fig. 8).

Natural history

This species was recorded only from Gruta do Morcego Branco, a relatively small limestone cave located in a small patch of high altitude Brazilian Atlantic Forest in Ubajara National Park (a so-called '*brejo de altitude*'). This conservation unit contains 11 limestone caves, from which 115 invertebrate species have been recorded, including 53 species at Gruta do Morcego Branco (Silva and Ferreira 2009). The specimens of *M. ubajara* were collected in sympatry with *M. piaui*, and also in sympatry and syntopy with *Mesabolivar spinulosus*. These three species were absent in the other limestone cave sampled, Gruta de Ubajara, the larger cave of the Ibiapaba complex (Silva and Ferreira 2009).

At both expeditions to the area (September 2012, dry period; May 2013, rainy period) the spiders were observed in the entire

cave except at the cave entrance. Specimen counts were 48 and 98 individuals in the dry and rainy seasons respectively, but these counts were performed at different sites within the cave, owing to flooding in the area that had been sampled in the dry season.

The mean height above the ground at which specimens were found was 115 cm (141 observations; range: 10 to >200 cm). This was significantly higher (U = 115, p-value (bilateral) = 0.0106) than the sympatric pholcid *Mesabolivar spinulosus*, which was found at a mean height of 55 cm (five observations; range: 10–97 cm), suggesting that the two pholcids occupy different microhabitats within the cave (Fig. 67).

Most individuals (~80%) were observed outside webs on the cave walls, while others were observed in barely visible sheet webs (mostly ~10 × 10 cm), with anchoring lines fixed to the walls and its recesses. The spiders appear to actively select their position on the cave walls, as 76% of the individuals (100 observations) were observed less than 50 cm from a conspecific, while only 9% were observed more than 100 cm from the next conspecific.

Feeding was observed five times, with two individuals feeding on beetles (Carabidae), one on a true bug (Heteroptera; Fig. 4), one on an unidentified Diptera, and one on a bee (Apidae, *Trigona* sp.). Females with egg sacs were observed at both expeditions (11 in September 2012; 17 in May 2013). Egg sacs contained 17–34 eggs ($N = 3$) and were weakly enveloped with silk lines. Four male–female pairs (less than 10 cm from each other) were observed in September 2012 ($N = 1$) and May 2013 ($N = 3$). Sex ratio (males/females) was 0.42, indicating a female-biased population ($\chi^2 = 18.893$, d.f. = 1, $P < 0.0001$, with Yates correction).

At disturbance, most specimens ran away quickly (21 observations); others slowly walked a short distance (13 observations) or showed no reaction (8 observations). Other reactions were rare (Fig. 69).

Etymology

The species name is a noun in apposition, derived from the type locality.

Discussion

Transfer versus new genus

The taxonomic implications of the data are not self-evident. New World '*Leptopholcus*' could either be transferred to *Micropholcus* or be considered a separate genus. Each option has pros and cons and we chose the first option even though our new delimitation of *Micropholcus* is at first sight rather counter-intuitive. Together with *Pholcus* and *Aucana* it is now one of only three genera (among the 90 extant pholcid genera currently known) occurring on both sides of the Atlantic. Old and New World (especially Caribbean) representatives are conspicuously different in their habitus, with Old World species having a short oval abdomen while New World species have an elongated or even worm-shaped abdomen (Figs 1–4).

We opted for a transfer of New World '*Leptopholcus*' to *Micropholcus* primarily because we were not able to find any morphological synapomorphies that would have supported creation of a new genus for New World '*Leptopholcus*'. In fact, New World '*Leptopholcus*' are best described as a group in which most plesiomorphic character states of the *Pholcus* group of genera are combined (e.g. male chelicerae with proximal lateral processes and distal apophyses with modified hairs; male palpal morphology in general and bulbal processes in particular; spigots on male gonopore and on spinnerets; female epigynum with 'knob' – for details see descriptions above and Huber *et al*. 2005; Huber and Wunderlich 2006).

The Cuban species

Our data provide new substance to an old and intractable controversy about Cuban '*Leptopholcus*' (now *Micropholcus*). Franganillo (1930, 1931) initially described two species: *Leptopholcus delicatulus* Franganillo, 1930 from western Cuba and *L. conicus* Franganillo, 1931 from western and eastern Cuba. The type series of the former includes only females while the types of the latter are lost (Huber and Pérez 1998). Later, Franganillo (1936) synonymised the two species (erroneously giving priority to *L. conicus*). Bryant (1948) synonymised the Cuban species with the Puerto Rican *Micromerys dalei* Petrunkevitch, 1929 but the Cuban *L. delicatulus* was revalidated by Huber and Pérez (1998).

This was the status quo until recent collections in western, central and eastern Cuba revealed the existence of two easily distinguishable male genital morphs, one restricted to western Cuba (*delicatulus*?), the other widely distributed all over the island (*conicus*?). Our new molecular data support the existence of two species on Cuba (Fig. 7), but we treat them all as *M. delicatulus* because a re-examination of the types of *L. delicatulus* (deposited at the Instituto de Ecología y Sistematica, La Habana) should be performed before deciding on the use of Franganillo's (1930, 1931) names.

Sihala: *the next surprise?*

The genus *Sihala* was established for a Sri Lankan species originally described as *Pholcus ceylonicus* O. Pickard-Cambridge, 1869 and a closely related species from southern India (Huber 2011). While its inclusion in the *Pholcus*-group of genera is well supported, its detailed relationships remain obscure. The distinctive modified hair on the tip of the male palpal trochanter apophysis (Huber and Benjamin 2005: figs 3e, f; Huber 2011: fig. 104) reminds strongly of *Micropholcus* and New World '*Leptopholcus*' but otherwise the spiders appear as different as two Pholcinae can be. As is the case of New World '*Leptopholcus*', molecular data may well uncover another unexpected relationship and give further weight to the idea that adaptive radiations and multiple convergent evolution of phenotypes have played a significant role in the diversification of Pholcidae (Dimitrov *et al*. 2013).

Competitive exclusion

Our data lend further support to the idea that New World '*Leptopholcus*' (now *Micropholcus*) are largely excluded from high precipitation areas by the very species-rich and abundant New World pholcid genus *Metagonia* Simon, 1893 (Huber *et al*. 2005; Huber and Wunderlich 2006). *Metagonia* is diverse and abundant in the humid Amazon and Atlantic forests of Brazil, but very rare in the arid corridor in-between, where *Micropholcus*

occurs. The only large-scale humid forests in the New World where *Micropholcus* is present (and often abundant) are located on the Caribbean islands, where *Metagonia* is conspicuously absent (except for two eyeless cave-dwelling species on Jamaica and Cuba; Gertsch 1986; Pérez and Huber 1999). Whenever *Micropholcus* was found in a more humid Brazilian environment (e.g. gallery forest enclave or *brejo de altitude*), this was located within the drier Cerrado and Caatinga domains.

Female-biased sex ratios

Both species studied in detail (*M. piaui* and *M. ubajara*) had significantly female-biased populations. Spider populations and communities are often described as male-biased, in part probably resulting from the higher activity of male individuals, which makes them easier to collect (Álvares *et al*. 2004; Machado *et al*. 2007). However, Carvalho *et al*. (2010) considered female-biased populations as a natural pattern in *Metagonia taruma* Huber, 2000 and in an unidentified species of *Mesabolivar*, as the spiders were collected using active methods (beating tray and nocturnal hand searches). Female-biased Pholcidae populations were also reported by Huber and Schütte (2009) for two species of *Metagonia* sampled by diurnal hand collecting. A robust biological explanation such as proposed for the highly female-biased sex ratio in the social spider *Anelosimus domingo* Levi, 1963 (based on cytogenetics; Avilés *et al*. 2000) is not available for the Pholcidae species studied.

Diversity of defensive behaviours

Quantitative behavioural data of Pholcidae spiders are scarce and largely limited to the reproductive repertoire (e.g. Huber 1996; Huber and Eberhard 1997; Uhl 1998; Peretti *et al*. 2006). The defensive behaviours previously described for Pholcidae include body vibration, running away, jumping to the ground followed by thanatosis, leg autotomy, camouflage and cryptic colouration and behaviour (e.g. Huber 2011, 2013; Huber *et al*. 2013). The defensive behaviours observed for the three long-legged species presented here (Figs 68, 69), which lived in similar microhabitats, differed among species. While each species had in its repertoire a range of responses to disturbance, each appeared to prefer a different strategy: running away in *M. ubajara*; no reaction or flat posture against the cave wall in *M. piaui*; and jumping to the floor in *Mesabolivar spinulosus*.

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