

Two new species of litter-dwelling *Metagonia* spiders (Araneae, Pholcidae) document both rapid and slow genital evolution

Bernhard A. Huber,¹ Cristina A. Rheims² and Antonio D. Brescovit³

¹Zoological Research Institute and Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany; ²Laboratório de Artropódes, Instituto Butantan, Avenida Vital Brazil, 1500, CEP 05503–900, São Paulo, SP, Brazil; ³Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

Keywords:

Araneae, genitalia, leaf-litter, *Metagonia*, Pholcidae, rapid evolution

Accepted for publication:

27 January 2005

Abstract

Huber, B.A., Rheims, C.A., Brescovit, A.D. 2005. Two new species of litter-dwelling *Metagonia* spiders (Araneae, Pholcidae) document both rapid and slow genital evolution. — *Acta Zoologica* (Stockholm) 86: 33–40

The observation that genitalia, rather than other characters, are useful in distinguishing species has resulted in the statement that genitalia evolve relatively rapidly. In this paper we claim that relatively rapid evolution of genitalia may often be restricted to the shapes, numbers, and sizes of individual structures. In contrast, the more basic pattern, including the presence or absence of structures and their interrelationships (the bauplan), does not seem to evolve more rapidly than other (nongenital) aspects of morphology. We document this idea by contrasting two litter-dwelling pholcid species, *Metagonia petropolis* sp. n. and *M. paranapiacaba* sp. n., with their mostly leaf-dwelling congeners. Significant differences occur with regard to nongenital aspects of morphology as well as shapes of individual genital structures, but the bauplan of their genitalia is basically the same.

Bernhard A. Huber, Zoological Research Institute and Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany. E-mail: b.huber.zfmk@uni-bonn.de

Introduction

There is a wide consensus that genitalia and other sexual-contact structures commonly evolve more rapidly than other morphological characters (reviews in Eberhard 1985; Hosken and Stockley 2004). This relatively rapid evolution, coupled with a relative uniformity of genitalia within populations and supposed reproductive communities (Eberhard *et al.* 1998; Palestini *et al.* 2000; Tatsuta *et al.* 2001), explains the importance of genitalia in species discrimination in many animal taxa, including spiders (Huber 2004). Nongenitalia, on the other hand, have traditionally been preferred by taxonomists for the delimitation of genera and higher categories (Platnick 1975: 'As is usual in spiders, the genera are defined by somatic characters and the species groups by genital characters'; see also Griswold 1993; Foelix 1996). However, in one important sense, genitalia may evolve relatively slowly rather than relatively rapidly compared with other characters, i.e. with regard to their bauplan, which probably reflects the mechanics of copulation. The high percentages of

genital characters in recent matrices for cladistic analyses document this conservative aspect of genital evolution at species-group, generic, and higher levels (an average of 58% of characters in the eight matrices cited in Huber 2004). In pholcids, some of the most valuable characters at family and subfamily levels refer to genital or other sexual-contact structures (e.g. characters 36, 40, 47 and 52 in Huber 2000). Further support comes from individual cases of slow genital evolution coupled with prominent changes in nongenital morphology (Huber 1998, 2002). The present paper describes two new species of *Metagonia* that illustrate (1) species-specificity in the details, i.e. rapid evolution of genitalia with respect to shapes and sizes of individual structures, and (2) conspicuous changes in overall morphology because of changes in ecology without any effect on the genital bauplan of the genus, i.e. relatively slow evolution of genitalia with respect to the basic bauplan.

The genus *Metagonia* Simon, 1893 is one of the most species-rich pholcid genera in the Neotropics. The present count is at about 80 nominal species, but dozens of undescribed

species exist in collections, and many more probably remain uncollected (Huber 2000). The genus is also interesting from a biogeographical point of view. Unlike most other Neotropical genera that belong to the New World clade, *Metagonia* is more closely related to a large clade with an almost exclusive Old World distribution (Huber 2000). Little is known about the biology of *Metagonia* species (Gertsch 1986; Huber 1997). Most forest species seem to have adapted to a cryptic life on the underside of alive (i.e. green) leaves, with pale greenish bodies, very thin and long legs, elongated abdomens, and sometimes even elongated egg-sacs. Similar morphologies have been described for other (Old World) genera adapted to the same microhabitat (Deeleman-Reinhold 1986). Other species occur in caves, with extensive speciation documented in Mexico. Some of these have evolved troglomorphic features (e.g. loss of eyes), but most have retained morphologies similar to those of the leaf-dwelling species. Finally, a number of species live close to the ground, 'under objects and detritus on the soil' (Gertsch 1986). A very unusual species with short legs and globular abdomen described recently (*M. globulosa* Huber 2000) probably belongs in this ecological group, but its microhabitat remains unknown. The present paper describes two further short-legged species with globular abdomens, both collected from the leaf litter.

Taxonomy

The style of the following descriptions follows that in Huber (2000). Measurements are in mm unless indicated otherwise. Material is deposited in the collections of the Instituto Butantan, São Paulo (IBSP, A. Brescovit), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto da Rocha), and Zoological Research Institute and Museum Alexander Koenig, Bonn (ZFMK, B. Huber).

Genus *Metagonia* Simon, 1893

Metagonia petropolis sp. n.

Type material. Male holotype, BRAZIL, Rio de Janeiro, Petrópolis, Fazenda Ranchinho da Roça (~22°30'S, 43°06'W), 8–15 February 2000, 'Equipe BIOTA' (pitfall traps) (IBSP 41195). *Paratypes.* Same data as for holotype, 28 male, 17 female (IBSP: 41169, 41175–41176, 41180–41201; MZSP: two male, two female, ZFMK: four male, three female).

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

Diagnosis. Easily distinguished from *Metagonia paranapiacaba* sp. n. and *M. globulosa* Huber by the armature of the male clypeus (Figs 2C and 3A), by the shape and position of the apophysis on the male palpal femur (Fig. 2A), by the

shape of the procurus (Fig. 2A,B), and by the epigynum and internal female genital structures (Figs 1C and 2D,E). Distinguished from most other congeners also by the short legs and the globular abdomen.

Description. Male (holotype): total length 1.70 (1.84 with clypeus), carapace width 0.76. Leg 1: 8.52 (2.07 + 0.27 + 2.25 + 3.03 + 0.90), tibia 2: 1.17, tibia 3: 0.87, tibia 4: 1.40. Tibia 1 length/diameter (L/d): 32. Habitus as in Fig. 1(A,B). Prosoma and legs ochre-yellow, slightly darker mark medially on carapace, including ocular area, abdomen grey with large darker marks except ventrally. Ocular area barely elevated, thoracic furrow absent; distance PME–PME 60 µm; diameter PME 80 µm; distance PME–ALE 10 µm; AME absent. Clypeus with distinctive pair of apophyses (Figs 2C and 3A). Sternum wider than long (0.54/0.48), unmodified. Chelicerae as in Fig. 2(C), with pair of distal apophyses (Fig. 3D), with stridulatory ridges and cuticular humps near clypeal apophyses (Fig. 3B). Palps as in Fig. 2(A,B); coxa unmodified, trochanter without apophysis, femur with distinctive apophysis prolaterally (Fig. 2A), with stridulatory pick proximally (Fig. 3F); procurus relatively complex distally, with distinctive hinged process (Fig. 2B), with many cuticular scale-like spines (Fig. 3G), with capsulate tarsal organ; bulb simple, with tubular embolus as only projection, ending in spine (Fig. 3C). Retrolateral trichobothrium of tibia 1 at 22%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with over 10 pseudosegments, very indistinct proximally; tarsus 4 ventrally with comb hairs. Gonopore with four epiandrous spigots (Fig. 3E). Anterior lateral spinneret (ALS) with several piriform gland spigots (Fig. 3H).

Variation: The marks on carapace and abdomen are variably distinct. Tibia 1 in 26 males: 2.07–2.33 (mean 2.18).

Female (paratypes): In general similar to male. Tibia 1 in 15 females: 1.80–2.07 (mean 1.89). Female external genitalia a slightly protruding large brown plate (Figs 1C and 2D), internal genitalia with distinctive asymmetric sclerotized elements (Fig. 2D,E). ALS spigots as in male (Fig. 3I).

Distribution. Known only from type locality.

Material examined. Only types above.

Metagonia paranapiacaba sp. n.

Type material. Male holotype, BRAZIL, São Paulo, Paranapiacaba, Estação Biológica do Alto da Serra (23°46.7'S, 46°18.6'W), 750–890 m above sea level, 14–15 December 2003, Huber, Schulz, Rheims & Indicatti, from the underside of dead leaves on the ground (IBSP 41218). *Paratypes:* same data as for holotype, 12 males, 16 females (IBSP 41219, MZSP: two males, two females, ZFMK: four males, four females).

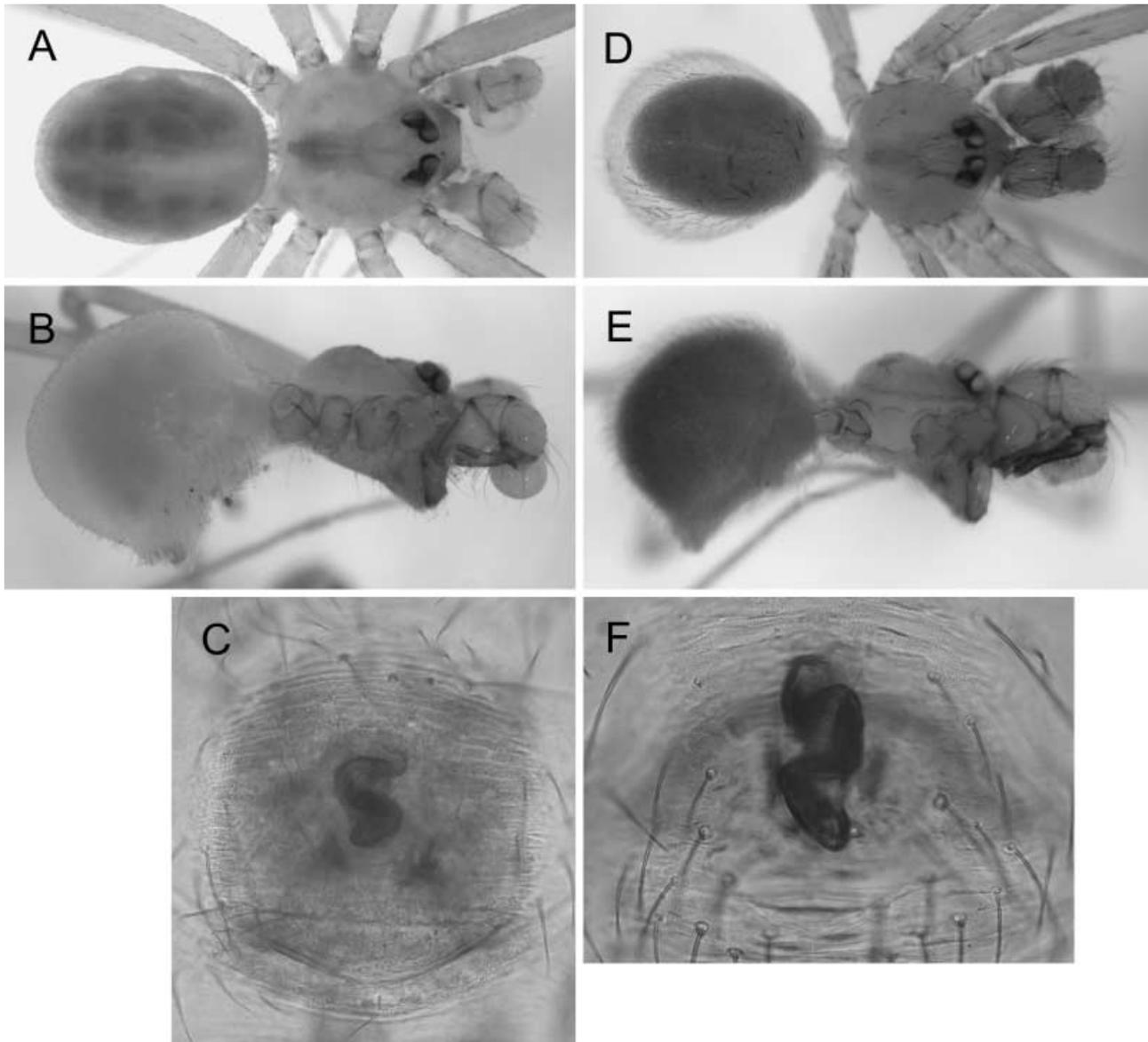


Fig. 1—*Metagonia petropolis* sp. n. (A–C) and *M. paranapiacaba* sp. n. (D–F). —A, D. Males, dorsal views. —B, E. Males, lateral views. —C, F. Cleared female genitalia, ventral views.

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

Diagnosis. Easily distinguished from *M. petropolis* and *M. globulosa* by the armature of the male clypeus (Figs 4C and 5A,B), by the shape and position of the apophysis on the male palpal femur (Fig. 4A), by the shape of the procurus (Fig. 4A,B), and by the epigynum and internal female genital structures (Figs 1F and 4D,E). Distinguished from most other congeners also by the short legs and the globular abdomen.

Description. Male (holotype): total length 1.46 (1.60 with clypeus), carapace width 0.66. Leg 1: 7.86 (1.90 + 0.23 + 2.13 + 2.67 + 0.93), tibia 2: 1.13, tibia 3: 0.80, tibia 4: 1.33. Tibia 1 L/d: 32. Habitus as in Fig. 1(D,E). Prosoma and legs ochre-yellow, abdomen monochromous grey. Ocular area not elevated, only triads on very low elevations (Fig. 5A), thoracic furrow absent; distance PME–PME 45 μ m; diameter PME 80 μ m; distance PME–ALE 10 μ m; AME absent. Clypeus with distinctive pair of apophyses (Figs 4C and 5A,B). Sternum wider than long (0.50/0.40), unmodified. Chelicerae as in Fig. 4(C), with pair of distal

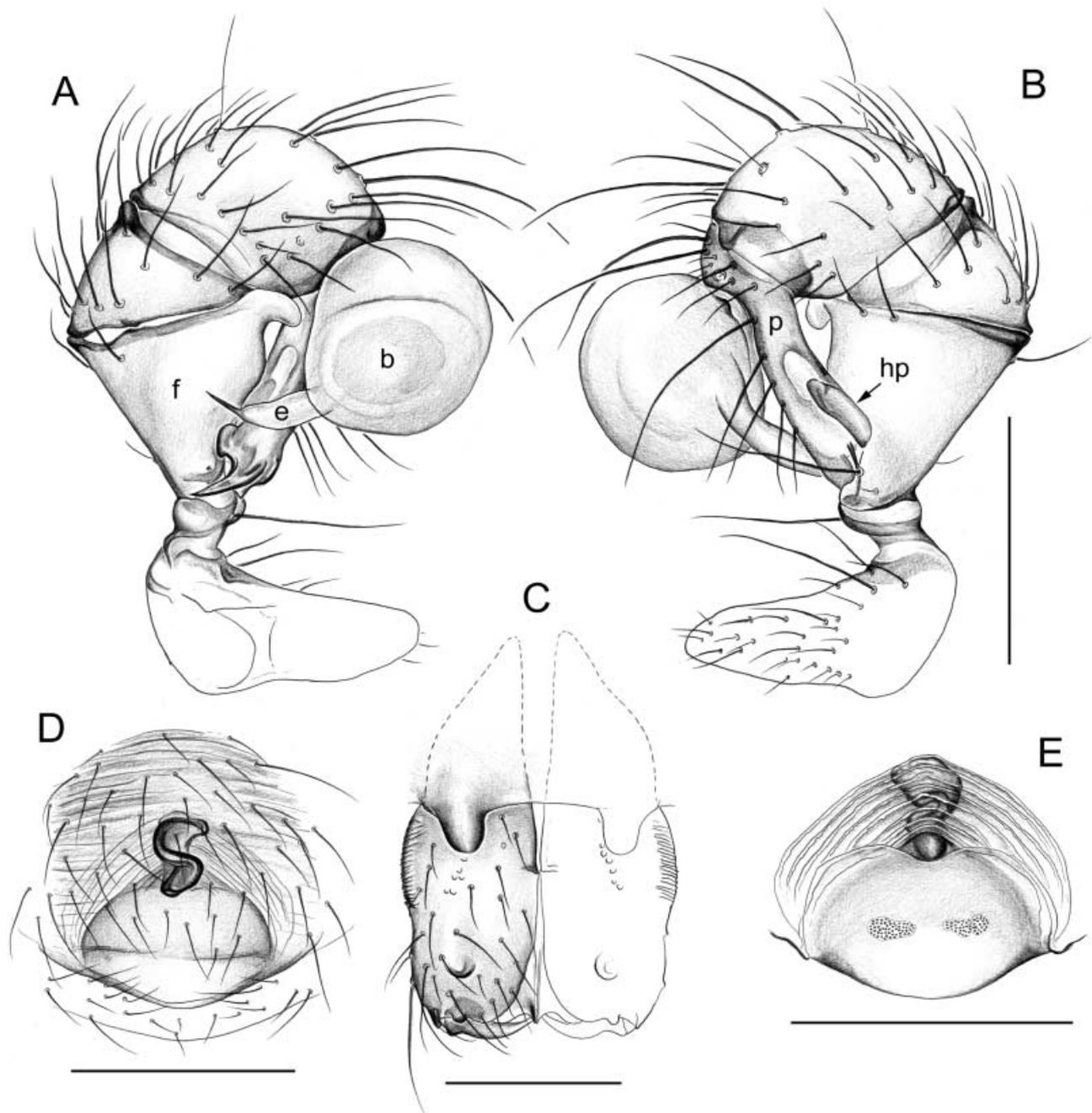


Fig. 2—*Metagonia petropolis* sp. n. —**A, B**. Left male palp in prolateral (A) and retrolateral (B) views. —**C**. Male clypeus and chelicerae, frontal view. —**D, E**. Cleared female genitalia, ventral (D) and dorsal (E) views. Scale lines: 0.3 mm (A, B, D, E), 0.2 mm (C). Abbreviations: b, genital bulb; e, embolus; f, femur; hp, hinged process; p, procursus.

apophyses (Fig. 5D), without stridulatory ridges. Palps as in Figs 4(A,B); coxa unmodified, trochanter without apophysis, femur with distinctive apophysis prolaterally (Fig. 4A); procursus relatively complex distally, with distinctive hinged process, with capsulate tarsal organ (Fig. 5C); bulb simple, with tubular embolus as only projection, ending with spine

(Fig. 5E). Retrolateral trichobothrium of tibia 1 at 28%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with about 13 pseudosegments, indistinct proximally; tarsus 4 ventrally with comb hairs (Fig. 5I). Gonopore with four epiandrous spigots (Fig. 5F). ALS as in female (see below).

Variation: Tibia 1 in 12 males: 2.10–2.30 (mean 2.19).

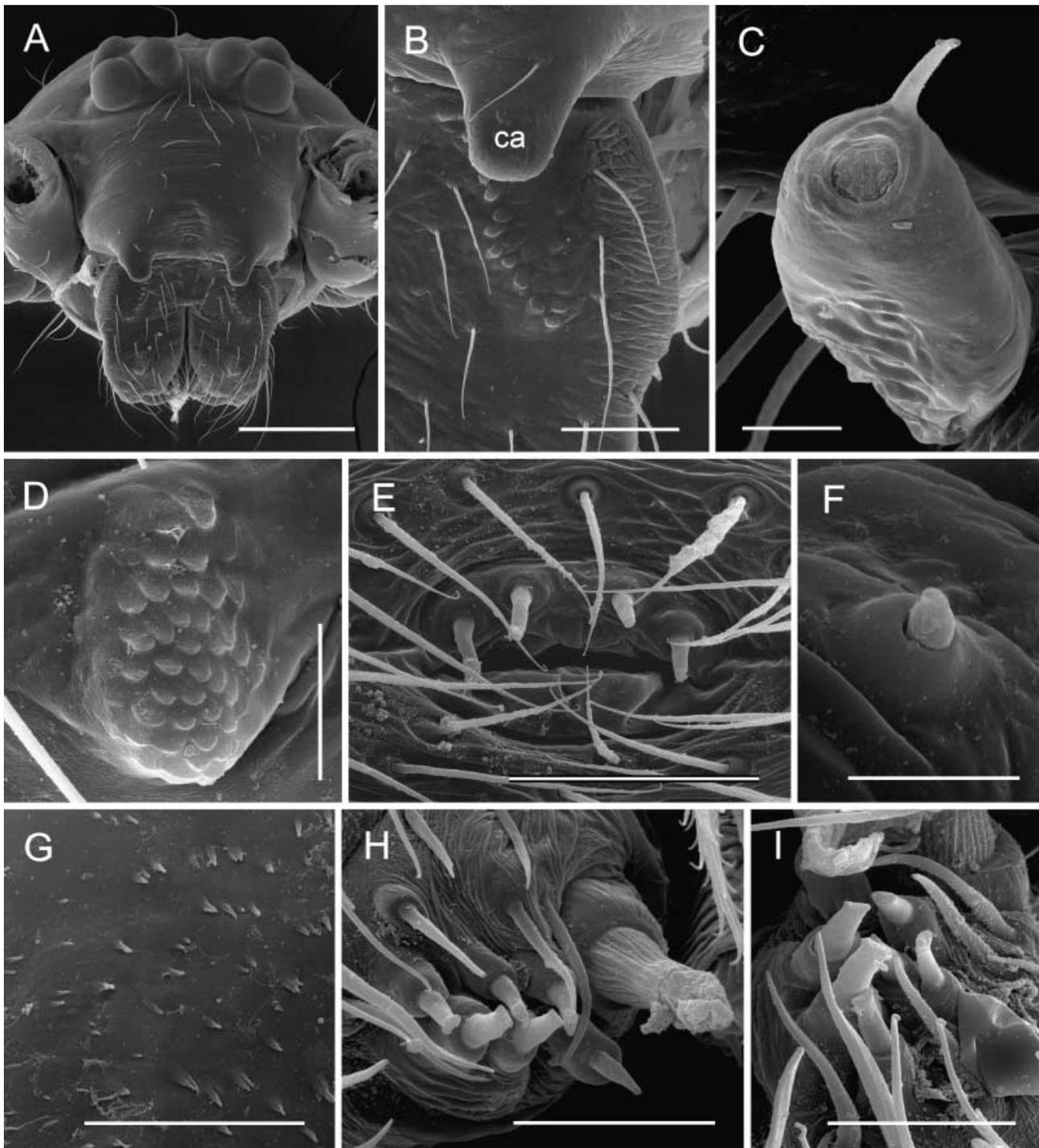


Fig. 3—*Metagonia petropolis* sp. n. —**A**. Male, frontal view. —**B**. Male clypeus apophysis (ca) and chelicera with stridulatory ridges and frontal humps. —**C**. Embolus with sperm duct opening and distal spine. —**D**. Male cheliceral apophysis. —**E**. Male gonopore with four epiandrous spigots. —**F**. Stridulatory pick on male palpal femur. —**G**. Cuticular spines on procurus. —**H**. Male anterior lateral spinneret (ALS). —**I**. Female ALS. Scale lines: 200 μm (A), 50 μm (B, E), 20 μm (C, D, G–I), 10 μm (F).

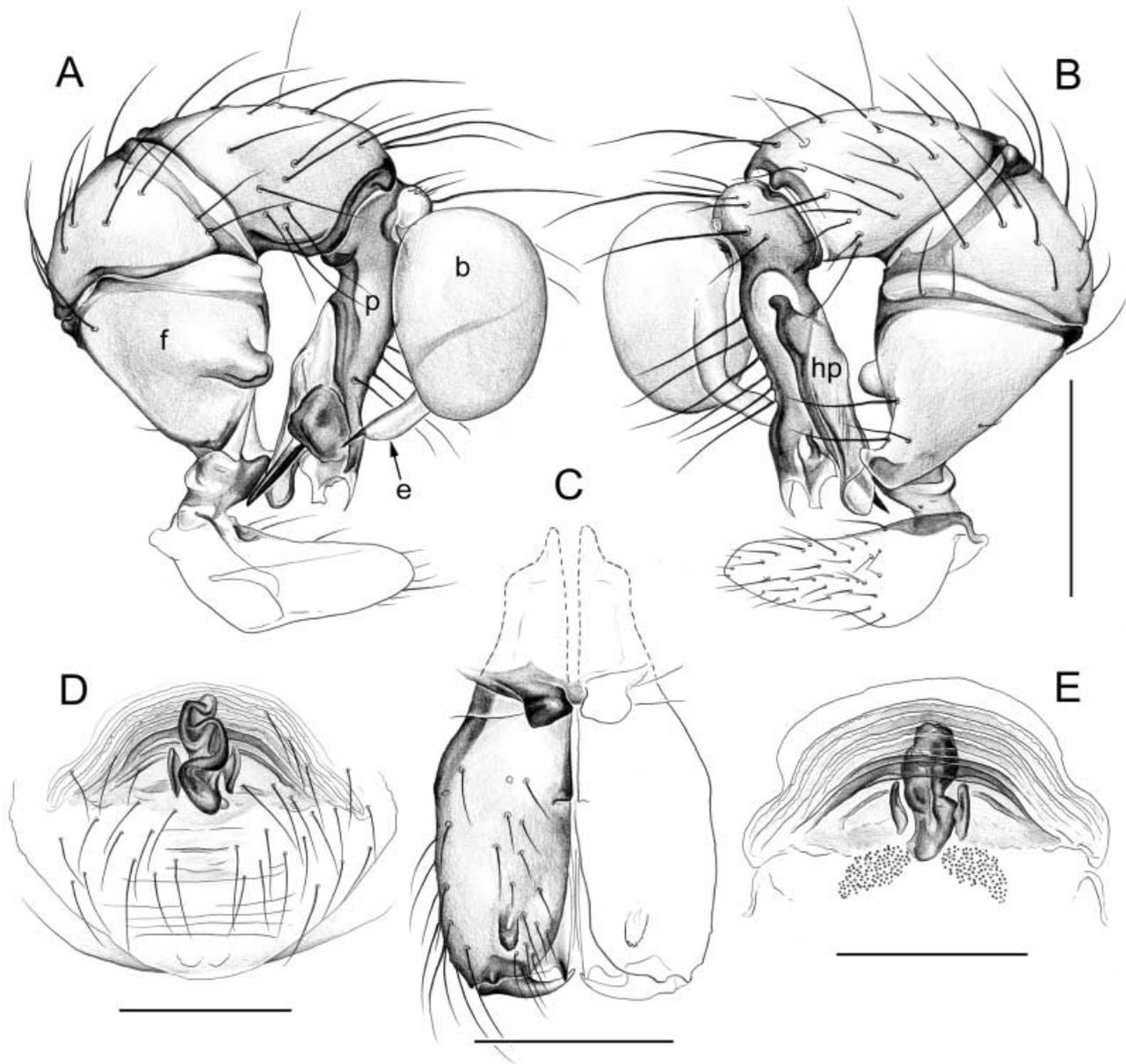


Fig. 4—*Metagonia paranapiacaba* sp. n. —**A, B**. Left male palp in prolateral (A) and retrolateral (B) views. —**C**. Male clypeus and chelicerae, frontal view. —**D, E**. Cleared female genitalia, ventral (D) and dorsal (E) views. Scale lines: 0.3 mm (A, B), 0.2 mm (C–E).

Female (paratypes): In general similar to male. Tibia 1 in 16 females: 1.82–2.10 (mean 2.00). Female external genitalia slightly to strongly protruding, only a small triangular area slightly sclerotized (Figs 1F and 4D), Internal genitalia with distinctive sclerotized asymmetric elements (Fig. 4D,E). ALS with several piriform gland spigots (Fig. 5H).

Distribution. Known only from type locality.

Material examined. Only types above.

Discussion

Rapid and slow genital evolution

Rapid genital evolution is ubiquitous in animals with internal fertilization (Eberhard 1985; Hosken and Stockley 2004) and barely needs further documentation. All the diagnostic characters listed above that distinguish the two species from each other and from the closest known relative are genital (the clypeus is not genital in a strict sense, but it is also

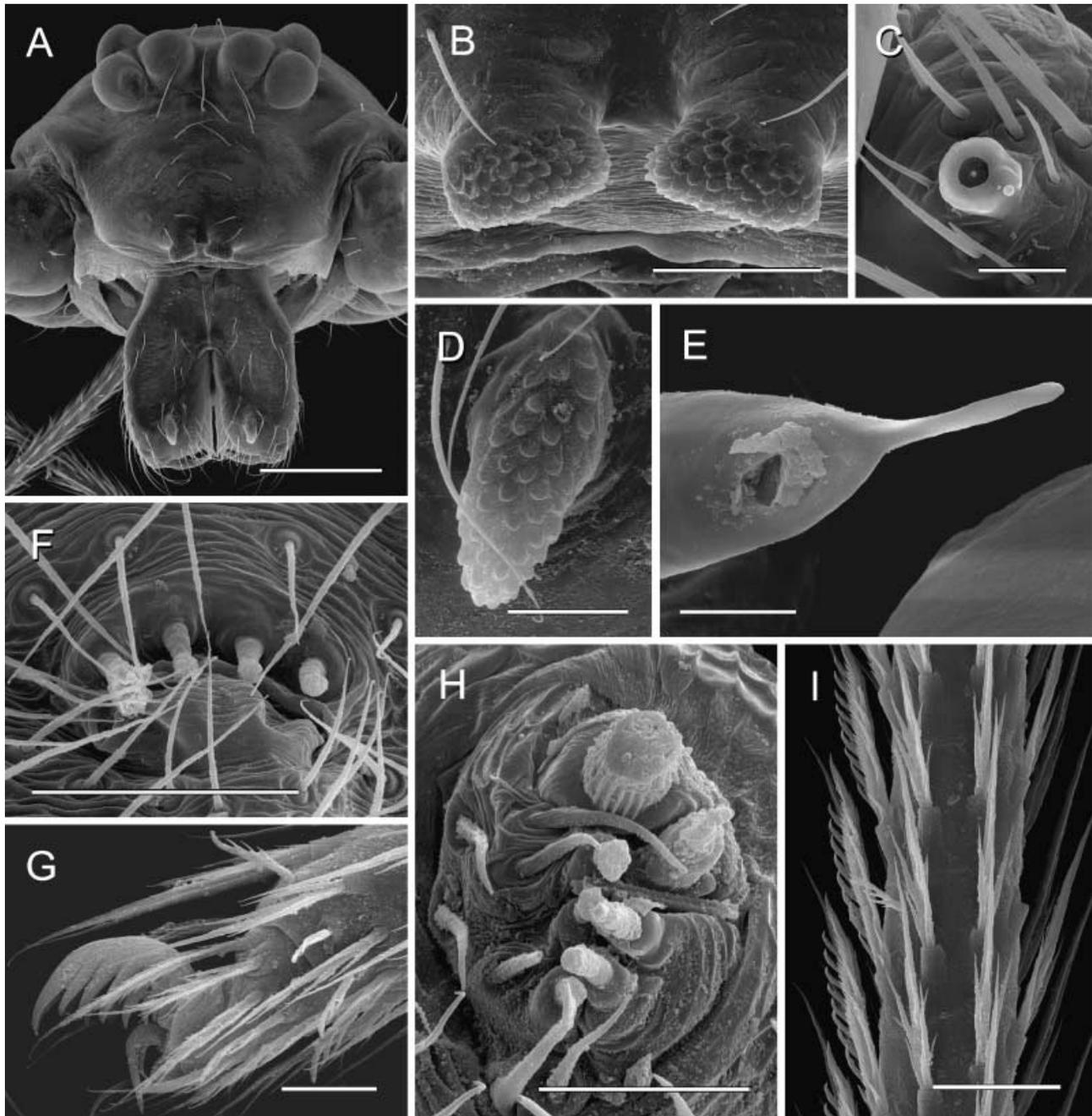


Fig. 5—*Metagonia paranaapiacaba* sp. n. —**A**. Male, frontal view. —**B**. Male clypeus apophyses. —**C**. Male palpal tarsal organ. —**D**. Male cheliceral apophysis. —**E**. Embolus with sperm duct opening and distal spine. —**F**. Male gonopore with four epiandrous spigots. —**G**. Male tarsus 3 tip with claws. —**H**. Female anterior lateral spinneret (ALS). —**I**. Female tarsus 4 with ventral row of comb hairs (left side). Scale lines: 200 μm (A), 50 μm (B, F), 30 μm (I), 20 μm (C–E, G, H).

employed during copulation in pholcids: Huber 1997). The point we wish to make is that this rapidity is largely restricted to changes of shapes, numbers, and sizes of individual structures. The more basic pattern, including the presence/absence of individual structures and their interrelation-

ships (the bauplan), does not seem to evolve more rapidly than other (nongenital) aspects of morphology. In the present case, the bauplan of *Metagonia* genitalia is characterized by a hinged process on the procurus, a bulb with a tubular embolus as single projection, asymmetric female internal

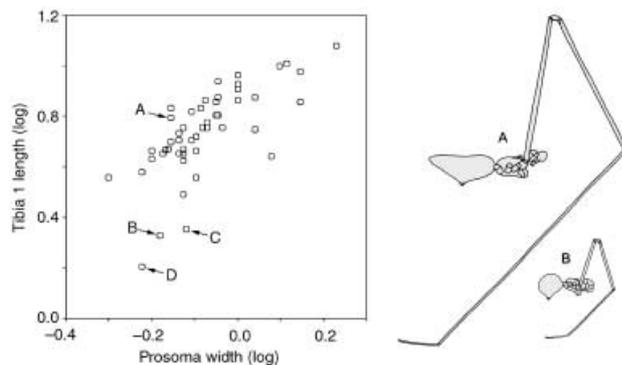


Fig. 6—Scatter of tibia 1 length on prosoma width (both log-transformed) in the 54 species of *Metagonia* for which these data are available in the taxonomic literature. Two species with similar prosoma width are marked on the graph and drawn with one first leg at the same scale: —**A.** *Metagonia rica*, —**B.** *M. paranapiacaba*. Two further short-legged species are marked in the graph: —**C.** *Metagonia petropolis*, —**D.** *M. globulosa*.

genitalia, and a modified male clypeus. All these characters are important synapomorphies of the genus or of species groups within *Metagonia* (Huber 2000). Their conservative nature reflects relatively slow evolution. Since the genus is based on cladistic analysis (Huber 2000) which in turn uses all recognizable similarities (not just bauplan similarities) as potential synapomorphies, the argument is not circular.

Rapid nongenital evolution

The species described herein differ markedly from most known congeners by their small size, short legs (also relative to size, Fig. 6), the globular abdomen, and the darker coloration. All of these characteristics are likely adaptations to a life in the leaf litter. A cladistic analysis within the genus *Metagonia* has not been made, but it seems likely that leaf-dwelling is the plesiomorphic condition and litter-dwelling is the derived condition. Leaf-dwelling is the dominant or exclusive mode of life in four of the five operational species groups identified by Huber (2000), including the group that is possibly sister to all others (group 3 in Huber 2000). Whatever the direction of change, the major changes of overall morphology have not visibly affected the genital bauplan. The latter has thus evolved relatively slowly.

Acknowledgements

We thank Rafael P. Indicatti and Roland Schulz for help with field work, Rosangela S. Bianchini from the Estação Biológica do

Alto da Serra for logistical support, and an anonymous referee for helpful criticism. This study was financially 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

- Deeleman-Reinhold, C. L. 1986. Leaf-dwelling Pholcidae in Indo-Australian rain forests. – *Proceedings of the International Congress of Arachnology* 9 (Panama, 1983): 45–48.
- Eberhard, W. G. 1985. *Sexual Selection and Animal Genitalia*, Harvard University Press, Cambridge, MA.
- Eberhard, W. G., Huber, B. A., Rodriguez, S. R. L., Briceño, R. D., Salas, I. and Rodriguez, V. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. – *Evolution* 52(2): 415–431.
- Foelix, R. F. 1996. *Biology of Spiders*, 2nd edn. Oxford University Press, G. Thieme Verlag, New York, Oxford.
- Gertsch, W. J. 1986. The spider genus *Metagonia* (Araneae: Pholcidae) in North America, Central America, and the West Indies. – *Texas Memorial Museum, Speleological Monographs* 1: 39–62.
- Griswold, C. E. 1993. Investigations into the phylogeny of the lycosoid spiders and their relatives (Arachnida: Araneae: Lycosoidea). – *Smithsonian Contributions to Zoology* 539: 1–39.
- Hosken, D. J. and Stockley, P. 2004. Sexual selection and genital evolution. – *Trends in Ecology and Evolution* 19: 87–93.
- 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. 1998. Notes on the neotropical spider genus *Modisimus* (Pholcidae, Araneae), with descriptions of thirteen new species from Costa Rica and neighboring countries. – *Journal of Arachnology* 26: 19–60.
- 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. 2002. Rapid evolution and species-specificity of arthropod genitalia: fact or artifact? – *Organisms Diversity and Evolution* 3: 63–71.
- Huber, B. A. 2004. The significance of copulatory structures in spider systematics. In Schult, J. (Ed.): *Studien zur Theorie der Biologie, Band 5, Biosemiotik – Praktische Anwendung und Konsequenzen für die Einzeldisziplinen*, pp. 89–100. VWB-Verlag für Wissenschaft und Bildung, Berlin.
- Palestrini, C., Rolando, A. and Laiolo, P. 2000. Allometric relationships and character evolution in *Onthophagus taurus* (Coleoptera: Scarabaeidae). – *Canadian Journal of Zoology* 78: 1199–1206.
- Platnick, N. I. 1975. A revision of the palpimanid spiders of the new subfamily Otiiothopinae (Araneae, Palpimanidae). – *American Museum Novitates* 2562: 1–32.
- Tatsuta, H., Mizota, K. and Akimoto, S.-I. 2001. Allometric patterns of heads and genitalia in the stag beetle *Lucanus maculifemoratus* (Coleoptera: Lucanidae). – *Annals of the Entomological Society of America* 94: 462–466.