

# Cryptic Female Exaggeration: the Asymmetric Female Internal Genitalia of *Kaliana yuruani* (Araneae: Pholcidae)

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**ABSTRACT** Males of the Venezuelan pholcid spider *Kaliana yuruani* have unique genitalia, with the procursi about six times as long as usual in the family. The present article describes the previously unknown female, searching for a morphological correlate in the female genitalia to the male's exaggeration. Reconstruction of histological serial sections reveals an internal female complexity that is unequalled in pholcid spiders. An intricate system of ducts and folds is arranged in an asymmetric way, making this the third known case of genital asymmetry in spiders. The term "cryptic female exaggeration" is used in analogy to cryptic female choice, pointing to the fact that from the outside, the female genitalia do not appear unusual. I propose that cryptic female exaggeration may be relatively common in copulatory structures if male exaggerations need to be evaluated according to the female choice by mechanical fit model. Finally, the evolution of genital asymmetry in spiders is contrasted with that in insects. *J. Morphol.* 267:705–712, 2006. © 2006 Wiley-Liss, Inc.

**KEY WORDS:** exaggeration; cryptic female choice; sexual selection; Venezuela; *Kaliana*; Pholcidae

Even though the term "exaggerated", being a relative term, may be considered not particularly useful, exaggerations have played an important role in evolutionary biology ever since Charles Darwin. One of the key questions that Darwin (1871) tried to answer in his seminal book on sexual selection was how to explain exaggerated male sexual traits like the peacock tail, beetle horns, or elk antlers. Such exaggerations are common in males (e.g., Andersson, 1994; Emlen and Nijhout, 2000), and an evolutionary explanation poses no serious problems despite controversy regarding the details (e.g., Kokko and Johnstone, 2002; Kokko et al., 2003). Females of most species are generally thought to invest more in offspring than males, and females are thus under selection to choose among males (Trivers, 1972). Various heritable and nonheritable benefits of choice for the female have been proposed, like good genes, good parents, sexy sons, or fecundity advantages, food, parental care, and a good territory (Andersson, 1994). Male characters may thus become subject to directional selection and as a consequence become exaggerated. Exaggerated male characters have repeatedly been shown to involve

costs to the male (e.g., Reinhold et al., 1998; Gack and Peschke, 2004; Knell et al., 2004; Skroblin and Blows, 2005; further references in Emlen, 2001; Kotiaho, 2001), and costs may be an important factor in the diversification of sexual traits (Emlen, 2001).

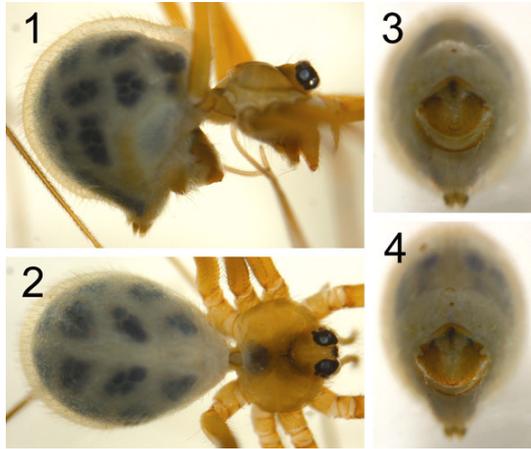
Female exaggeration is an apparently much rarer phenomenon. Partly this may result from the fact that sexual role reversals are relatively rare (cf. Bonduriansky, 2001). In some cases, female exaggeration is not related to sexual selection (e.g., in soldier ants with huge heads and mandibles); in others it apparently is. For example, exaggerated female sexual swellings in primates are thought to be correlated with sexual selection (Nunn, 1999). In spiders, female insemination ducts are often exaggerated, and this exaggeration has been attributed to female choice (Eberhard, 1996). In certain species of the New World pholcid genus *Mesabolivar*, females have exaggerated external genitalia suggesting substantial costs (Huber et al., 2005). In these species, female exaggeration is functionally correlated with extravagant male cheliceral morphology, and circumstantial data indicate that females may rather benefit indirectly by superior offspring (suggesting female choice) than directly by increased fecundity (which would suggest antagonistic coevolution) (Eberhard, 2004; Huber et al., 2005).

The pholcid spider *Kaliana yuruani* was previously known from only one male specimen (Huber, 2000). The most extraordinary traits in the male are the procursi, projections from the palpal tarsi that occur in all pholcid spiders. Usually, each procursus is about as long as the palpal femur, but in *K. yuruani* it is approximately six times as long (Figs. 29, 30). Since the procursi are inserted into the female

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Figs. 1-4. *Kaliana yuruani*, female habitus, lateral (1) and dorsal (2) views. Female abdomen, ventral (3) and anterior-ventral (4) views.

during copulation in all pholcid species studied so far (Huber, 1994, 1995, 1997, 1998, 2002; Uhl et al., 1995; Huber and Eberhard, 1997), the obvious question is whether there is a corresponding female exaggeration. The present article answers this question, giving a description of the female internal genitalia of *K. yuruani*, along with an interpretation of their exceedingly complex morphology.

## MATERIALS AND METHODS

Specimens of *Kaliana yuruani* Huber, 2000 were collected in Bolívar, Venezuela (see details below). Material studied is depos-

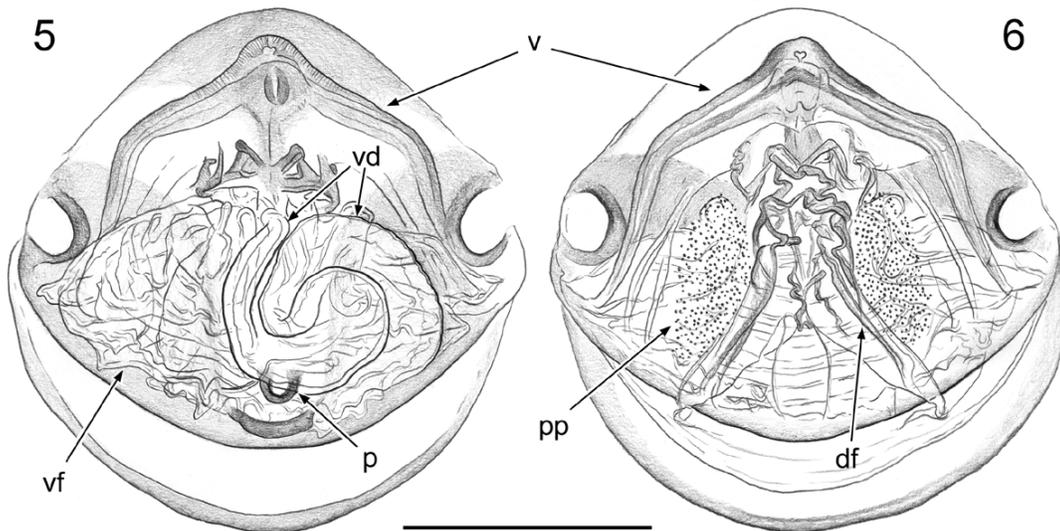
ited in the following institutions: Museo de Historia Natural La Salle, Caracas (MHNLS), Alexander Koenig Zoological Research Museum, Bonn (ZFMK).

Abdomens of three females were cleared in NaOH. The genitalia of one of these were stained with Chlorazol black and used for standard taxonomic drawings. These were done with a camera lucida on a Nikon Labophot-2 compound microscope. The other two abdomens were dried in HMDS (Brown, 1993), and studied with a Hitachi S-2460 scanning electron microscope. After taking photos from the outside, the cuticle covering the internal structures was peeled off with needles, the object was recoated, and photos were taken of internal structures. One female abdomen was embedded in ERL-4206 epoxy resin and serially sectioned with a diamond knife on a Microm HM 350 rotation microtome (sagittal sections, thickness: 1  $\mu$ m). Sections were stained with a mixture of azur II (1%) and methylene blue (1%) in an aqueous borax solution (1%) at  $\sim 70^{\circ}\text{C}$  for about 30 sec. All 104 sections were photographed with a Nikon Coolpix 995 digital camera (1600  $\times$  1200 pixels) using a Nikon Labophot-2 compound microscope, and reconstructed using the program Reconstruct (Fiala, 1996-2005).

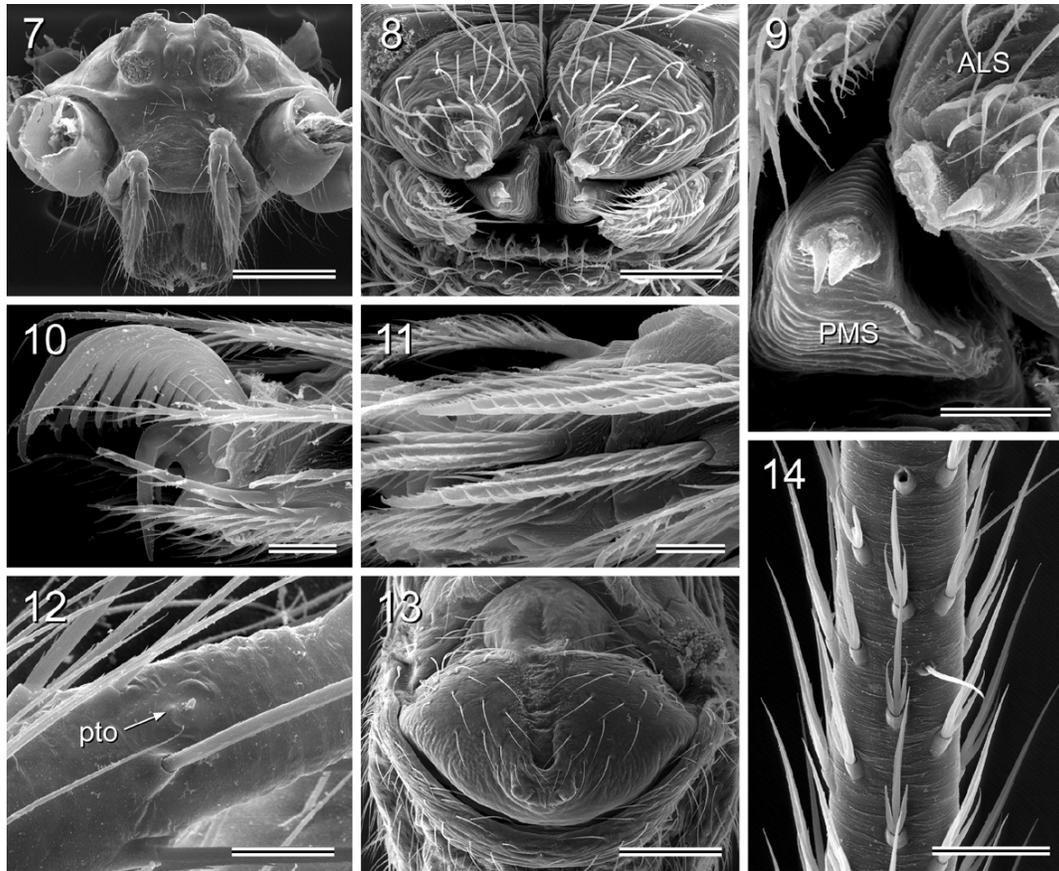
## RESULTS

### Female *Kaliana yuruani*

**Description.** Habitus is as in Figures 1 and 2. Total body length ranges from 2.0–2.3 mm, carapace width is 0.85 mm. Leg measurements of one specimen: leg 1: 15.5 mm (3.8 + 0.3 + 3.6 + 6.3 + 1.5), tibia 2: 2.2, tibia 3: 1.5, tibia 4: 2.3; tibia 1 in 6 other females: 3.5–4.6 (mean 4.2). Eyes are in similar arrangement as in the male (cf. fig. 1095 in Huber, 2000), but triads are closer together (PME-PME: 115  $\mu$ m, vs. 210  $\mu$ m in males) and the ocular area is less elevated (Figs. 1, 7). Clypeus and chelicerae are unmodified. The palpal tarsal organ is exposed (Fig. 12). Tarsus 1 claws are as in Figure 10. Prolateral trichobothrium is present on all tibiae. Tarsus 4 is provided with a patch of serrated hairs distally (Fig.



Figs. 5, 6. *Kaliana yuruani*, cleared female genitalia in ventral (5) and dorsal (6) views. df, dorsal folds; p, pocket; pp, pore plate; v, valve; vd, ventral duct; vf, ventral folds. Scale line: 0.3 mm.



Figs. 7–14. *Kaliana yuruani*, female. 7: Prosoma, frontal view. 8: Spinnerets. 9: Anterior lateral spinneret (ALS) and posterior median spinneret (PMS). 10: Tarsus 1 claws. 11: Serrated hairs on tarsus 4. 12: Palpal tarsal organ (pto). 13: Epigynum, ventral view. 14: Metatarsus 1 hairs. Scale lines: 10  $\mu\text{m}$  (10, 11), 20  $\mu\text{m}$  (9, 12), 40  $\mu\text{m}$  (14), 60  $\mu\text{m}$  (8), 200  $\mu\text{m}$  (13), 300  $\mu\text{m}$  (7).

11). All legs are densely covered with short hairs (Fig. 14). Spinnerets are as in Figures 8 and 9, with widened and pointed spigot on ALS and two pointed spigots on PMS. Epigynum is protruding (Fig. 1), with a distinct median pocket on the frontal sclerite (Fig. 13) and a narrower posterior sclerite (Figs. 3, 4). Cleared genitalia are as in Figures 5 and 6.

**Distribution.** *Kaliana yuruani* is now known from four localities in Bolívar state, Venezuela (type locality and three new localities below).

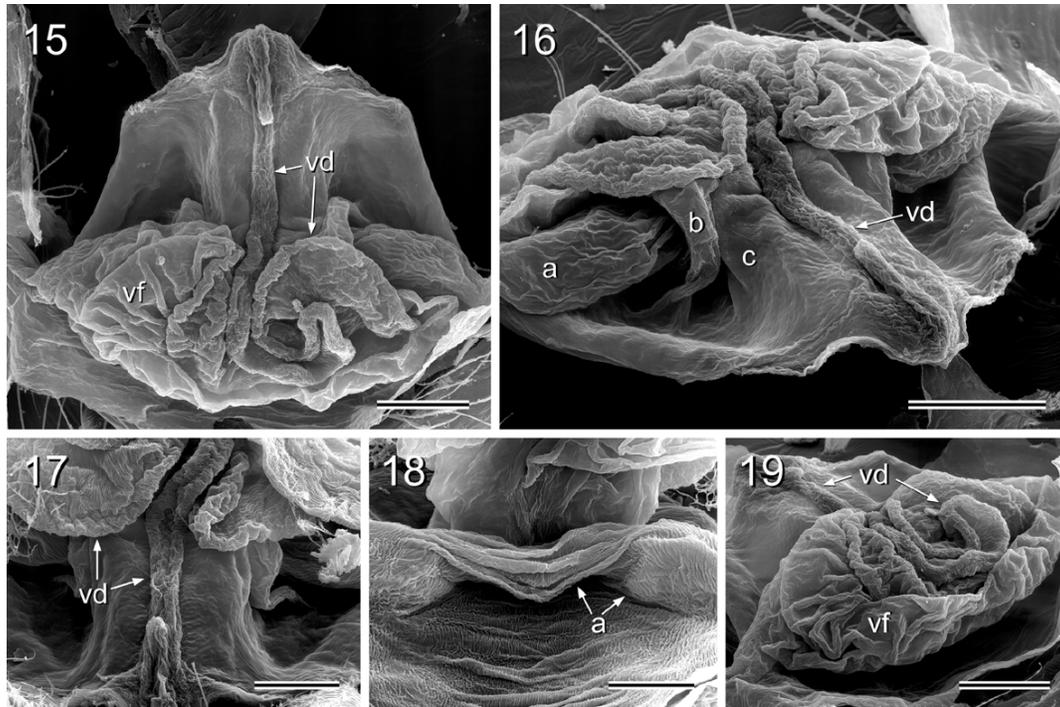
**New material examined.** Venezuela: *Bolívar*: at km 109 from El Dorado (6°01'N, 61°23.5'W), ~800 m above sea level (a.s.l.), under dead leaves on ground, 3.xii.2002 (B.A.Huber), 5♀, 5♂ subadult in 80% ethanol (1♀ in MHNLS, other material in ZFMK) and 2♀, 2♂ subadult, 6 juveniles in 100% ethanol (ZFMK); at km 102 from El Dorado (6° 04' N, 61°24' W), ~500 m a.s.l., under dead leaves on ground, 2.xii.2002 (B.A.Huber) 2♀, 1♂, 1♂ subadult (1♀ sectioned, 1♀ in MHNLS, males in ZFMK); for-

est near Pozo de la Felicidad (~5 km SE Canaima, 6° 11.5' N, 62° 47' W), ~450 m a.s.l., near ground, 6.xii.2002 (B.A.Huber) 1♀ (MHNLS).

### Female Internal Genitalia

For the purpose of description, the internal female genitalia of *Kaliana yuruani* can be divided into three components: the uterus externus, a complex system of cuticular folds ventral of the uterus externus, and a ventral duct connecting this system of folds with the anterior part of the uterus externus (Fig. 28).

**Uterus externus.** The morphology of the uterus externus is relatively simple, symmetric, and mostly in agreement with that of other pholcids (e.g., Uhl, 1994; Huber 1998, 2002). A slit-like posterior gonopore opens into a flattened space delimited by a dorsal and a ventral plate (Fig. 20). The dorsal plate



Figs. 15-19. *Kaliانا yuruani*, female internal genitalia (treated with NaOH), after removal of ventral cuticle. 15: Ventral view, showing asymmetry of ventral duct and ventral folds. 16: Oblique (ventral-anterior-left) view. 17: Ventral duct. 18: Rolled-up transversal fold (a) after lifting the overlying system of folds (only the lateral parts of this fold are visible in Fig. 16). 19: Oblique (ventral-posterior-right) view. a, b, c, ventral folds of uterus externus; vd, ventral duct; vf, ventral folds. Scale lines: 70  $\mu\text{m}$  (17, 18), 100  $\mu\text{m}$  (15, 16, 19).

carries the usual pair of glands that discharge into the uterus externus as well as some simple folds, some of which serve as muscle attachment sites (Figs. 20, 21). Frontally, a simple “valve” separates the uterus externus from the unsclerotized uterus internus (Fig. 23). All the unusual complexity arises from modifications of the ventral plate.

**Ventral cuticular folds.** Two independent systems of mostly membranous folds emanate from the uterus externus ventrally. The first is a symmetric transversal fold that is rolled up and whose thin cuticle is medially heavily pleated (‘a’ in Figs. 18, 22, 26, 28). The second is by far more complex. It originates from the uterus externus by two symmetric folds in tandem position (‘b’ and ‘c’ in Figs. 16, 22, 26, 28). These two folds merge and give rise posteriorly to an asymmetric system of heavily pleated folds with very thin cuticle. At about the position where folds ‘b’ and ‘c’ merge lies the origin of the third component, the ventral duct.

**Ventral duct.** This asymmetric duct leads from the ventral cuticular folds to the uterus externus in the area of the “valve” (‘vd’ in Figs. 16, 28). The cuticle of this duct is partly very thick, but the staining properties (light to dark blue, not green)

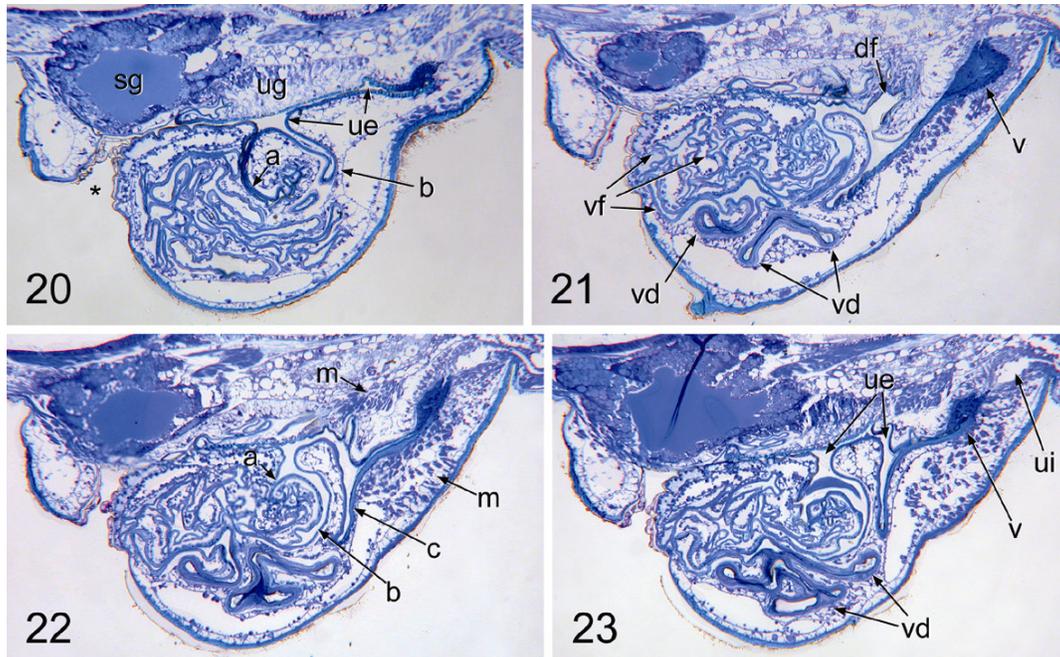
indicate that it is flexible rather than sclerotized. No glands or glandular pores were seen in the ventral cuticular folds and the ventral duct (sections and SEM images).

**Asymmetry.** The “handedness” of the female internal genitalia was clearly established in only four specimens (three cleared abdomens + sectioned abdomen). Taking the posterior part of the ventral duct as the most easily visible reference component (Fig. 5), these females were all “left-handed.” In untreated specimens, the asymmetry is not visible.

## DISCUSSION

### Cryptic Female Exaggeration

The term “cryptic female choice” was coined to account for the observation that females may exert choice among males in ways that are not easily discovered by traditional observation by researchers and that may be difficult to control by conspecific males (Thornhill, 1983). In analogy, the term “cryptic female exaggeration” is introduced here for female exaggeration that is not immediately apparent using traditional methodology. In the present case it refers to morphology, but in principle it might apply



Figs. 20-23. *Kaliana yuruani*, sagittal sections of female copulatory organ (anterior side on the right). 20: Section through right side. 21-23: Sections through left side. For position of sections, see also Figure 24. a, b, c, ventral folds of uterus externus; df, dorsal cuticular fold; m, muscles; sg, silk gland; ue, uterus externus; ug, uterus gland; ui, uterus internus; v, "valve"; vd, ventral duct; vf, ventral folds; asterisk marks entrance to uterus externus.

to exaggeration of other characters too, like chemical compounds, physiology, or behavior.

Costs of mate choice for females may involve expenditure of time and energy, an increase in an individual's vulnerability to predators, etc. (Pomiankowski, 1987; Milinski and Bakker, 1992; Kraak and Weissing, 1996; Gibson and Langen, 1996). Morphological costs of mate choice for females have to my knowledge barely been discussed previously (Huber et al., 2005). I suggest that this need not necessarily indicate that it is an exceptional phenomenon, but that it might be a consequence of the cryptic nature of female morphological exaggeration. Female choice based on morphology may be largely limited to copulatory organs ("female choice by mechanical fit," sensu Eberhard, 1985), and female copulatory organs are often to a large degree internal structures. As such, they are more difficult to study, but recent studies on spider internal genitalia have revealed an often unexpected complexity (e.g., Burger et al., 2003; Huber, 2004). To what extent such complexity and exaggeration is costly in the sense of having a negative influence on the possessor's fitness remains to be established (cf. Kotiaho, 2001).

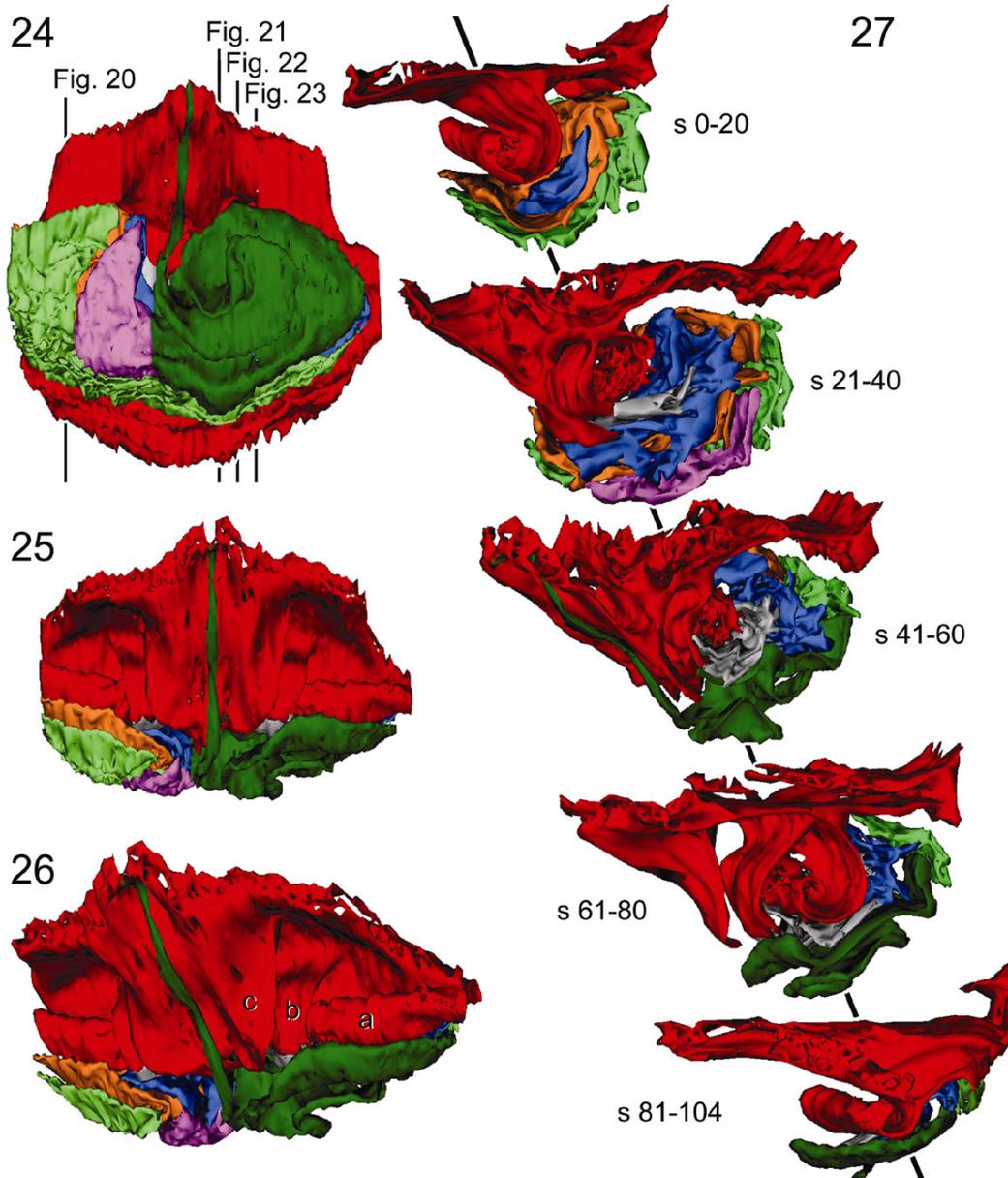
In conclusion, for methodological and maybe sociological reasons, there is still a relative neglect of

females in the context of sexual selection and genital evolution (Eberhard, 1985; Méndez and Córdoba-Aguilar, 2004). I predict that detailed investigations of species with exaggerated male genitalia will often reveal cryptic female exaggeration. In a context of female choice by mechanical fit, the need to evaluate male exaggerations may force females to evolve exaggerations themselves.

#### Asymmetry in Spider Genitalia

Asymmetry in spiders is extremely rare (Huber, 2004). Only two cases of genital asymmetry were previously known, in the pholcid genus *Metagonia* (Huber, 2004) and in the theridiid genus *Asygyna* (Agnarsson, 2006). In *Metagonia*, many species have antisymmetric female genitalia (Huber, 1997, 2000), and one species (*M. mariguitarensis*) has evolved directionally asymmetric female and male genitalia (Huber, 2004). In *Asygyna*, females are antisymmetric, males are symmetric (Agnarsson, 2006). *Kaliana yuruani* agrees with these two cases in having asymmetric female but symmetric male genitalia.

The situation in spiders contrasts sharply with that in insects. In insects, 1) asymmetric genitalia have evolved many dozens, maybe hundreds of



Figs. 24-27. Reconstructions of the internal spaces (as opposed to SEM images) of the internal female genitalia of *Kaliana yuruani* using Reconstruct (Fiala 1996-2005). 24: Ventral view, with sections shown in Figures 20-23 indicated by lines. 25: Frontal view. 26: Oblique (ventral-anterior-left) view (a, b, c, ventral folds of uterus externus). 27: Reassembled blocks of sections from left side (upper left) to right side (lower right), showing structures hidden in Figures 24-26 (s 0-20, sections 0-20; etc.). red, uterus externus with entire ventral fold a and beginning of ventral folds b and c; dark green, ventral duct; blue, gray, orange, light green, pink, ventral cuticular folds.

times (see e.g., Gielis, 1993; Hodges, 1998; Kaila, 2004; Sihvonen, 2005, on Lepidoptera; Hebsgaard et al., 2004 on Heteroptera; unpubl. data on other orders); 2) it is usually the males that are asym-

metric, leading to the conclusion that male asymmetry evolves before female asymmetry; 3) asymmetry usually occurs in the form of directional asymmetry. A plausible explanation for these fun-

damental differences rests on the different proximate factors that are likely responsible for asymmetry in the two groups. In insects, the most reasonable hypothesis assumes that directionally asymmetric copulatory positions have selected for asymmetric male (and sometimes female) genitalia (Ludwig, 1932). In spiders, copulatory positions are symmetrical or antisymmetrical (males change between two reversed image positions or use any of the two). Both in *Metagonia* and in *Kaliana*, space constraints seem to be the proximate factors selecting for asymmetry. In both genera, females have developed a complex system of ducts and folds in the limited space between uterus externus and ventral body wall (for *Metagonia*, see fig. 25 in Huber, 1997, and figs. 1, 2 in Huber, 2004). Exaggeration of these structures beyond a certain limit may only be possible at the expense of reducing one side and as a consequence becoming asymmetrical. In *Asygya*, this explanation may not fit, but serial sections have not been made and the internal situation is difficult to establish based on cleared preparations only.

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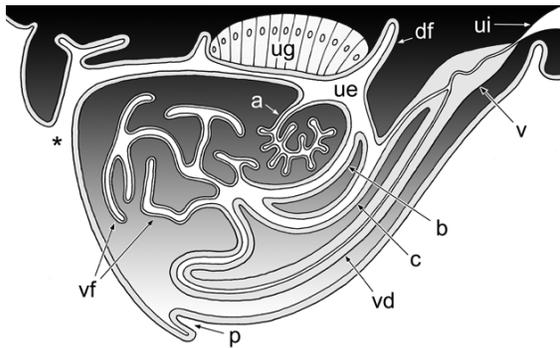
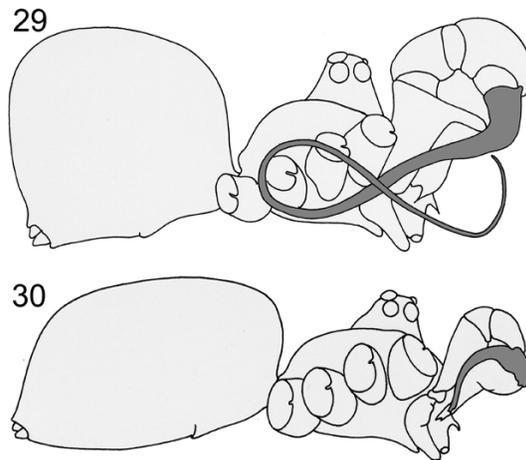


Fig. 28. Schematic representation of the female genitalia of *Kaliana yuruani*. Internal structures, especially the ventral system of folds, heavily simplified. a, b, c: ventral folds of uterus externus; df, dorsal cuticular fold; p, median pocket; ue, uterus externus; ug, uterus gland; ui, uterus internus; v, valve; vd, ventral duct; vf, ventral folds; asterisk marks entrance to uterus externus.



Figs. 29, 30. The exaggerated male genitalia of *Kaliana yuruani* (procursus dark gray) in comparison with the closely related *Mesabolivar cyaneomaculatus*. Legs omitted. Redrawn from Huber (2000).

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