

Female genital dimorphism in a spider (Araneae: Pholcidae)

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Abstract

Discontinuous individual variation among members of the same sex, in the same life stage, within a population, is an important phenomenon for our understanding of more fundamental issues in evolutionary biology. One set of morphological characters is conspicuously rare in the literature on intrasexual polymorphisms: genitalia. In this paper we report the first case of a female genital polymorphism, the first not only for spiders but apparently for animals in general. We argue that the overwhelming use of genitalia in species identification practiced by many invertebrate taxonomists presents a strong bias against discovering polymorphisms in genitalia. Further methodological and practical aspects of invertebrate taxonomy are discussed that taken together make the discovery of genital polymorphisms very unlikely, no matter whether or not the phenomenon is rare.

Key words: spider, genital dimorphism

INTRODUCTION

Intrasexual polymorphism is defined as discontinuous individual variation among members of the same sex, in the same life stage, within a population. This kind of polymorphism is relatively common in certain groups of animals, such as pterygote insects, where winged and wingless morphs have different dispersal strategies (Roff, 1986). It may also be related to mimicry, such as in certain papilionid butterflies, where females of one species mimic several different distasteful models from other butterfly families (Goldschmidt, 1945; Clarke & Sheppard, 1969), or to alternative mating strategies, such as in certain horned beetles, where males with well-developed horns are better fighters, while males with poorly developed horns reduce direct competition by avoiding the 'majors' either in space or time (Eberhard, 1980). A well-known example from vertebrates is salmon species where large 'hooknose' males are specialized at fighting while small 'jacks' are specialized at sneaking (Gross, 1985).

Various authors have emphasized the importance of polymorphisms for our understanding of more fundamental issues in evolutionary biology (e.g., West-Eberhard, 1989; Eberhard & Gutiérrez, 1991; Mayr &

Ashlock, 1991). They bear on the role of developmental constraints on morphology (Gould, 1989), on the possible importance of polyphenisms in speciation and macroevolution (West-Eberhard, 1986, 1989), on the evolution of dispersal (Roff, 1986), on sexual selection theory (Emlen, 1994), and in certain cases have been said to suggest the existence of selective differences between apparently neutral characters (Mayr, 1963).

One set of morphological characters is conspicuously rare in the literature on intrasexual polymorphisms: genitalia. More than that, in studies on dimorphisms it is sometimes even stressed that the genitalia of the respective species are monomorphic (Müller, 1984; Maelfait, de Keer & Meester, 1990). Especially striking is the sciarid fly, *Plastosciera pernicioso*. In this species, 'essentially all' external morphological features were said to be dimorphic between macropterous and 'micropterous' (actually wingless) morphs of both males and females, with the remarkable exception of the genitalia (Steffan, 1973, 1975). Are genitalia really an exception?

In many animal groups, genitalia have evolved rapidly and divergently and are considered useful characters in species-level taxonomy (Eberhard, 1985). In some groups, such as in spiders, genitalia are used with an overwhelming priority in species identification. This approach seems justified both by the diversity of genital structures and the lower allometric values and coefficients of variation of genital vs non-genital structures (Eberhard *et al.*, 1998). However, as a result, taxono-

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mists are biased against discovering polymorphisms in genitalia. The only two cases in the literature known to us are the seasonal dimorphisms in cicadas of the genus *Euscelis*, where the male copulatory organs differ between spring and summer generations (e.g. Kunze, 1959); and the dimorphism in the thrips *Iotatubothrips kranzae*, where macropterous males have significantly longer genitalia than micropterous males (Mound, Crespi & Tucker, 1998); the polymorphism of the male hypopygium in the empideid fly *Microphor holosericus* (Meigen) (Ulrich, 1988); the polymorphism of the supposedly 'genetalic' sternites 8 of male *Scopula* and *Glossotrophia moths* (Hausmann, 1999). Other than that, Johnson (1995) reported dimorphic male genetalic styli in *Merope tuber* (Mecoptera), but here the term 'genetal' may be misleading. Nothing is known about the function of these structures, and it is possible that they are used as weapons in battles between males rather than in copulation (Eberhard *et al.*, 1998). The present paper reports the first instance of a female genital polymorphism.

The pholcid spider species where this phenomenon was discovered has just been described as *Ciboneya antraia* Huber & Pérez González, 2001, and belongs to a new genus endemic to Western Cuba. The spiders live in crevices in caves and flee rapidly when disturbed. Thus, we could collect only a relatively small sample of 27 females and 15 males, all on 1 day in a single cave (a few further individuals have been collected in other caves, but these are not included in the following analysis). Males showed the usual low degree of variation (coefficient of variation corrected for bias: $V^* = 2.3$ and 3.1 in two genital characters; 4.5 - 6.0 in

three non-genital characters; for detailed description of characters see Huber & Pérez González, 2001) and no indication of any dimorphism. Females varied strongly ($V^* = 13.6$ - 53.1 [!] in three genital, 11.3 and 13.2 in two non-genital characters), and came in two morphs (Fig. 1) that were easily distinguished even with naked eye in the field: 'macrogyne', which have the frontal part of the external genitalia (epigynum) stretched forward, reaching under the prosoma; and slightly smaller 'microgyne', which have the frontal part of the epigynum slightly bent backwards (Fig. 1). The epigyna are sclerotized, meaning that the two morphs are end products and cannot be converted into each other by simply bending the frontal part back and forth. Only one intermediate specimen could not be easily assigned to any of the two morphs ('i', Fig. 1). Both female morphs co-occurred in the same microhabitat. In the laboratory, microgyne and macrogyne mothers produced daughters of both morphs (Table 1), proving conspecificity. The sons ($n=16$; see Table 1) of these females (of the mothers) showed the same low degree of variation as above, and again, no sign of dimorphism in any trait.

The individual history of the specimens measured varied as follows: some were collected as adults and immediately preserved in ethanol (16 females: eight macrogyne, seven microgyne, one intermediate), others were collected as adults but preserved later (nine females: two macrogyne, seven microgyne; six males), and still others were collected as penultimate instars and killed after maturing in the laboratory (two females: one macrogyne, one microgyne; nine males). We do not consider it a problem to lump the data of all these specimens for several reasons: morphologically, indivi-

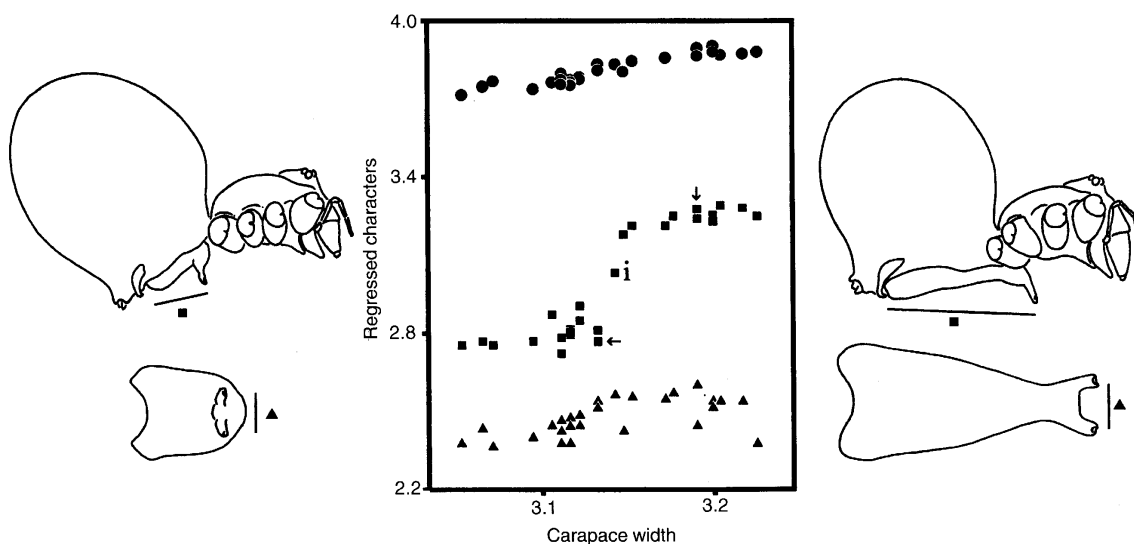


Fig. 1. Regressions of tibia 1 length (circles), epigynum length (squares) and distance between epigynal pockets (triangles) on carapace width (measurements in μm , \log_{10} transformed). The strong compression of the Y axis makes the top and bottom slopes almost horizontal and quite meaningless per se, but it emphasizes the difference to the sigmoidal relation between epigynum length and carapace width. "i" = intermediate morph; arrows point to illustrated individuals.

Table 1. Rearing experiment: six mothers, the morphs of their female offspring, and numbers of their male offspring. All daughters were clearly either macrogynes or microgynes; no intermediate morph was reared in the laboratory.

Mothers	Daughters (macrogynes/ microgynes)	Sons (monomorphic)
Macrogyne	4/6	14
Macrogyne	0/2	0
Microgyne	2/3	2
Microgynes (data pooled; $n=3$)	1/1	0

duals reared from the penultimate stage in the laboratory did not differ perceptibly from individuals collected as adults. This was even true for daughters reared in the laboratory from eggs: they were either perfect macrogynes or perfect microgynes (see below) and could not be distinguished from individuals of the respective morphs that had been collected as adults. (Note, however, that the F_1 generation was not included in the morphometric analyses).

Regressions of genital and non-genital body parts on prosoma width as an indicator of overall size (all data log transformed) showed that all male characters (two genital, two non-genital) and most female characters (two genital, one non-genital) showed the usual linear relationship between body parts (all characters illustrated in Huber & Pérez González, 2001). The only exception was epigynum length, which showed a remarkably distinct discontinuity (Fig. 1). As typical for dimorphisms, the curve of epigynum length was sigmoidal with a clear 'switch point'.

A number of open questions results from this finding. First, how common are genital polymorphisms? We have no evidence that they are anything more than rare curiosities, and acknowledge that the paradigm of genital usefulness in taxonomic recognition is not going to change until refuted by far more examples. However, the important point is that there is equally no evidence that they are not common. The fact that certain particular types of polymorphisms are widespread in entire families and orders (Mayr, 1963) invites a more thorough search at least in spiders. Several methodological and practical aspects of invertebrate taxonomy act together to make the discovery of genital polymorphism very unlikely: the dominant role of genital structures in species identification mentioned above; the frequent use of low sample sizes (often one specimen) for species description, resulting from the high frequencies of singletons and extremely low specimen numbers in museum collections; the absence of data on the reproductive biology of most invertebrates.

Second, what could be the proximate and ultimate explanations for this female genital polymorphism? Circumstantial evidence points to a conditional strategy, where environmental factors during ontogeny determine the morph of the adult spider: microgynes (defined by

the shape of their epigynum, not by their body size) are consistently smaller than macrogynes; most females reared in the laboratory (12 out of 19) became microgynes (irrespective of their mother's morph; see Table 1), presumably as a result of the unnatural rearing conditions (details of rearing in Huber & Pérez González, 2001); in the laboratory, microgynes produced significantly fewer eggs per egg-sac (7-13 in six microgynes vs 24 and 29 in two macrogynes).

However, explaining the different morphs in terms of different conditions during development does not answer the question about what microgynes gain by making their epigynum so short: there is no obvious difference in cost between developing the frontal part of the epigynum pointing forward like in macrogynes or backward. Most of the ultimate explanations for polymorphisms discussed in the literature (e.g. different dispersal strategies; alternative adaptations to seasonal environmental fluctuations; multiple mimicry; alternative resource acquisition) make little sense in the present case. The only reasonable hypothesis seems to invoke alternative mating strategies. The interesting implication of this hypothesis is that individuals of the dimorphic sex are predicted to compete for access to the other sex. This means, in the present case, that males should also constitute a valuable resource for females. The possible type of male investment forming the basis of this scenario is unknown. Obviously, what is needed next is a detailed study of the natural history of this species.

The final open question refers to the old lock-and-key idea of genital mechanics: how is this particular dimorphism related to the mechanics of copulation? The basics of copulation in pholcid spiders are well studied (reviews in Huber & Eberhard, 1997; Huber, 1999), and comparative data strongly suggest that a pair of apophyses on the male fangs (detailed illustrations in Huber & Pérez González, 2001) grasp the pockets at the tips of the fork *at the front* of the female epigynum while the distal parts of the pedipalps are inserted into the female internal genitalia *at the rear* of the epigynum. Thus, the dimorphic measure 'epigynum length' is not just an irrelevant aspect of the female genitalia, but one of seemingly crucial importance for the mechanics of copulation.

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