

Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (González-Sponga) (Pholcidae: Araneae)

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Abstract

The asymmetric male and female genitalia of the spider *Metagonia mariguitarensis* (González-Sponga) are described, based on semi-thin serial sections and SEM photographs, and several male genital and non-genital characters are measured and analysed statistically. Left male genital bulbs are significantly larger than right bulbs while right palpal tibiae are significantly stronger than left tibiae, suggesting a functional segregation into a more predominantly displaying right palp and a more predominantly sperm-transferring left palp. Despite several structural differences between right and left male palps, however, there is no indication of qualitative differences: both bulbs transfer sperm, and both palps are provided with the full set of muscles. The female internal genitalia are provided with an unpaired receptacle that is connected to the uterus externus by a wide and complicated duct and to the valve separating uterus externus from uterus internus by a short narrow duct. This resembles entelegyne genitalia, but the functional details remain unknown. The evolution of asymmetric genitalia is discussed in a wider framework, with the conclusion that the causes of asymmetry in spiders may be different from those in other arthropods such as insects and copepods.

Key words: genitalia, copulatory organs, directional asymmetry, Pholcidae, *Metagonia*

INTRODUCTION

Spiders are highly symmetric organisms. There is barely anything in spider morphology to be included in the long list of asymmetries ranging from protozoan cell structures to fiddler crab claws and mammalian hearts (Ludwig, 1932). An exception is fluctuating asymmetry, which is ubiquitous in bilaterally symmetric organisms and has also been studied in spiders (e.g. Huber, 1996; Uetz & Smith 1999). Other obvious exceptions include teratologies (e.g. Scioscia, 1995), males that obligatorily detach one palp during ontogeny (Knoflach & van Harten, 2000), asymmetries owing to regenerated limbs (Uetz *et al.*, 1996), internal asymmetries regarding locations of symmetric organs (Millot, 1931), or structures that are symmetric *per se* but that are wrinkled and folded to result in an asymmetric appearance (e.g. the scapes on the epigyna of certain araneid and pholcid spiders: Levi, 1973; Huber, 2003). All these cases are either genetic accidents or manipulations of a symmetric phenotype.

The only exceptions seem to occur in representatives of the pholcid genus *Metagonia*, in which the female

internal genitalia of several species are asymmetric. In most species studied with regard to this detail, these are cases of anti-symmetry, i.e. there is parity between right- and left-sided individuals (Huber, 1997). The only case of directional asymmetry occurs in *M. mariguitarensis*, where all of 48 females examined (herein) were same-sided. This species is also the only known spider with asymmetric male genitalia. This exceptional situation prompted González-Sponga (1998) to create a new genus with the telling name *Anomalaia*, but there is strong evidence for inclusion of the species in the large genus *Metagonia* Simon (Huber, 2000).

Metagonia mariguitarensis is very rare in collections. In a large revision of New World pholcid spiders (Huber, 2000), only four male and six female specimens were available, and González-Sponga's type series (four males, 12 females) in Caracas is not publicly accessible. However, preliminary measurements suggested that this species might offer the unique possibility to measure opposing selective forces acting on genitalia separately by comparing allometric values.

Allometric values of specific characters on indicators of body size have provided a wealth of data with implications on possible selective pressures acting on these characters. For example, structures used as weapons in male-male fights or as visual display characters in the context of

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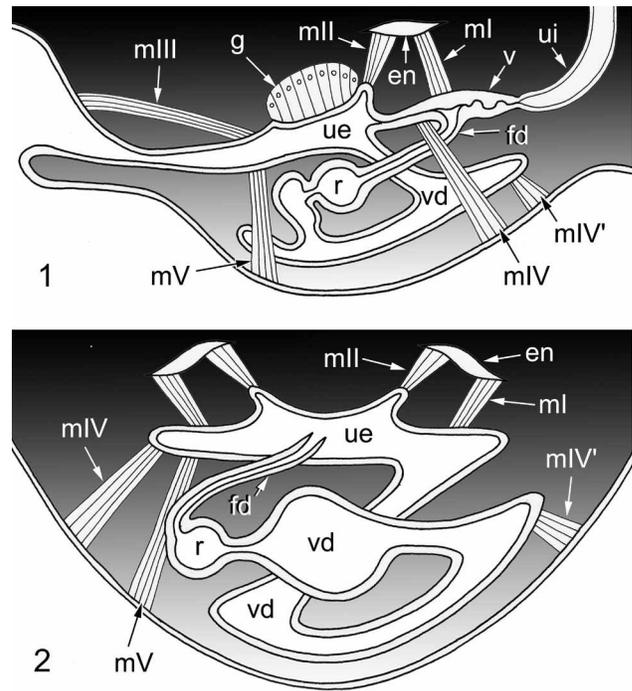
sexual selection tend to show high allometric values (often >1 ; Petrie, 1992; Green, 1992), while structures operating in the tactile channel tend to have lower slopes (Eberhard *et al.*, 1998; Tatsuta *et al.*, 2001). Genitalia thus tend to show low slopes, but this is a simplified picture for various reasons: (1) not all genital structures fit a corresponding structure in the opposite sex; (2) some structures on the genitalia may function in the context of visual display, as for example hair tufts in jumping spider palps, or be under selection for strength as has been suggested for enlarged male spider palps (Huber, 1999). This reflects the fact that there is no clear boundary between genitalia and non-genitalia, and that genitalia are multifunctional organs.

Preliminary measurements suggested that the right male palp of *M. mariguitarensis* may have assumed a more stimulatory function while the left palp may have taken over the sperm transfer function. The resulting prediction was that the right palp should be positively allometric, the left one negatively. This prediction was tested based on a series of 38 males and 39 females collected in Venezuela in 2002.

MATERIALS AND METHODS

The spiders were collected at the type locality, Marigüitar (10°26.5'N, 63°54.5'W), Estado Sucre, Venezuela, at about 30 m a.s.l., from the underside of banana leaves, on 29 November 2002 by the author. They are presently deposited at the Zoological Research Institute and Museum Alexander Koenig, Bonn, but will later be partly transferred to the Museo de La Salle, Caracas. Drawings were made with a camera lucida on a Leitz Dialux 20 compound microscope. For SEM photos, specimens were cleaned ultrasonically, dried in HMDS (Brown, 1993), and photographed with a Hitachi S-2460 scanning electron microscope. For histological sections, the objects were dehydrated, embedded in ERL-4206 epoxy resin after vacuum impregnation, serially sectioned with a Microm HM 350 rotation microtome (1 μ m) using a diamond knife, and stained with a mixture of azur II (1%) and methylene blue (1%) in an aqueous borax solution (1%) at 70°C for *c.* 20 s. Photographs were made with a Nikon Coolpix 950 digital camera (1600 x 1200 pixels) mounted on a Leitz Dialux 20 compound microscope.

Measurements were made with an ocular grid on a Nikon SMZ1500 dissecting microscope. Tibia length was measured dorsally; eye distance was defined as distance between outer margins of posterior lateral eyes; carapace width was measured at maximum width; for other measures see Figs 16-19. Statistical analysis was carried out with SPSS 11.0. Ordinary least squares (OLS) regressions of log-transformed characters were calculated for all traits on eye distance as an indicator of body size (for critique and justification of method see Green, 1999; Eberhard, Huber & Rodriguez, 1999). Eye distance was used rather than carapace width (the usual indicator of



Figs 1-2. Female copulatory organ in lateral and frontal views. en, endosternite; fd, 'fertilisation duct'; g, gland; mI-V, muscles I-V; r, receptacle; ue, uterus externus; ui, uterus internus (oviduct); v, valve; vd, ventral duct.

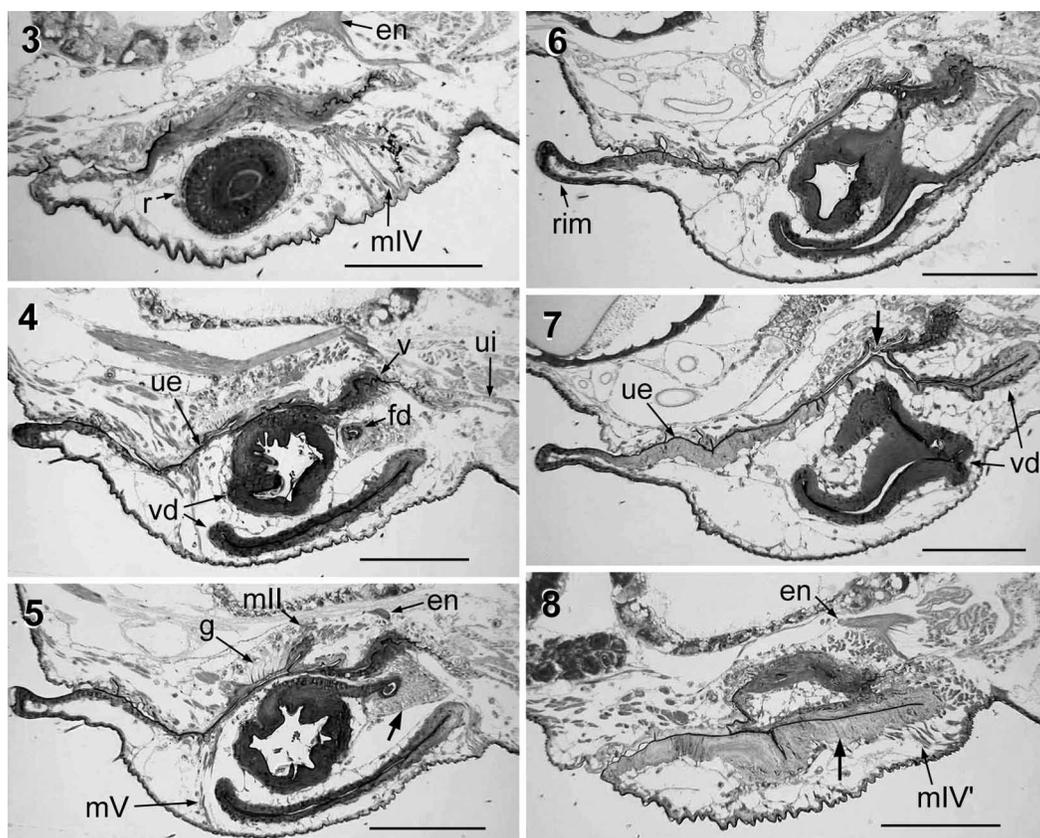
body size in spiders) because carapace borders seemed to be too soft and indistinct.

RESULTS

Female morphology

Externally, the female copulatory organ is a simple, bulging area of barely sclerotized, unpigmented, wrinkled cuticle. The only external structure visible in the dissecting microscope is a sclerotized rim at the posterior margin (Fig. 6). This rim is apparently perfectly symmetrical.

Internally, two basic components of the copulatory organ can be distinguished: the uterus externus, i.e. that part of the uterus that is lined by cuticle, and a complicated system of folds and ducts between uterus externus and ventral body wall (Figs 1 & 2). The uterus externus is slightly asymmetric, but otherwise built as in all pholcids studied: it bears a pair of dorsal pore plates through which glands excrete their products (Figs 1, 5 & 9) and a 'valve' that separates it from the uterus internus (Figs 1 & 4). Large numbers of sperm were present in the uterus externus in one of the two females sectioned. These sperm were embedded in a matrix (Figs 9 & 10) seemingly identical to that present in the male genital bulb (see below). The asymmetry of the uterus externus concerns primarily the cuticular lining: on the left side, very thick (but apparently not rigid) cuticle (Figs 8, arrow & 9) marks the entrance to the ventral system



Figs 3-8. Semi-thin sagittal sections of the female copulatory organ, from right to left. en, endosternite; fd, 'fertilisation duct'; g, gland; mI-V, muscles I-V; r, receptacle; ue, uterus externus; ui, uterus internus (oviduct); v, valve; vd, ventral duct. Arrows, glands connected to ventral duct (Fig. 5), connection between uterus externus and ventral duct (Fig. 7), and thick cuticular lining of uterus externus on left side (Fig. 8). Scale bars = 100 μ m.

of folds and ducts, while the right side is lined by the usual thin cuticle. Several muscles insert on the uterus externus and the valve (Figs 1-14): three pairs of dorsal muscles (mI-III) all of which are symmetrical (originating posteriorly from the body wall and dorsally from a pair of endosternites), and two ventral muscles both of which are asymmetrical (present only on the right side: mIV, mV).

The second basic component, the system of folds and ducts, can – for the purpose of description – be divided into three sections: (1) a duct leading from the uterus externus to the receptacle (Figs 1 & 2; vd); (2) the heavily sclerotized receptacle (Figs 1 & 2; r); (3) a narrow duct leading from the receptacle to the 'valve' separating uterus externus and uterus internus (Figs 1 & 2; fd). In both females sectioned, few sperm were found in section 1, but they were tightly packed in sections 2 and 3. In all three areas, sperm were not embedded in any visible matrix. Glands apparently open into section 3 (Fig. 5, arrow), but not into sections 1 and 2. Only one muscle inserts on this second component: frontally on the duct leading from the uterus externus to the receptacle (on the left side). The origin corresponds to muscle mIV, suggesting homology (therefore mIV').

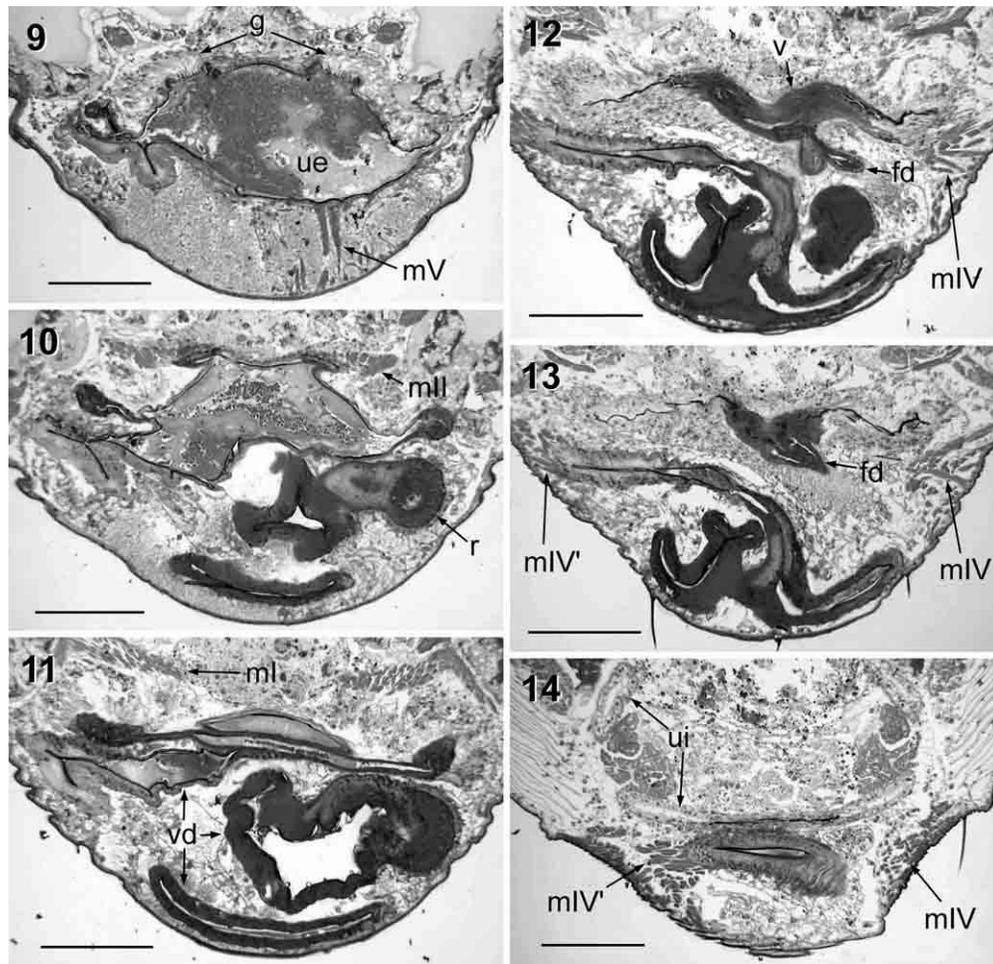
The uterus internus (oviduct) as well as the ovaries appear perfectly symmetrical.

Male morphology

In pholcids, the male chelicerae contact the female during copulation, which probably explains their modifications and diversity (Huber, 1999). In *M. mariguitarensis*, the male chelicerae bear a pair of lateral projections, a pair of frontal apophyses close to the fangs, and a number of modified (globular) hairs at the bases of the apophyses (Figs 18 & 19). There is no clear indication of asymmetry (see below).

All palpal segments with the exception of the coxa are asymmetric: the right trochanter is slightly larger but similar in shape (Figs 25 & 26); the right femur is longer and its entire proximal part is different in shape (Figs 25 & 26); the right patella is larger; the right tibia is strongly inflated (Fig. 16); the right procurus bears a much longer dorsal sclerite and a much longer hinged process with a weaker and simpler tip (Figs 20-24); the right bulb is smaller; the right embolus is much thinner and longer (Figs 27 & 28). Some of these characters were measured and are treated quantitatively below.

Internally, there is apparently no qualitative difference between left and right palps. Both tibiae contain the same sets of muscles (m25-28; terminology from Ruhland &



Figs 9-14. Semi-thin cross sections of the female copulatory organ, from posterior to frontal. en: endosternite, fd: 'fertilisation duct', g: gland, mI-V: muscles I-V, r: receptacle, ue: uterus externus, ui: uterus internus (oviduct), v: valve, vd: ventral duct. Scale bars = 100 μ m.

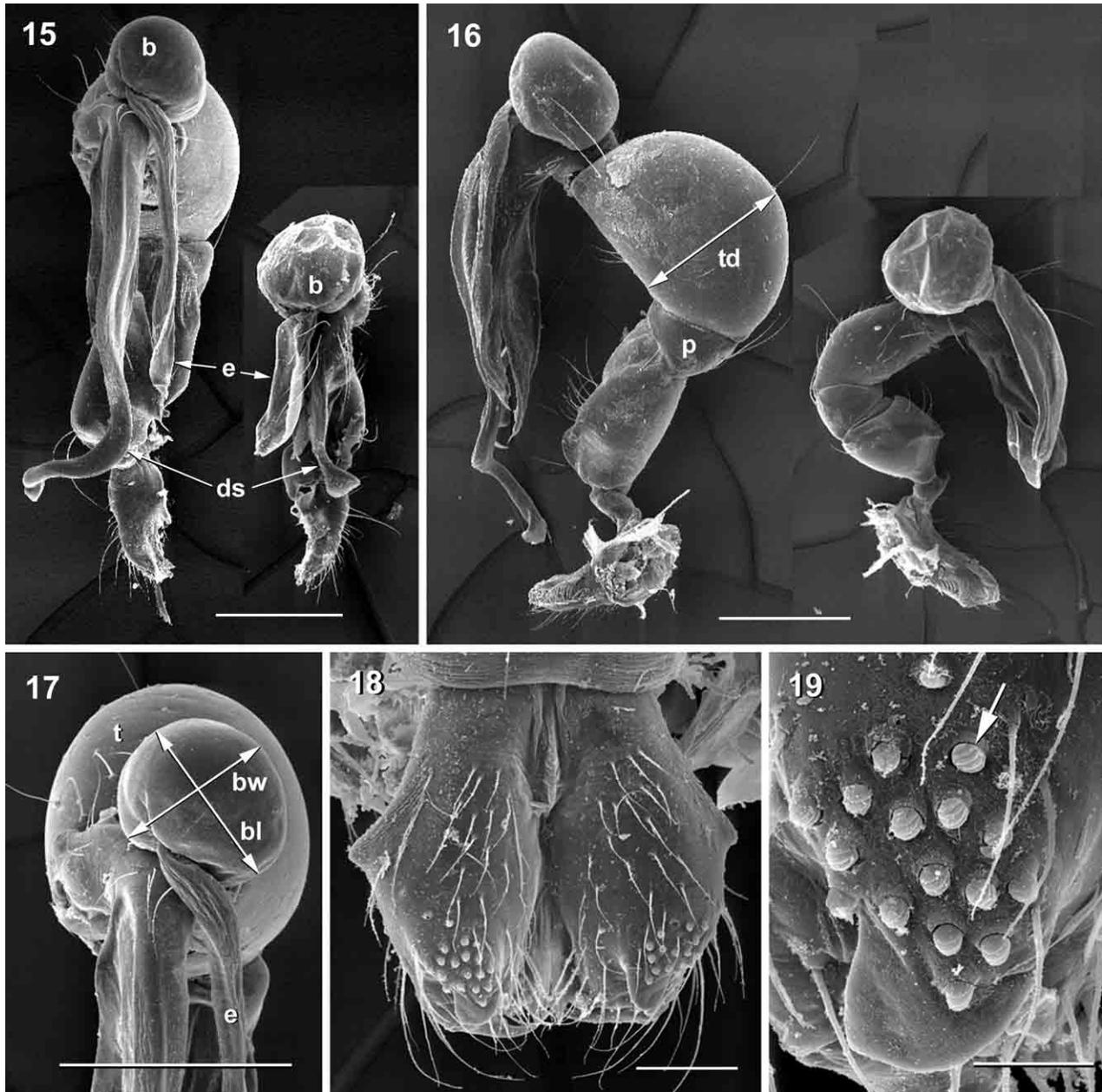
Rathmayer, 1978), with quantitative differences only; both bulbs are moved by the same two muscles: the m29 originating dorsally in the tibia (Fig. 30), and the m30 originating in the cymbium (Figs 29 & 32); both bulbs contain a mixture of sperm and matrix (Figs 34 & 35) similar to that found in the uterus externus of one female (see above). This mixture is also found in the embolus (Fig. 33), strongly suggesting that both components are actually transferred to the female. However, the right procurus contains a thick epithelium that might have glandular function (Fig. 32, arrow), but exit ducts could not be found. This epithelium was not found in two right palps sectioned.

Measurements

Table 1 gives sample sizes, ranges, means, standard deviations, coefficients of variation, significance values of Kolmogorov-Smirnov tests for normal distribution, estimates of measurement error, and slopes of OLS regressions.

The right palpal tibia ($b=0.87$) does not have an allometric value >1 , but almost the same value as the highest in the data set (tibia 1 length: $b=0.88$). This is in contrast to the left palpal tibia that has a much lower value ($b=0.58$). Measures of the bulb result in low values as is usual for genitalia, but slopes of the right bulb were not statistically significant.

Right bulbs were significantly smaller than left bulbs (both in 'length' and in 'width'; paired samples t -tests: $P<0.001$ for both measures), while right palpal tibiae were significantly larger than left palpal tibiae (paired samples t -test: $P<0.001$). No significant asymmetry occurred in the male chelicerae (paired samples t -test: $P=0.07$), and 15 of 38 specimens had identical numbers of modified hairs on both sides. However, the Kolmogorov-Smirnov test indicated that the distribution of the difference left minus right was not normal: there seemed to be a slight but significant trend for higher numbers of hairs on the left side. Walking leg asymmetry was minimal, i.e. only fluctuating (differences left minus right were normally distributed with means of -0.1 mm and 0.0 mm respectively).



Figs 15-19. SEM photos of the male pedipalps and chelicerae: **15** palps in dorsal view; **16** palps in prolateral view, showing the measure 'tibia diameter'; **17** right bulb in dorsal view, showing the bulbal measures; **18** chelicerae, frontal view; **19** modified hairs on left chelicera (one hair marked with arrow). b, bulb; bl, bulb length; bw, bulb width; ds, dorsal sclerite; e, embolus; p, patella; t, tibia; td, tibia diameter. Scale bars = 400 μm (15-17), 100 μm (18), 30 μm (19).

DISCUSSION

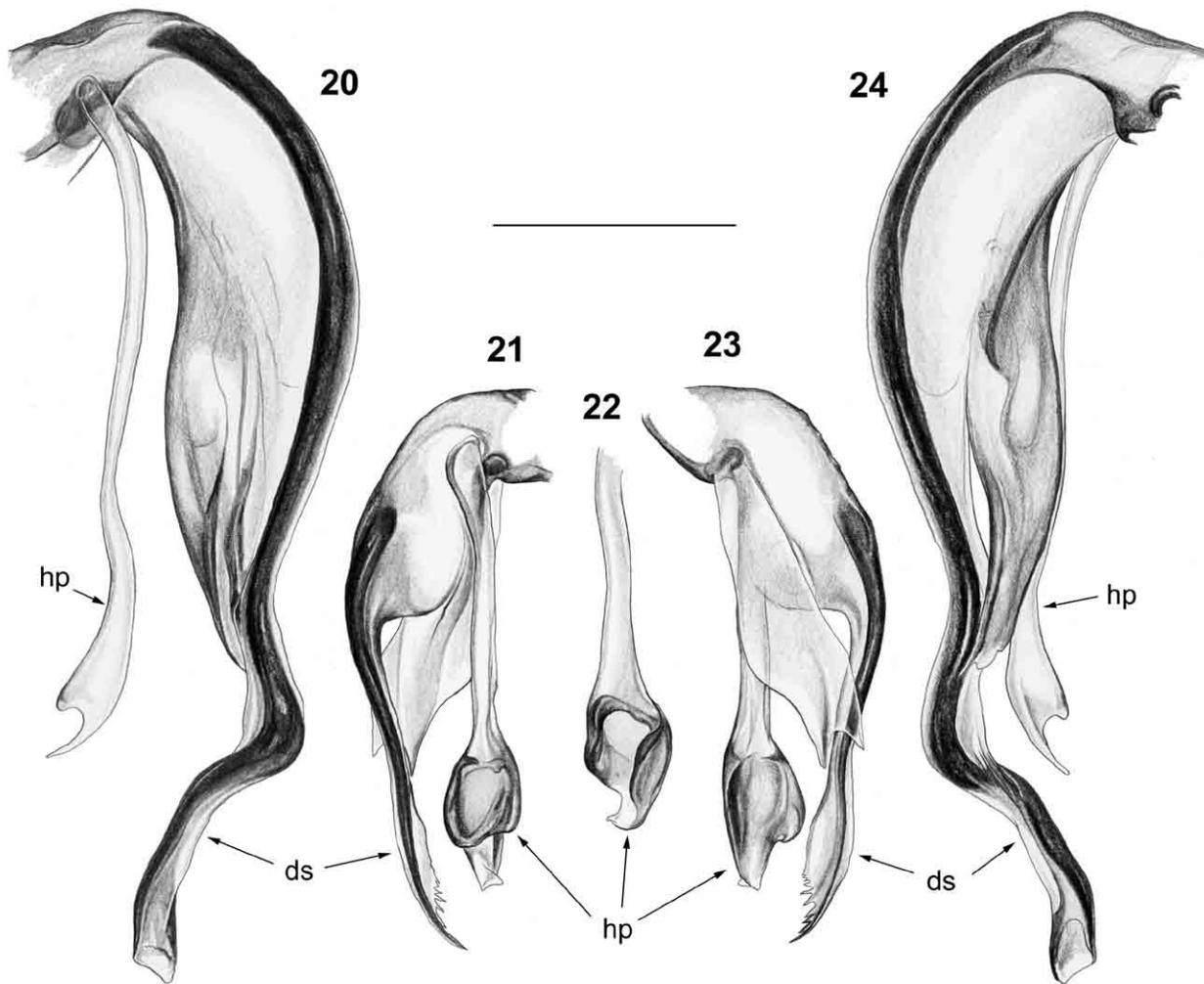
Morphometrics

The significant differences in genital bulb size and palpal tibia size indicate that there is indeed a tendency towards functional segregation between right and left male palps. However, both palps retain the ability to transfer sperm, and both palps retain the full set of palpal muscles. This may explain why the slopes are not as different as predicted. In particular, the right palp is not positively allometric as predicted for pure display structures. The

use of substituted measures (e.g., tibia diameter instead of cross sectional area) may make it difficult to interpret the slopes of allometric measures (Smith, 1980), but this is only true if shapes are different and cross sections of right and left palpal tibiae in *M. mariguitarensis* are both approximately round (as in Fig. 17).

Pseudoentelegyny

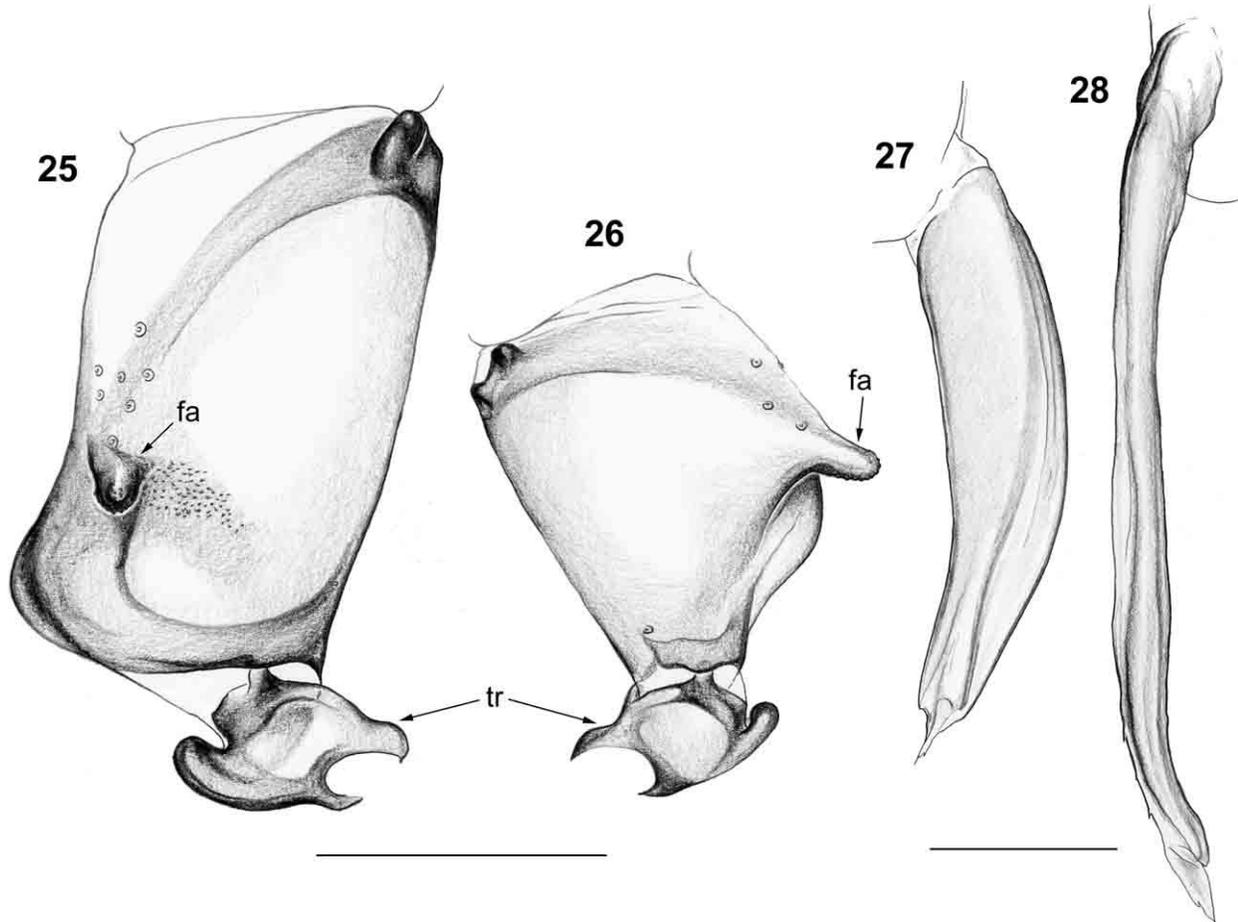
The term pseudoentelegyny was coined in a previous paper on *Metagonia* (Huber, 1997), and needs some



Figs 20-24. Illustrations of right and left tarsal processes (procursi) of the male pedipalps: right procurus, **20** prolateral and **24** retrolateral views; left procurus, **21** prolateral and **22** retrolateral views; **22** left hinged process in ventral view. ds, dorsal sclerite; hp, hinged process. Scale bar = 300 μ m.

Table 1. Male characters measured (mm), with sample sizes (*n*), ranges, means, standard deviations (SD), coefficients of variation (CV), significance values of Kolmogorov-Smirnov tests for normal distribution (KS), estimates on measurement error, and slopes of regressions on eye distance as an indicator of body size, using ordinary least squares (OLS) regression. As walking leg tibiae proved to be symmetrical, means of right and left sides are used in the regressions for tibia 1 and tibia 4 lengths. Means are also used for numbers of modified hairs on the chelicerae as asymmetry is minimal at best. Slopes significantly different from 0 are indicated by *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Characters	<i>n</i>	Range	Mean	SD	CV	KS	Measurement error (\pm mm)	OLS
Right tibia 1	30	4.03-4.97	4.50	0.24	5.3	0.84	0.05	0.88 ***
Left tibia 1	37	4.00-4.97	4.50	0.23	5.1	0.76	0.05	
Right tibia 4	38	2.30-2.87	2.63	0.13	4.9	0.78	0.03	0.74 ***
Left tibia 4	37	2.32-2.88	2.63	0.13	4.9	0.95	0.03	
Carapace width	37	0.68-0.83	0.75	0.036	4.8	0.71	0.01	0.41 *
Eye distance	38	0.43-0.52	0.48	0.019	4.0	0.86	0.01	-
Right palpal tibia	38	0.41-0.52	0.47	0.020	4.3	0.64	0.01	0.87 ***
Left palpal tibia	38	0.19-0.23	0.21	0.009	4.3	0.62	0.01	0.58 ***
Right bulb width	38	0.20-0.28	0.23	0.019	8.3	0.43	0.01	0.41 <i>n.s.</i>
Left bulb width	38	0.26-0.31	0.28	0.012	4.3	0.62	0.01	0.46 **
Right bulb length	38	0.26-0.31	0.28	0.013	4.6	0.95	0.01	0.35 <i>n.s.</i>
Left bulb length	38	0.31-0.33	0.32	0.007	2.2	0.03	0.01	0.26 *
Right chelicera hairs	38	12-20	15.47	1.87	12.1	0.26	0	0.61 <i>n.s.</i>
Left chelicera hairs	38	13-21	15.89	1.98	12.5	0.13	0	



Figs 25-28. Illustrations of right (25) and left (26) male palpal femora in prolateral views, and left (27) and right (28) emboli in prolatero-dorsal views. fa: femur apophysis, tr: trochanter. Scale bars = 200 μ m.

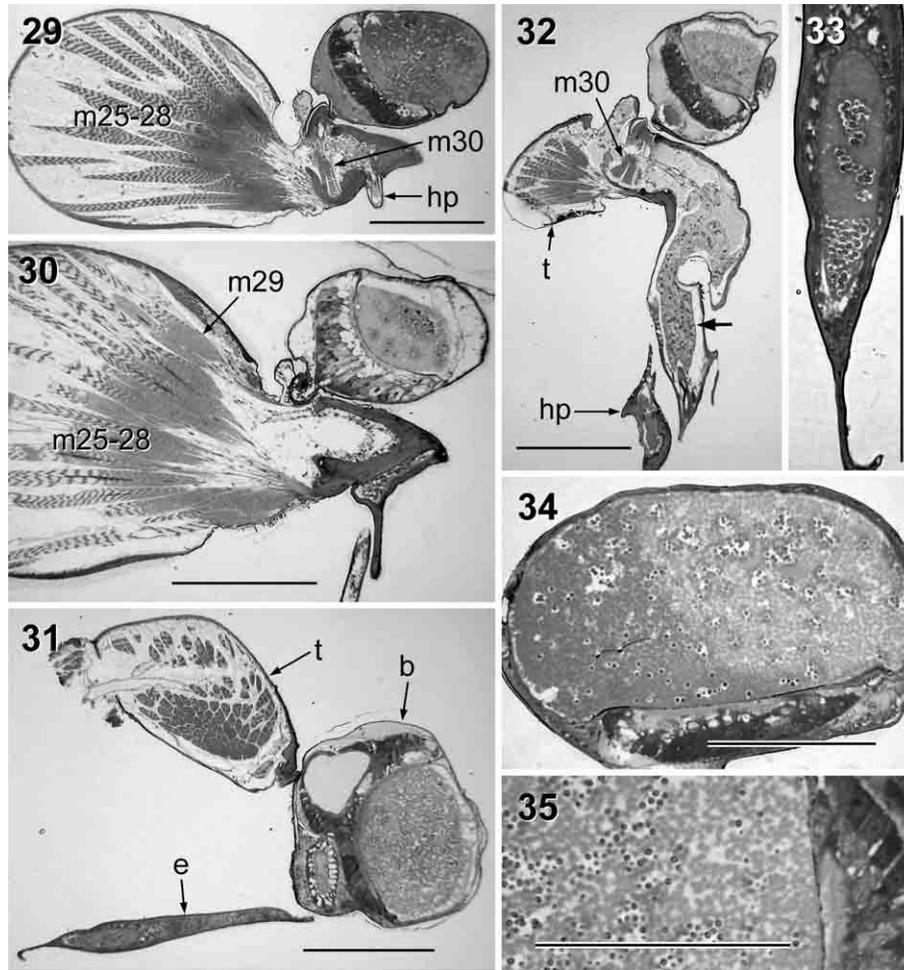
clarification. A structural similarity with 'true' entelegyne female spider genitalia is evident but not absolute by any means. True entelegyny implies (1) separation of ducts leading to and from the sperm storing organ, (2) paired arrangement of ducts and receptacles; (3) an external copulatory duct opening. In *M. mariguitarensis* and some other representatives of *Metagonia* (Huber, 1997), the first criterion is met, but not the second and third: the receptacle is unpaired, and the duct leading to the receptacle starts in the uterus externus, not visible from outside (Figs 1 & 7). Given the occurrence of the situation in only one clade of *Metagonia* and the unpaired nature of the system, there is no doubt that true entelegyny and pseudoentelegyny evolved independently.

A functional similarity with true entelegyny is not proven but plausible. The male deposits sperm with matrix in the uterus externus. It is not known how sperm gets separated from the matrix and into the receptacle. Two routes exist: via the duct between uterus externus and receptacle or via the duct between receptacle and valve. Only in the former case it would be justified to speak of an entelegyne condition. The way out of the receptacle is probably via the duct between receptacle and valve, as the other option would imply by far too much volume for the relatively low numbers of sperm.

Functional considerations

In all pholcids studied with regard to genital mechanics, the male procurus is inserted into the female uterus externus. If we assume this to be the case in *M. mariguitarensis* too, there are only two options for the large dorsal sclerite (Fig. 20) of the right male procurus: either the tip only is inserted, or it is inserted into the ventral duct leading to the receptacle. This seems probable because the symmetrical male chelicerae and female external genitalia strongly suggest that the copulatory position of the male towards the female is symmetrical as usual in pholcids. This position results in contralateral insertion, with the right palp being inserted into the left side of the female genitalia. The left side of the uterus externus is characterised by thick, light-staining cuticle (Fig. 9), which is also true for the first section of the duct leading to the receptacle. Thus, the right procurus might indeed be inserted at least into this first section of the ventral duct system.

This would be different from the only other *Metagonia* species studied with respect to genital mechanics: in *M. rica* Gertsch, no male structure is inserted into the duct leading to the receptacle (Huber, 1997). However, comparison with that species is difficult, because the



Figs 29-35. Semi-thin sagittal sections of male pedipalps: **29, 30** right tibia, tarsus, and bulb; **31, 32** left tibia, tarsus and bulb; **33** right embolus; **34** right bulb; **35** left bulb. b, bulb; e, embolus; hp, hinged process; m25-28, muscles moving the tarsus; m29-30, muscles moving the bulb; t, tibia. Scale bars = 200 μ m (29-32), 100 μ m (33-35).

hinged processes of *M. mariguitarensis* are clearly not capable of spreading open the female uterus externus, as is the case in *M. rica*.

Evolution of genital asymmetry

Compared with the considerable number of studies on fluctuating asymmetry accumulated over the last decade (see references in Lens *et al.*, 2002; Kruuk *et al.*, 2003), our understanding of the causes of directional and anti-symmetry has barely increased since Ludwig's (1932) comprehensive treatment. This is surprising as asymmetries are ubiquitous, and asymmetric genitalia in particular are a strikingly common phenomenon in many groups including platyhelminths, nematodes, cephalopods, insects, 'cyprinodont' fish and birds (Ludwig, 1932; Tuxen, 1970). Asymmetric genitalia evolved many times independently (e.g. at least four times in Heteroptera: R. Schuh, pers. comm., 'many' times in Diptera: McAlpine, 1981), but apart from scattered speculations, no recent attempt at a general explanation

is known to me. However, clarifying the causes of asymmetry might cast some light on the causes of spider symmetry.

Ludwig (1932) identified two major causes for asymmetric genitalia (Fig. 36): (1) female internal asymmetry owing to space constraints; (2) asymmetric copulatory positions. In the first scenario (apparently realized in cephalopods and birds), internal female asymmetry results in asymmetry of the female copulatory organ, and this in turn selects for asymmetric male genitalia. In the second scenario (presumably realized in nematodes, copepods, and insects), the female is symmetric but for some other reason an asymmetric copulatory position is taken, and this in turn selects for male asymmetry (see also McAlpine, 1981; Verma, 1994).

In *Metagonia*, the cephalopod/bird scenario is more probable: several close relatives of *M. mariguitarensis* as well as two other species groups identified by Huber (2000) have asymmetric female but symmetric male genitalia, suggesting that in this genus female asymmetry arose first; the symmetric male chelicerae of *M. mariguitarensis* suggest that the copulatory position

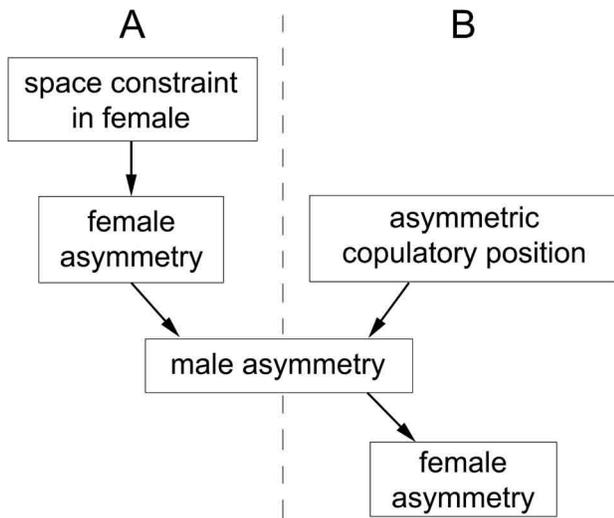


Fig. 36. Diagram showing the evolution of asymmetric copulatory organs, derived from data and discussions in Ludwig (1932): the scenario possibly realised in (a) some birds and cephalopods; (b) some insects, nematodes, and copepods; (a) is more probable for spiders (see text).

is symmetric in this species as in all pholcids. Even the ultimate cause may be the same as that suggested for cephalopods and birds: there is very little space between the uterus externus and the ventral body wall for a receptacle with ducts (Figs 3-8).

Why has male asymmetry not evolved more often in *Metagonia*? The answer may be because in all species except *M. mariguitarensis* there is parity between left- and right-sided females. When the chances of males encountering females of either morph are approximately equal, there is no selection for male asymmetry.

In this context it is important to note that many spiders do indeed assume an asymmetrical copulatory position but nevertheless retain their symmetric genitalia (Helvesen, 1976). However, there is a fundamental difference in this regard between spiders and insects: spiders shift from one side to the other (or, at least, have the option to copulate with either side). Taken together, the two asymmetric positions are symmetrical and there is consequently no selection for asymmetry.

Species limits

When redescribing *M. mariguitarensis*, specimens were available from northern Brazil (Roraima) and Peru (Loreto, Huánuco, Madre de Dios) (Huber, 2000). Despite some differences, all specimens were assigned to the same species because too few individuals were available to assess intrapopulation variability. Measurements of right palpal tibia diameter revealed little variation within the Mariguitar population (Table 1), and the single Roraima male falls into the range of these Venezuelan specimens (0.43 mm). However, the Peruvian male illustrated in Huber (2000: fig. 265) is far outside this range (0.68 mm),

suggesting that Peruvian specimens might represent a separate species. Clearly, more sampling is needed, especially in Peru and northern Brazil.

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