Description of the female of *Orsolobus pucara* Forster & Platnick 1985, with comments on the functional morphology of the female genitalia in Dysderoidea (Araneae: Dysderoidea: Orsolobidae)

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Abstract.   The female of *Orsolobus pucara* Forster & Platnick 1985 is described and its genitalia examined using the scanning electron microscope (SEM). A small phylogenetic matrix with female genital and sexual behavior characters was made with the aim to study the evolution of these characters in the superfamily Dysderoidea. This is the first time that the female genitalia of a species of the family Orsolobidae have been studied in detail with SEM. The anterior portion of the female genitalia is a sclerotized structure with gland ducts and sites for muscle attachments. The posterior portion has a membranous receptaculum and a sclerotized plate that serves as attachment for muscles. We discuss the probable function of genital characters in a phylogenetic context. The anterior sclerotized elements of the female genitalia of some Dysderidae, Orsolobidae and Oonopidae species and the anterior receptaculum in the Segestriidae seem to be homologous structures because of the presence of gland ducts and sperm. However, both of these characteristics are lost in some species of these families, the anterior portion of the female genitalia being transformed into a highly modified structure serving mainly as attachment for muscles implicated in sexual behavior mechanisms.

Keywords: Character evolution, complex genitalia, reproductive behavior, spiders, taxonomy

The family Orsolobidae Cooke is a group of haplogyne spiders with six eyes that can by distinguished by the presence of an elevated tarsal organ (Fig. 7D). These active hunting spiders are distributed in eastern and western Australia, New Zealand, South Africa, Argentina, Falkland Islands, Chile and Brazil (Forster & Platnick 1985; Griswold & Platnick 1987; Platnick & Brescovit 1994; Brescovit el al. 2004; Baehr 2009).

The Orsolobidae, together with the Dysderidae, Oonopidae and Segestriidae, are grouped in the haplogyne superfamily Dysderoidea by the occurrence of a second portion of the internal female genitalia associated with the posterior wall of the bursal cavity (Forster & Platnick 1985; Ramírez 2000). Although the female genitalia of many haplogyne spiders are simple, such as in the Filistatidae and Caponiidae, the genital structures of other families (among them the Orsolobidae and Oonopidae) appear rather complex (Burger & Kropf 2007). In some species the anterior section of the female genitalia (AFG henceforth) has a very complex organization. It has been proposed that the degree of complexity might involve mechanisms of cryptic female choice, sperm dumping, and genital organization similar to the entelegyne condition (Uhl 2000; Huber 2002; Burger et al. 2003, 2006; Huber et al. 2005; Burger 2007; Burger & Kropf 2007). The oonopid genus *Scaphiella* Simon 1891 is in fact functionally entelegyne, since they have separate copulatory and fertilization openings and ducts (see Burger 2009). The same condition occurs in the diverse genus *Escaphiella* Platnick & Dupérré 2009 (Platnick & Dupérré 2009).

Although Forster & Platnick (1985) illustrated the diversity of female genital structures in the Orsolobidae, the fine structure of this group is unknown, thus precluding more detailed functional hypotheses. Also, homologies are difficult to explore when comparing, for example, the simple genitalia of segestriid genera like *Segestria* Latreille 1804 or *Ariadna* Audouin 1826 with the complex configurations found in oonopids like *Antoonops* Fannes & Jocqué 2008 or *Opopaea*

fosuma Burger 2002 (probably to be transferred to another genus in the future). For details compare fig. 2b in Grismado 2008 with fig. 3 in Burger et al. 2003).

With this work we wish to provide the first SEM images of the female genitalia in the family. Also, we compare the morphology of the female genitalia of *O. pucara* with other species of Dysderoidea. We used published data about the functional mechanisms of the genitalia across the superfamily to infer similar patterns in *O. pucara* and the Orsolobidae in general, to detect possible homologies and to discuss the evolution of the female genital characters. Detailed images of the male palp are also presented, and other anatomical structures of the female are illustrated.

METHODS

Specimens are deposited in the collection of arachnids of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN-Ar, Cristina Scioscia).

The format of descriptions and morphologic terminology follows in general Forster & Platnick (1985). In describing the female genitalia, we used the criterion followed by Platnick et al. (1999) for naming structures situated anteriorly or posteriorly to the uterus externus. Abbreviations used for eyes and legs are standard in arachnology. Measurements are in millimeters. After dissection, the female genitalia were digested in hot KOH and mounted in temporary preparations with lactic acid. The male palp was cleared with clove oil. A camera lucida mounted on a compound microscope (Olympus BH–2) was used to make drawings. Photographs of preserved spiders were made with a digital camera (Nikon DXM1200) mounted on a stereoscopic microscope (Nikon SMZ 1500). The focal planes were combined with Helicon Focus 3.10.3 (online at http://helicon.com.ua/heliconfocus/). Scanning electron micrographs were taken under high vacuum with a FEI XL30 TMP after critical point drying and Au–Pd coating. A small phylogenetic matrix with genital and sexual behavioral

Table 1.—Terminal included in the phylogenetic analysis and the data source where the characters were constructed.

Family	Terminal	Data source
Caponiidae	*Nops* MacLeay 1839	Izquierdo & Labarque pers. obs.
Segestriidae	*Ariadna boesenbergi*	Grismado 2008; Izquierdo & Labarque pers. obs.
Dysderidae	*Dysdera erythrina*	Uhl, 2000
	Hapactea lepida (C.L. Koch 1838)	Burger & Kropf 2007
Orsolobidae	*Orsolobus pucara*	Forster & Platnick 1985; Izquierdo & Labarque pers. obs.
	Osornolobus Forster & Platnick 1985	Forster & Platnick 1985
Oonopidae	*Scaphiella hespera* Chamberlin 1924	Burger 2009
	Antoonops corbulo Fannes & Jocqué 2008	Fannes & Jocqué 2008
	Silhouettella loricatula (Roewer 1942)	Burger et al. 2006
	Opopaea fosuma	Burger et al. 2003
	Orchestina (sp.1)	Izquierdo & Labarque pers. obs.; Burger et al. 2010
	Orchestina (sp. 2)	Izquierdo & Labarque pers. obs.
	Grymeus	Burger 2010
	Lionneta	Burger 2010
	Myrmopopaea	Burger 2010

characters includes morphological and behavioral characters described in the literature and from our personal observations (Fig. 8). The terminals and sources are listed in Table 1. The phylogenetic tree was taken from the previous analyses of Platnick et al. (1991) and Ramírez (2000). The Oonopidae was considered monophyletic, but without any internal structure, except for two groups supported by potential evidence: the *Lionneta* Benoit 1979, *Grymeus* Harvey 1987 and *Myrmopopaea* Reimoser 1933 clade (see Burger 2010) and the genus *Orchestina* Simon 1882 (jumping oonopids). Characters were mapped on this tree using TNT (Goloboff et al. 2008). The aim of this small analysis is to explore the evolution of the female genitalia characters in the Dysderoidea; a full reanalysis of dysderoid relationships is beyond the scope of this contribution.

SYSTEMATICS

Orsolobus pucara Forster & Platnick 1985
(Figs. 1–7)

Female diagnosis.—Easily distinguished from other females of the genus by the shape of the median rod, bifurcated at the tip and with a flattened projection directed ventrally (Figs. 3 A, B).

Description.—(MACN-Ar 16120). Total length 3.47, carapace 1.40 wide, opisthosoma 1.80 wide. Leg length I: 6.49, II: 5.90, III: 4.93, IV: 6.44; palp length 2.08. Carapace pale orange with several setae in the surface (Fig. 1); legs and maxillary endites pale yellow, sternum and labium pale orange. Opisthosoma pale yellowish with many dots of pigment, visible by transparency through the cuticle (Figs. 1A–C). Spinnerets yellow. ALE and PLE contiguous, PME–ALE separation 0.08. Chelicerae length 1.02 with two teeth on promargin (contiguous) and two on retromargin (slightly separated) (Fig. 7A). Sternum 1.03 long, 0.87 wide, more widened between coxae 2 and 3, sternum with cuticular projections toward coxae (Fig. 1F). Spination: Leg III: Tibia p 0-1-0, r 0-1-0, v p1ap; metatarsus p 0-1-1, r 1ap (displaced to dorsal), v 2ap. Leg IV: Tibia r 1ap, v 2ap; metatarsus p 1-1-1, r 0-1-1, v p1-p1-2. Palp: Tarsus d p1, p 1, v 2ap. Tarsal organ with about ten cuticular lobes and two rounded receptors on

Leg I (Fig. 7D) and about ten cuticular lobes and one (maybe two) receptor on leg IV. Retroclaw and proclaw with fifteen teeth on both outer and inner margins (Fig. 7C). Trichobothrial socket with proximal hood at the same level as the cuticle and with the same sculpture (Fig. 7E). Distal hood very short and with same sculpture as cuticle. Base of the trichobothrial seta slightly swollen and with oblique rings (Fig. 7E). AFG heavily sclerotized, formed by only one anterior median plate (mp, Fig. 3A) with four basal spurs, two of them directed dorsally and two ventrally. Between them arises the anterior median rod (mr), which bears numerous gland ducts near its base (Figs. 3C, 4C, E). The tip of the median rod is bifurcated and has several scars corresponding to the places of muscles attachments (Fig. 4D). The median rod has a flattened projection directed ventrally that may also bear muscle insertions (Fig. 3B). Posterior part of the female genitalia (PFG) with a membranous posterior receptaculum formed by a tube–like section that ends in a sack structure. Between them are two sclerotized plates (Fig. 3A, asterisk on Fig. 3B) that may act as supporting structures for the receptaculum or as attachments for muscles that control the aperture of these structures. External surface of the sack structure with many gland ducts formed by short bases (BS) and distal piriform caps (DC) (Fig. 5A). The gland ducts are sparsely distributed or grouped in two or three on the receptaculum surface and communicate into the lumen through simple pores (Figs. 5A, B). There is a "posterior plate" (pp, Figs. 3A, 4A) in close connection with the AFG. The posterior plate has a convex shape in the median line and extends toward both sides, acquiring a flattened shape (fa, "flattened lateral apodemes", Fig. 4B). The position of the uterus externus has been unknown until now. We found that it is located between the anterior median plate of the AFG and the posterior plate of the PFG (Figs. 3A, B, 4B).

Variability.—We have examined the female genitalia of two additional females from Neuquén and Rio Negro provinces (Argentina), one of them collected together with two males. The tip of the median rod and the size of the gland region differ in both specimens, but the morphology of the other plates does not vary. However, relative positions of the plates may be slightly variable, making the immediate determination
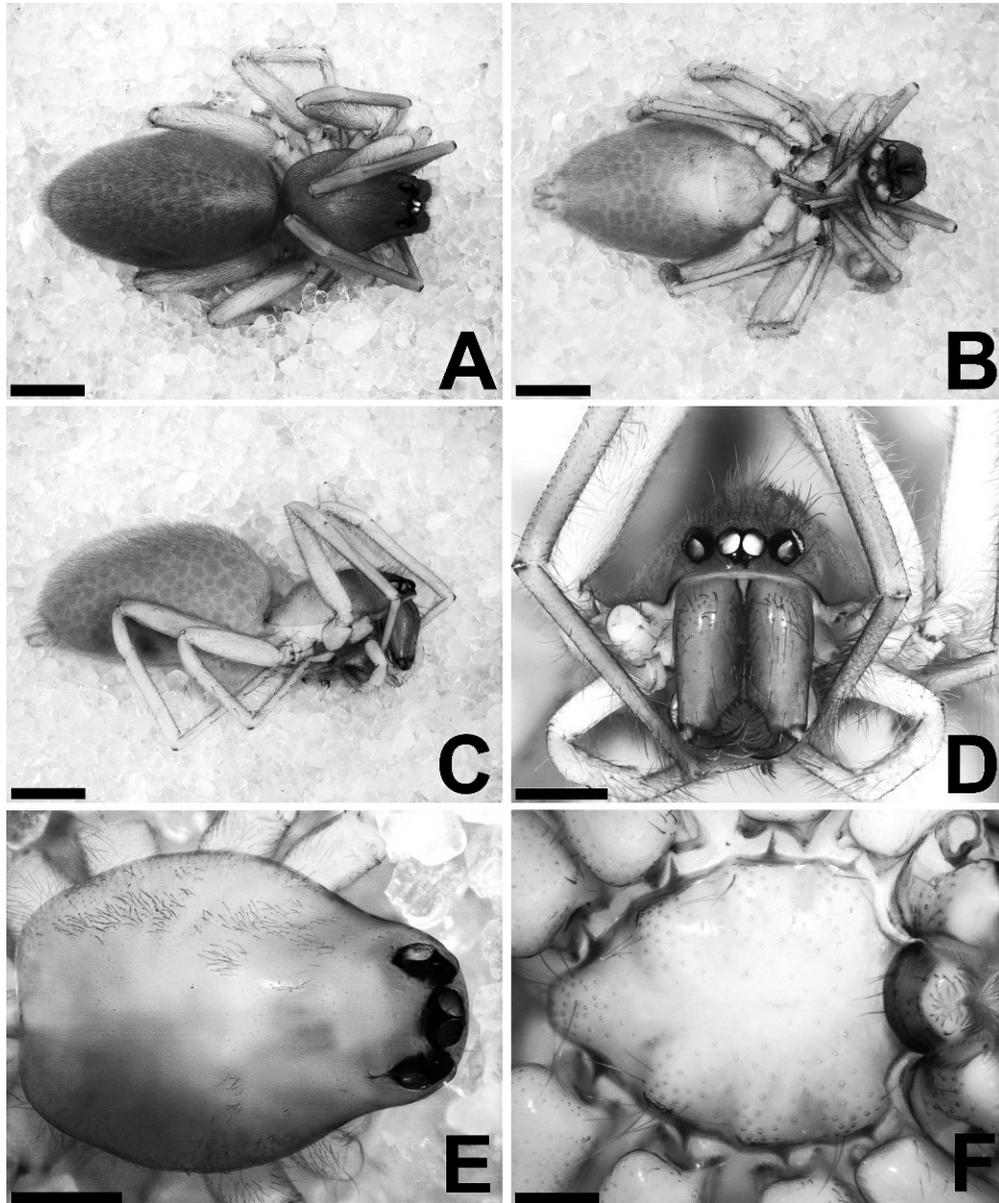
Figures 1 A–F.—*Orsolobus pucara* (MACN-Ar 16120). Female. A. Habitus dorsal; B. Habitus ventral; C. Habitus lateral; D. Eyes anterior; E. Dorsal shield of opisthosoma; F. Sternum. Scale bars: A–C = 1 mm, D, E = 0.5 mm, F = 0.25 mm.
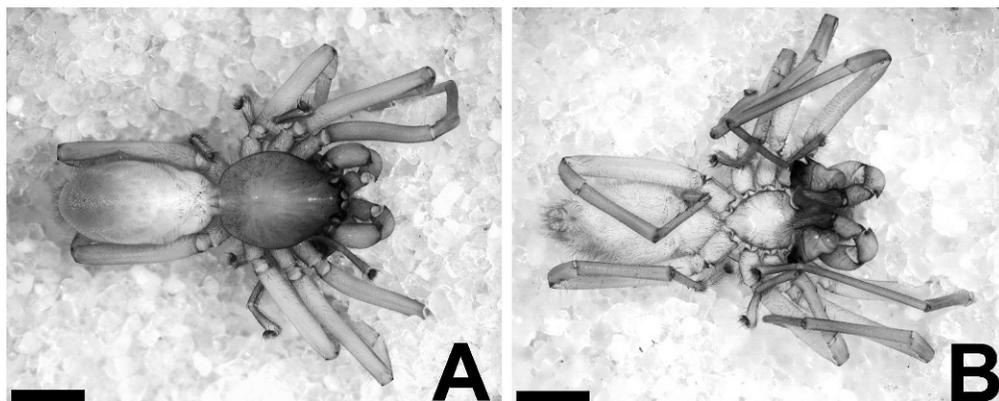
Figures 2 A, B.—*Orsolobus pucara* (MACN-Ar 16567). Male habitus. A. Dorsal; B. Ventral. Scale bars: 1 mm.
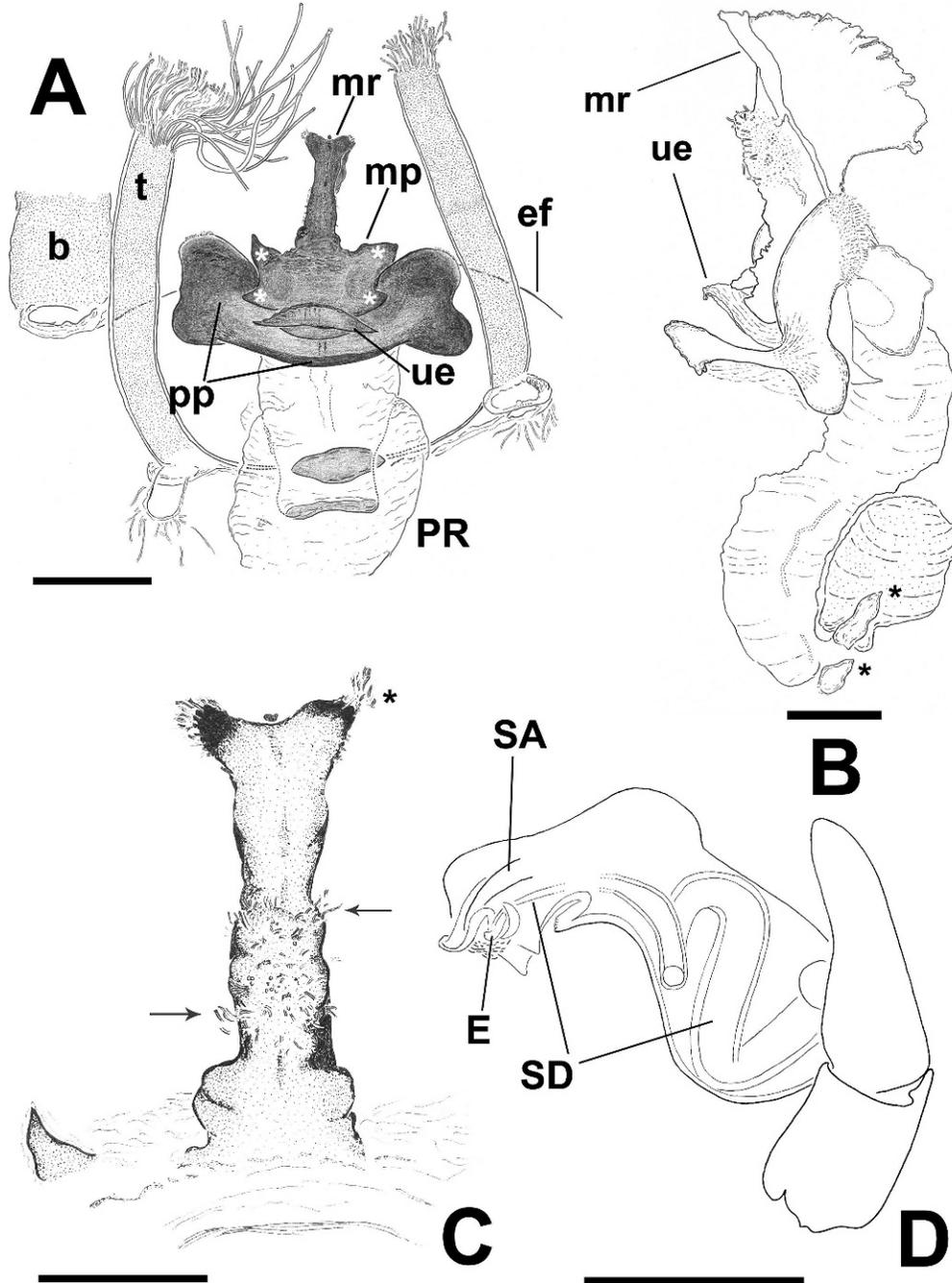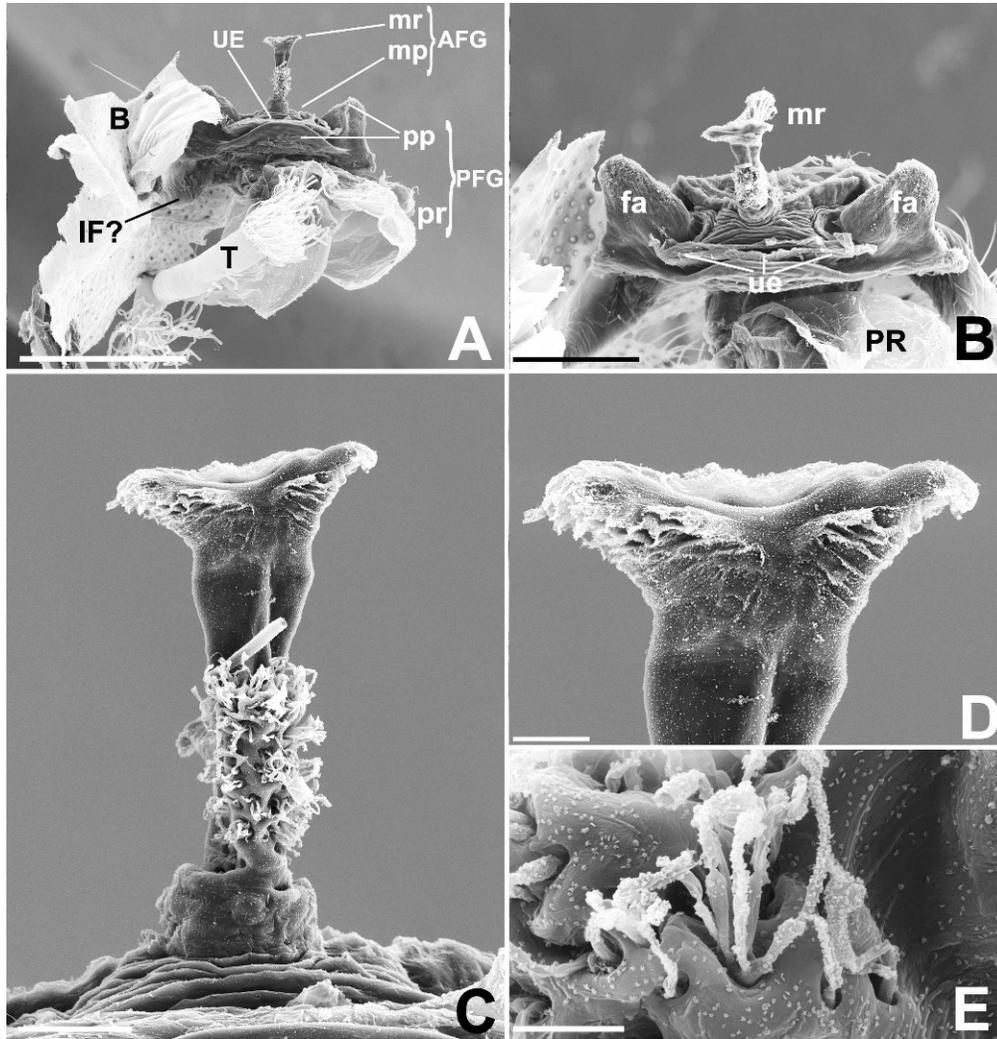
Figures 3 A–D.—*Orsolobus pucara* (MACN-Ar 10873). Genitalia. A–C. Female vulva. A. Dorsal view; B. Lateral view, asterisk on the two sclerotized plates; C. Anterior median rod, arrowheads to the gland ducts, asterisk on rest of digested muscles. D. Male palp, left prolateral view. Abbreviations: b = booklung, pp = posterior plate, E = embolus, ef = epigastric furrow, mp = median plate, mr = anterior median rod, PR = posterior receptaculum, SA = spine-shaped apophysis, SD = spermatic duct, t = tracheal trunk, ue = uterus externus. Scale bars: A = 0.25 mm, B, C = 0.1 mm, D = 0.5 mm.

of the species difficult. For correct determination, it is necessary to dissect and digest the genitalia and then observe the preparation from several points of view.

Male.—Described by Forster & Platnick (1985). We provide an additional description of the palp of one male (MACN-Ar 16567) collected together with several females. Internal course of the spermatic duct (SD) as in Fig. 3D. Embolus (E) short, with a wide aperture at the tip (Fig. 6B). The base of the embolus seems to originate from a fold of a striated laminar membrane (LM Figs. 6B, C). Spine-shaped apophysis (SA, Figs. 6B, C) close to the dorsal lobe (DL, Figs. 6C, D). Dorsal subterminal lobe spine-shaped, ventral subterminal lobe slightly flattened (DSL & VSL, Fig. 6A).

Other material examined.—ARGENTINA: *Neuquén Province*: Cerro Bayo, 1304 m, 40.74796°S, 71.59779°W, March 2005, V. Werenkraut, pitfall traps (cod. M3S5M05), 2 males

Figures 4 A–E.—*Orsolobus pucara* (MACN-Ar 10873). Internal female genitalia. A. Entire dorsal view; B. Anterior portion in anterior view; C. Anterior median rod; D. Tip of the median rod showing the points of muscle attachments and rest of digested muscles; E. Gland ducts on the base of the median rod. Abbreviations: AFG = anterior portion of the female genitalia, B = booklung, pp = posterior plate, EC = external cuticle, fa = flattened apodemes, IF? = interpulmonary fold?, mp = median plate, mr = median rod, PFG = posterior portion of female genitalia, PR = posterior receptaculum, T = tracheal trunk, ue = uterus externus. Scale bars: A = 0.5 mm, B = 0.2 mm, C = 0.05 mm, D = 0.01 mm, E = 0.01 mm.
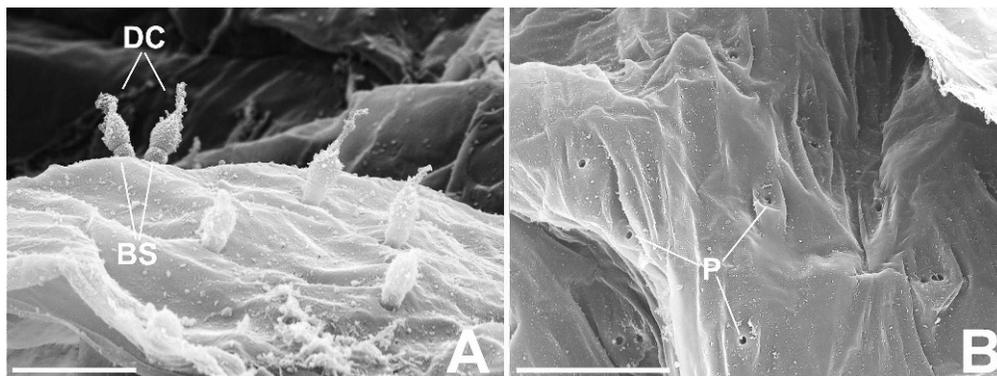
Figures 5 A, B.—*Orsolobus pucara* (MACN-Ar 10873). Posterior receptaculum. A. External surface showing the gland ducts; B. Internal surface showing the pores of the gland ducts. Abbreviations: BS = base of the gland duct, DC = distal cap of the gland duct, P = pores. Scale bars: 0.02 mm.
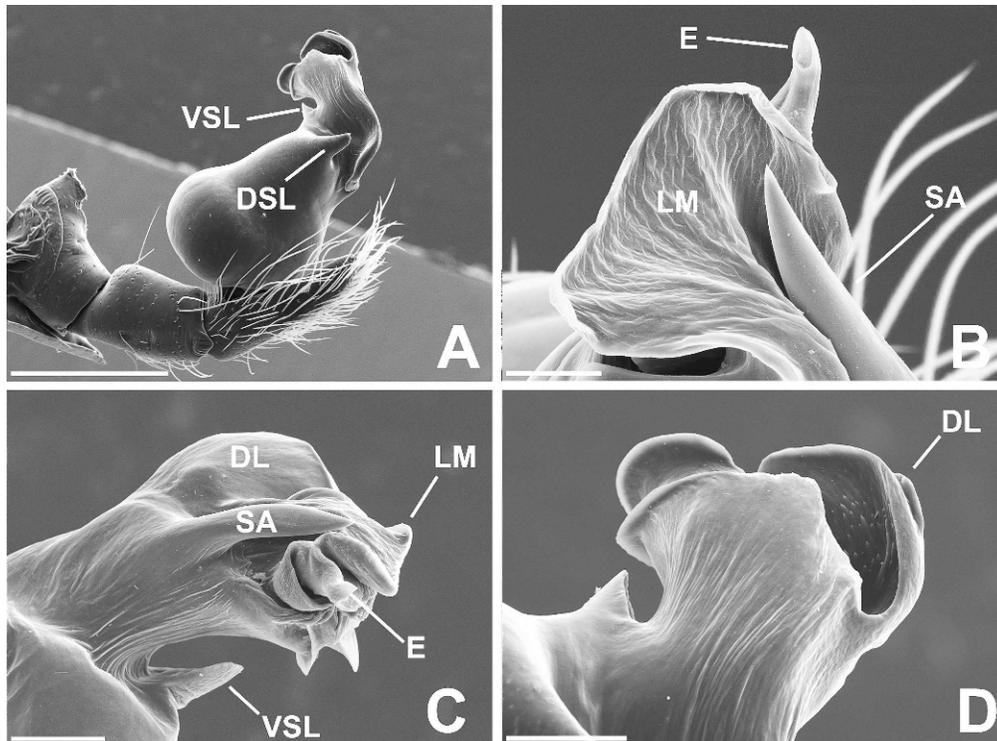
Figures 6 A–D.—*Orsolobus pucara* (MACN-Ar 16567). Left male palp. A. Retrolateral view; B. Tip of the copulatory bulb in dorsal-apical view; C. Ditto in prolateral view; D. Ditto retrolateral view. Abbreviations: DL = dorsal lobe, DSL = dorsal subterminal lobe, E = embolus, LM = laminar membrane, SA - spine-apophysis, VSL = ventral subterminal lobe. Scale bars: A = 0.5 mm, B = 0.05 mm, C, D = 0.1 mm.

(MACN-Ar 19559); same data January 2006 (cod. M3S5E06), 1 female (MACN-Ar 19560); *Rio Negro Province*: Cerro López, 1502m, 41.09948°S, 71.55801°W, March 2006, V. Werenkraut, pitfall traps (cod. M1S8M06), 1 female (MACN-Ar 19558). CHILE: *Región IX*, *Cautín Province*: Huerquehue National Park, Laguna Toro, in *Nothofagus* (Nothofagaceae)-*Araucaria* (Araucariaceae)-*Chusquea* (Poaceae) forest, 995m, 39°08′18.7″S, 71°42′30.9″W, 7 February 2005, M. Ramírez & F. Labarque, 1 female (MACN-Ar 16120), voucher codes ARAMR001025; same data 1 male and 2 immature (MACN-Ar 16568); 1 female (MACN-Ar 16570) voucher code ARAMR001026, preparation code MAI-137; 1 female (MACN-Ar 10873), voucher code ARAMR000999, preparation codes MAI-99, 124, 138–140; 1 male and 1 female (MACN-Ar 16567), male voucher code ARAMR000972, preparation codes MAI-58, 69, female voucher code ARAMR000971, preparation codes MAI-23, 63–68, 78; 1 male (MACN-Ar 16571), voucher code ARAMR001021, preparation code MAI-128; Villarica Natl. Park, sector Quetrupillén, in forest of *Araucaria*, *Nothofagus* and *Chusquea*, 1280m, 39°27′42.1″S, 71°50′44.2″W, 8 February 2005, 1 male and 3 immature (MACN-Ar 16569), M. Ramírez & F. Labarque.

Distribution.—Previously known from Argentina, Neuquén Province, here reported for Rio Negro Province and from Chile, Cautín Province (Región IX).

Natural history.—*Orsolobus pucara* was captured beating the vegetation in a *Nothofagus* and *Araucaria* forest, especially on *Chusquea* bamboos (Ramírez & Labarque pers. obs.) in Chile and with pitfall traps in Neuquén and Río Negro Provinces (Argentina).

DISCUSSION

Female genitalia, functional morphology.—The peculiar morphology of the anterior female genitalia appears to be adapted for muscle attachment. The places for muscle attachment seem to be restricted to the tip of the median rod and its ventral projections and to the flattened apodemes of the posterior plate. Forster & Platnick (1985) have noted that the lumen of the median rod of some species of Orsolobidae is sometimes heavily charged with sperm. The presence of different gland types in the anterior and posterior portions of the genitalia has been taken as indicative of two functionally different sites for sperm storage in the dysderid *Dysdera erythrina* (Walckenaer 1802) (Uhl 2000). These glands would produce secretions generating different conditions of sperm storage, although other secretions might be transferred by the male together with the spermatozoa (Burger & Kropf 2007). The presence of gland ducts in the anterior median rod of *Orsolobus pucara* suggests some storage function as well, and therefore a double function: attachment for muscles and sperm storage. Some of the muscles in the anterior portion of the female genitalia could be implicated in mechanisms of sexual selection, as occurs in other families. For example, the muscles M3, M4 and M7 can move some plates, which leads to the closing of the uterus externus in *Triaeris stenaspis* Simon 1891; whereas in *Brignolia recondita* (Chickering 1951) the muscle M3 seems to enable females to move a bulge close to
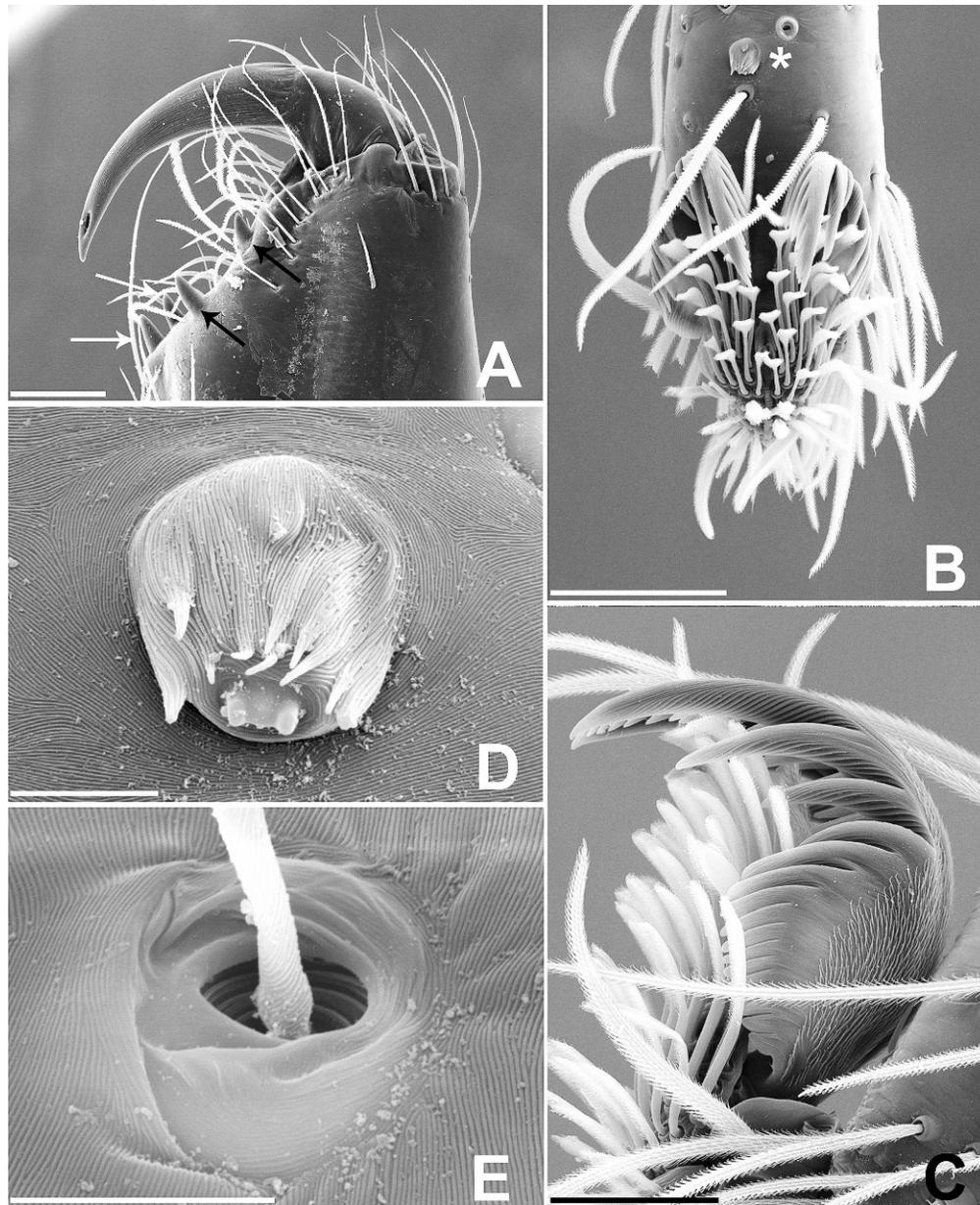
Figures 7 A–E.—*Orsolobus pucara* (MACN-Ar 16567). Female. Left chelicera. A. Posterior view, black arrowheads to the retromarginal teeth, white arrowheads to the promarginal teeth. B–E. Left leg I structures. B. Tarsal claws in dorsal-apical view, asterisk on the distal tarsal organ; C. Claws in retrolateral view; D. Tarsal organ; E. Metatarsal trichobothrial socket. Scale bars: A–C = 0.1 mm, D, E = 0.01 mm.

the genital opening, which may lead to the ejection of sperm (Burger 2009, under *Opopaea recondita*).

In species of the genera *Myrmopopaea*, *Grymeus* and *Lionneta*, the surface of the posterior receptaculum is pervaded with papillae that resemble those present in the genital structures of water mites (Burger 2010). Likewise, these papillae are present in the segestriid genus *Ariadna* (P. Michalik pers. comm.). Apparently, the papillae might have a function in osmoregulatory processes and could be involved in sperm activation (Burger 2010). However, the gland ducts on the posterior receptaculum of *Orsolobus pucara* are slightly different compared with these species, hence its involvement in

osmoregulatory processes is still unclear. Similar gland ducts have been observed in the oonopid *Unicorn catleyi* Platnick & Brescovit 1995 (M.A. Izquierdo pers. obs.).

Phylogenetic context.—If the female genitalia of all Dysderoidea are compared in an hypothetical evolutionary context with the hope of identifying homolog structures (Fig. 8), Segestriidae and almost all the Dysderidae fit well with the notion of a typical Dysderoidea (that is, well delimited anterior and posterior receptacles), while the Orsolobidae and Oonopidae have complex anterior female genitalia with bizarre sclerotized elements. However, it is still possible to find similar structures and infer common mechanisms. The median
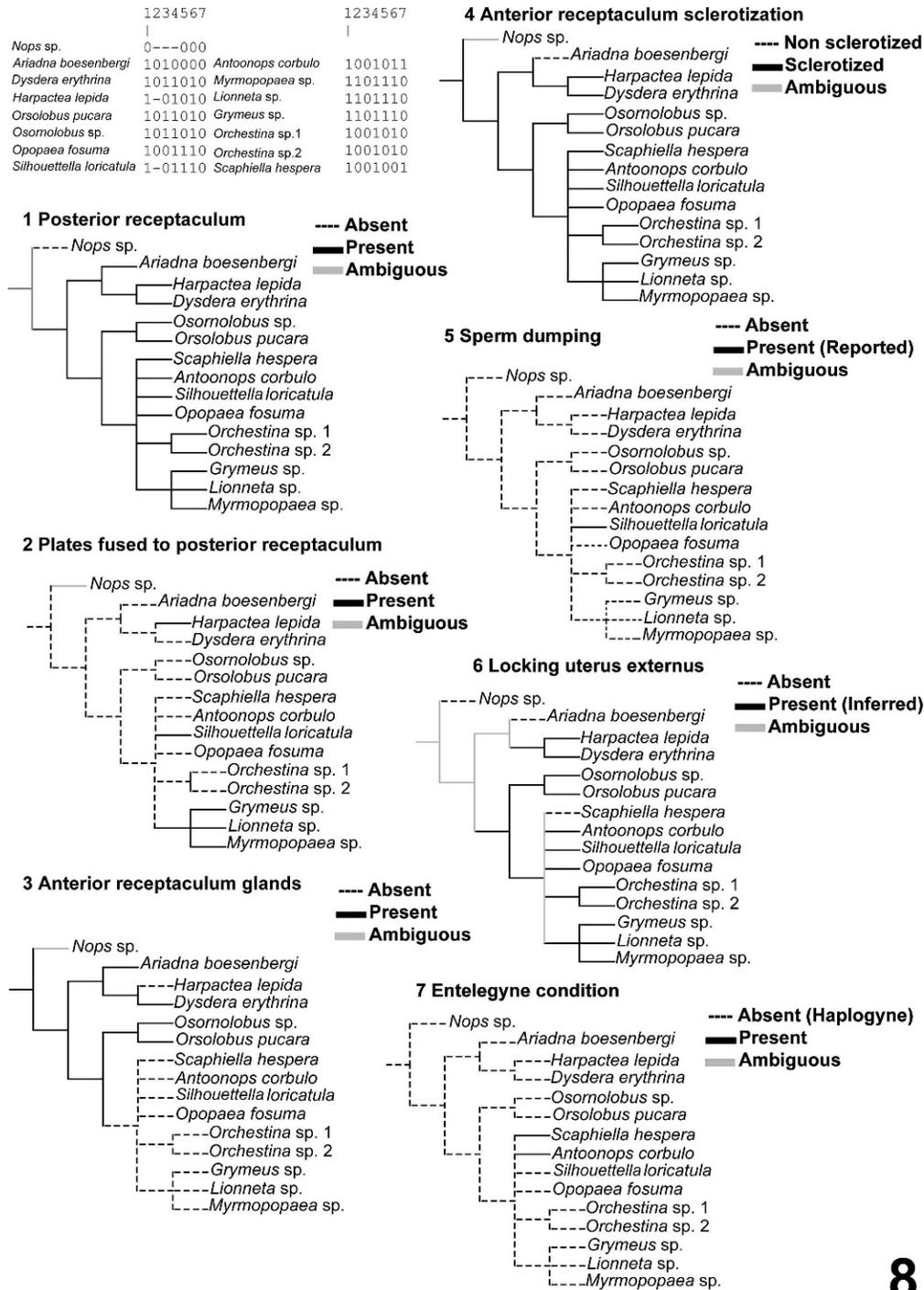
	1234567		1234567
Nops sp.	0---000		
Ariadna boesdenbergi	1010010	*Antoonops corbulo*	1001011
Dysdera erythrina	1011010	*Myrmopopaea* sp.	1101110
Harpactea lepida	1-01010	*Lionneta* sp.	1101110
Orsolobus pucara	1011010	*Grymeus* sp.	1101110
Osornolobus sp.	1011010	*Orchestina* sp.1	1001010
Opopaea fosuma	1001110	*Orchestina* sp.2	1001010
Silhouettella loricatula	1-01110	*Scaphiella hespera*	1001001

Figure 8.—Data matrix (upper left corner) and optimization for seven genital and sexual behavior characters.

rod and the lateral apodemes of the posterior plate in *Orsolobus* are very similar to other species of Dysderoidea (compare Fig. 3A with fig. 2 in Burger & Kropf 2007 and fig. 3 in Burger et al. 2006). The presence of gland ducts and sperm inside the anterior median rod suggests that these and similar structures in the Oonopidae and other Orsolobidae are homologous with the membranous anterior receptaculum found in Dysderidae and Segestriidae (see Grismado 2008

figs. 1A, 2A, 8H–O; Uhl 2000). As Forster and Platnick (1985) mention, there is a tendency for the storage function of the anterior genitalia to become reduced as the posterior receptaculum becomes larger. The absence of gland ducts in the oonopids analyzed here (Character 3, Fig. 8) and the sclerotization of the anterior receptaculum (Character 4, Fig. 8) seem to indicate a switch in the function of the anterior receptacle, from sperm storage to attachment of

muscles involved in copulatory and post-copulatory mechanisms. Gland ducts in the anterior female genitalia have recently been observed in undescribed oonopids from the molles spiny group (C.J. Grismado pers. comm.), *Heteroonops* Dalmas 1916 (N.I. Platnick & N. Dupérré pers. comm.), and in *Unicorn catleyi* (M.A. Izquierdo & Rubio unpubl. data).

All the Dysderoidea included in the matrix except *Ariadna boesenbergi* Keyserling 1877 and *Scaphiella hespera* Chamberlin 1924 have a mechanism of uterus externus locking (Character 6, Fig. 8) that would prevent the spermatozoa from getting into it during copulation (Burger et al. 2006). The locking mechanism is possible because of the combined presence of muscles and sclerotization of the anterior receptaculum (or part of it) and additional plates, both serving as attachments for those muscles. When the muscles contract, the plates contact each other and lock the uterus (for detailed morphology see Uhl 2000; Burger & Kropf 2007; Fannes & Jocqué 2008; Burger 2009, 2010; Burger et al. 2003, 2006, 2010). The absence of sclerotization in the female genitalia of the segestriid *Ariadna boesenbergi* suggests that this mechanism is not present in this species and probably in the whole family. The absence of locking mechanism in *Escaphiella hespera* is consistent with the development of a unidirectional sperm flux in the genitalia, a configuration typical for the Entelegynae (Character 7, Fig. 8). In *E. hespera* there are two ducts: one of them connects the copulatory opening with the posterior receptaculum and the other connects the posterior receptaculum with the uterus externus (Burger 2009). This configuration suggests that the locking mechanism of the uterus externus is not necessary in this species, since the males have no direct contact with this structure during copula. The locking mechanism has been reported for another group of gamasomorphine species (not analyzed here; see Burger et al. 2006), and it is probably present in the genus *Orchestina* as well (Burger et al. 2010; Izquierdo & Labarque pers. obs.).

Sperm dumping is a common means of cryptic female choice by which the females discard sperm from current or previous matings (Eberhard 1996). In Dysderoidea sperm dumping has been reported only in *Silhouettella loricatula* (Roewer 1942) (Burger 2007; Burger et al. 2006). However, this mechanism of cryptic female choice has been suggested for other gamasomorphine oonopids of the genera *Opopaea* and *Xyphinus* Simon 1893, *Gamasomorpha* Karsch 1881, *Grymeus*, *Lionneta* and *Myrmopopaea* (Burger et al. 2003; Burger 2010). This behavior seems possible only with the combined presence of sclerotized structures and muscles in the female genitalia.

ACKNOWLEDGMENTS

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