TESIS DE DOCTORADO EN CIENCIAS BIOLOGICAS

TITULO

Las arañas saltadoras del género *Orchestina* Simon en América: revisión y análisis filogenético mediante caracteres morfológicos y moleculares (Arachnida: Araneae, Oonopidae)

(Tomo II)

por

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DEFENSA ORAL Y PÚBLICA

Lugar y Fecha:

Calificación:

TRIBUNAL

Firma: ……………………………….. Aclaración: ………………………….

Firma: ……………………………….. Aclaración: ………………………….

Firma: ……………………………….. Aclaración: ………………………….

11 APÉNDICES

11.1 Apéndice

Lista de caracteres. Se indica entre paréntesis el número de carácter, con un signo + aquellos aditivos, con un asterisco (*) aquellos utilizados en el marco del proyecto PBI, con (#) aquellos utilizados por Henrard & Jocqué 2012 y con (!) caracteres nuevos propuestos en esta tesis.

Caracteres válidos para ambos sexos (0-29)

Textura del carapacho (0) (*)

0-liso

1-fuertemente reticulado

2-granulado

Patrón de coloración del carapacho (1) (*)

0-sin patrón

1-con un patrón reticulado

2-patrón tipo *Xiombarg*

Forma del carapacho en vista lateral (2) (! modificado del proyecto PBI)

0-con un declive suave hacia posterior

1-convexo

2-aplanado anteriormente, deprimido posteriormente

Fóvea torácica (3) (*)

0-ausente

1-presente

Setas marginales del carapacho (4) (*)

0-ausentes

1-presentes

PME (5) (!)

0-ausentes

1-presentes

PLE (6) (!)

0-ausente

1-presente

Fila posterior de ojos en vista dorsal (7) (*)

0-recta

1-recurva

2-procurva

Distancia entre los ALE (8)(+) (*)

0-separados por menos que su radio

1-separados entre su radio y diámetro

2-separados por más que su diámetro

Distancia entre los ALE y PLE (9) (+) (*)

0-en contacto

1-separados por menos que el radio de los ALE

2-separados entre el radio y el diámetro de los ALE

Surcos del esternón (10) (*)

0-sin surcos entre las coxas I-II, II-III, III-IV

1-con surcos entre las coxas I-II, II-III, III-IV

Triángulos precoxales (11) (*)

0-ausentes

1-presentes

Margen posterior del esternón (12) (*)

0-a nivel de las coxas IV

1-sobrepasando el margen posterior de las coxas IV

Espiráculos posteriores (13) (*)

0-conectados por un surco

1-no conectados

Posición del opistosoma-pedicelo (14) (*)

0-escudo no extendido más allá del pedicelo

1-escudo ausente pero opistosoma extendido más allá del pedicelo

2-escudo ausente pero abdomen no extendido más allá del pedicelo

Patrón de coloración del opistosoma (15) (!)

0-ausente

1-presente

Patrón de coloración del opistosoma (16) (*)

0-con un patrón reticulado y V invertida

1-con cheurones

2-con otro patrón de coloración

Artejo basal de las ALS (17) (!)

0-entero

1-atravesado por una diagonal membranosa

Forma del pedicelo (18) (*)

0-sin modificaciones

1-acanalado

2-con un anillo de setas

Anillo de setas largas alrededor de las hileras (19) (*)

0-ausentes

1-presentes

Colulo (20) (*)

0-ausente

1-presente

Forma del fémur IV (21) (*)

0-no engrosado

1-mucho más engrosado que en el resto de las patas

Uña inferior en pata IV (22) (*)

0-asuente

1-presente

Forma de la base de la tricobotria (23) (*)

0-redondeada

1-estrecha longitudinalmente

Pata III (24) (!)

0-dirigida hacia adelante

1-no dirigida hacia adelante

Uñas tarsales (25) (#)

0-unipectinadas

1-bipectinadas

Órgano tarsal (26) (!)

0-expuesto

1-encapsulado

Forma del órgano tarsal (27) (!)

0-elevado

1-no elevado

Borde proximal del órgano tarsal estrecho (28) (!)

0-ausente

1-presente

Receptores en los órganos tarsales I-IV (29) (!)

0-4.4.3.3

1-3.3.2.2

Caracteres válidos para hembras (30-72)

Clípeo en vista dorsal (30)(+) (*)

0-ensanchado casi el diámetro de los PME o AME o más

1-ensanchado menos del diámetro de los PME o AME

2-inconspicuo

Porción anterior del carapacho en vista dorsal (31) (+) (!)

0-separado claramente del resto del carapacho

1-levemente separado del resto del carapacho

2-no separado claramente del resto del carapacho

Forma del clípeo en vista anterior (32) (*)

0-curvado hacia abajo

1-recto

Forma del clípeo en vista lateral (33) (*)

0-vertical

1-proyectado hacia adelante

Fila posterior de ojos en vista frontal (34) (*)

0-recta

1-procurva

Distancia entre los PME (35)(+) (*)

0-en contacto a lo largo de casi toda su longitud

1-en contacto por menos de la mitad de su longitud

2-separados por menos que su radio

Distancia entre los PLE y PME (36) (+) (*)

0-en contacto

1-separados por menos que el radio de los PME

2-separados entre el radio y el diámetro de los PME

3-separados por más que el diámetro de los PME

Posición de las setas del esternón (37) (*)

0-igualmente distribuidas

1-densas en los laterales

2-agrupadas en las bases de las coxas

Forma del esternón (38) (*)

0-más ancho que largo

1-tan ancho como largo

2-más largo que ancho

Textura del esternón (39) (*)

0-suave

1-finamente reticulado

2-rugoso

Extensiones laterales del esternón (40) (*)

0-sin extensiones

1-con extensiones redondeadas entre las coxas

2-con extensiones delgadas entre las coxas

Número de dientes en el promargen de los quelíceros (41) (*)

0-sin dientes

1-con dos dientes

2-con tres o más dientes

Forma del labio (42) (*)

0-rectangular

1-triangular

2-hexágono alargado

Margen anterior del labio (43) (*)

0-cóncavo en el medio

1-recto en el medio

2-profuendamente escotado en el medio

Sérrula (44) (*)

0-ausente

1-presente

Uña del palpo (45) (*)

0-ausente

1-presente

Forma del opistosoma (46) (*)

- 0-ovoide
- 1-cilíndrico
- 2-globular

Escudo dorsal (47) (+) (*)

- 0-ausente
- 1-levemente esclerotizado
- 2-fuertemente esclerotizado

Escudo epigástrico (48) (+) (*)

- 0-ausente
- 1-levemente esclerotizado
- 2-fuertemente esclerotizado

Escudo post-epigástrico (49) (+) (*)

- 0-ausente
- 1-levemente esclerotizado
- 2-fuertemente esclerotizado

Forma de escudo epigástrico (50) (*)

- 0-rodeando al pedicelo

1-no rodeando al pedicelo

Extensión del escudo post-epigástrico (51) (*)

0-sólo alrededor del surco epigástrico

1-cubriendo casi toda la longitud del opistosoma

Espinas en las patas I (52) (*)

0-ausentes

1-presentes

Espinas en las patas II (53) (*)

0-ausentes

1-presentes

Espinas en las patas III (54) (*)

0-ausentes

1-presentes

Espinas en las patas IV (55) (*)

0-ausentes

1-presentes

Receptáculo posterior (56) (#)

0-ausente

1-presente

Unión posterior de los músculos M2 (57) (!)

0-a una barra transversal

1-a una placa

2-a una barra con proyecciones anteriores

3-en apodemas unidos al receptáculo posterior

4-a barras paralelas dirigidas posteriormente

Forma del receptáculo anterior (58) (!)

0-rotado dorsalmente

1-recto

Glándulas del receptáculo anterior (59) (!)

0-ausentes

1-presentes

Unión anterior de los músculos M2 (60) (!)

0-directa en el ápice del receptáculo anterior

1-en apodemas laterales cortos, menores a la longitud del receptáculo anterior

2-en apodemas laterales largos, de casi la misma longitud que la longitud del receptáculo anterior

3-en apodemas laterales muy largos, mayores a la longitud del receptáculo anterior

Lumen del receptáculo anterior (61) (+) (!)

0-ausente

1-presente, pero poco desarrollado

2-presente, bien desarrollado, región anterior formando cavidades

Bolsillos externos en la zona epigástrica (62) (#, modificado)

0-ausentes

1-presentes

Proximidad de los bolsillos externos (63) (+) (!)

0-adyacentes

1-separados una o dos veces el diámetro de su apertura

2-separados por varias veces el diámetro de su apertura

Posición de los bolsillos externos (64) (!)

0-cercanos al surco epigástrico

1-separados del surco epigástrico, cercanos al pedicelo

Bolsillos internos (65) (!)

0-ausentes

1-presentes

Tamaño de los bolsillos internos (66) (+) (!)

0-pequeños

1-medianos

2-masivos

Rebordes en la región epigástrica (67) (!)

0-ausentes

1-presentes

Proximidad de los rebordes de la región epigástrica (68) (!)

0-adyacentes

1-separados

Bordes esclerotizados en los extremos del surco epigástrico (69) (!)

0-ausentes

1-presentes

Cámaras laterales adicionales en el receptáculo anterior (70) (!)

0-ausentes

1-presentes

Forma del receptáculo anterior (71) (!)

0-recto, sin proyecciones laterales

1-con proyecciones laterales redondeadas masivas

2-con una proyección ventral redondeada

3-con proyecciones laterales no redondeadas

4-con una región dorsal masiva redondeada

Base del receptáculo anterior (72) (!)

0-redondeado

1-no redondeado

Caracteres válidos para machos (73-120)

Bandas laterales esclerotizadas en el carapacho (73) (!)

0-presentes

1-ausentes

Área cefálica (74) (+) (!)

0-separado claramente del resto del carapacho

1-levemente separado del resto del carapacho

2-no separado claramente del resto del carapacho

Clípeo en vista frontal (75) (*)

0-curvado hacia abajo

1-recto

2-sinuoso

Clípeo en vista dorsal (76) (+) (!)

0-extendido casi el diámetro de los PME o AME o más

1-extendido menos del diámetro de los PME o AME

2-inconspicuo

Forma del clípeo en vista lateral (77) (* modificado)

0-vertical

1-proyectado hacia adelante

2-dirigido posteriormente

Fila posterior de ojos en vista frontal (78) (*)

0-recta

1-recurva

2-procurva

Ojos laterales en vista dorsal (79) (+) (!)

0-ALE y PLE cubriendo el margen del carapacho

1-sólo ALE cubriendo el margen del carapacho

2-ALE y PLE no cubriendo el margen del carapacho

Forma del esternón (80) (*)

0-más ancho que largo

1-tan ancho como largo

2-más largo que ancho

Patrón de coloración del esternón (81) (* modificado)

0-uniforme

1-con una banda esclerotizada corta desde la base del labio

2-con dos bandas oscuras desde la base del labio

3-con dos regiones pálidas en la base de las láminas maxilares

4-con un patrón irregular color púrpura

5-con una banda central larga color púrpura

Proyecciones en el margen anterior de los quelíceros (82) (* modificado)

0-sin modificaciones

1-con proyecciones romas

2-con proyecciones cónicas

Dientes en el promargen de los quelíceros (83) (*)

0-sin dientes

1-con un diente

2-con dos dientes

3-con tres o más dientes

Setas en el promargen de los quelíceros (84) (#)

0-sin un grupo de setas

1-con un grupo de tres setas largas

Largo de los quelíceros (85) (+) (!)

0-más cortos que las láminas maxilares

1-aproximadamente del mismo largo que las láminas maxilares

2-más largos que las láminas maxilares

Macrosetas en el margen anterior de los quelíceros (86) (!)

0-presentes

1-ausentes

Proyecciones en el promargen de los quelíceros (87) (!)

0-sin proyecciones

1-con una proyección triangular

Margen interno de los quelíceros (88) (!)

0-sin modificaciones

1-con una o más proyecciones triangulares fuertes

Forma del labio (89) (*)

0-rectangular

1-triangular

2-hexágono elongado

Labio fusionado al esternón (90) (*)

0-no fusionado

1-fusionado

Setas modificadas en el labio (91) (#)

0-ausentes

1-presentes, en forma de hoja

Sérrula (92) (*)

0-ausente

1-presente

Margen lateral de láminas maxilares (93) (!)

0-normales

1-excavadas

Margen anterior de láminas maxilares (94) (!)

0-sin modificaciones

1-con una proyección apical pequeña

2-con una proyección apical fuerte

Forma del opistosoma (95) (*)

0-ovoide

1-cilíndrico

2-globular

Escudo epigástrico (96) (+) (*)

0-ausente

1-levemente esclerotizado

2-fuertemente esclerotizado

Escudo post-epigástrico (97) (+) (*)

0-ausente

1-levemente esclerotizado

2-fuertemente esclerotizado

Forma del escudo epigástrico (98) (*)

0-rodeando al pedicelo

1-no rodeando al pedicelo

Extensión del escudo post-epigástrico (99) (+) (*)

0-alrededor del surco epigástrico

1-cubriendo casi la longitud total del opistosoma

Espinas en la pata I (100) (*)

0-ausentes

1-presentes

Espinas en la pata II (101) (*)

0-ausentes

1-presentes

Espinas en la pata III (102) (*)

0-ausentes

1-presentes

Espinas en la pata IV (103) (*)

0-ausentes

1-presentes

Región proximal de la tibia I (104) (#)

0-normal

1-ensanchada

Poro espermático (105) (*)

0-no visible

1-visible

Unión de la patela con la tibia en el palpo (106) (*)

0-basal

1-sub-basal

Largo de la tibia del palpo (107) (+) (*)

0-menor a dos veces el ancho del fémur

1-dos o tres veces el ancho del fémur

2-más de tres veces el ancho del fémur

Forma de la tibia del palpo (108) (+) (!)

0-ensanchada una vez el ancho del fémur

1-ensanchada entre una a una vez y medio el ancho del fémur

2-ensanchada cerca de dos veces el ancho del fémur

3-ensanchada entre dos y dos veces y medio el ancho del fémur

4-ensanchada tres veces el ancho del fémur

Cimbio fusionado al bulbo (109) (*)

0-no fusionado

1-fusionado

Forma del cimbio en vista dorsal (110) (!)

0-ovoide

1-estrecho

2-redondeado

Longitud del cimbio (111) (*)

0-no sobrepasando el extremo del bulbo copulador

1-sobrepasando el extremo del bulbo copulador

Ancho del bulbo copulador en vista lateral (112) (!)

0-menor al ancho de la tibia

1-cercano al ancho de la tibia

2-una a una vez y medio el ancho de la tibia

3-dos o más veces el ancho de la tibia

Forma del bulbo copulador (113) (!)

0-esférico-ovoide

1-región terminal claramente diferenciada de la región basal

2-angosto hacia la punta

3-macizo

Ducto espermático (114) (# modificado)

0-conspicuo, bien esclerotizado

1-levemente esclerotizado

Recorrido del ducto espermático (115) (# modificado)

0-no espiralado

1-espiralado una vez

2-espiralado más de una vez

Conductor glandular (116) (!)

0-ausente

1-presente

Apófisis adicional en el bulbo copulador (117) (!)

0-ausente

1-presente, espiniforme o en forma tubular en el margen retrolateral

2-presente, de otra forma

3-presente, pero más de una

Esclerotización de la apófisis espiniforme (118) (!)

0-levemente esclerotizada

1-fuertemente esclerotizada, color negro

Proyección redondeada cercana a la base del émbolo en vista retrolateral (119) (!)

0-presente

1-sin dicha proyección

Testículos (120) (+) (!)

0-pares

1-parcialmente fusionados

2-completamente fusionados

11.2 Apéndice

Sinapomorfías para *Orchestina* y nodos internos (ver figura 220). Se indica entre paréntesis el número de carácter correspondiente.

Nodo 169 (Género *Orchestina*)

- Margen posterior del esternón (12)
  - A nivel de las coxas IV → sobrepasando el margen posterior de las coxas IV
- Forma del pedicelo (18)
  - sin modificaciones → con un anillo de setas
- Anillo de setas largas alrededor de las hileras (19)
  - ausentes → presentes
- Forma del fémur IV (21)
  - no engrosado → mucho más engrosado que el resto de las patas
- Forma del clípeo en vista lateral en las hembras (33)
  - vertical → proyectado hacia adelante

Nodo 168 (*Orchestina* excepto *O. pavesiiformis*)

- Setas marginales del carapacho (4)
  - Presentes→Ausentes

Nodo 167 (*Orchestina* excepto Sudamérica)

- Patrón de coloración del carapacho (1)
  - sin patrones→con un patrón reticulado

Nodo 162

Setas en el promargen de los quelíceros (84)

Sin un grupo de setas → con un grupo de tres setas largas

Nodo 163

Setas modificadas en el labio del macho (91)

ausentes → presentes, en forma de hoja

Forma del cimbio en vista dorsal (110)

ovoide → redondeado

Nodo 164

Unión posterior de los músculos M2 (57)

a una placa → a una barra con proyecciones anteriores

Nodo 175

Forma del receptáculo anterior (71)

Recto, sin proyecciones → con una región dorsal masiva redondeada

Nodo 179

Apófisis adicional en el bulbo copulador (117)

ausente → presente, espiniforme o en forma tubular en el margen retrolateral

Nodo 181

Rebordes en la región epigástrica (67)

ausentes → presentes

Nodo 187

Bolsillos internos (65)

ausentes → presentes

Nodo 189

Base del receptáculo anterior (72)

no redondeado → redondeado

Nodo 193

Proyección redondeada cercana a la base del émbolo en vista retrolateral (119)

sin dicha proyección →presente

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Notnops calderoni	2	0	2	0	1	0	0	?	2	?	0	0	0	1	1	0	?	0	0	0	0	0	1	?	1	0	0	1	0	?	0	1	0	1	?	?	?	1	1	0	0
Dysdera crocata	2	0	0	1	1	1	1	2	1	0	0	1	0	1	1	0	?	1	0	0	1	0	0	0	1	0	0	1	0	?	2	0	1	0	2	1	1	0	2	3	2
Harpactea hombergi	2	0	0	1	1	1	1	2	0	0	0	1	0	1	1	0	?	1	0	0	?	0	1	?	1	0	0	1	0	?	2	0	0	0	2	1	0	1	2	1	2
Ariadna araucana	0	0	0	0	1	1	1	2	2	0	0	1	0	1	1	0	?	1	0	0	1	0	1	?	0	0	0	1	0	?	2	1	1	0	1	0	2	0	2	0	0
Ariadna boesenbergi	0	0	0	0	1	1	1	2	2	0	0	1	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	?	2	1	1	0	1	2	2	0	2	0	0
Segestria florentina	0	0	0	0	1	1	1	1	2	0	?	1	0	1	0	1	1	1	0	0	1	0	1	0	0	0	0	1	0	?	1	1	0	0	1	1	2	1	2	0	1
Orsolobus pucara	0	0	1	0	1	1	1	1	2	0	0	1	1	1	1	0	?	1	0	0	1	0	0	0	1	1	0	0	0	?	2	0	0	0	1	1	2	0	2	0	0
***Tasmanoonops* sp**	0	0	2	0	1	1	1	1	2	0	0	1	1	1	1	0	?	1	0	0	1	0	0	?	1	1	0	0	0	?	1	0	0	0	0	1	2	0	0	0	0
Puan chechehet	0	2	1	0	1	1	1	1	2	0	0	1	0	1	1	1	1	1	0	0	1	0	0	0	1	0	1	1	0	?	0	0	0	0	0	1	2	0	0	0	0
Unicorn catleyi	0	2	1	0	1	1	1	1	2	0	0	1	0	1	1	1	1	1	0	0	1	0	0	?	1	0	1	1	0	?	0	0	0	0	2	1	2	0	0	0	0
Xiombarg plaumanni	0	2	1	0	1	1	1	1	2	0	0	0	0	1	1	1	1	1	0	0	1	0	0	?	1	0	1	1	0	?	2	0	1	0	2	1	2	0	0	0	0
Birabenella homonota	1	0	2	0	1	1	1	1	2	2	1	0	0	0	0	0	?	?	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	2	2	0	1	2	1
***Oonopinae* sp2**	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	?	1	0	0	0	0	0	?	1	1	0	1	1	1	1	0	0	0	0	0	1	0	1	0	0
***Oonopinae* sp1**	0	0	1	0	1	1	1	1	1	1	0	1	0	1	0	0	?	1	0	0	0	0	0	?	1	1	0	1	1	1	1	0	0	0	0	0	1	0	2	0	0
Neotrops pombero	0	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	?	1	0	0	1	0	0	?	1	1	0	1	1	1	1	0	0	0	2	0	1	0	1	0	0
Neotrops waorani	0	0	1	0	1	1	1	1	1	0	0	1	0	1	0	0	?	1	0	0	1	1	0	?	1	1	0	1	1	1	1	0	0	0	2	0	1	0	2	0	0
Neoxyphinus termitophilus	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0	0	?	0	1	0	0	0	0	?	1	1	0	1	1	1	1	1	1	0	2	0	0	0	1	0	0
***Reductoonops* sp**	0	0	2	0	1	0	0	?	0	?	1	0	0	1	1	0	?	0	0	0	0	0	0	?	1	?	0	1	1	1	0	1	0	0	?	?	?	2	0	0	0
"*Gamasomorpha*" sp	2	0	2	0	1	1	1	1	1	0	1	0	0	0	0	0	?	0	0	0	1	0	0	?	1	1	0	1	1	1	1	0	0	0	2	0	2	0	1	3	0
Orchestina cornuta	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	1	0	1	0	0	2	0	2	0	0
Orchestina debakkeri	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina macrofoliata	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	?	?	2	1	1	1	0	0	1	1	0	1	1	0	0	1	0	1	0	0	2	0	1	0	0
Orchestina gigabulbus	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina saaristoi	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina clavulata	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina tubulata	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina truncatula	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
***Orchestina* AUSTRALIA**	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	2	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina kamehameha	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	2	1	2	1	1	1	0	?	1	1	0	1	1	0	0	1	0	1	0	0	2	0	2	0	0
Orchestina moaba	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina nadleri	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina quasimodo	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	?	1	1	0	1	1	0	0	1	0	1	0	0	2	0	2	0	0
Orchestina saltitans	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	1	0	1	0	0	2	0	2	0	0
Orchestina utahana	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina cachai	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina cajamarca	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina caleta	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina cali	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	2	0	0	1	0	0	2	0	2	0	0
Orchestina campana	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina chiriqui	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina griswoldi	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina jaiba	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina justini	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	1	0	0
Orchestina labarquei	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina luispi	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina pandeazucar	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina pizarroi	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina platnicki	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	1	0	0
Orchestina quijos	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina heredia	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina ranchogrande	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina saltabunda	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina ucumar	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	1	2	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina pavesiiformis	0	0	1	0	1	1	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina guatemala	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	?	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0
Orchestina bolivar	0	0	1	0	0	1	1	1	2	0	0	0	1	1	1	0	?	?	2	1	1	1	0	?	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?
Orchestina crypta	0	1	1	0	0	1	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	?	1	1	0	1	1	0	0	0	0	1	0	0	2	0	2	0	0

Apéndice 11.4. Matriz de datos morfológica, (ver Apéndice 11.2 para consultar caracteres aditivos).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
Notnops calderoni	0	0	1	1	0	1	0	0	0	?	?	0	?	?	0	0	?	?	?	?	?	0	?	?	0	?	0	?	0	?	?	?	1	1	0	0	1	?	1	1	0
Dysdera crocata	2	1	2	0	1	1	0	1	0	1	?	0	0	1	1	1	0	1	1	0	2	0	?	?	0	?	0	?	0	0	0	1	1	0	0	2	0	2	1	2	0
Harpactea hombergi	1	0	0	1	1	1	0	1	0	1	?	0	0	1	1	1	0	1	?	0	1	0	?	?	0	?	0	?	0	0	0	1	1	1	0	2	0	2	1	2	0
Ariadna araucana	2	0	0	1	1	1	0	1	0	1	?	1	1	1	1	1	?	?	1	?	?	0	?	?	0	?	0	?	0	0	?	1	1	1	1	2	0	2	2	2	0
Ariadna boesenbergi	2	0	0	1	1	1	0	1	0	1	?	1	1	1	0	1	?	?	1	?	?	0	?	?	0	?	0	?	0	0	?	1	1	1	1	2	0	2	2	2	0
Segestria florentina	2	0	0	1	1	1	0	1	0	1	?	1	1	1	1	1	0	1	1	?	1	0	?	?	0	?	0	?	0	0	?	1	1	1	0	1	0	1	2	2	0
Orsolobus pucara	1	0	0	1	1	1	0	1	0	1	?	0	0	1	1	1	0	1	1	1	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	2	0	1	1	2	0
***Tasmanoonops* sp**	1	0	1	1	1	1	0	1	0	1	?	0	0	1	1	1	0	1	1	0	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	2	0	0	1	2	0
Puan chechehet	0	2	1	1	0	2	0	1	0	1	?	1	1	1	1	1	0	1	1	0	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	0	0	0	2	0	0
Unicorn catleyi	0	0	0	1	0	2	0	1	0	1	?	1	1	1	1	1	0	1	1	0	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	0	0	2	?	0	0
Xiombarg plaumanni	0	1	1	1	0	2	0	1	0	1	?	0	0	0	0	1	0	1	1	0	2	0	?	?	0	?	0	?	0	?	0	1	1	0	1	2	0	2	1	0	0
Birabenella homonota	0	?	0	1	0	0	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	0	?	?	0	?	0	?	0	0	1	1	1	0	0	1	0	0	2	1	0
***Oonopinae* sp2**	0	2	0	1	0	0	0	1	1	1	0	1	1	1	1	0	1	1	1	0	?	0	?	?	0	?	0	?	0	0	0	1	1	0	0	1	0	0	0	1	0
***Oonopinae* sp1**	0	2	0	1	0	0	0	1	1	1	0	1	1	1	1	0	1	1	0	1	0	0	?	?	0	?	0	?	0	0	0	1	1	0	0	2	0	0	1	2	0
Neotrops pombero	0	2	0	1	0	0	0	1	1	1	0	1	1	1	1	0	1	1	0	0	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	1	0	2	1	1	0
Neotrops waorani	0	2	0	1	0	0	0	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	2	0	2	1	2	0
Neoxyphinus termitophilus	0	1	1	1	0	0	2	2	2	0	1	1	1	1	1	1	4	1	?	0	0	0	?	?	0	?	0	?	0	0	0	1	1	1	1	2	0	1	2	1	0
***Reductoonops* sp**	0	1	0	1	0	1	0	1	0	0	?	0	0	0	0	?	0	1	?	0	0	0	?	?	0	?	0	?	0	0	0	1	1	1	0	0	0	?	2	2	0
"*Gamasomorpha*" sp	0	1	0	1	0	0	2	2	2	0	1	0	0	0	0	1	3	1	0	2	0	0	?	?	0	?	0	?	0	0	0	1	1	0	0	0	0	2	2	1	0
Orchestina cornuta	0	1	0	1	0	0	0	1	0	1	?	0	0	0	0	0	2	1	?	1	?	0	?	?	0	?	0	?	0	0	0	1	1	1	0	0	0	0	1	1	5
Orchestina debakkeri	0	1	0	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1	0	2	1	1	1	0	0	?	0	?	0	0	3	1	1	0	1	0	1	0	1	1	5
Orchestina macrofoliata	0	1	0	1	0	0	0	1	0	1	?	0	0	0	0	0	2	0	0	1	1	0	?	?	0	?	0	?	0	0	0	1	1	2	0	0	1	0	2	1	5
Orchestina gigabulbus	0	1	0	1	0	0	0	1	0	1	?	0	0	0	0	0	2	0	?	1	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	0	1	0	1	1	5
Orchestina saaristoi	0	1	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	1	1	0	?	?	0	?	0	?	0	0	2	1	1	0	0	0	1	0	1	2	5
Orchestina clavulata	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1	?	1	1	0	?	?	0	?	0	?	0	0	0	1	1	0	0	0	1	0	1	1	5
Orchestina tubulata	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	2	0	0	1	2	1	1	0	0	?	0	?	0	0	0	1	1	1	0	0	1	0	1	0	4
Orchestina truncatula	0	0	1	?	0	0	0	1	0	1	?	0	0	0	0	0	2	1	?	2	0	0	?	?	0	?	0	?	0	0	4	1	1	1	0	0	1	0	1	2	5
***Orchestina* AUSTRALIA**	0	0	1	?	0	0	0	1	0	1	?	0	0	0	0	1	1	1	?	1	1	0	?	?	0	?	0	?	0	0	2	1	1	0	0	0	1	0	1	2	4
Orchestina kamehameha	0	2	1	0	0	0	0	1	0	1	?	0	0	0	0	?	2	0	?	1	1	1	2	0	0	?	0	?	0	0	0	1	1	2	0	0	1	2	2	1	5
Orchestina moaba	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	1	2	0	?	1	1	1	0	1	0	?	0	?	0	0	0	1	1	2	0	0	0	0	2	2	1
Orchestina nadleri	0	1	1	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1	?	1	1	0	?	1	0	?	0	?	0	0	0	1	1	0	0	0	1	0	1	0	1
Orchestina quasimodo	0	0	1	1	0	0	0	1	0	1	?	0	0	0	1	1	2	0	?	2	1	1	2	1	0	?	0	?	0	0	0	1	1	2	0	0	1	0	2	2	1
Orchestina saltitans	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	1	?	1	?	1	0	0	?	?	0	?	0	?	0	0	0	1	1	1	0	0	0	0	2	2	4
Orchestina utahana	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	1	2	0	?	1	1	1	2	1	0	?	0	?	0	0	0	1	1	2	0	0	1	0	2	2	1
Orchestina cachai	0	0	1	1	0	0	0	1	0	1	?	0	0	0	1	0	1	1	?	1	2	1	2	0	0	?	1	0	0	0	0	1	1	0	0	0	?	0	1	1	0
Orchestina cajamarca	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	2	1	0	?	?	1	0	0	?	0	0	3	1	1	1	0	1	1	0	1	1	0
Orchestina caleta	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	1	2	0	?	?	0	?	1	1	0	0	0	1	1	0	0	0	?	0	1	2	0
Orchestina cali	0	0	1	1	0	0	0	1	0	1	?	0	0	0	1	1	1	1	1	1	1	0	?	?	1	0	0	?	0	0	1	1	1	0	0	2	1	0	1	2	0
Orchestina campana	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1	?	1	1	0	?	?	1	0	0	?	0	0	1	1	1	0	0	0	1	0	1	2	0
Orchestina chiriqui	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	2	1	0	?	?	1	0	0	?	0	0	0	0	1	0	0	0	1	0	1	2	0
Orchestina griswoldi	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	?	1	1	?	2	1	0	?	?	1	0	0	?	0	0	0	0	1	1	0	0	1	0	1	2	0
Orchestina jaiba	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	0	1	2	1	2	0	0	?	1	0	0	0	0	1	1	0	0	0	1	0	1	2	0
Orchestina justini	0	2	1	1	0	0	0	0	0	?	?	0	0	0	1	1	2	1	?	2	0	0	?	?	0	?	0	?	0	0	4	1	1	0	0	0	0	0	2	1	5
Orchestina labarquei	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	2	1	0	?	?	1	0	0	?	0	0	1	1	1	0	0	0	1	0	1	2	0
Orchestina luispi	0	2	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	0	3	2	0	?	?	0	?	0	?	0	1	2	1	1	0	0	0	1	0	1	1	0
Orchestina pandeazucar	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	1	2	1	?	0	0	?	1	1	0	0	0	1	1	0	0	0	?	0	1	2	0
Orchestina pizarroi	0	0	1	1	0	0	0	1	0	1	?	0	0	0	1	0	1	1	?	1	2	1	?	0	0	?	1	1	0	0	0	1	1	0	0	0	1	0	1	2	0
Orchestina platnicki	0	0	1	1	0	0	0	1	0	1	?	?	?	?	?	1	1	1	?	2	1	0	?	?	1	0	0	?	0	0	3	1	1	0	0	0	?	0	1	1	2
Orchestina quijos	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	0	1	0	?	?	1	1	0	?	0	0	3	1	1	1	2	0	1	0	2	0	2
Orchestina heredia	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	2	1	0	?	?	1	0	0	?	0	0	1	1	1	1	0	0	1	0	1	0	0
Orchestina ranchogrande	0	0	1	1	0	0	0	1	0	1	?	?	?	?	?	1	1	1	?	1	1	0	?	?	1	0	0	?	0	0	0	1	1	0	0	0	?	0	1	1	2
Orchestina saltabunda	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1	?	2	1	0	?	?	1	0	0	?	0	0	3	1	1	1	0	1	0	0	2	1	0
Orchestina ucumar	0	0	1	1	0	0	0	1	0	1	?	0	0	0	1	0	1	1	?	1	2	0	?	?	0	?	0	?	1	0	2	1	1	0	0	?	1	0	2	2	0
Orchestina pavesiiformis	0	0	0	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1	?	1	?	1	1	0	0	?	0	?	0	0	0	1	1	0	0	0	1	0	2	2	0
Orchestina guatemala	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	1	1	?	2	1	0	?	?	1	0	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?
Orchestina bolivar	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	1	0	2	1	0
Orchestina crypta	0	0	1	1	0	0	0	1	0	1	?	0	0	0	0	0	2	1	?	1	1	0	?	?	0	?	0	?	0	0	4	1	1	1	1	0	1	0	2	2	5

Apéndice 11.4 *(continuación)*. Matriz de datos morfológica, (ver Apéndice 11.2 para consultar caracteres aditivos).

	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Notnops calderoni	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	?	0	0	?	1	?
Dysdera crocata	0	3	0	2	1	0	0	1	0	0	0	0	0	1	0	0	?	?	0	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	?	1	1
Harpactea hombergi	0	2	0	1	1	0	0	0	0	0	1	0	0	1	0	0	?	?	0	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	?	1	?
Ariadna araucana	0	3	0	1	1	0	0	0	0	0	1	0	0	1	0	0	?	?	1	1	1	1	0	0	0	2	1	0	0	0	1	0	0	1	0	0	?	1	0
Ariadna boesenbergi	0	3	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	1	1	1	0	0	0	0	1	1	0	2	0	1	0	0	1	0	0	?	1	0
Segestria florentina	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	?	?	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	?	1	0
Orsolobus pucara	0	2	0	1	1	0	0	0	0	0	1	0	0	1	0	0	?	?	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	?	1	0
***Tasmanoonops* sp**	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	?	?	0	0	1	1	0	0	0	0	0	0	1	0	3	0	0	1	0	0	?	1	0
Puan chechehet	0	0	0	1	1	0	0	2	0	0	1	0	0	0	0	0	?	?	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	1	?
Unicorn catleyi	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	1	?
Xiombarg plaumanni	0	0	0	2	1	0	0	0	0	0	1	0	0	2	0	0	?	?	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	0	?	1	?
Birabenella homonota	0	0	0	2	1	0	0	?	0	0	1	0	?	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	?	0	0	?	1	?
***Oonopinae* sp2**	0	0	0	1	1	0	0	2	0	0	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	1	0	2	0	0	1	1	1	?	1	0	?	1	2
***Oonopinae* sp1**	0	0	0	1	1	0	0	2	0	0	1	1	?	0	1	1	1	0	1	1	1	1	0	0	0	1	0	2	0	0	0	1	1	?	1	0	?	1	2
Neotrops pombero	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	?	1	0	?	1	2
Neotrops waorani	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	?	1	0	?	1	2
Neoxyphinus termitophilus	0	1	0	1	1	0	0	0	0	0	0	0	0	0	2	2	0	1	1	1	0	0	0	1	0	1	0	1	0	1	2	2	1	?	0	0	?	1	2
***Reductoonops* sp**	0	0	0	1	1	0	0	1	0	0	?	0	0	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?	0	0	?	1	?
***"Gamasomorpha"* sp**	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	?	0	0	?	1	2
Orchestina cornuta	0	?	1	1	1	0	0	1	0	1	0	0	?	0	0	0	?	?	0	0	0	0	0	0	1	2	2	0	2	0	1	1	0	1	0	0	?	1	?
Orchestina debakkeri	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	?	?	0	0	0	0	0	0	0	2	1	0	0	0	1	1	0	1	0	0	?	1	?
Orchestina macrofoliata	0	0	0	2	1	0	0	1	0	1	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	2	2	0	2	0	0	1	0	1	0	0	?	1	?
Orchestina gigabulbus	0	?	1	?	1	0	0	1	0	1	0	0	?	0	0	0	?	?	0	0	0	0	0	0	1	2	4	0	2	0	2	1	0	1	0	0	?	1	?
Orchestina saaristoi	0	0	0	1	1	0	0	?	0	0	1	0	1	2	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina clavulata	0	0	0	1	1	0	0	1	0	0	1	0	2	0	0	0	?	?	0	0	0	0	0	0	0	2	3	0	0	0	1	0	0	2	0	0	?	1	?
Orchestina tubulata	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	2	3	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina truncatula	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	2	3	0	2	0	1	1	0	1	0	0	?	1	?
***Orchestina* AUSTRALIA**	0	0	0	1	1	0	0	0	0	0	?	0	2	0	0	0	?	?	0	0	1	1	0	0	0	2	1	0	0	0	1	0	0	1	0	0	?	1	?
Orchestina kamehameha	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	2	3	0	0	0	2	0	0	1	0	0	?	1	?
Orchestina moaba	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	1	0	0	2	1	0	0	0	1	0	0	1	0	0	?	1	2
Orchestina nadleri	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	1	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina quasimodo	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	1	1	0	0	2	2	0	0	0	1	0	0	1	0	0	?	1	?
Orchestina saltitans	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	1	0	0	?	1	?
Orchestina utahana	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	1	0	0	?	1	?
Orchestina cachai	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	1	0	0	0	2	2	0	0	0	2	1	0	2	0	1	0	1	2
Orchestina cajamarca	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina caleta	0	0	0	1	1	0	0	0	0	0	1	0	?	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	1	1	0	2	0	0	?	1	?
Orchestina cali	0	0	0	1	1	0	0	0	0	0	1	0	?	0	0	0	?	?	0	0	0	1	0	0	0	2	2	0	0	0	2	1	0	2	0	0	?	1	?
Orchestina campana	0	0	0	1	1	0	0	0	0	0	1	0	?	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina chiriqui	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina griswoldi	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	1	2	0	0	2	0	0	?	1	?
Orchestina jaiba	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina justini	2	0	1	1	1	0	0	2	0	1	0	0	0	0	0	0	?	?	0	0	0	1	0	0	1	2	2	0	2	0	1	0	0	1	0	0	?	1	?
Orchestina labarquei	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina luispi	0	0	0	1	1	0	0	0	0	0	?	0	2	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina pandeazucar	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	1	0	2	0	1	0	1	?
Orchestina pizarroi	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina platnicki	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	1	0	2	0	0	?	1	?
Orchestina quijos	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina heredia	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	1	1	0	0	1	2	4	0	0	0	1	0	0	2	0	0	?	1	?
Orchestina ranchogrande	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	0	?
Orchestina saltabunda	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	3	0	0	2	0	0	?	0	?
Orchestina ucumar	0	0	0	2	1	0	0	0	0	0	1	0	1	0	0	0	?	?	0	0	0	1	0	0	0	2	2	0	0	0	1	1	0	2	0	0	?	1	2
Orchestina pavesiiformis	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	?	?	0	0	0	0	0	0	0	2	2	0	0	0	2	0	0	2	0	0	?	1	?
Orchestina guatemala	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Orchestina bolivar	0	0	0	1	1	0	0	0	0	0	1	0	0	?	0	0	?	?	0	0	0	0	0	?	0	2	2	0	0	0	2	0	0	2	0	0	?	0	?
Orchestina crypta	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	?	?	0	0	0	0	1	0	1	2	4	0	2	0	1	0	0	1	0	0	?	1	?

Apéndice 11.4 *(continuación)*. Matriz de datos morfológica, (ver Apéndice 11.2 para consultar caracteres aditivos).

Especie	Sexo	Número de colección	Otro código	Origen de las secuencias	Observación
Notnops calderoni	1♀	MACN-Ar 30468	…	MACN-Proyecto PBI	
Aridna boesenbergi	1♀	…	…	MACN-Proyecto PBI	Se envió el especimen entero
Ariadna araucana	1♀	MACN-Ar 30473	CJG-Hual-7	MACN-Proyecto PBI	
Harpactea holmbergi	1♀	MACN-Ar 31304	…	MACN-Proyecto PBI	
***Tasmanoonops* sp**	1♀	MACN-Ar 11174	ARAMR000690	MACN-AToL	
Orsolobus pucara	1♂	MACN-Ar 28669	…	MACN-Proyecto PBI	
Unicorn catleyi	1♂	MACN-Ar 22100	PBI_OON 15059	MACN-Proyecto PBI	
Puan chechehet	1♂	MACN-Ar 27622	PBI_OON 43348	MACN-Proyecto PBI	
Puan chechehet	1♀	MACN-Ar 27629	PBI_OON 43360	MACN-Proyecto PBI	
Birabenella homonota	1♂	MNSC	PBI_OON 14989	MACN-Proyecto PBI	
***Reductoonops* sp**	5♂13♀1 J	MACN-Ar 31436	PBI_OON 15086	MACN-Proyecto PBI	
"*Gamasomorpha*" sp	1♂	MACN-Ar 15876	PBI_OON 14775	MACN-Proyecto PBI	
Neoxyphinus termitophilus	1♀	MACN-Ar	PBI_OON 14778	MACN-Proyecto PBI	Se envió el especimen entero
Neotrops waorani	1♂	MACN-Ar 26905	PBI_OON 30832	MACN-Proyecto PBI	
Neotrops pombero	1♀	MACN-Ar 13172	PBI_OON 14770	MACN-Proyecto PBI	
Orchestina saaristoi	1♀	MRAC	…	MRAC-Proyecto PBI	
Orchestina macrofoliata	3♂5♀	MRAC 228778	PBI_OON 16775	MRAC-Proyecto PBI	
Orchestina gigabulbus	1♀	MRAC	…	MRAC-Proyecto PBI	
Orchestina cornuta	1♀	MRAC 228790	PBI_OON 16797	MRAC-Proyecto PBI	
Orchestina cornuta	9♀	MRAC 228913	PBI_OON 33331	MRAC-Proyecto PBI	
Orchestina ucumar	1♀	MACN-Ar 18056	PBI_OON 14909	MACN-Proyecto PBI	
Orchestina totoralillo	1♀	MNSC	PBI_OON 30844	MACN-Proyecto PBI	
Orchestina cachai	1♀	MACN-Ar 15875	PBI_OON 14774	MACN-Proyecto PBI	
***Orchestina* MI026**	1♀	MACN-Ar 28652	PBI_OON 30872	MACN-Proyecto PBI	
Orchestina quijos	1♀	MACN-AR 28894	PBI_OON 30857	MACN-Proyecto PBI	
Orchestina golem	1♀	MACN-Ar 28651	PBI_OON 30843	MACN-Proyecto PBI	
Orchestina chiriqui	1♀	MACN-Ar 29886	PBI_OON 42292, SAB1DFB026, SPIPA603-10	MACN-Proyecto PANCODING	
Orchestina campana	1♀	MACN-Ar 29905	PBI_OON 42299, SCU2NHH019, PA880	MACN-Proyecto PANCODING	
Orchestina labarquei	1♀	MACN-Ar 29889	PBI_OON 42305, SFB1D9H029, PA895	MACN-Proyecto PANCODING	

Apéndice 11.5. Ejemplares voucher utilizados para la obtención de datos moleculares.

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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.

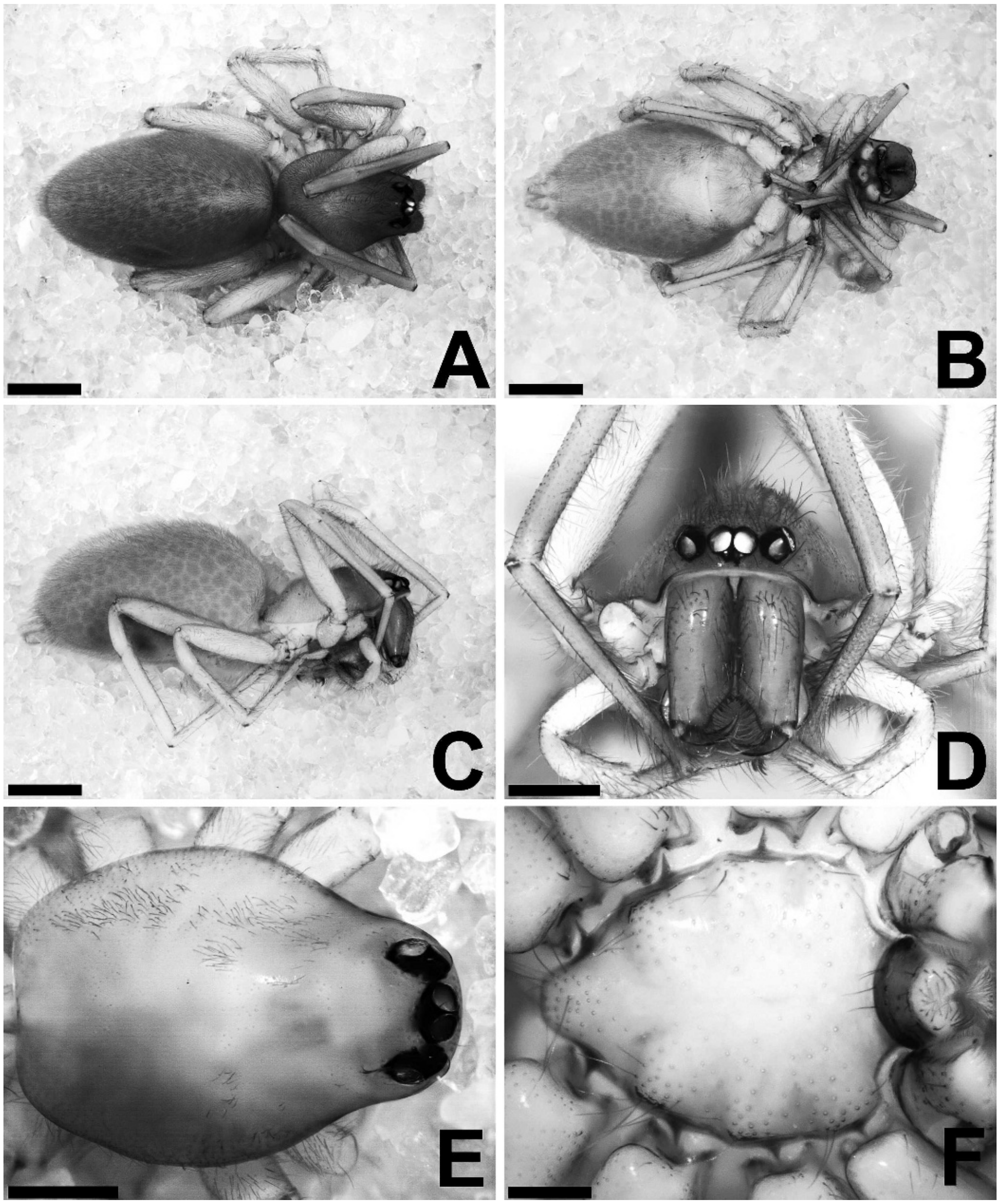
SYSTEMATICS

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

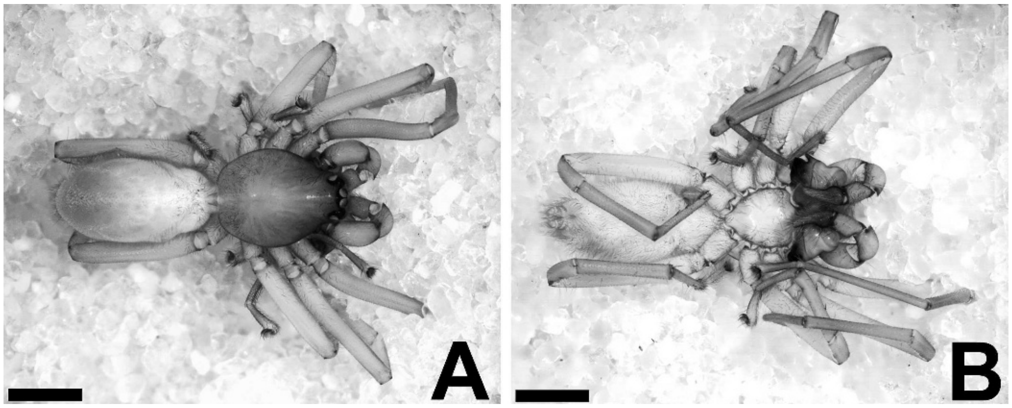
Female diagnosis.—Easily distinguished from other females of the genus by the shape of the median rod, bifurcated at the tip and with a flattened projection directed ventrally (Figs. 3 A, B).

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).

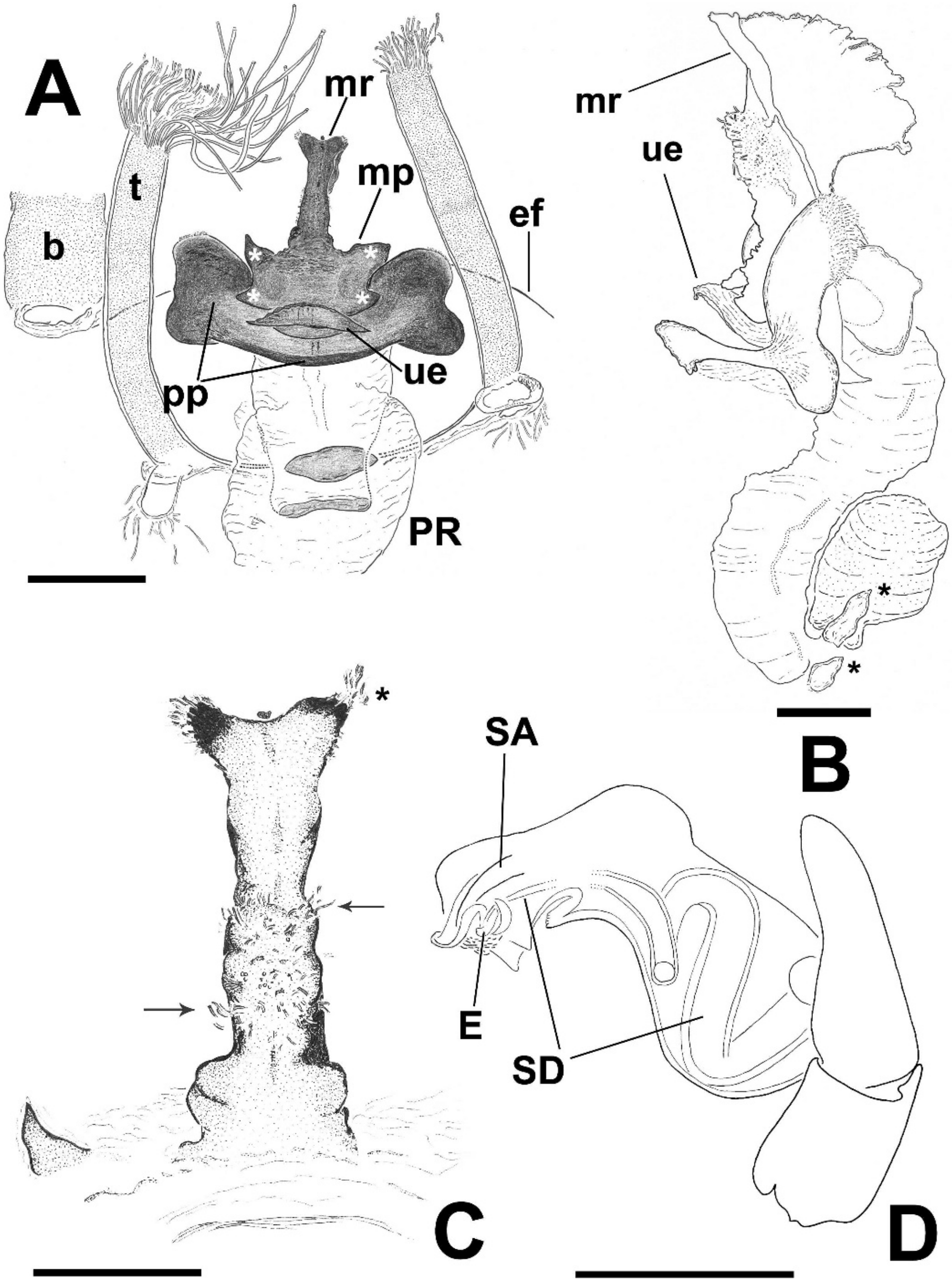
Variability.—We have examined the female genitalia of two additional females from Neuquén and Rio Negro provinces (Argentina), one of them collected together with two males. The tip of the median rod and the size of the gland region differ in both specimens, but the morphology of the other plates does 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.

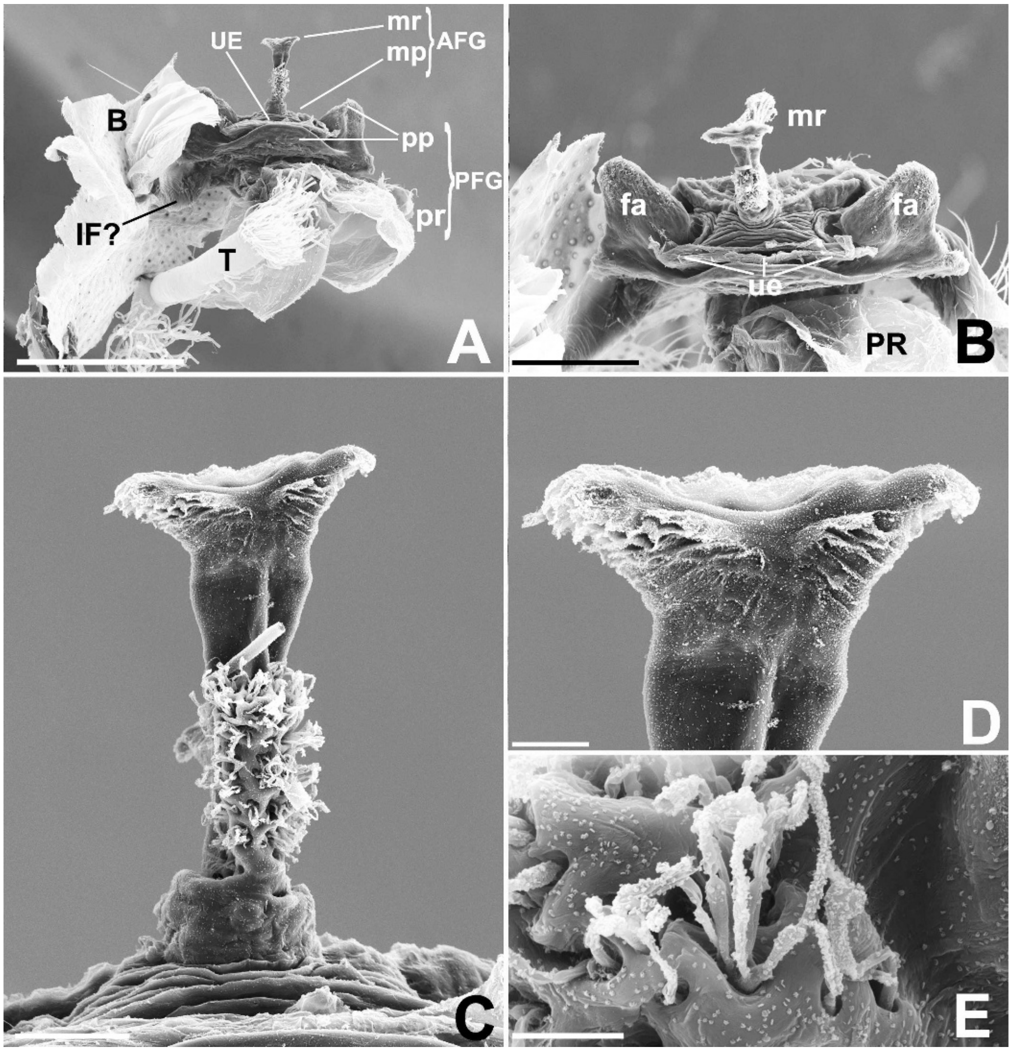


Figures 3 A–D.—*Orsolobus pucara* (MACN-Ar 10873). Genitalia. A–C. Female vulva. A. Dorsal view; B. Lateral view, asterisk on the two sclerotized plates; C. Anterior median rod, arrowheads to the gland ducts, asterisk on rest of digested muscles. D. Male palp, left prolateral view. Abbreviations: b = 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.

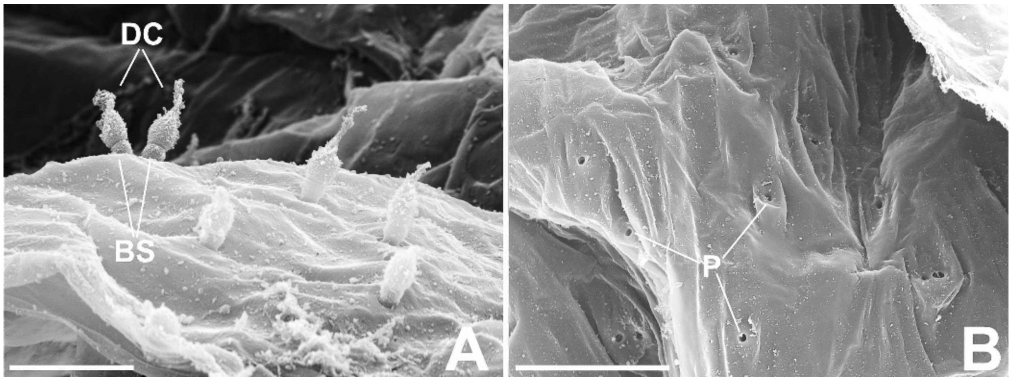
of the species difficult. For correct determination, it is necessary to dissect and digest the genitalia and then observe the preparation from several points of view.

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).

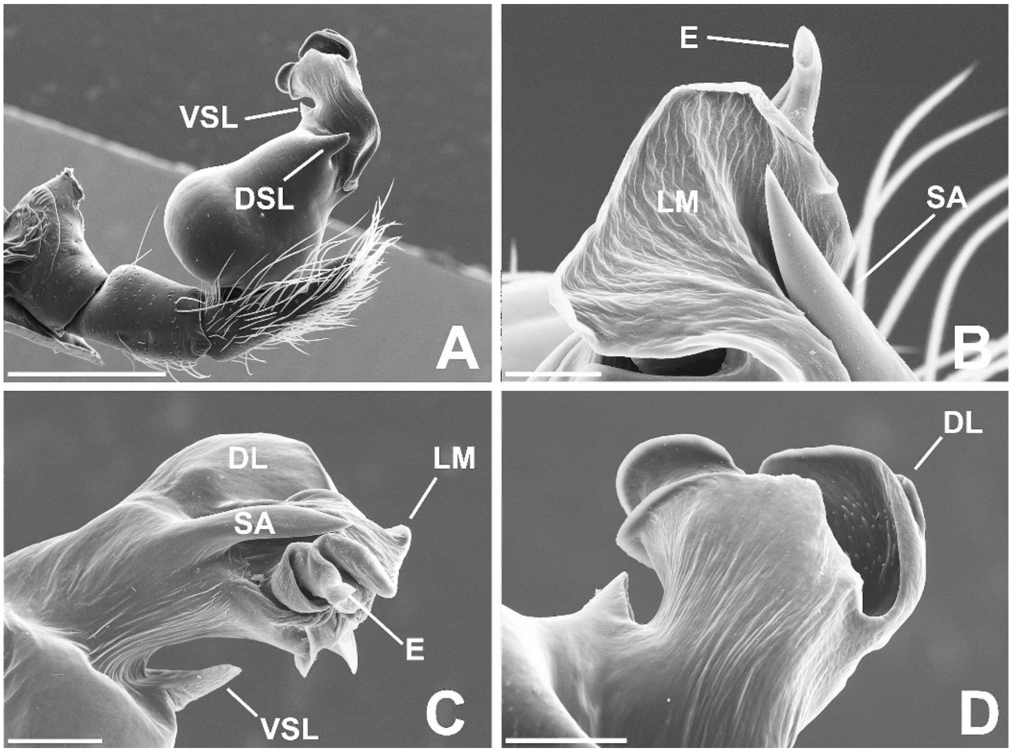
Other material examined.—ARGENTINA: *Neuquén Province*: Cerro Bayo, 1304 m, 40.74796°S, 71.59779°W, March 2005, V. Werenkraut, pitfall traps (cod. M3S5M05), 2 males



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.

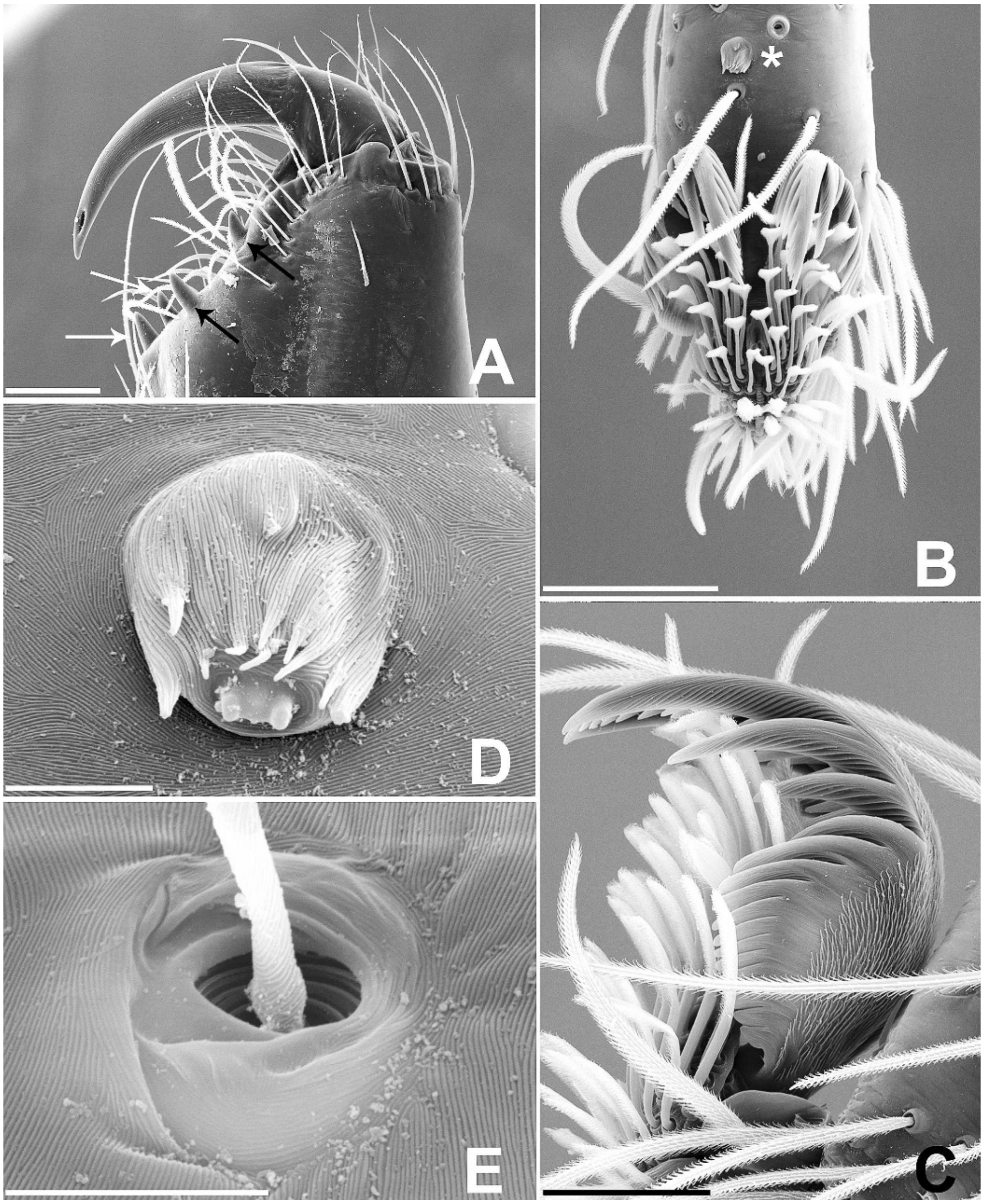
(MACN-Ar 19559); same data January 2006 (cod. M3S5E06), 1 female (MACN-Ar 19560); *Rio Negro Province*: Cerro López, 1502m, 41.09948°S, 71.55801°W, March 2006, V. Werenkraut, pitfall traps (cod. M1S8M06), 1 female (MACN-Ar 19558). CHILE: *Región IX*, *Cautín Province*: Huerquehue National Park, Laguna 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

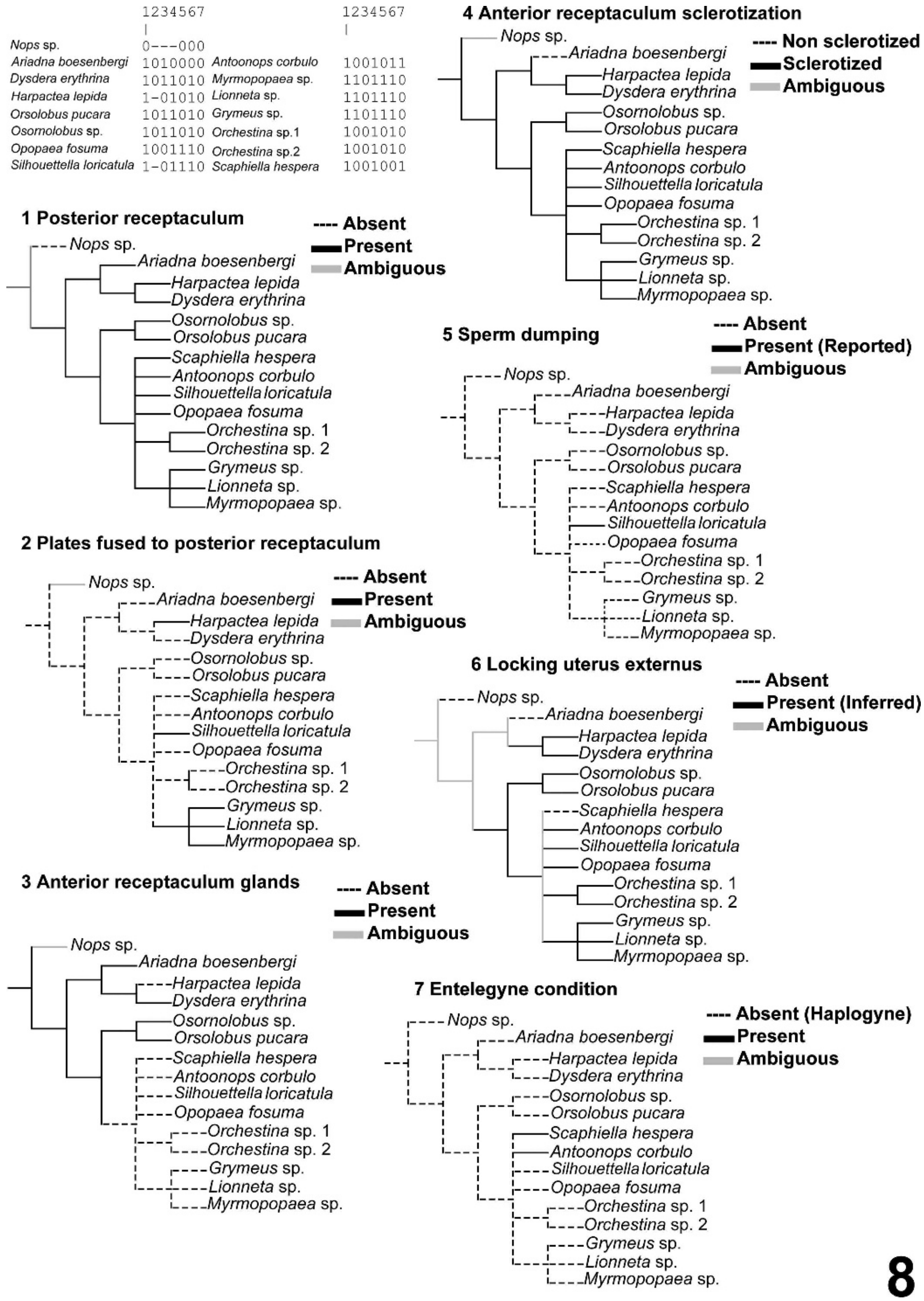


Figures 7 A–E.—*Orsolobus pucara* (MACN-Ar 16567). Female. Left chelicera. A. Posterior view, black arrowheads to the retromarginal teeth, white arrowheads to the promarginal teeth. B–E. Left leg I structures. B. Tarsal claws in dorsal-apical view, asterisk on the distal tarsal organ; C. Claws in retrolateral 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 boesenbergi	1010000	*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.

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LITERATURE CITED

Baehr, B.C. & H.M. Smith. 2008. Three new species of the Australian orsolobid spiders genus *Hickmanolobus* (Araneae: Orsolobidae). Records of the Western Australian Museum 24:325–336.

Brescovit, A.D., L.A. Bertoncello, R. Ott & A.A. Lise. 2004. Description and ecology of two new species of the brazilian spider genus *Losdolobus* Platnick & Brescovit (Araneae, Dysderoidea, Orsolobidae). Revista Ibérica de Aracnología 9:249–257.

Burger, M. 2007. Sperm dumping in a haplogyne spider. Journal of Zoology 273:74–81.

Burger, M. 2009. Female genitalia of goblin spiders (Arachnida: Araneae: Oonopidae): a morphological study with functional implications. Invertebrate Biology 128:340–358.

Burger, M. 2010. Complex female genitalia indicate sperm dumping in armored goblin spiders (Arachnida, Araneae, Oonopidae). Zoology 113:19–32.

Burger, M., W. Nentwig & C. Kropf. 2003. Complex genital structures indicates cryptic female choice in haplogyne spiders (Arachnida, Araneae, Oonopidae, Gamasomorphinae). Journal of Morphology 255:80–93.

Burger, M., W. Graber, P. Michalik & C. Kropf. 2006. *Silhouettella loricatula* (Arachnida, Araneae, Oonopidae): A haplogyne spider with complex female genitalia. Journal of Morphology 267: 663–667.

Burger, M. & C. Kropf. 2007. Genital morphology of the haplogyne spider *Harpactea lepida* (Arachnida, Araneae, Dysderidae). Zoomorphology 126:45–52.

Burger, M., M. Izquierdo & P. Carrera. 2010. Female genital morphology and mating behavior of *Orchestina* (Arachnida: Araneae: Oonopidae). Zoology 113:100–109.

Eberhard, W.G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey.

Fannes, W. & R. Jocqué. 2008. Ultrastructure of *Antoonops*, a new, ant–mimicking genus of afrotropical Oonopidae (Araneae) with complex internal genitalia. American Museum Novitates 3614:1–30.

Forster, R.R. & N.I. Platnick. 1985. A review of the austral spiders family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. Bulletin of the American Museum of Natural History 181:1–229.

Goloboff, P.A., J.S. Farris & K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Grismado, C.J. 2008. A taxonomic revision of the spider genus *Ariadna* Audouin, 1826 in Argentina and Chile, with the description of five new species (Arachnida, Araneae, Segestriidae). Zoosystema 30:333–360.

Griswold, C.E. & N.I. Platnick. 1987. On the first African spiders of the family Orsolobidae (Araneae, Dysderoidea). American Museum Novitates 2892:1–14.

Huber, B.A. 2002. Functional morphology of the genitalia in the spider *Spermophora senoculata* (Pholcidae, Araneae). Zoologischer Anzeiger 241:105–116.

Huber, B.A., A.D. Brescovit & C. Rheims. 2005. Exaggerated female genitalia in two new spiders (Araneae, Pholcidae), with comments on genital evolution by female choice versus antagonistic coevolution. Insect Systematics & Evolution 36:285–292.

Platnick, N.I., J.A. Coddington, R.R. Forster & C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders

(Araneae, Araneomorphae). American Museum Novitates 3016: 1–73.

Platnick, N.I. & A.D. Brescovit. 1994. A new genus of the spider family Orsolobidae (Araneae, Dysderoidea) from Brazil. American Museum Novitates 3112:1–6.

Platnick, N.I. & N. Dupérré. 2009. The American goblin spiders of the new genus Escaphiella (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 328:1–151.

Platnick, N.I., C.J. Grismado & M.J. Ramírez. 1999. On the genera of the spider subfamily Otiothopinae (Araneae, Palpimanidae). American Museum Novitates 3257:1–25.

Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of Haplogyne spiders (Araneae, Araneomorphae). Journal of Arachnology 28:149–157.

Uhl, G. 2000. Two distinctly different sperm storage organs in female *Dysdera erythrina* (Araneae, Dysderidae). Arthropod Structure & Development 29:163–169.

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Female genital morphology and mating behavior of *Orchestina* (Arachnida: Araneae: Oonopidae)

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ABSTRACT

The unusual reproductive biology of many spider species makes them compelling targets for evolutionary investigations. Mating behavior studies combined with genital morphological investigations help to understand complex spider reproductive systems and explain their function in the context of sexual selection. Oonopidae are a diverse spider family comprising a variety of species with complex internal female genitalia. Data on oonopid phylogeny are preliminary and especially studies on their mating behavior are very rare. The present investigation reports on the copulatory behavior of an *Orchestina* species for the first time. The female genitalia are described by means of serial semi-thin sections and scanning electron microscopy. Females of *Orchestina* sp. mate with multiple males. On average, copulations last between 15.4 and 23.54 min. During copulation, the spiders are in a position taken by most theraphosids and certain members of the subfamily Oonopinae: the male pushes the female back and is situated under her facing the female's sternum. Males of *Orchestina* sp. possibly display post-copulatory mate-guarding behavior. The female genitalia are complex. The genital opening leads into the uterus externus from which a single receptaculum emerges. The dorsal wall of the receptaculum forms a sclerite serving as muscle attachment. A sclerotized plate with attached muscles lies in the posterior wall of the uterus externus. The plate might be used to lock the uterus during copulation. The present study gives no direct evidence for cryptic female choice in *Orchestina* sp. but suggests that sexual selection occurs in the form of sperm competition through sperm mixing.

Introduction

Mating behavior observations in combination with a thorough investigation of the genital morphology have large potential consequences for the understanding of the reproductive biology of a particular species (e.g., Huber, 1994, 1995; Uhl et al., 1995; Huber and Eberhard, 1997; Burger, 2007). Especially fine genital morphological details help to understand the evolution of the genitalia and to explain their function in the context of sexual selection (Eberhard, 1985, 1996, 2004a, b; Galis, 1996; Hellriegel and Ward, 1998; Burger et al., 2003, 2006a, c; Huber, 2003, 2006; Alberti and Michalik, 2004; Burger and Kropf, 2007; Burger, 2008, 2009, 2010).

The unusual reproductive biology of many spider species makes them compelling targets for evolutionary studies (Eberhard, 2004a). According to the classification of Simon (1893), araneomorph spiders were separated into the two groups Haplogynae and Entelegynae based on the gross morphology of their genitalia. In contrast to the more complex female genitalia of entelegynes, haplogynes are traditionally considered to have simple female genitalia (Wiehle, 1967; Austad, 1984; Uhl, 2002). Almost 3000 described species in 17 families belong to the Haplogynae (Platnick, 2009) and their monophyly seems to be well founded based on the origin of a cheliceral lamina, the basal fusion of the chelicerae, the fusion of the tegulum and subtegulum, and the loss of tartipores (Coddington and Levi, 1991; Platnick et al., 1991; Ramirez, 2000).

Investigations of genital morphology and copulatory mechanics in spiders have been carried out for entelegynes (e.g., van Helsdingen, 1965; Huber, 1993, 2004b; Uhl and Vollrath, 1998; Uhl and Gunnarsson, 2001; Berendonck and Greven, 2002, 2005; Dimitrov et al., 2007; Useta et al., 2007) and haplogynes (Huber, 1994, 1995, 1997, 1998, 2002, 2004a, b, 2006; Uhl, 1994, 1998, 2000, 2002; Uhl et al., 1995; Huber and Eberhard, 1997; Senglet, 2001; Burger et al., 2003, 2006a, c; Burger, 2007, 2008, 2009, 2010; Burger and Kropf, 2007; Fannes and Jocqué, 2008).

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However, data on mating behavior and genital morphology are still missing for a majority of the haplogyne families.

Oonopidae are a highly diverse spider family belonging to the Haplogynae. They comprise a variety of species with rather complex internal female genitalia that do not correspond to the conventional type of haplogyne genitalia described by e.g. Wiehle (1967) (Dumitresco and Georgesco, 1983; Saaristo, 2001; Burger et al., 2003, 2006a; Burger, 2007, 2009, 2010; Fannes and Jocqué, 2008). The family is widespread in many habitats on all continents (except Antarctica) (e.g., Gerhardt, 1933; Chickering, 1951; Dumitresco and Georgesco, 1983; Harvey, 1987; Saaristo, 2001) and systematically placed within the group of the Dysderoidea (Coddington and Levi, 1991; Platnick et al., 1991). Especially the life history of most oonopids is unknown and descriptions of their mating behavior are very rare (Bristowe, 1929, 1930; Gerhardt, 1930, 1933; Burger, 2007). Relationships among oonopids are still largely unknown and many, perhaps most, of the genera have yet to be described. Two subgroups are conventionally recognized within Oonopidae (Simon, 1893) and often treated as subfamilies – the armored "loricati" or Gamasomorphinae and the soft-bodied "molles" or Oonopinae, which are presumably more basal oonopids. Chamberlin and Ivie (1945) highlighted the distinctiveness of the genus *Orchestina* from other oonopid genera by erecting the subfamily Orchestininae – a hypothesis which was not further considered in subsequent studies.

The present study reports on the copulatory behavior of a member belonging to the oonopine genus *Orchestina* for the first time. The female genitalia are described in detail by means of serial semi-thin sections and scanning electron microscopy. In addition, the male palp is briefly described. Mating behavior and functional aspects of the female genitalia are discussed in the context of previous studies on haplogynes.

Material and methods

Specimens

4 ♀ (PBI_OON 14890, PBI_OON 14905 MACN–Ar 17674, PBI_OON 14907 MACN–Ar 17675, PBI_OON 14908 MACN–Ar 17676), 4 ♂ (PBI_OON 14879 MACN–Ar 17718, PBI_OON 14882 MACN–Ar 17714, PBI_OON 14922 MACN–Ar 17678, PBI_OON 14924 MACN–Ar 17677), Argentina, Jujuy, Parque Nacional Calilegua, Seccional Aguas Negras, 23°45′43.3″S, 64°51′04.7″W (±10 m, WGS84), elev. 605 m (GPS), col. C. Grismado, M. Izquierdo, F. Labarque, G. Rubio, M. Burger, P. Michalik, P. Carrera, A. Ojanguren, C. Mattoni, 6–11 December 2008, beating foliage; 2 ♀ (PBI_OON 14895 MACN–Ar 18016, PBI_OON 14896 MAC–Ar 18015), 2 ♂ (PBI_OON 14895 MACN–Ar 18016), same data, col. M. Izquierdo, L. Zapata, M. Akmentins, 27–31 January 2009. The material is deposited in the collection of arachnids of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN–Ar, Cristina Scioscia).

Mating behavior

The spiders were mature when collected and thus their mating history was unknown. The specimens collected on December 6–11, 2008 were brought to the Laboratorio de Biología Reproductiva y Evolución of the Universidad Nacional de Córdoba. The females were individually kept in plastic boxes (9 cm × 6.5 cm × 2.5 cm) with ground gypsum. A small plastic cap (2.5 cm diameter) containing a humid paper towel (5 cm × 10 cm) was added in each box. The towel was moistened every other day with a few drops of water. The males were individually kept in Eppendorf tubes (1.5 ml) together with a small paper towel moistened every other day. The spiders were not fed. Three females and three males were used for the mating behavior studies.

Copulations were observed with a binocular microscope (Nikon SMZ 1500, Nikon Instruments Inc., Tokyo, Japan) with attached digital camera. Photographs of the matings were taken at different focus levels, combined into a single shot using the software CombineZP, and partially edited using Adobe Photoshop Elements 2.0 (Adobe Systems Inc., San Jose, CA, USA).

For each pairing, the male was carefully removed from his tube and placed into the female's box. The first palpal insertion by the male was taken as the beginning of copulation. The end of copulation was defined as the moment when the spiders physically separated, which was also the moment when the copulatory organs were decoupled. In the results section, copulation durations are given as averages ± standard deviation. Post-copulatory behavior was observed for 15 min in each case before the spiders were separated. All females were mated three times in the lab (once with each male) and were given a resting period of 1–3 days between each copulation. The copulations are referred to as first, second, and third copulation, respectively. One female was mated twice on the same day with a resting period of 1 h between the copulations. The females were sacrificed one day after their third copulation using ethanol.

Light microscopy

The opisthosomas of the three females observed in the mating tests were dehydrated in a graded ethanol series, embedded in soft-grade acrylic resin (LR White; London Resin Co., London, UK) and semi-thin serially sectioned (1 μm) with a microtome (Sorvall JB-4, Thermo Fischer Scientific Inc., Waltham, MA, USA) using glass knives. The sections were stained with toluidine blue (1%) in an aqueous borax solution (1%) at approximately 90 °C for 30–60 s. Light microscopic studies were performed with an Olympus BH-2 (Olympus Corp., Tokyo, Japan) and a Leica DM2500 (Leica Microsystems GmbH, Wetzlar, Germany). The sections were photographed with a Leica DFC500 digital camera (Leica Camera AG, Solms, Germany) and partly edited using Adobe Photoshop Elements. The palp of one mated male (PBI_OON 14924) was detached, embedded in Hoyer's medium and slide-mounted. Drawings were made with an ink pen on finely granulated paper under an Olympus BH-2 light microscope with attached drawing tube and then shaded with a graphite pen. The drawings were scanned and edited using Adobe Photoshop Elements 2.0. The genitalia of one female (PBI_OON 14896) were embedded in clove oil, slide-mounted and observed under an Olympus BH-2 light microscope. Photographs were taken with a digital camera (Nikon DXM1200; Nikon Instruments Inc., Tokyo, Japan) and the focal planes were combined with Helicon Focus 3.10.3 (http://helicon.com.ua/heliconfocus/).

Scanning electron microscopy

The genitalia of two females (PBI_OON 14895) were dissected and kept in a borax–pancreatin solution for 1–2 h according to the protocol of Alvarez-Padilla and Hormiga (2007). After digestion the genitalia were flushed with a micropipette in distilled water until all the soft tissues were removed. The female genitalia and one male palp (PBI_OON 14924) were dehydrated in a graded ethanol series (80–100%), critical-point dried, and gold-sputtered. Scanning electron micrographs were taken under high vacuum with a FEI XL30 TMP (FEI Company, Hillsboro, OR, USA).

Results

Mating behavior

Pre-copulatory behavior

All of the females were sitting inside a little sheet web, which they had constructed on the side or in a corner of the box. When a male was placed in the female's box, he usually walked around. When he came into contact with the threads of a female's web, the male commenced searching for the female. He usually walked over the web for several times and searched for an opening. The female then reacted by turning (if necessary) and facing him. No male was ever seen filling his pedipalps with sperm prior to copulation. The male quickly advanced toward the female until both spiders touched each other's front legs (Fig. 1A). From there, the male either took the copulatory position directly by pushing the female back and creeping under her (Fig. 1B) or both palpated each other with their front legs first. In the latter cases, both spiders typically raised their cephalothorax and touched each others' metatarsi and tarsi of the first legs. The bouts lasted approximately 3–8 s. It could not be determined whether the palpating was initiated by the female or the male.

Special cases

(i) One male displayed a slightly different behavior prior to each of his three copulations: after coming in contact with the female (as described above), the male seemed to hesitate. He moved back and away from the female again. The female followed him and touched his first legs slightly. The male usually did not react and the female moved back again. This behavior could be repeated several times before the male finally made a quick advance toward the female and took the copulatory position. (ii) In one pairing [third pairing of the female; different male than in (i)], the female showed seemingly aggressive behavior. As soon as the male approached her, she scared him away with vigorous vibrations of the body, especially the front legs. The male moved back and stayed outside of the web for a few seconds. Then he approached the female again and she showed the same behavior. This behavior was repeated four times before the male managed to creep under the female and to take the copulatory position. The female moved back and tried to turn around but the male managed to copulate anyway. (iii) The female that was mated twice on the same day left the web after the second copulation and constructed a new web in another corner of the box. When a male was placed into the box the next day, he came in contact with the threads of the old web and commenced searching for the female there. He stayed inside the web. After approximately 15 min the male was removed from the web by the authors and brought close to the female. He immediately approached the female and displayed the pre-copulatory behavior described above.

Copulatory behavior

The first copulations lasted 18.11 ± 3.04 min, the second copulations 15.40 ± 3.35 min, and the third copulations 23.54 ± 5.29 min. In the copulatory position the male was under the female facing her sternum (Fig. 1C). The male palps were inserted simultaneously and moved alternately during the entire copulation. Only one palp moved at a time whereas the other remained motionless. The palp moved up and down and back and forth. The palp movements stopped approximately 2 min before the end of copulation. In some cases, the female slightly tapped the male with her prosoma approximately 30 s before separation. When the spiders separated, the male quickly moved back and both spiders palpated each other with the front legs for a few seconds. Sometimes, the female scared the male away with vibrations of her body and then turned around.

Post-copulatory behavior

After the separation, the male stayed close to the female's web (Fig. 1D) and showed intense self-grooming. He often ran his pedipalps through the chelicerae. The male kept walking over the female's web and spun threads over it. When he contacted the female by typically touching her front legs with his front legs, she scared him away with slight movements of the front legs and turned around. Sperm re-induction by the male could not be observed.

Morphology of the female genitalia

The slit-like genital opening (GO in Figs. 2A, B, 3A, B, 4A) of female *Orchestina* sp. lies in the epigastric furrow. It is bordered by a thick sclerotized ridge (Ri1 in Figs. 2A, B, 3A, D, 4A) anteriorly and paired short sclerotized ridges (Ri2 in Figs. 2A, 3A) posteriorly. Anterior of the genital opening, the cuticle of the opisthosoma forms paired semicircular apodemes (Ap in Figs. 2A, 3A, 4A, B) connected by a thin sclerotized ridge (Ri3 in Figs. 2A, B, 3A, 4B). The genital opening leads into the uterus externus (UE in Figs. 2B, 3B, 4D), which forms a median anterior fold (Fo in Figs. 2B, 3B). Laterally, the uterus externus is reduced to a short fold (arrowheads in Fig. 2A). A single bulge-like receptaculum (Re in Figs. 2A, B, 3A–D, 4C) emerges anteriorly from the uterus externus. The receptaculum is reduced to a small fold laterally (arrows in Fig. 2A). In all of the investigated females, spermatozoa (Sp in Fig. 3C, D) surrounded by secretion (Sec in Fig. 3C) were present in the receptaculum. On semi-thin sections, the spermatozoa appear as small dark particles (see Fig. 3C). The dorsal wall of the receptaculum forms a massive sclerite (Sc in Figs. 2A, B, 3A, B, D, 4B, C), which extends considerably toward anterior. The anterior part of the sclerite shows two lateral protrusions (Pr in Figs. 2A, C, 3A, E, 4B, C). Inside the anterior part of the sclerite, a large hollow space (see Figs. 2A, B, 3A, B, E) connects to the lumen of the receptaculum via a small circular cavity (Ca in Figs. 2A, B, 3A, E). The hollow space in two of the investigated females seemed to contain a small amount of secretion (Sec in Fig. 3D). The cavity continues into a curved slit (Sl in Figs. 2A, B, 3A, B, E) proceeding through the posterior part of the sclerite. The slit is connected with the lumen of the receptaculum (see Fig. 2B). A thin lamella (La in Figs. 2B, 3C) emerges posteriorly from the sclerite and reaches into the lumen of the receptaculum. A hook-like posterior extension (Ho in Figs. 2A, B, 3B) of the sclerite reaches into a depression (Dp in Figs. 2A, B, 3B) of a massive plate (Pl in Figs. 2A–C, 3A, B, D, E, 4B–D). The ventral extensions of the plate (Ex1 in Figs. 2A, 4B, D) are fused with the posterior wall of the uterus externus (see Fig. 4D). The plate is curved forward and expands considerably toward dorsal (see Figs. 2B, 3B, 4B, C). It forms massive lateral extensions dorsally (Ex2 in Figs. 2A, C, 3A, 4B, C).

The plate (Pl in Fig. 2C) serves as attachment site for various muscles. A paired muscle set (M1 in Fig. 2C) runs from the lateral parts of the plate toward ventral and attaches on the cuticle of the opisthosoma. Another muscle set (M2 in Figs. 2C, 3A, E) connects the lateral extensions of the plate (Ex2 in Fig. 2C) with the lateral protrusions (Pr in Fig. 2C) of the sclerite. The anterior part of the sclerite serves as attachment site for muscles (M3 in Figs. 2C, 3A, B, E) running to the ventral cuticle of the opisthosoma. Paired thin muscles (M4 in Figs. 2C, 3A) originate on the lateral extensions of the plate and are directed laterally, ending on the cuticle of the opisthosoma.

Morphology of the male palp

The tibia of the male palp of *Orchestina* sp. is swollen (see Fig. 5). The large, pyriform palpal bulb (PBu in Fig. 5)

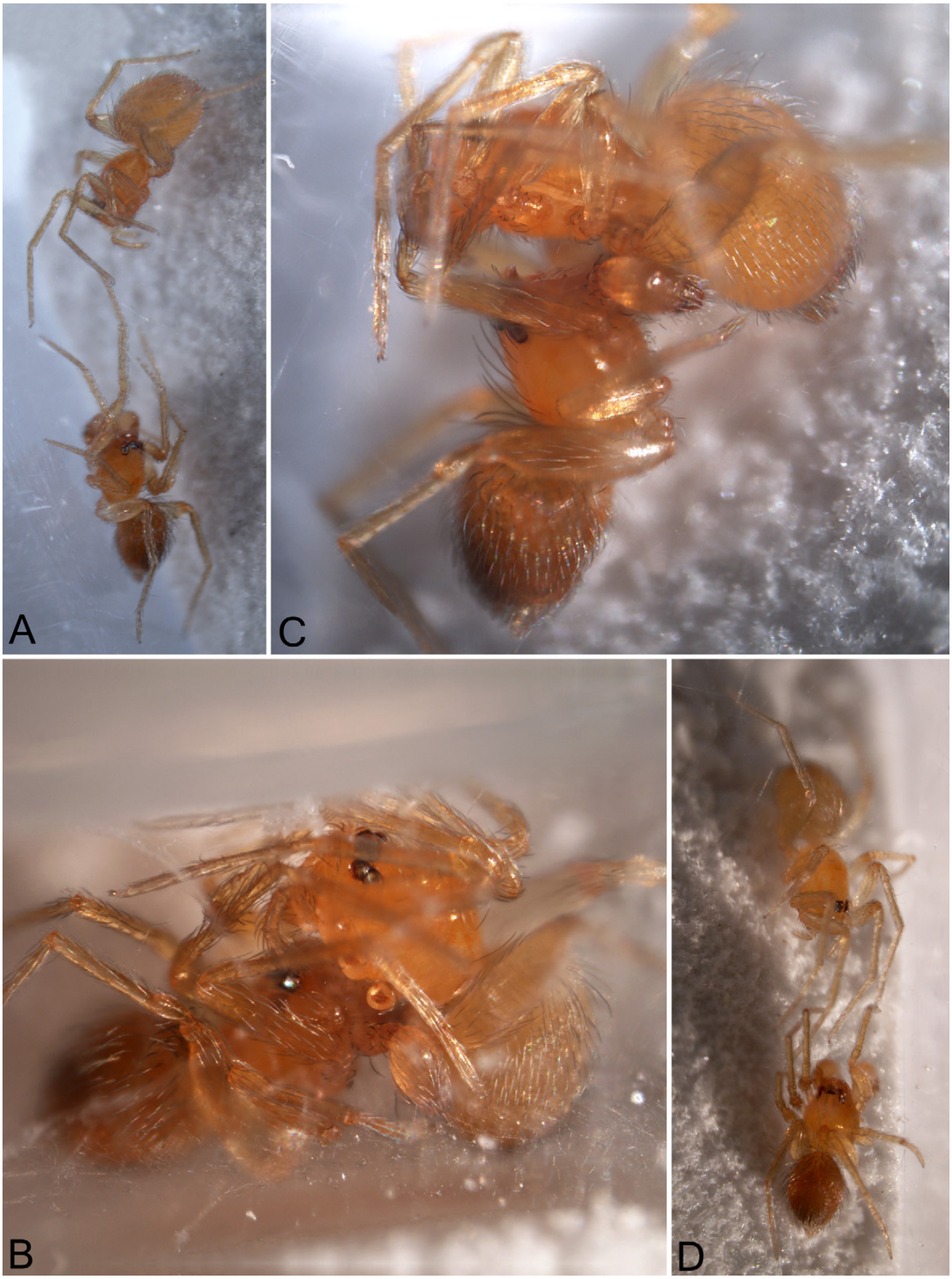

Fig. 1. Female and male of *Orchestina* sp. prior, during, and after copulation. Male at the bottom in (A), (C), (D), on the left in (B). (A) Male approaches female prior to copulation and both spiders touch each other's front legs. (B) Male pushes female back and creeps under her to take copulatory position. (C) Spiders in copula. (D) Male stays close to female after copulation.

continues into a short embolus (Em in Figs. 4E, F, 5) with the opening (EOp in Fig. 4E, F) situated at the tip. A small denticle (De in Figs. 4E, 5) is present at the base of the embolus on the prolateral side. The sclerotized sperm duct (SD in Fig. 5) is strongly curved and visible through the cuticle of the palpal bulb. Some areas of the sperm duct have pores (see arrowheads in Fig. 5) into which presumably gland ducts are leading.

Discussion

Mating behavior

Male spiders often display extensive courtship behavior prior to copulation (e.g., Maklakov et al., 2003; Cross et al., 2008; Gibson and Uetz, 2008). However, in haplogynes, the courtship by

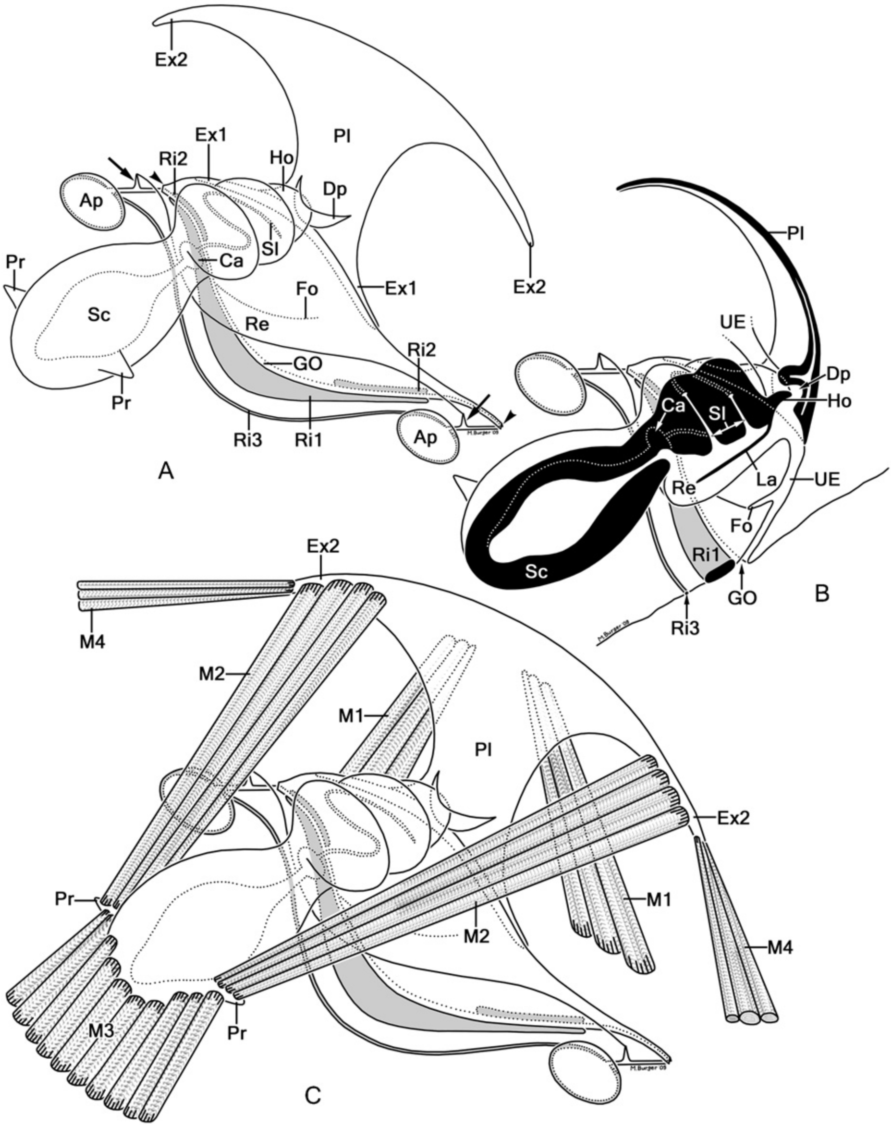

Fig. 2. Schematic drawings of female genitalia of *Orchestina* sp. (A) Overview. Arrowheads indicate lateral parts of the uterus externus, arrows point to lateral parts of the receptaculum (see text for details). (B) Median longitudinal section. (C) Genitalia with muscles. Abbreviations: Ap, apodeme; Ca, circular cavity; Dp, depression; Ex1, Ex2, lateral extensions of plate; Fo, fold; GO, genital opening; Ho, hook-like extension; La, lamella; M1–M4, muscles 1–4; Pl, plate; Pr, protrusion; Re, receptaculum; Ri1–Ri3, sclerotized ridges; Sc, sclerite; Sl, slit; UE, uterus externus.

males (if there is any at all) is restricted to vibrations of the opisthosoma or simple leg and palp movements (e.g., Bristowe, 1929; Gerhardt, 1929; Uhl et al., 1995; e.g., Bartos, 1998; Huber, 2002; Burger et al., 2006a). In the observed matings of *Orchestina* sp., male and female palpated each other with the front legs before copulation, which could represent some sort of pre-copulatory courtship behavior. Some of the variations – especially in the pre-copulatory behavior – described under "special cases" might be explained by the different mating history of the spiders. The palpation of the legs prior to copulation was also described for the oonopine *Oonops placidus* by Gerhardt (1930). Interestingly, Gerhardt (1930) also stressed the fact that the palps in *O. placidus* were inserted simultaneously but moved differently from other haplogynes that insert both palps at the same time such as certain dysderids (e.g., Jackson and Pollard, 1982) and pholcids (e.g., Huber, 1995; Uhl et al., 1995): only one palp moved at a time, whereas the other remained motionless. The present study shows that the same pattern of palp movements occurs in *Orchestina* sp.

In the most "primitive" copulatory position the male approaches the female frontally and creeps under her by pushing her back. The palps are inserted simultaneously or alternately (see von Helversen, 1976). This position is taken by most theraphosids (e.g., Gerhardt, 1929; Yáñez et al., 1999) and certain haplogynes such as *Segestria bavarica* (Gerhardt, 1929) and *Dysdera crocata* (Jackson and Pollard, 1982). The "primitive" copulatory position also occurs in members of the oonopine genera *Oonops* (Bristowe, 1929; Gerhardt, 1930; see also von Helversen, 1976) and *Orchestina* (as the present study shows), which are presumably more basal oonopids. A more "derived" copulatory position has evolved convergently in different spider groups: the male moves back and both spiders turn their ventral sides toward each other facing in the same direction (von Helversen, 1976). This position is adopted by certain gamasomorphine oonopids such as *Xestaspis nitida* (Gerhardt, 1933), *Grymeus robertsi* (Harvey, 1987), and *Silhouettella loricatula* (Bristowe, 1930; Burger, 2007), as well as by certain members of the family Tetrablemmidae (Burger et al., 2006a; Edwards and Edwards, 2006).

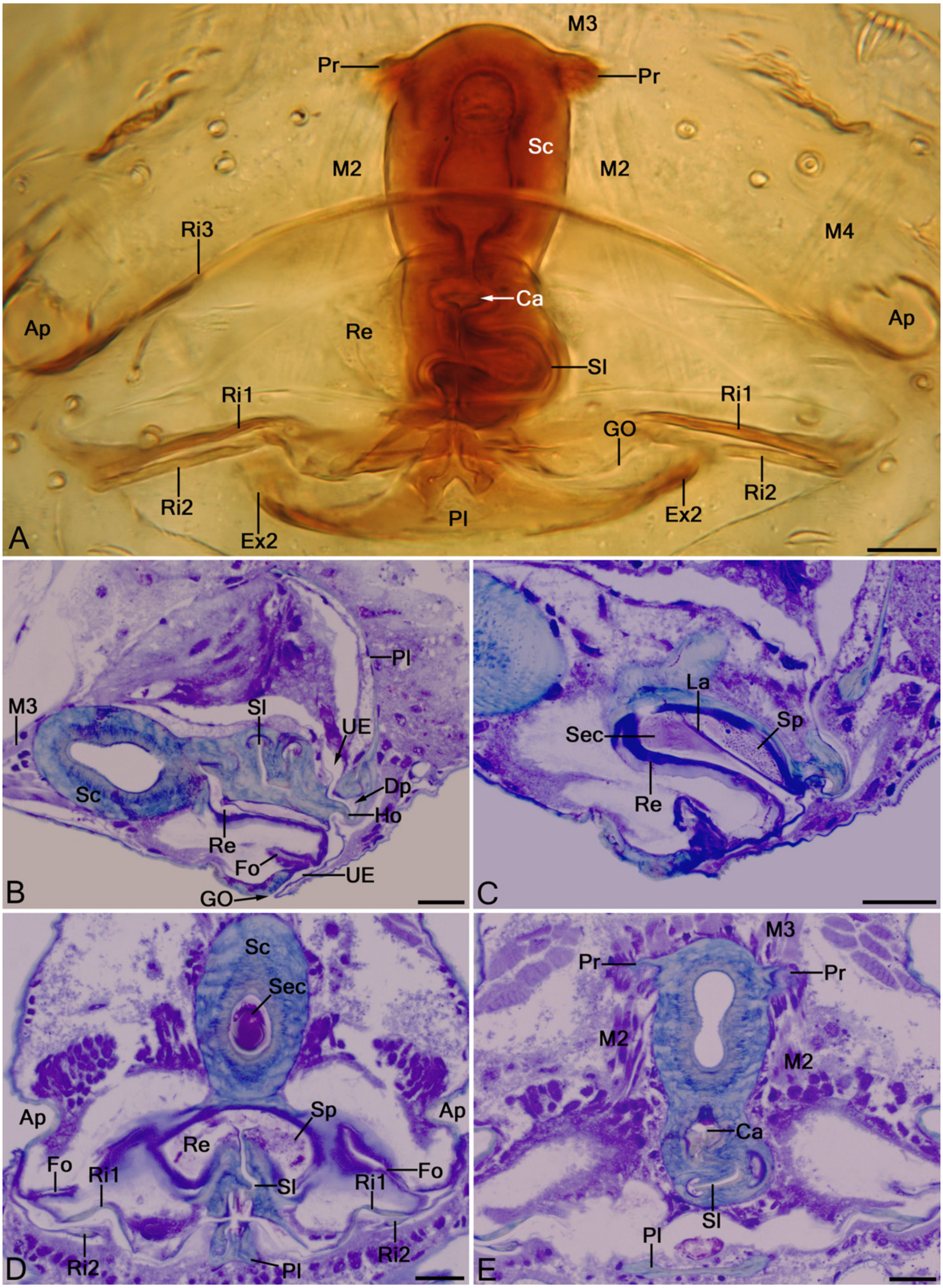

Fig. 3. Female genitalia of *Orchestina* sp., light microscopy. (A) Slide-mounted genitalia embedded in clove oil, dorsal view. (B) Median longitudinal section showing sclerite and plate. (C) Longitudinal section showing receptaculum that contains spermatozoa and secretion. (D) Horizontal section showing ventral part of receptaculum and sclerite. (E) Horizontal section showing dorsal part of sclerite with attached muscles. Scale bars: 20 μm. Abbreviations: Ap, apodeme; Ca, circular cavity; Dp, depression; Ex2, lateral extension of plate; Fo, fold; GO, genital opening; Ho, hook-like extension; La, lamella; M2–M4, muscles 2–4; Pl, plate; Pr, protrusion; Re, receptaculum; Ri1–Ri3, sclerotized ridges; Sc, sclerite; Sec, secretion; Sl, slit; Sp, spermatozoa; UE, uterus externus.

After copulation, the male of *Orchestina* sp. always stayed close to the female and sometimes spun threads over her web. Males accompanying females after copulation were observed in other haplogynes, such as the pholcid *Physocyclus globosus* (Eberhard, 1992; Huber and Eberhard, 1997). In some insects and spiders, the male guards the female prior to or after copulation in order to restrict access of other males to the female, thus guarding and protecting his own transferred ejaculate (e.g., Sillén-Tullberg, 1981; Schöfl and Taborsky, 2002; Prenter et al., 2003; Wynn and Vahed, 2004). However, whether the behavior displayed by male

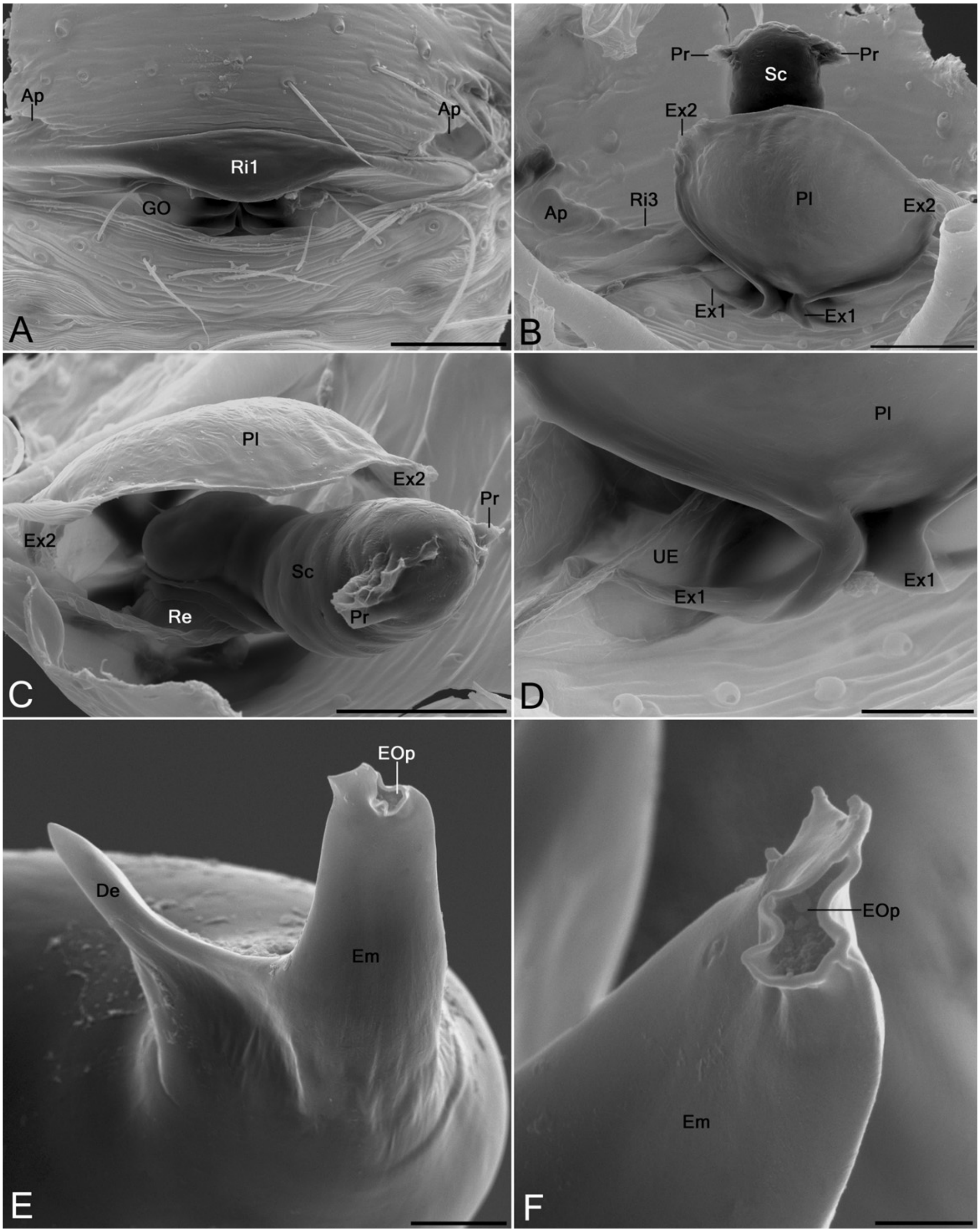

Fig. 4. Female and male genitalia of *Orchestina* sp., scanning electron micrographs. (A) Female genital region, ventral view. (B) Internal female genitalia showing sclerite and plate, dorsal view. (C) Internal female genitalia showing sclerite and plate, antero-dorsal view. (D) Detail of plate, postero-lateral view. (E) Left embolus of male, antero-lateral view. (F) Left embolus of male with opening, apical view. Scale bars: 50 μm (A–C), 20 μm (D), 10 μm (E), 3 μm (F). Abbreviations: Ap, apodeme; De, denticle; Em, embolus; EOp, embolus opening; Ex1, Ex2, lateral extensions of plate; GO, genital opening; Pl, plate; Pr, protrusion; Re, receptaculum; Ri1, Ri3, sclerotized ridges; Sc, sclerite; UE, uterus externus.

Orchestina sp. serves as post-copulatory mate guarding remains unknown at this point.

Morphology of the female genitalia

Previous studies proved that the female genitalia of certain oonopids are astonishingly complex and clearly differ from the concept proposed for the group Haplogynae (Dumitresco and Georgesco, 1983; Burger et al., 2003, 2006a; Burger, 2007, 2009, 2010; Fannes and Jocqué, 2008). A widely accepted theory nowadays is that complicated genital structures have evolved under sexual selection by cryptic female choice (Thornhill, 1983; Eberhard, 1985, 1996), which is defined as female behavior, physiology or morphology that biases sperm precedence in favor of certain males against others after the beginning of copulation (Eberhard and Cordero, 1995).

The female genital structures of *Orchestina* sp. are complex and resemble the genitalia of the oonopine *Stenoonops reductus*

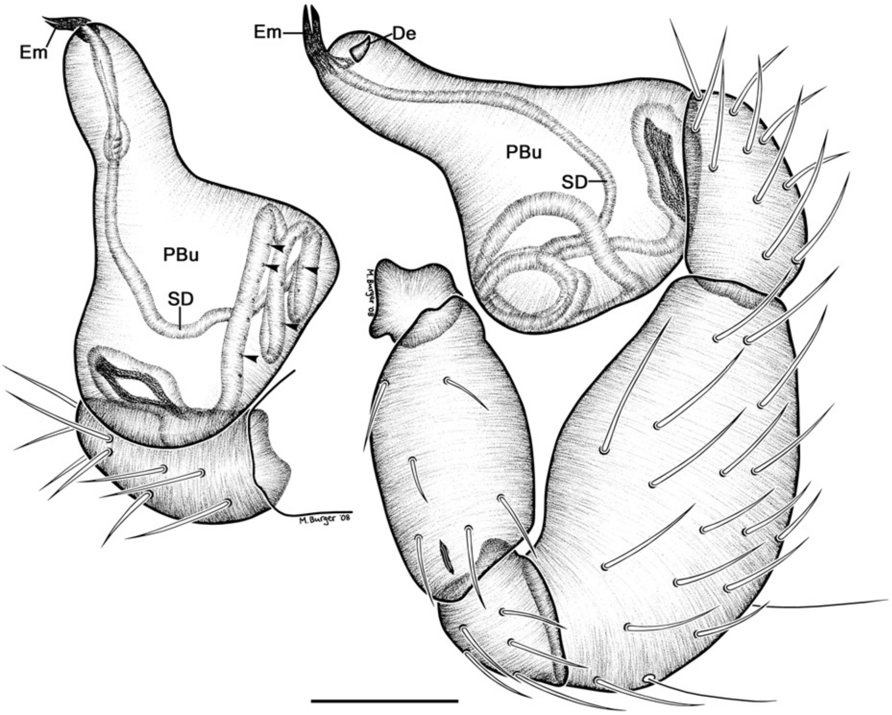

Fig. 5. Drawings of right palp of male *Orchestina* sp., prolateral view; retrolateral view of palpal bulb on the left. Arrowheads pointing to pores on sperm duct. Scale bar: 100 µm. Abbreviations: De, denticle; Em, embolus; PBu, palpal bulb; SD, sperm duct.

(Burger, 2009) and the dysderid *Harpactea lepida* (Burger and Kropf, 2007). In all three species, there is a massive anterior sclerite with an internal lumen and a large sclerotized plate with extensions situated in the posterior wall of the uterus externus. Both of these sclerotized structures serve as attachments for muscles (M1–M4 in Fig. 2C; M4 lacking in *H. lepida*) whose arrangement is also comparable in the three species. Interestingly, a number of gamasomorphine oonopids show a modified sclerite situated in the uterus wall. Apparently, the sclerite can be moved back and forth by muscle contractions, suggesting that the uterus externus can be locked, which might prevent sperm from getting into it during copulation (Burger et al., 2003, 2006b; Burger, 2010, 2009). The sclerotized plate (Pl in Fig. 2A–C) in *Orchestina* sp. might have the same function. However, for *S. reductus* and *H. lepida* it was suggested that the plate helps to move the spermatozoa into the receptacula (*S. reductus*; see Burger, 2009) and the uterus externus (*H. lepida*; see Burger and Kropf, 2007), respectively.

The present study shows that the anterior sclerite in *Orchestina* sp. extends from the sclerotized dorsal wall of the receptaculum where sperms are stored. A similar situation occurs in *H. lepida* where roundish sclerotized structures containing sperm are connected with the anterior sclerite (Burger and Kropf, 2007). The large sperm storage organs in *Stenoonops reductus*, however, have no connection to the anterior sclerite (Burger, 2009). Forster and Platnick (1985) proposed that the development of a posterior diverticulum as sperm storage organ represents a synapomorphy for the Dysderoidea (including the families Orsolobidae, Oonopidae, Dysderidae, and Segestriidae). According to these authors the primitive dysderoid genitalia consisted of an anterior receptaculum in association with a posterior secretory gland system, which was modified into a posterior diverticulum (or receptaculum) in certain dysderoid genera (Forster and Platnick, 1985). Apparently, in the investigated *Orchestina* sp. in the present study the posterior diverticulum is missing, which is also seen in orsolobids belonging to the genus *Subantarctia* (Forster and Platnick, 1985). In some gamasomorphine oonopids, however, the anterior receptaculum seems to be reduced (compare Burger et al., 2003, 2006b; Burger, 2010).

A study on the gamasomorphine *Silhouettella loricatula* showed that females of this species dump sperm of previous males during subsequent matings and thus might be able to exert cryptic female choice (Burger, 2007). Sperm dumping was suggested for other gamasomorphines according to the morphology of the female genital tracts (Burger et al., 2003; Burger, 2010). The present study gives no morphological or behavioral evidence for sperm dumping in *Orchestina* sp. However, sperm ejection during or after copulation cannot be ruled out completely. The female genital morphology of *Orchestina* sp. suggests that the ejaculates of different males mix inside the receptaculum as it occurs in the pholcid *Pholcus phalangioides* (Uhl, 1998; Yoward, 1998). In conclusion, the present study gives no direct evidence for cryptic female choice in *Orchestina* sp., but rather suggests that sexual selection occurs in the form of sperm competition through sperm mixing (see Birkhead and Møller, 1998), which could be influenced by post-copulatory mate guarding by the male.

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References

Alberti, G., Michalik, P., 2004. Feinstrukturelle Aspekte der Fortpflanzungssysteme von Spinnentieren (Arachnida). In: Thaler, K. (Ed.), Diversität und Biologie von Webspinnen, Skorpionen und anderen Spinnentieren. Denisia 12, pp. 1–62.

Alvarez-Padilla, F., Hormiga, G., 2007. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. J. Arachnol. 35, 538–542.

Austad, S.N., 1984. Evolution of sperm priority patterns in spiders. In: Smith, R.L. (Ed.), Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, London, pp. 223–249.

Bartos, M., 1998. Quantitative analyses of male courtship behaviour in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). In: Selden, P.A. (Ed.), Proceedings of the 17th European Colloquium of Arachnology. British Arachnological Society, Burnham Beeches, Edinburgh, pp. 171–176.

Berendonck, B., Greven, H., 2002. Morphology of female and male genitalia of *Latrodectus revivensis* Shulov, 1948 (Araneae, Theridiidae) with regard to sperm priority patterns. In: Toft, S., Scharff, N. (Eds.), European Arachnology 2000. Aarhus University Press, Aarhus, pp. 157–167.

Berendonck, B., Greven, H., 2005. Genital structures in the entelegyne widow spider *Latrodectus revivensis* (Arachnida; Araneae; Theridiidae) indicate a low ability for cryptic female choice by sperm manipulation. J. Morphol. 263, 118–132.

Birkhead, T.R., Møller, A.P., 1998. Sperm Competition and Sexual Selection. Academic Press, London.

Bristowe, W.S., 1929. The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. Proc. Zool. Soc. London 1929, 309–358.

Bristowe, W.S., 1930. A supplementary note on the mating habits of spiders. Proc. Zool. Soc. London 1930, 395–413.

Burger, M., 2007. Sperm dumping in a haplogyne spider. J. Zool. 273, 74–81.

Burger, M., 2008. Functional morphology of armored spiders (Arachnida: Araneae: Tetrablemmidae). J. Morphol. 269, 1073–1094.

Burger, M., 2009. Female genitalia of goblin spiders (Arachnida: Araneae: Oonopidae): a morphological study with functional implications. Invertebr. Biol. 128, 340–358.

Burger, M., 2010. Complex female genitalia indicate sperm dumping in armored goblin spiders (Arachnida, Araneae, Oonopidae). Zoology 113, 19-32, doi: 10.1016/j.zool.2009.04.002.

Burger, M., Kropf, C., 2007. Genital morphology of the haplogyne spider *Harpactea lepida* (Arachnida, Araneae, Dysderidae). Zoomorphology 126, 45–52.

Burger, M., Nentwig, W., Kropf, C., 2003. Complex genital structures indicate cryptic female choice in a haplogyne spider (Arachnida, Araneae, Oonopidae, Gamasomorphinae). J. Morphol. 255, 80–93.

Burger, M., Jacob, A., Kropf, C., 2006a. Copulatory behavior and web of *Indicoblemma lannaianum* from Thailand (Arachnida, Araneae, Tetrablemmidae). J. Arachnol. 34, 176–185.

Burger, M., Graber, W., Michalik, P., Kropf, C., 2006b. *Silhouettella loricatula* (Arachnida, Araneae, Oonopidae): a haplogyne spider with complex female genitalia. J. Morphol. 267, 663–677.

Burger, M., Michalik, P., Graber, W., Jacob, A., Nentwig, W., Kropf, C., 2006c. Complex genital system of a haplogyne spider (Arachnida, Araneae, Tetrablemmidae) indicates internal fertilization and full female control over transferred sperm. J. Morphol. 267, 166–186.

Chamberlin, R.V., Ivie, W., 1945. On some Nearctic mygalomorph spiders. Ann. Entomol. Soc. Am. 38, 549–558.

Chickering, A.M., 1951. The Oonopidae of Panama. Bull. Mus. Comp. Zool. 106, 207–245.

Coddington, J.A., Levi, H.W., 1991. Systematics and evolution of spiders (Araneae). Annu. Rev. Ecol. Syst. 22, 565–592.

Cross, F.R., Jackson, R.R., Pollard, S.D., 2008. Complex display behaviour of *Evarcha culicivora*, an East African mosquito-eating jumping spider. New Zeal. J. Zool. 35, 151–187.

Dimitrov, D., Alvarez-Padilla, F., Hormiga, G., 2007. The female genital morphology of the orb weaving spider genus *Agriognatha* (Araneae, Tetragnathidae). J. Morphol. 268, 758–770.

Dumitresco, M., Georgesco, M., 1983. Sur les Oonopidae (Araneae) de Cuba. Résultats des Expéditions Biospéologiques Cubano-Roumaines à Cuba 4, 65–114.

Eberhard, W.G., 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge.

Eberhard, W.G., 1992. Notes on the ecology and behaviour of *Physocyclus globosus* (Araneae, Pholcidae). Bull. Br. Arachnol. Soc. 9, 38–42.

Eberhard, W.G., 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey.

Eberhard, W.G., 2004a. Why study spider sex: special traits of spiders facilitate studies of sperm competition and cryptic female choice. J. Arachnol. 32, 545–556.

Eberhard, W.G., 2004b. Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. Evolution 58, 1947–1970.

Eberhard, W.G., Cordero, C., 1995. Sexual selection by cryptic female choice on male seminal products – a new bridge between sexual selection and reproductive physiology. Trends Ecol. Evol. 10, 493–496.

Edwards, R.L., Edwards, A.D., 2006. Life history and ecology of the armored spider *Monoblemma muchmorei* (Araneae, Tetrablemmidae). J. Arachnol. 34, 599–609.

Fannes, W., Jocqué, R., 2008. Ultrastructure of *Antoonops*, a new, ant-mimicking genus of Afrotropical Oonopidae (Araneae) with complex internal genitalia. Am. Mus. Novit. 3614, 1–30.

Forster, R.R., Platnick, N.I., 1985. A review of the Austral spider family Orsolobidae (Arachnida, Araneae) with notes on the superfamily Dysderoidea. Bull. Am. Mus. Nat. Hist. 181, 1–230.

Galis, F., 1996. The application of functional morphology to evolutionary studies. Trends Ecol. Evol. 11, 124–129.

Gerhardt, U., 1929. Zur vergleichenden Sexualbiologie primitiver Spinnen, insbesondere der Tetrapneumonen. Z. Morph. Ökol. Tiere 14, 699–764.

Gerhardt, U., 1930. Biologische Untersuchungen an südfranzösischen Spinnen. Z. Morph. Ökol. Tiere 19, 184–227.

Gerhardt, U., 1933. Neue Untersuchungen zur Sexualbiologie der Spinnen, insbesondere der Arten der Mittelmeerländer und der Tropen. Z. Morph. Ökol. Tiere 27, 1–75.

Gibson, J.S., Uetz, G.W., 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. Anim. Behav. 75, 1253–1262.

Harvey, M.S., 1987. *Grymeus*, a new genus of pouched oonopid spider from Australia (Chelicerata: Araneae). Mem. Mus. Vict. 48, 123–130.

Hellriegel, B., Ward, P.I., 1998. Complex female reproductive tract morphology: its possible use in postcopulatory female choice. J. Theor. Biol. 190, 179–186.

Huber, B.A., 1993. Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). Can. J. Zool. 71, 2437–2447.

Huber, B.A., 1994. Genital morphology, copulatory mechanism and reproductive biology in *Psilochorus simoni* (Berland, 1911) (Pholcidae; Araneae). Neth. J. Zool. 44, 85–99.

Huber, B.A., 1995. Copulatory mechanism in *Holocnemus pluchei* and *Pholcus opilionoides*, with notes on male cheliceral apophyses and stridulatory organs in Pholcidae (Araneae). Acta Zool. Stockholm 76, 291–300.

Huber, B.A., 1997. On American *Micromerys* and *Metagonia* (Araneae, Pholcidae), with notes on behavior and natural history. Zool. Scr. 25, 341–363.

Huber, B.A., 1998. Genital mechanics in some neotropical pholcid spiders (Araneae: Pholcidae), with implications for systematics. J. Zool. 244, 587–599.

Huber, B.A., 2002. Functional morphology of the genitalia in the spider *Spermophora senoculata* (Pholcidae, Araneae). Zool. Anz. 241, 105–116.

Huber, B.A., 2003. Rapid evolution and species-specificity of arthropod genitalia: fact or artifact? Org. Divers. Evol. 3, 63–71.

Huber, B.A., 2004a. Evolutionary transformation from muscular to hydraulic movements in spider (Arachnida, Araneae) genitalia: a study based on histological serial sections. J. Morphol. 261, 364–376.

Huber, B.A., 2004b. Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (Gonzalez-Sponga) (Pholcidae: Araneae). J. Zool. 262, 317–326.

Huber, B.A., 2006. Cryptic female exaggeration: the asymmetric female internal genitalia of *Kaliana yuruani* (Araneae: Phoicidae). J. Morphol. 267, 705–712.

Huber, B.A., Eberhard, W.G., 1997. Courtship, copulation and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Can. J. Zool. 74, 905–918.

Jackson, R.R., Pollard, S.D., 1982. The biology of *Dysdera crocata* (Araneae, Dysderidae): intraspecific interactions. J. Zool. London 198, 197–214.

Maklakov, A.A., Bilde, T., Lubin, Y., 2003. Vibratory courtship in a web-building spider: signalling quality or stimulating the female? Anim. Behav. 66, 623–630.

Platnick, N.I., 2009. The World Spider Catalog, version 9.5. American Museum of Natural History, online at 〈http://research.amnh.org/entomology/spiders/catalog/index〉. Accessed on 20 May 2009.

Platnick, N.I., Coddington, J.A., Forster, R.R., Griswold, C.E., 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Am. Mus. Novit., 1–73.

Prenter, J., Elwood, R.W., Montgomery, W.I., 2003. Mate guarding, competition and variation in size in male orb-web spiders, *Metellina segmentata*: a field experiment. Anim. Behav. 66, 1053–1058.

Ramirez, M.J., 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araenae, Araneomorphae). J. Arachnol. 28, 149–157.

Saaristo, M.I., 2001. Dwarf hunting spiders or Oonopidae (Arachnida, Araneae) of the Seychelles. Insect Syst. Evol. 32, 307–358.

Schöfl, G., Taborsky, M., 2002. Prolonged tandem formation in firebugs (*Pyrrhocoris apterus*) serves mate-guarding. Behav. Ecol. Sociobiol. 52, 426–433.

Senglet, A., 2001. Copulatory mechanisms in *Hoplopholcus*, *Stygopholcus* (revalidated), *Pholcus*, *Spermophora* and *Spermophorides* (Araneae, Pholcidae), with additional faunistic and taxonomic data. Mitt. Schweiz. Entomol. Ges. 74, 43–67.

Sillén-Tullberg, B., 1981. Prolonged copulation: a male 'postcopulatory' strategy in a promiscuous species, *Lygaeus equestris* (Heteroptera: Lygaeidae). Behav. Ecol. Sociobiol. 9, 283–289.

Simon, E., 1893. Histoire Naturelle des Araignées, vol. 1, part 2. Roret, Paris, pp. 257–488.

Thornhill, R., 1983. Cryptic female choice and its implication in the scorpionfly *Harpobittacus nigriceps*. Am. Nat. 122, 765–788.

Uhl, G., 1994. Genital morphology and sperm storage in *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). Acta Zool. Stockholm 75, 1–12.

Uhl, G., 1998. Mating behaviour in the cellar spider, *Pholcus phalangioides*, indicates sperm mixing. Anim. Behav. 56, 1155–1159.

Uhl, G., 2000. Two distinctly different sperm storage organs in female *Dysdera erythrina* (Araneae: Dysderidae). Arthropod. Struct. Dev. 29, 163–169.

Uhl, G., 2002. Female genital morphology and sperm priority patterns in spiders (Araneae). In: Toft, S., Scharff, N. (Eds.), European Arachnology 2000. Aarhus University Press, Aarhus, pp. 145–156.

Uhl, G., Gunnarsson, B., 2001. Female genitalia in *Pityohyphantes phrygianus*, a spider with a skewed sex ratio. J. Zool. 255, 367–376.

Uhl, G., Vollrath, F., 1998. Genital morphology of *Nephila edulis*: implications for sperm competition in spiders. Can. J. Zool. 76, 39–47.

Uhl, G., Huber, B.A., Rose, W., 1995. Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). Bull. Br. Arachnol. Soc. 10, 1–9.

Useta, G., Huber, B.A., Costa, F.G., 2007. Spermathecal morphology and sperm dynamics in the female *Schizocosa malitiosa* (Araneae, Lycosidae). Eur. J. Entomol. 104, 777–785.

van Helsdingen, P.J., 1965. Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneida, Linyphiidae), with notes on the function of the genital organs. Zool. Meded. 41, 15–42.

von Helversen, O., 1976. Gedanken zur Evolution der Paarungsstellung bei den Spinnen (Arachnida, Araneae). Entomol. Germ. 3, 13–28.

Wiehle, H., 1967. *Meta* – eine semientelegyne Gattung der Araneae. Senckenbergiana 48, 183–196.

Wynn, H., Vahed, K., 2004. Male *Gryllus bimaculatus* guard females to delay them from mating with rival males and to obtain repeated copulations. J. Insect Behav. 17, 53–66.

Yáñez, M., Locht, A., Macías-Ordóñez, R., 1999. Courtship and mating behavior of *Brachypelma klaasi* (Araneae, Theraphosidae). J. Arachnol. 27, 165–170.

Yoward, P.J., 1998. Sperm competition in *Pholcus phalangoides* (Fuesslin, 1775) (Araneae, Pholcidae) – shorter second copulations gain a higher paternity reward than first copulations. In: Selden, P.A. (Ed.), Proceedings of the 17th European Colloquium of Arachnology. British Arachnological Society, Burnham Beeches, Edinburgh, pp. 167–170.

Male genital mutilation in the high-mountain goblin spider, *Unicorn catleyi*

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Abstract

Male genital mutilation is a common mechanism by which males reduce sperm competition by plugging female insemination ducts with different parts of its own genital system. This behavior is frequent in many spider families but is uncommon in Haplogynae. The reproductive biology of Dysderoidea is not well studied and the data is fragmentary; male genital mutilation has been reported only for one species of Oonopidae. This study provides evidence of male genital mutilation in *Unicorn catleyi* Platnick and Brescovit (Araneae: Oonopidae). Pieces of the embolus were found in the female posterior receptaculum. This behavior is a strategy used by the males in order to guarantee their paternity and not for escape from female attacks as has been reported for other species of Araneae, since cannibalism is unlikely in this species. The presence of embolus in the posterior receptaculum suggests this is the first place where sperm is received. The similarity of the female genitalia of *U. catleyi* to those of Orsolobidae, along with sclerotization of the seminal duct in the male copulatory bulb that is also present in *Orchestina*, *Xiombarg,* and Orsolobidae, provide strong evidence of the basal position of this genus in the family Oonopidae.

Keywords: female genitalia, Haplogynae, mating plugs, Oonopidae, spider reproduction
Abbreviations: AFG, anterior portion of the female genitalia; **AMP**, anterior median plate; **PFG**, posterior portion of the female genitalia; **PMP**, posterior median plate
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Introduction

Spider reproduction comprises a wide variety of morphological and behavioral strategies that include male sacrifice, production of mating plugs, extreme sexual size dimorphism, and polyandrous females (Nessler et al. 2007a; Miller 2007; Uhl et al. 2010). After mating, males of some animals, including arthropods and nematodes, deposit a mating plug that is thought to prevent or reduce intromission by other males. In this way, males increase the likelihood of their paternity (Jackson 1980; Robinson 1982; Matsumoto and Suzuki 1992; Barker 1994; Simmons 2001; Aisenberg and Eberhard 2009; Peretti 2010). In spiders, plugs might be formed by secretions generated by accessory glands in the male palp or female genital tract (Exline and Levi 1962; Leopold 1976; Masumoto 1993; Elgar 1998; Uhl et al. 2010), while in other cases are formed by fragments of male copulatory organs or even entire male palps that break off during copulation and remain in the insemination duct of the female (Levi 1968, 1983; Nessler et al. 2007b). Plugs have been reported in at least 41 families, some of which are not phylogenetically related groups (Uhl et al. 2010).

Embolus tips act as mating plugs in some species. It has been proposed that the breakage of the male pedipalp may facilitate male survival from the regular female cannibalistic attacks, since ectomizing a part of the palp may allow the male to quickly jump off the female immediately after copulation (Nessler et al. 2007b). Alternatively, mating plugs are considered an adaptive strategy to reduce sperm competition in order to guarantee paternity (Austad 1982; Nessler et al. 2007b; Uhl et al. 2010). Mating plugs are not frequent in haplogine spiders and only one case has been reported for Dysderoidea in the family Oonopidae (Platnick and Dupérré 2009).

The spiders of the genus *Unicorn* Platnick & Brescovit (Araneae: Oonopidae) are relatively large oonopids from South America, with a total length of 2.2-2.8 mm. The genus includes six species known from Chile, Bolivia, and semi-desert areas of western Argentina. The genus presents sexual dimorphism in some characteristics; males have a clypeal horn and an expanded palpal tibia but no sexual differences are observed in the body size. Virtually nothing is known about the natural history of *Unicorn*. They are uncommon in collections and are difficult to find. With the exception of *U. socos* collected at 469 meters, the genus is distributed at high elevations from 1100-3780 meters, where the dominant physiognomy is the semi-desert biome. It has been proposed that this genus, along with the genera *Orchestina* and *Xiombarg*, is probably one of the most basal members of the Oonopidae (Platnick and Brescovit 1995).

The purpose of this paper is to report and describe the male genital mutilation in the genus *Unicorn* from observations of specimens of *U. catleyi* Platnick and Brescovit (Araneae: Oonopidae) discussing its probable function in the species. Also, brief additional descriptions of the male and female genitalia are provided using scanning electron microscopy.

Materials and Methods

Material examined

Collections of *Unicorn catleyi.* Salta province, Argentina, road to Muñiano, route 51 between Santa Rosa de Tastil and Muñiano, elevation

3100-4000 MASL, 22 August 2006, G.D. Rubio collector, pitfall traps 2 males, 2 females, preserved in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (CL Scioscia) (MACN-Ar 22099, PBI_OON 00015060, preparation codes MAI 270, 271, 279-281, 300, 328). Same data 15 November 2006, 1 male (MACN-Ar 22100, PBI_OON 00015059). In order to explore the male palp morphology in species of the same genus, additional material was examined: *Unicorn argentina*. Mendoza province, Argentina: Ñacuñan reserve, 20 October 1997. S Lagos collector, pitfall traps; 2 males, 1 female, (PBI_OON 00015084, preparation codes MAI 327) in Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, Entomology, Sergio A Roig).

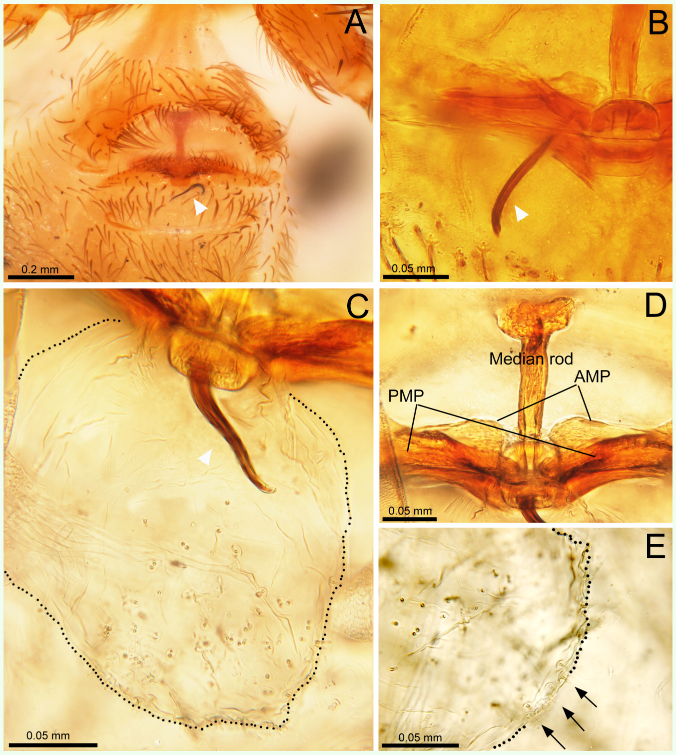

Figure 1. *Unicorn catleyi,* female genitalia. (A) Epigastric region in ventral view; (B) internal genitalia cleared in a clove oil in dorsal view; (C) digested genitalia in lactic acid; (D) anterior elements of the genitalia; (E) posterior receptaculum. Arrowheads point to the embolus tip, black arrows point to the gland ducts of the posterior receptaculum, black dots delineate the margins of the posterior receptaculum. AMP, anterior median plate; PMP, posterior median plate. High quality figures are available online.

The description of the male and female genitalia generally follows that of Platnick and Brescovit (1995) and Forster and Platnick (1985). Male and female genital systems were dissected, embedded in clove oil, mounted on a slide, and observed under an Olympus BH-2 compound microscope (Olympus, www.olympus.com). Photographs of compound microscope and stereomicroscope preparations were made with Nikon DXM1200 (Nikon, www.nikon.com) and Leica DFC 290 (www.leica-microsystems.com) digital cameras, and the focal planes combined with Helicon Focus 3.10.3 and 4.62 Pro (www.heliconsoft.com). The genitalia of one female was digested in a borax-pancreatin solution for 1-2 hours according to the protocol of Alvarez-Padilla and Hormiga (2007), and then flushed with a micropipette in distilled water until all the soft tissues were removed. Genitalia were then observed in a lactic acid medium using a compound microscope. For SEM observations, two male palps and the digested female genitalia were dehydrated in a graded ethanol series (80-100%), critical point dried, and Au-Pd coated. SEM micrographs were taken under high vacuum with a FEI XL30 TMP (FEI, www.fei.com).

Results

The females examined contained an embolus tip inside the posterior receptaculum; in one specimen the embolus was observed across the abdominal cuticle through the transparent (Figure 1A). Only after the complete digestion of the genitalia was it possible to observe the embolus tip inside the posterior receptaculum. Because of the cleaning process during dissection, the original position of the embolus (Figure 1B) changed slightly inside the posterior receptaculum (Figure 1C).

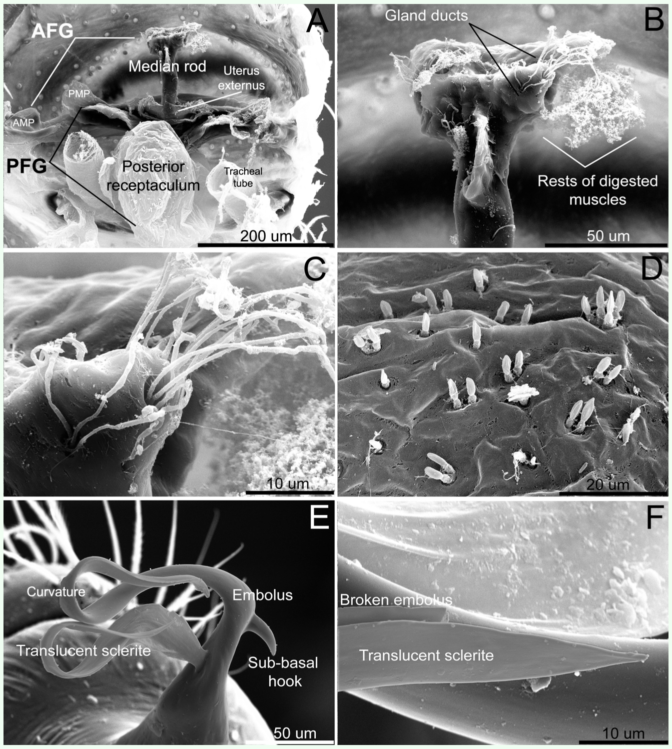

Figure 2. *Unicorn catleyi*, male and female genitalia in SEM images. A-D: female genitalia, (A) dorsal view; (B) apical portion of the anterior median rod; (C) gland ducts of the anterior median rod; (D) gland ducts of the posterior receptaculum. E-F: male genitalia, (E) entire embolus and translucent sclerite; (F) broken embolus and translucent sclerite. AFG, anterior portion of the female genitalia; AMP, anterior median plate; PFG, posterior portion of the female genitalia; PMP, posterior median plate. High quality figures are available online.

Female genitalia

The anterior portion of the female genitalia (Figure 2A) is a highly sclerotized structure formed by a conspicuous median rod and an anterior median plate extended to both right and left sides (Figures 1D, 2A). The median rod bears many gland ducts and the remainder of digested muscles near the tip (Figures 2B, 2C). The posterior portion of the female genitalia is shown in Figure 2A with a posterior median plate extended to both left and right sides (Figures 1D, 2A) and a globose, membranous receptaculum bearing many gland ducts on its surface (Figures 1A, 1E). The uterus externus is located between the base of a median rod and the posterior median plate (Figure 2A).

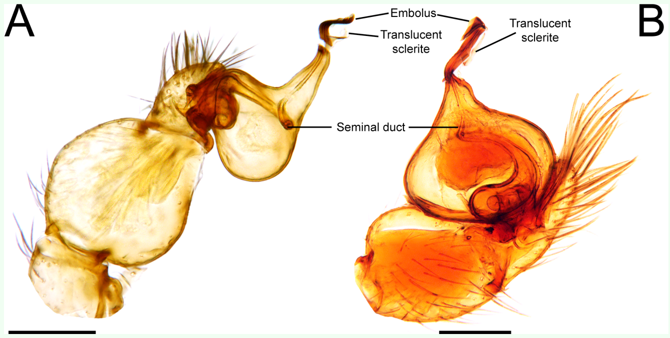

Figure 3. Male copulatory bulb of *Unicorn* spp. cleared in a clove oil. (A) *Unicorn catleyi*; (B) *U. argentina.* Scale bars = 0.2 µm. High quality figures are available online.

Male palp

The embolus with sub-basal hook, long and describing a pronounced curve at the tip is shown in Figure 2E. The SEM images reveal that the male embolus lacks a suture line were it could break off during copulation. The curvature in the embolus might act as a lever mechanism allowing the embolus to break off at this point. However the breakage also occurs ahead of this curvature, near the tip of the embolus (Figure 2F). There is a translucent sclerite originating near the embolus base (Figure 2E). Because of the translucent nature of this sclerite, it can be more or less joined to the embolus and can sometimes be placed in different positions making it difficult to detect. The male copulatory bulb has a sclerotized seminal duct (Figure 3A). This character was also confirmed by the examination of specimens of *Unicorn argentina* (Mello-Leitão 1940) (Figure 3B). The male palp drawings of Platnick and Brescovit (1995) suggest the presence of a seminal duct in the other species of the genus. Also, the seminal duct is present in the genus *Orchestina* (Saaristo and van Harten 2006, Izquierdo personal observation) and *Xiombarg* as revealed in the original drawing of Brignoli (1979).

Discussion

Male genital mutilation and its possible functions

Two studies regarding the occurrence of plugs support the hypothesis that the plug provides paternity protection. Miller (2007) suggests that mating plugs formed from fragments of male genitalia are an adaptive mechanism when post-mating male-male competition is intensive. Studies on *A. bruennichi* are inconsistent with the alternative hypothesis that the damage occurs as the male attempts to escape attack by the female (Nessler et al. 2007b).

More observations of behavior are needed to make accurate predictions of the sexual strategies of this species. This issue represents a challenge since the species is difficult to find in the field, and indirect methods, such as pitfall traps, are often needed to collect them. Given this, we can only make assumptions or predictions in analyzing the genital morphology of the specimens. Our observations could be consistent with the ideas of Miller (2007) and Nessler et al. (2007b). Cannibalistic attacks are more evident in those arthropod species with remarkable body size dimorphism (Wilder and Rypstra 2008). In general, female spiders are larger than the cannibalized males. Although cannibalism in *U. catleyi* should not be dismissed, this behavior might be rare since males and females are not sexually dimorphic in body size. Additional data in favor of this hypothesis is that males with the broken embolus in only one palp were found in pitfall traps, suggesting that they remain alive after copulation. In addition, the presence of only one embolus fragment in the female genital tract of this species may reflect the efficiency of the embolus tip in preventing future insertions by the palp of other males. However, more specimens are needed to make predictions of greater accuracy.

Predictions of the pattern of sperm priority are difficult to make; many more specimens need to be studied. In most haplogyne spiders, the female genitalia exhibit a dead end design (Uhl 2002). These spiders should exhibit last male sperm priority, as the last sperm to enter should lie closest to the single fertilization duct. If there is no mixing of sperm from several males, then this arrangement of the female genitalia is a disadvantage for the first mating males. If this hypothesis is correct, the formation of a mating plug by the first mating males could represent an adaptive switch by which these males have an advantage over the second males. If mating with the first males only is indeed the norm in *U. catleyi*, as suggested by the discovery of single embolus tips in females, then first males not only overcome the morphological difficulties of the female genitalia but also may increase paternity. The exactly place where the sperm transference takes place has been difficult to determine in several species of Dysderoidea. However, the presence of the male embolus inside the posterior receptaculum might suggest that this is the place where the sperm transference occurs.

Some details of reproductive strategies have been documented in related species of Dysderoidea. Platnick and Dupérré (2009) reported the presence of an embolus fragment in the female genitalia of one species of the oonopid genus *Scaphiella,* while Řezác (2009) described the traumatic insemination in *Harpactea sadistica* in which males inseminate females with its needle-like intromittent organs by penetrating the female abdomen wall. In addition, Burger (2007) reported sperm dumping in the oonopid *Silhouettella loricatula* (Roewer 1942). As we see, the complexities in reproductive strategies and in the female genital morphology seem to be more abundant than expected for this haplogyne group of spiders.

Phylogenethic relationships

The female genitalia of *U. catleyi* resembles those described for orsolobids, such as *Orsolobus pucara* (see Izquierdo and Labarque 2010). In both species there is an anterior median, highly sclerotized sclerite, or median rod, with gland ducts on its surface and lateral plates. This sclerite serves as an attachment for muscles that might have a function in some mechanisms of sexual behavior such as sperm dumping, as has been described for the oonopid *Silhouettella loricatula* (Burger et al. 2006). Also, the gland ducts of the posterior receptaculum are extremely similar to those found in *O. pucara.* Because of the presence of gland ducts on the anterior median rod, Izquierdo and Labarque (2010) hypothesize the possible homology between this structure and the membranous anterior receptaculum found in Segestriidae and Dysderidae. It is possible that the anterior receptaculum has evolved to a sclerotized structure in order to provide attachment sites for muscles. In Oonopidae the sclerotized anterior receptaculum with a median rod is present in at least *Orchestina*, *Xiombarg*, and non-described species of soft-bodied oonopids (Cristian Grismado, personal communication), while it is a highly derived structure in other genera such as *Opopaea* (see Burger et al. 2003).

The sclerotization of the seminal duct in the male copulatory bulb in *Unicorn* and *Orchestina*, added to the similarity of the female genitalia of these genera with those of orsolobids, further supports its basal phylogenetic position in the Oonopidae, as has been proposed by Platnick and Brescovit (1995).

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References

Aisenberg A, Eberhard WG. 2009. Female cooperation in plug formation in a spider: effects of male copulatory courtship. *Behavioral Ecology* 20: 1236-1241.

Alvarez-Padilla F, Hormiga G. 2007. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. *Journal of Arachnology* 35: 538-542.

Austad SN. 1982. First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). *Evolution* 36: 777-785.

Barker DM. 1994. Copulatory plugs and paternity assurance in the nematode

Caenorhabditis elegans. *Animal Behaviour* 48: 147-156.

Brignoli P.M. 1979. Ragni del Brasile V. Due nuovi generi e quattro nuove specie dello stato di Santa Catarina (Araneae). *Revue Suisse de Zoologie* 86: 913-924.

Burger M. 2007. Sperm dumping in a haplogyne spider. *Journal of Zoology* 273: 74-81.

Burger M, Nentwig W, Kropf C. 2003. Complex genital structures indicate cryptic female choice in a haplogyne spider (Arachnida, Araneae, Oonopidae, Gamasomorphinae). *Journal of Morphology* 255: 80-93.

Burger M, Graber W, Michalik P, Kropf C. 2006. *Silhouettella loricatula* (Arachnida, Araneae, Oonopidae) A haplogyne spider with complex female genitalia. *Journal of Morphology* 267: 663-677.

Exline H, Levi HW. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). *Bulletin of the American Museum of Comparative Zoology* 127: 75-204.

Elgar MA. 1998. Sexual selection and sperm competition in arachnids. In: Birkhead TR, Møller AP, Editors. *Sperm Competition and Sexual Selection*. pp. 307-337. Academic Press.

Forster RR, Platnick NI. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. *Bulletin of the American Museum of Natural History* 181: 1-230.

Izquierdo MA, Labarque FM. 2010. Description of the female genitalia of *Orsolobus pucara* Forster & Platnick 1985 with comments on the functional morphology of the genitalia in Dysderoidea (Araneae, Dysderoidea, Orsolobidae). *Journal of Arachnology* 38: 551-520.

Jackson RR. 1980. The mating strategy of *Phidippus johnsoni* (Araneae: Salticidae), II: sperm competition and the function of copulation. *Journal of Arachnology* 8: 217-240.

Leopold RA. 1976. The role of male accessory glands in insect reproduction. *Annual Review of Entomology* 21: 199-221.

Levi HW. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). *Bulletin of the American Museum of Comparative Zoology* 136: 319-351.

Levi HW. 1983. The orb-weaver genera *Argiope*, *Gea* and *Neogea* from the western pacific region (Araneae: Araneidae, Argiopinae). *Bulletin of the Museum of Comparative Zoology* 150: 247-338.

Masumoto T. 1993. The effect of the copulatory plug in the funnel-web spider, *Agelena limbata* (Araneae: Agelenidae). *Journal of Arachnology* 21: 55-59.

Matsumoto K, Suzuki N. 1992. Effectiveness of the mating plug in *Atrophaneura alcinous* (Lepidoptera: Papilionidae). *Behavioral Ecology and Sociobiology* 30: 157-163.

Miller JA. 2007. Repeated evolution of male sacrifice behavior in spiders correlated with genital mutilation. *Evolution* 61: 1301-1315.

Nessler SH, Uhl G, Schneider JM. 2007a. A non-sperm transferring genital trait under sexual selection: an experimental approach. *Proceedings of the Royal Society* 274: 2337-2341.

Nessler SH, Uhl G, Schneider JM. 2007b. Genital damage in the orb-web spider *Argiope bruennichi* (Araneae: Araneidae) increases paternity success. *Behavioral Ecology* 18: 174-181.

Peretti AV. 2010. An ancient indirect sex model: single and mixed patterns in the evolution of scorpion genitalia. In: Leonard J, Córdoba-Aguilar A, Editors. *The Evolution of Primary Sexual Characters in Animals*. pp. 218-248. Oxford University Press.

Platnick NI, Brescovit AD. 1995. On *Unicorn*, a new genus of the spider family Oonopidae (Araneae, Dysderoidea). *American Museum Novitates* 3152: 1-12.

Platnick NI, Dupérré N. 2009. The American goblin spiders of the new genus *Escaphiella* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 328: 1-151.

Robinson MH. 1982. Courtship and mating behavior in spiders. *Annual Review of Entomology* 27: 1-20.

Řezác M. 2009. The spider *Harpactea sadistica*: co-evolution of traumatic insemination and complex female genital morphology in spiders. *Proceedings of the Royal Society* 276: 2697-2701.

Saaristo MI, Harten van A. 2006. The oonopid spiders (Araneae: Oonopidae) of mainland Yemen. *Fauna of Arabia* 21: 127-157.

Simmons LW. 2001. *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press.

Uhl G. 2002. Female genital morphology and sperm priority patterns in spiders (Araneae). In: Toft S, Scharff N, Editors. *European Arachnology 2000*. pp. 145-156. Aarhus University Press.

Uhl G, Nessler SH, Schneider J. 2007. Copulatory mechanism in a sexually cannibalistic spider with genital mutilation (Araneae: Araneidae: *Argiope bruennichi*). *Zoology* 110: 398-408.

Uhl G, Nessler SH, Schneider J. 2010. Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. *Genetica* 138: 75-104.

Wilder SM, Rypstra AL. 2008. Sexual size dimorphism mediates the occurrence of state-dependent sexual cannibalism in a wolf spider. *Animal Behaviour* 76: 447-454.

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Tarsal Organ Morphology and the Phylogeny of Goblin Spiders (Araneae, Oonopidae), With Notes on Basal Genera

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ABSTRACT

Based on a survey of a wide variety of oonopid genera and outgroups, we hypothesize new synapomorphies uniting the Oonopidae (minus the South African genus *Calculus* Purcell, which is transferred to the Orsolobidae). The groundplan of the tarsal organ in Oonopidae is hypothesized to be an exposed organ with a distinctive, longitudinal ridge originating from the proximal end of the organ, and a serially dimorphic pattern of 4-4-3-3 raised receptors on legs I–IV, respectively. Such organs typify the diverse, basal, and ancient genus *Orchestina* Simon. Several other genera whose members resemble *Orchestina* in retaining two plesiomorphic features (an H-shaped, transverse eye arrangement and a heavily sclerotized, thick-walled sperm duct within the male palp) are united by having tarsal organs that are partly (in the case of *Cortestina* Knoflach) or fully capsulate (in the case of *Sulsula* Simon, *Xiombarg* Brignoli, and *Unicorn* Platnick and Brescovit). The remaining oonopids are united by the loss of the heavily sclerotized palpal sperm duct, presumably reflecting a significant transformation in palpal mechanics. Within that large assemblage, a 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement seem to be retained only in the New Zealand genus *Kapitia* Forster; the remaining genera are apparently united by a reduction in the tarsal organ pattern to 3-3-2-2 raised receptors on legs I–IV and by the acquisition of a clumped eye arrangement. Three subfamilies of oonopids are recognized: Orchestininae Chamberlin and Ivie (containing only *Orchestina*; *Ferchestina* Saaristo and Marusik is placed as a junior synonym of *Orchestina*), Sulsulinae, new subfamily (containing *Sulsula*, *Xiombarg*, *Unicorn*, and *Cortestina*), and Oonopinae Simon (containing all the remaining genera, including those previously placed in the Gamasomorphinae). The type species of *Sulsula* and *Kapitia*, *S. pauper* (O. P.-Cambridge) and *K. obscura* Forster, are redescribed, and the female of *S. pauper* is described for the first time. A new sulsuline genus, *Dalmasula*, is established for *Sulsula parvimana* Simon and four new species from Namibia and South Africa.

INTRODUCTION

Goblin spiders (the family Oonopidae) have long been among the most poorly known groups of spiders; the bulk of the species and much of the generic-level diversity of the family have remained undescribed, and the phylogenetic relationships of its members have been poorly understood, at all levels. Thanks to a Planetary Biodiversity Inventory (PBI) project, initiated in September 2006 with support from the U.S. National Science Foundation (NSF), knowledge of these animals has expanded rapidly; at present, the PBI project involves over 45 participants in more than a dozen countries, and almost one-third of the total project budget comes from sources other than NSF, in several nations. Through the efforts of these participants, enough information has now accumulated to allow testing some preliminary hypotheses about the higher-level relationships of oonopids. We present here results based on investigations of the tarsal organ morphology of a wide variety of oonopids and their outgroups.

HISTORICAL BACKGROUND: OUTGROUPS

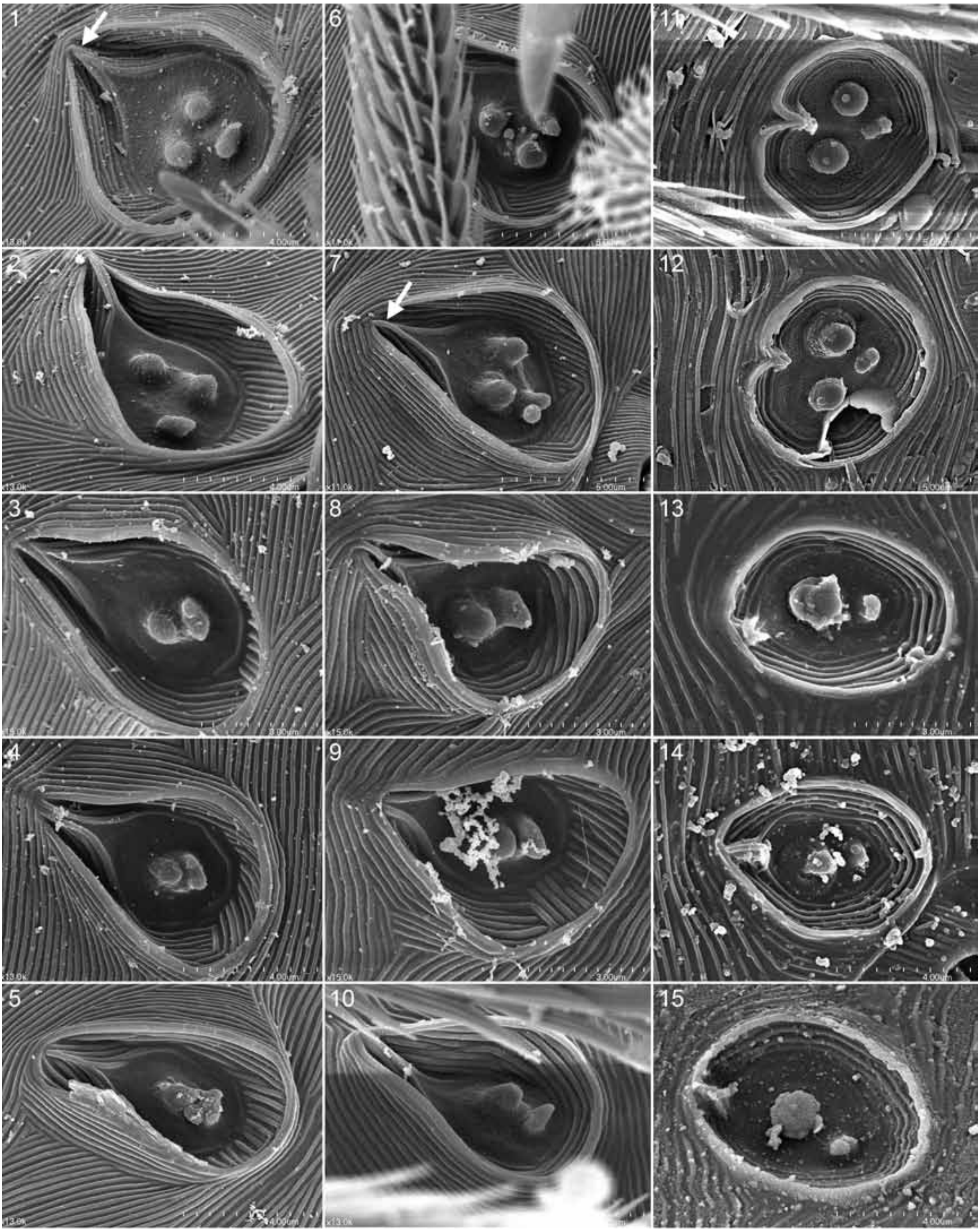
As treated in the classical literature (e.g., Simon, 1893; Dalmas, 1916; Chickering, 1951; Forster, 1956; Hickman, 1979), oonopids were poorly delimited, and certainly not a monophyletic group. Some of the major problems were solved by Forster and Platnick (1985), who used scanning electron microscopy of the tarsal organ (a chemosensory structure found near the tips of the legs and palps) to show that many of the austral genera previously assigned to the Oonopidae are actually more closely related to *Orsolobus* Simon (which was then placed in the Dysderidae) than they are to true oonopids. Forster and Platnick suggested that the monophyly of the superfamily Dysderoidea is supported by a peculiar specialization of the internal female genitalia (the development of a receptaculum associated with the posterior wall of the bursal cavity), and argued that four families of dysderoids should be recognized: the Dysderidae (primarily a Mediterranean group, but with one synanthropic, cosmopolitan species), Segestriidae (a worldwide group of three genera), Orsolobidae (a Gondwanan group, found in Australia, New Zealand, and southern South America, and subsequently discovered in southern Africa by Griswold and Platnick, 1987), and the Oonopidae. This grouping of families was also supported in more recent, matrix-based phylogenetic analyses by Platnick et al. (1991), which incorporated new data obtained by scanning electron microscopy of the spinneret spigots, and by Ramírez (2000), which added new data on respiratory system morphology.

The latter study placed the family Caponiidae as the sister group of dysderoids, based on the shared advancement of the posterior spiracles to a position just behind the epigastric furrow. Resolution within the Dysderoidea was not strongly supported in any of these studies; Platnick et al. (1991: 67) concluded that "familial relationships within the Dysderoidea (and the monophyly of the Oonopidae) remain uncertain" but favored a sister-group relationship between oonopids and orsolobids, and that sister-group relationship was also supported in the later analysis by Ramírez (2000).

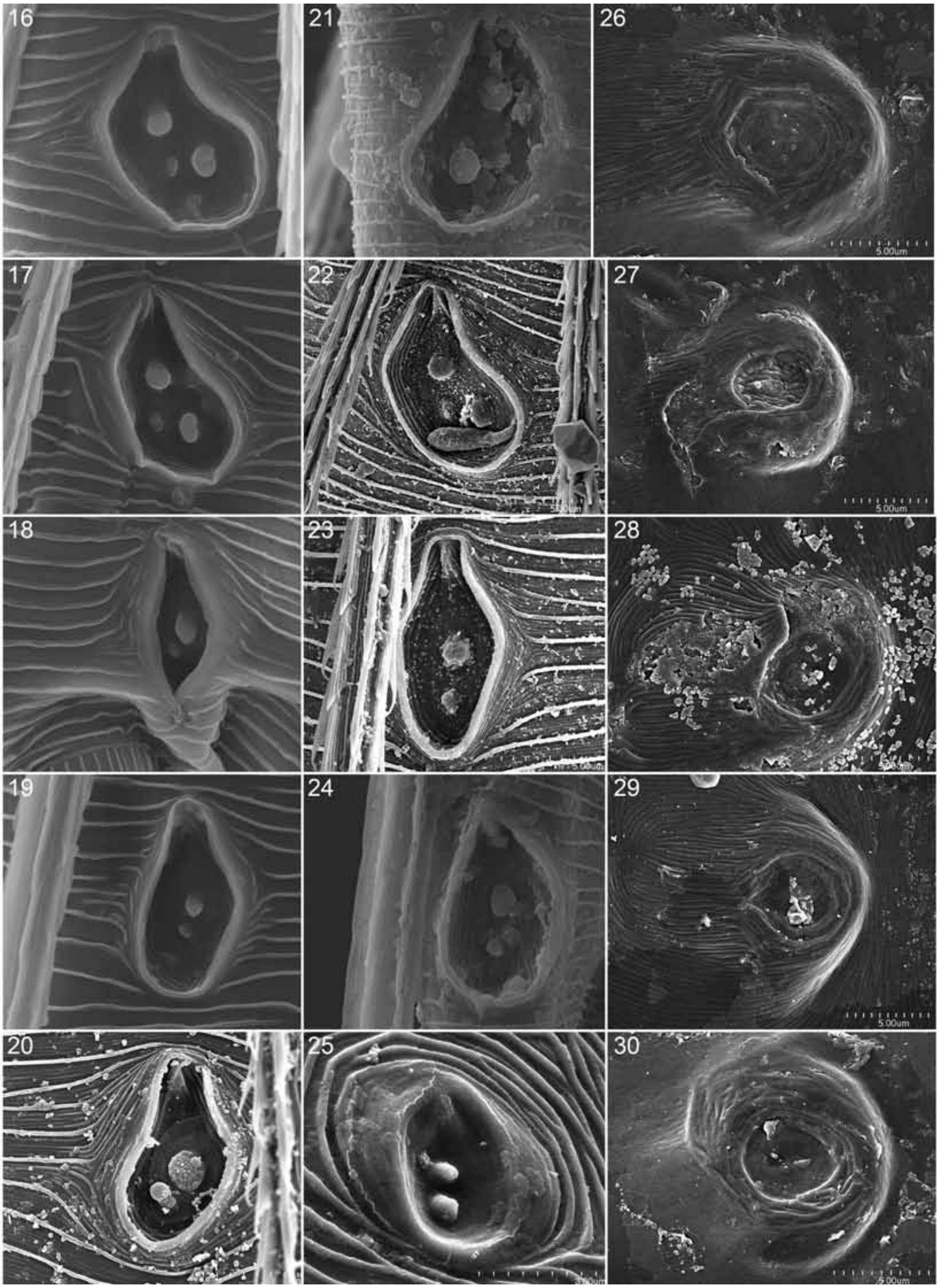
More recently, Burger and Michalik (2010) presented the first evidence in support of oonopid monophyly, showing that (unlike all other spiders previously observed) males of a wide variety of oonopid genera have an unpaired, completely fused testis. The single orsolobid species they examined, in contrast, had the paired, unfused testes typical of most other spiders. Interestingly, some dysderids and segestriids have been reported to have partially fused testes, but similar structures also occur in the more distantly related family Scytodidae (Michalik, 2009).

HISTORICAL BACKGROUND: INGROUP

The traditional classification of oonopids stems from the treatment of the family in Simon's (1893) classic volume on the *Histoire naturelle des araignées,* where he recognized two informal groups, the "Oonopidae molles," containing soft-bodied species in which the abdomen either lacks scuta entirely or has only a weakly sclerotized epigastric scutum, and the "Oonopidae loricatae," containing hard-bodied species in which the abdomen has additional (and more heavily sclerotized) scuta. Simon intended these groupings only as artificial aids to identification; he explicitly stated (1893: 292) "Pour en faciliter l'étude, je répartis les Oonopides en deux sections, qui ne correspondent cependant pas à des groupes naturels." Nevertheless, Petrunkevitch (1923) and subsequent workers recognized these groups formally, as the subfamilies Oonopinae and Gamasomorphinae, respectively. Neither Petrunkevitch nor the other workers who have used the names provided any phylogenetic justification for either of those subfamilies.



FIGURES 1–15. Tarsal organ, dorsal view, *Oonops pulcher* Templeton, female (1–5) and male (6–10), *Triaeris stenaspis* Simon, female (11–15). **1, 6, 11.** Leg I. **2, 7, 12.** Leg II. **3, 8, 13.** Leg III. **4, 9, 14.** Leg IV, **5, 10, 15.** Palp. Arrows point to the proximally situated, longitudinal ridge here considered synapomorphic for the Oonopidae.



FIGURES 16–30. Tarsal organ, dorsal view, *Ischnothyreus peltifer* (Simon), female (16–20) and male (21–25), *Segestria senoculata* (Linnaeus), female (26–30). **16, 21, 26.** Leg I. **17, 22, 27.** Leg II. **18, 23, 28.** Leg III. **19, 24, 29.** Leg IV. **20, 25, 30.** Palp.

Two later papers also attempted to establish formal, subfamilial groupings. Chamberlin and Ivie (1942: 6) erected a monotypic subfamily, the Orchestininae, but provided no relevant evidence, indicating only that "The genus *Orchestina* is sufficiently distinct from the other genera of the Oonopidae to warrant its separation into a separate subfamily." Their action seemingly ignored prior work, including that of Simon (1893: 292), who grouped *Orchestina* Simon with *Sulsula* Simon, and Dalmas (1916: 205), who added *Calculus* Purcell to this grouping, commenting that "Les trois genres *Orchestina*, *Calculus* et *Sulsula* sont les seuls de la famille offrant un groupe oculaire complêtement transverse." Much later, Dumitresco and Georgesco (1983: 103, 114) attempted to establish a subfamily containing only the gamasomorphine genera *Triaeris* Simon and *Ischnothyreus* Simon, but as they did not designate a type genus for the group, and did not base its name on either of the included genera, their subfamilial name "Pseudogamasomorphinae" is not available.

Given Simon's intentions, it is hardly surprising that modern workers have found at least the Oonopinae to be paraphyletic. Platnick and Dupérré (2010a) noted that two putatively synapomorphic features, the acquisition of a clumped eye arrangement (rather than a transverse, H-shaped arrangement with a strongly recurved posterior row) and the loss of the heavily sclerotized, thick-walled sperm duct within the male palp, place *Oonops* Templeton as more closely related to the gamasomorphines than to some of the other genera currently placed as oonopines (including *Orchestina* and several other basal groups that retain the plesiomorphic states of these characters). Platnick and Dupérré (2010a: 6) also indicated that the limits of the Gamasomorphinae are unclear, and suggested that "gamasomorphy" be treated "as a syndrome of increasing sclerotization that starts, phylogenetically, with the cephalothorax." Under that view, several genera placed as "molles" by Simon (1893) may be more closely related to the Gamasomorphinae than to *Oonops*. However, the monophyly of the classical Gamasomorphinae may be supported by at least one synapomorphic character, the presence of a sperm pore on the epigastric scutum of males.

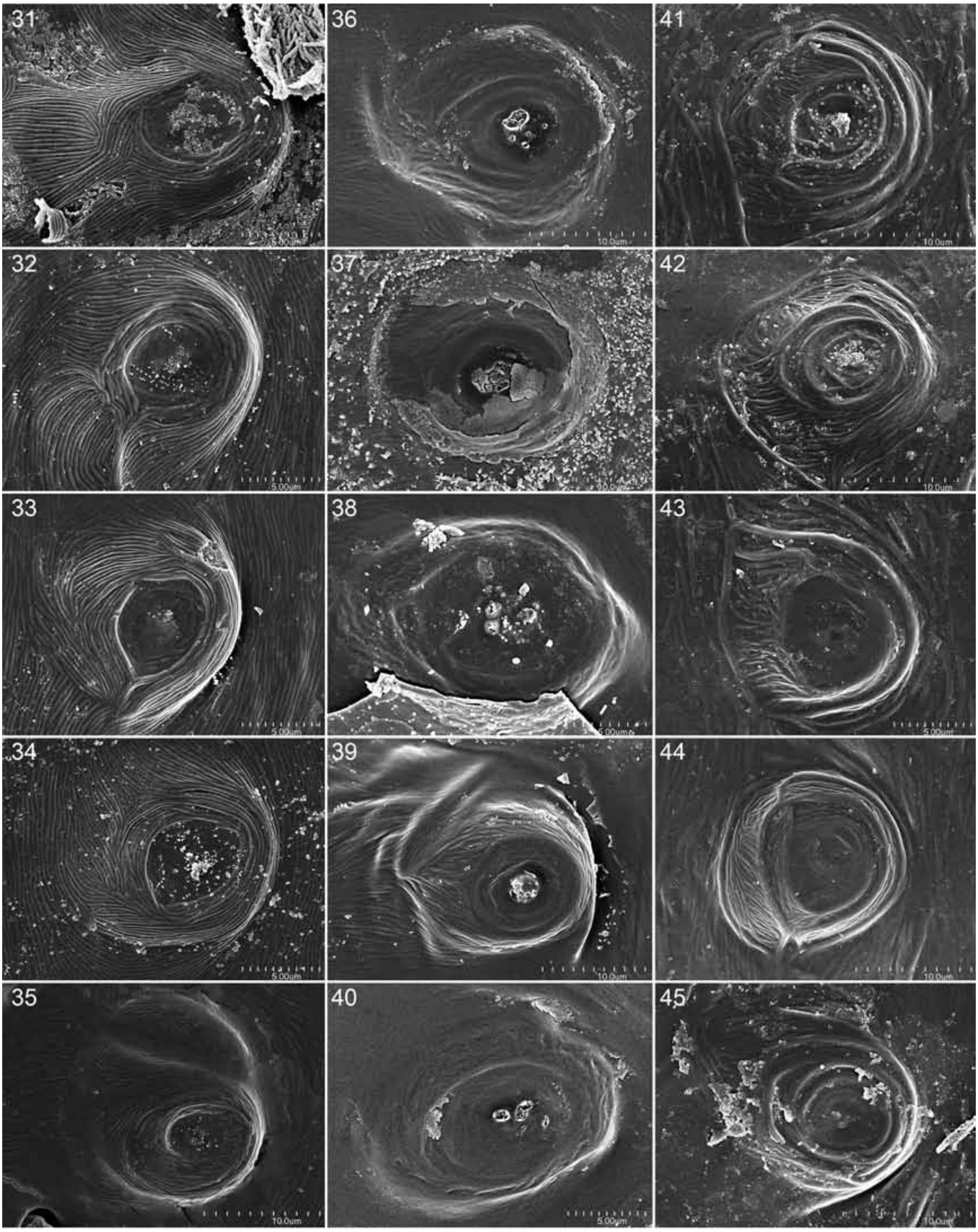
TYPICAL OONOPID TARSAL ORGANS

Study of a wide variety of oonopid genera indicates that the tarsal organ morphology most commonly encountered within the family is that shown by its type species, *Oonops pulcher* Templeton. In the first comprehensive study of spider tarsal organs, Blumenthal (1935: 669) indicated that in all cases where he succeeded in locating the tarsal organ, the organ occurred on the tarsus of each leg and on the palpal tarsus, always with the same structure (although not always with the same size). In that regard, as is frequently the case, oonopids simply don't play by the same rules as other spiders. As shown here for *O. pulcher* (figs. 1–10), both sexes typically show serial dimorphism in their tarsal organ morphology; on the anterior legs, the tarsal organ has three raised receptors (figs. 1, 2, 6, 7), whereas on the posterior legs (and palps) the tarsal organ has only two receptors (figs. 3–5, 8–10). In *O. pulcher* and most other oonopids, the two most proximal receptors on the anterior legs are arranged transversely, whereas the two receptors found on the posterior legs and palps are arranged longitudinally.

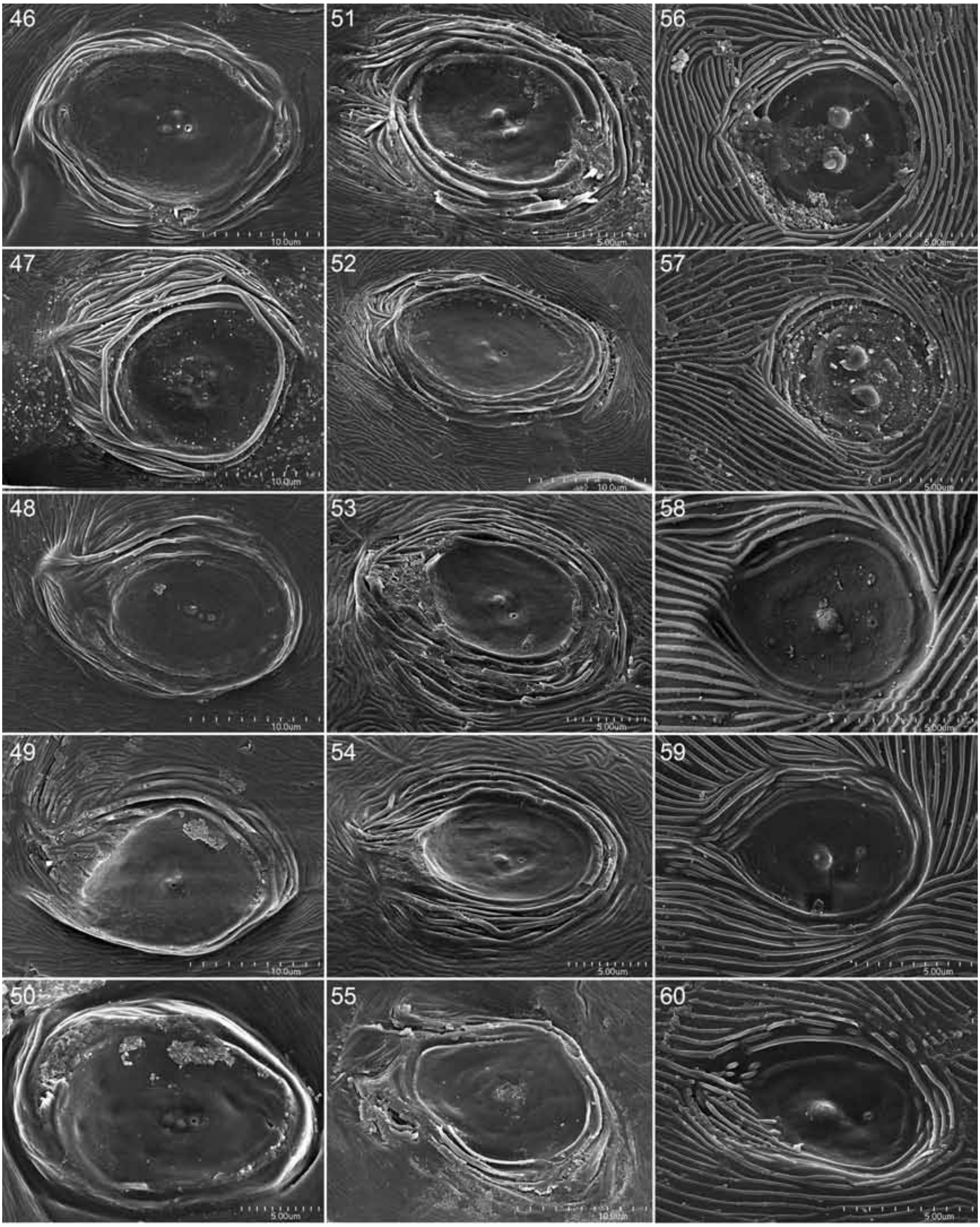
In addition to this unusual anterior/posterior dimorphism, most oonopid tarsal organs have a distinctive longitudinal ridge that originates at the proximal end of the tarsal organ (figs. 1, 7, arrows). Such ridges have not been detected, to date, in the relevant outgroup families (Orsolobidae, Dysderidae, Segestriidae, and Caponiidae). We therefore hypothesize that both the anterior/posterior, serial dimorphism in raised receptor number and orientation, and the presence of the proximal, longitudinal ridge, are synapomorphic for the Oonopidae.

To date, tarsal organs showing this typical morphology have been demonstrated to occur in the following oonopid taxa: *Antoonops corbulo* Fannes and Jocqué (see Fannes and Jocqué, 2008: fig. 47), *Australoonops granulatus* Hewitt (see Platnick and Dupérré, 2010b: figs. 755–759, 782, 796, 797), *Birabenella pizarroi* Grismado (see Grismado, 2010: fig. 14), *Brignolia parumpunctata* (Simon) (see Platnick et al., 2011: figs. 41–44, 49, 66, 77–80), *Camptoscaphiella paquini* Ubick (see Baehr and Ubick, 2010: figs. 91–94, 103–107), *Cavisternum clavatum* Baehr et al. (see Baehr et al., 2010: figs. 67–70), *Costarina plena* (O. P.-Cambridge; see Platnick and Dupérré, 2012: figs. 26–30, 56–60), *Coxapopha yuyapichis* Ott and Brescovit (see Ott and Brescovit, 2004: fig. 21), *Epectris apicalis* Simon (see Platnick and Dupérré, 2009a: figs. 137, 138), *Heteroonops castellus* (Chickering) (see Platnick and Dupérré, 2009c: figs. 287–290, 298), *H. spinimanus* (Simon) (see Platnick and Dupérré, 2009c: figs. 121–125), *Malagiella ranomafana* Ubick and Griswold (see Ubick and Griswold, 2011a: figs. 57–61), *Melchisedec thevenot* Fannes (see Fannes, 2010: fig. 44), *Molotra milloti* Ubick and Griswold (see Ubick and Griswold, 2011b: figs. 311–314), *M. molotra* Ubick and Griswold (see Ubick and Griswold, 2011b: figs. 123–128), *M. tsingy* Ubick and Griswold (see Ubick and Griswold, 2011b: figs. 266–268), *Niarchos barragani* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 59–63, 95–99), *N. foreroi* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 509–513, 542–546), *N. palenque* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 602–606, 633–637), *N. scutatus* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 250–254, 287–291), *Opopaea deserticola* Simon (see Platnick and Dupérré, 2009a: figs. 51–54), *Paradysderina watrousi* Platnick and Dupérré (see Platnick and Dupérré, 2011d: figs. 14, 25–28, 62, 67–70), *Pescennina arborea* Platnick and Dupérré (see Platnick and Dupérré, 2011b: figs. 119–123, 164–168), *Scaphidysderina palenque* Platnick and Dupérré (see Platnick and Dupérré, 2011a: figs. 149, 160–163, 183, 197–200), *Scaphiella williamsi* Gertsch (see Platnick and Dupérré, 2010a: figs. 510–514, 560–564), *Scaphios yanayacu* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 739–743, 786–790), *Semidysderina lagila* Platnick and Dupérré (see Platnick and Dupérré, 2011d: figs. 755, 766–769, 803, 809–812), *Simonoonops craneae* (Chickering) (see Platnick and Dupérré, 2011c: figs. 19–23, 50–54), *Stenoonops peckorum* Platnick and Dupérré (see Platnick and Dupérré, 2010b: figs. 33, 34, 66–70), and *S. pretiosus* (Bryant) (see Platnick and Dupérré, 2010b: figs. 379–383, 426–430).

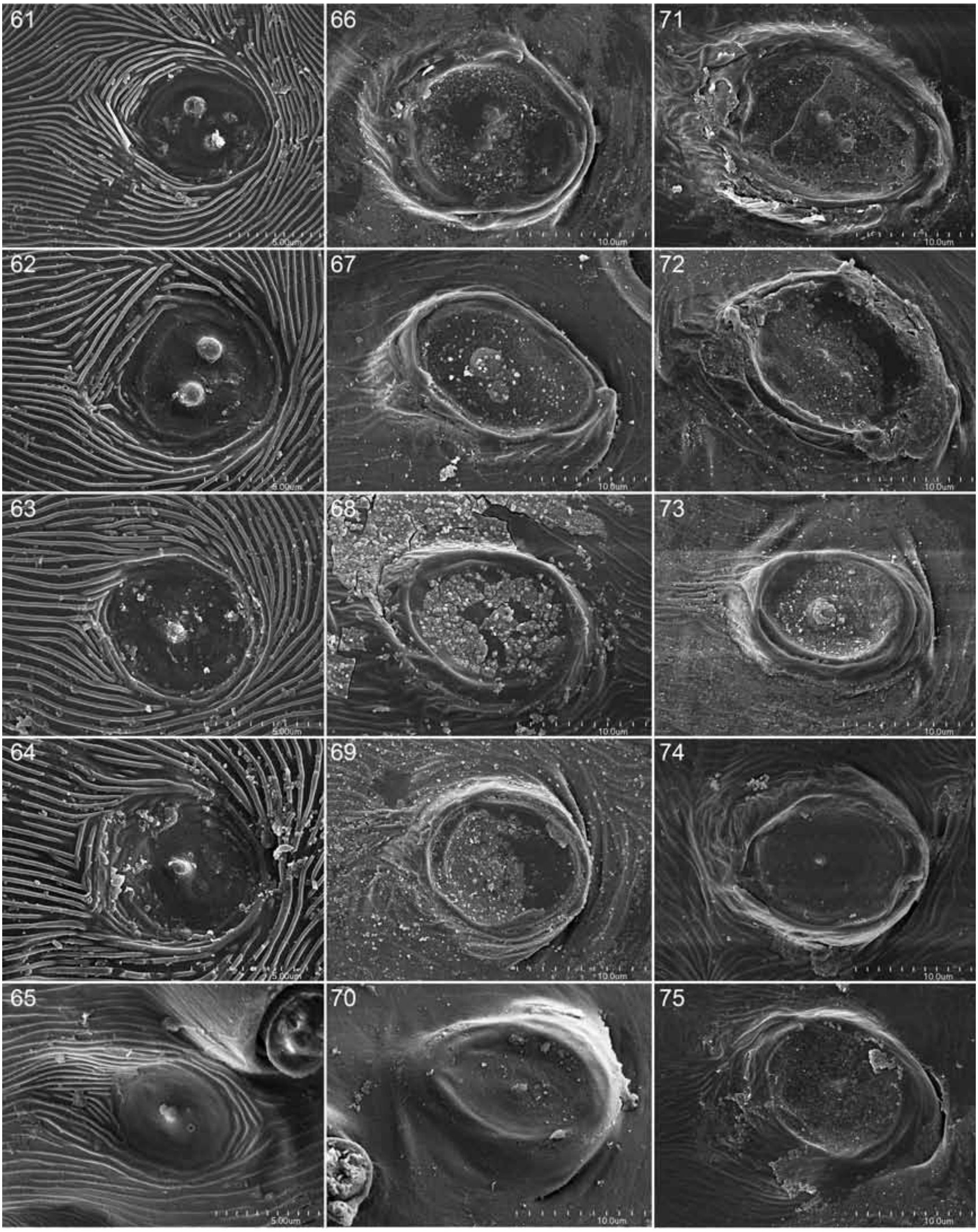
This range of taxa constitutes a reasonable sampling of oonopid diversity, particularly as studies in preparation show that tarsal organs of this type occur also in many taxa that are not yet revised or described, including members of the genera *Gamasomorpha* Karsch (Eichenberger et al., in press), *Neoxyphinus* Birabén (Abrahim et al., in press), *Zyngoonops* Benoit (Fannes, in prep.), *Lionneta* Benoit (Andriamalala, in prep.), and *Trilacuna* Tong and Li (Gris-



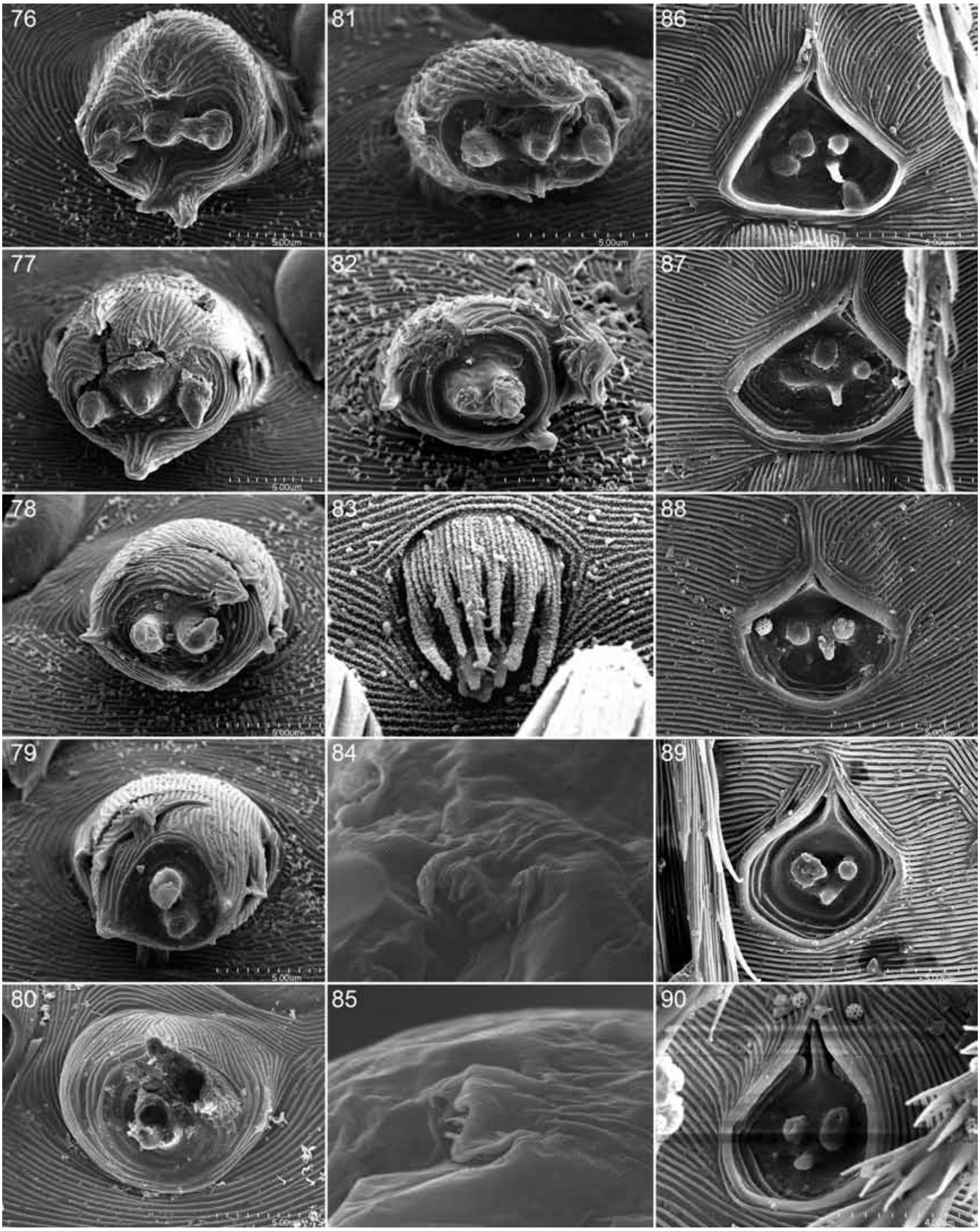
FIGURES 31–45. Tarsal organ, dorsal view, *Segestria senoculata* (Linnaeus), male (31–35), *Ariadna bicolor* (Hentz), female (36–40) and male (41–45). **31, 36, 41**. Leg I. **32, 37, 42.** Leg II. **33, 38, 43.** Leg III. **34, 39, 44.** Leg IV. **35, 40, 45.** Palp.



FIGURES 46–60. Tarsal organ, dorsal view, *Dysdera crocata* C.L. Koch, female (46–50) and male (51–55), *Harpactea lepida* (C.L. Koch), female (56–60). **46, 51, 56.** Leg I. **47, 52, 57.** Leg II. **48, 53, 58.** Leg III. **49, 54, 59.** Leg IV. **50, 55, 60.** Palp.



FIGURES 61–75. Tarsal organ, dorsal view, *Harpactea lepida* (C.L. Koch), male (61–65), *Harpactocrates drassoides* (Simon), female (66–70) and male (71–75). **61, 66, 71.** Leg I. **62, 67, 72.** Leg II. **63, 68, 73.** Leg III. **64, 69, 74.** Leg IV. **65, 70, 75.** Palp.



FIGURES 76–90. Tarsal organ, dorsal view (except 85, lateral view), *Tasmanoonops parvus* Forster and Platnick, female (76–80, proximal end at top of image except 79, proximal end at right of image) and male (81, 82), *Hickmanolobus* sp., female (83), *Calculus bicolor* Purcell (84, 85), *Orchestina* sp. from Africa, female (86–90). **76, 84–86.** Leg I. **77, 81, 83, 87.** Leg II. **78, 82, 88.** Leg III. **79, 89.** Leg IV. **80, 90.** Palp.

mado and Piacentini, in prep.), as well as in new genera from Brazil (Brescovit et al., in press), southern South America (Grismado and Ramírez, in prep.), Madagascar (Álvarez-Padilla et al., in press), and Australia (Baehr et al., in press).

The largest gap in the sampling that has been done to date concerns the two genera, *Triaeris* and *Ischnothyreus*, that were treated by Dumitresco and Georgesco (1983) as members of their stillborn subfamily "Pseudogamasomorphinae." We therefore present here scans of the tarsal organs of the type species of those genera, *Triaeris stenaspis* Simon (figs. 11–15) and *Ischnothyreus peltifer* (Simon) (figs. 16–25). Although the late Ray Forster doubted that *Ischnothyreus* is an oonopid, its type species has tarsal organs that are typical for the family. The longitudinal ridge is relatively short, but the same is true for many other typical oonopids (e.g., Platnick and Dupérré, 2011a: figs. 160–163).

OUTGROUP TARSAL ORGANS

The tarsal organs of the putative sister group of oonopids, the family Orsolobidae, have been documented in detail (see Forster and Platnick, 1985; Griswold and Platnick, 1987; Brescovit et al., 2004; Lise and Almeida, 2006; Baehr and Smith, 2008) because they constitute the best evidence for the monophyly of that family and provide many characters for grouping subsets of its members. Orsolobids resemble oonopids in many respects, but have distinctively elevated tarsal organs, usually accompanied by several cuticular lobes, that are unlike those of any other spiders studied to date (figs. 76–83). Interesting in that regard is one of the basal oonopid genera associated with *Orchestina* by Dalmas (1916), *Calculus*. The type (and only known) species of that genus, *Calculus bicolor* Purcell, is known only from juveniles from South Africa (Purcell, 1910); although they are poorly preserved, their tarsal organ morphology (figs. 84, 85) shows clearly that these juveniles are orsolobids rather than oonopids. Simon (1893: 294) identified similar juveniles from South Africa as members of *Sulsula pauper* (O. P.-Cambridge), a species otherwise then known only from Egypt. Dalmas (1916: 205) suggested that those South African juveniles actually belong to *C. bicolor* rather than *S. pauper*; we have scanned the tarsal organs of one of those juveniles, and can confirm that it does indeed belong to the Orsolobidae rather than the Oonopidae. On the basis of these results, we here transfer *Calculus* from the Oonopidae to the Orsolobidae.

The tarsal organs of the other dysderoid families, the Segestriidae and Dysderidae, are less well known. Blumenthal (1935) considered that all spider tarsal organs belong either to "der primitive Typus" or "die normale Form." His studies of the primitive type were based primarily on two species of *Segestria* Latreille, and his distinction was maintained by Forster (1980), who substituted the more descriptive terms "exposed" and "capsulate" for Blumenthal's primitive and normal types, respectively.

Forster and Platnick (1985: 219, figs. 958–962) provided characterizations of the tarsal organs for each of the dysderoid families, as well as a few scans of oonopid, dysderid, and segestriid tarsal organs. Here we present detailed sets of scans for several representative genera, including *Segestria* (figs. 26–35), *Ariadna* Audouin (figs. 36–45), *Dysdera* Latreille (figs. 46–55), *Harpactea* Bristowe (figs. 56–65), and *Harpactocrates* Simon (figs. 66–75). The primary relevance of these figures is to show that the typical oonopid tarsal organ morphology detailed above does not occur in those outgroup taxa.

The same is true for the putative sister group of dysderoids, the family Caponiidae. Caponiid tarsal organs have been well documented, for example, in *Cubanops alayoni* Sánchez-Ruiz et al. (see Sánchez-Ruiz et al., 2010: figs. 88–91, 112–115) and *Nopsides ceralbonus* Chamberlin (see Jiménez et al., 2011: figs. 34–37, 64–67). Those taxa show neither the anterior/posterior, serial dimorphism nor the proximally originating, longitudinal ridge characteristic of oonopids.

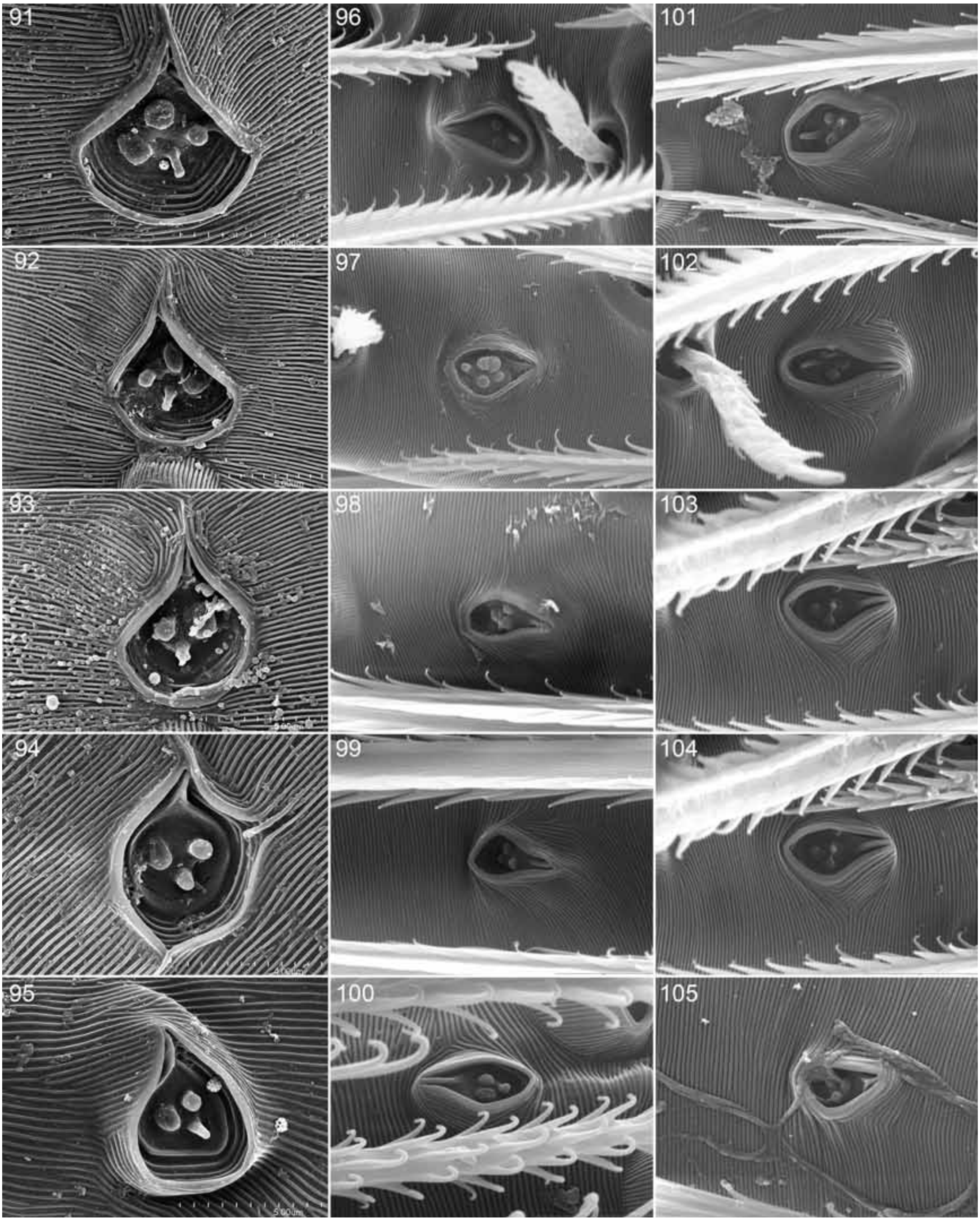
The tarsal organs of the dysderids we have examined offer several features of potential phylogenetic interest. In *Dysdera crocata* C.L. Koch, there is no longitudinal ridge, and there seem to be two different types of receptors. One type resembles the raised receptors of oonopids, except that they each seem to have a tiny pore (figs. 46, 51–54); the second type are just small pores, surrounded by an elevated rim (fig. 52). Because the raised receptors are relatively low and the small pores are easily occluded by dirt and debris, it is difficult to determine how many receptors are present on a given tarsal organ. For example, the tarsal organ of leg I seems to have four receptors in females (fig. 46), two raised and two rimmed, whereas in the male only one rimmed and two raised receptors are clearly visible on leg I (fig. 51). There may be some serial dimorphism as well; females seem to have one, rather than two, rimmed receptors on legs III, IV, and the palps (figs. 48–50).

In *Harpactea lepida* (C.L. Koch), the tarsal organ of leg I seems to have two rimmed and two raised receptors in males (fig. 61), and probably in females as well (fig. 56). Interestingly, in this species both sexes have two raised receptors on legs I and II, but only one on legs III, IV, and the palps (figs. 56–65). It seems likely that this pattern of serial dimorphism is a parallelism with oonopids, but the apparent presence of two rimmed receptors on the female palpal tarsal organ (fig. 60) suggests that it is also possible that one of the raised receptors has been transformed into a rimmed receptor, rather than lost. Our scans of *Harpactocrates drassoides* (Simon) are not clean enough to show the rimmed receptors, but they do indicate that a similar serial dimorphism occurs in that species, with two raised receptors on legs I and II, but only one on legs III, IV, and the palps (figs. 66–75).

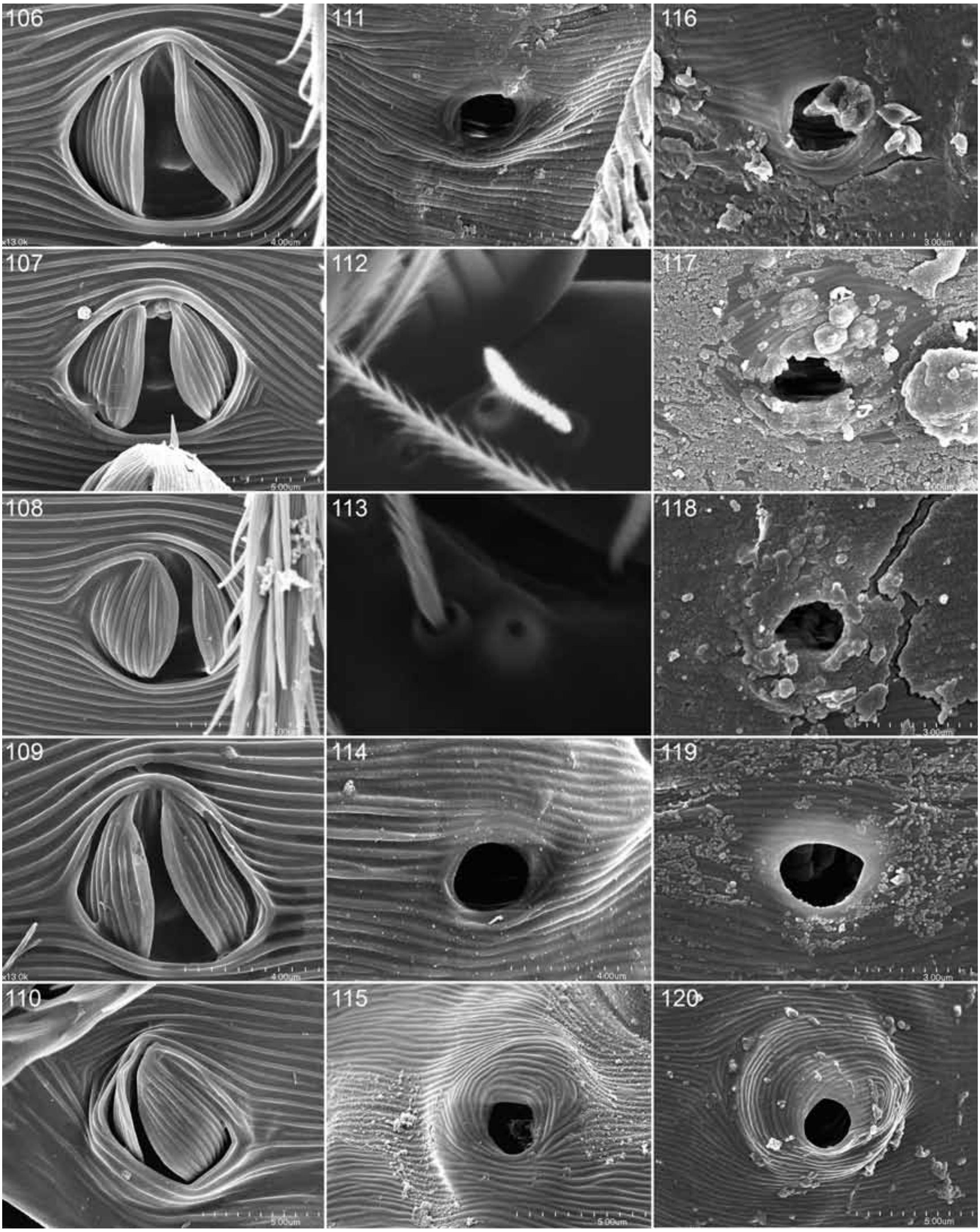
Interestingly, our scans of *Ariadna bicolor* (Hentz) indicate that the rimmed receptor type also occurs in that species (figs. 36, 41), and the same may also be true for *Segestria senoculata* (Linnaeus) (see fig. 31) and *Segestria florentina* (Rossi) (see Giroti and Brescovit, 2011: figs. 11–14). The rimmed receptors may therefore prove to be a synapomorphy uniting Dysderidae plus Segestriidae, although a much broader survey will be required to test that conjecture. Similarly, more thorough sampling of tarsal organ morphology is also likely to prove useful for future work on orsolobids, as our scans suggest that serial dimorphism occurs in both sexes of at least one species (figs. 76–82).

BASAL OONOPID TARSAL ORGANS

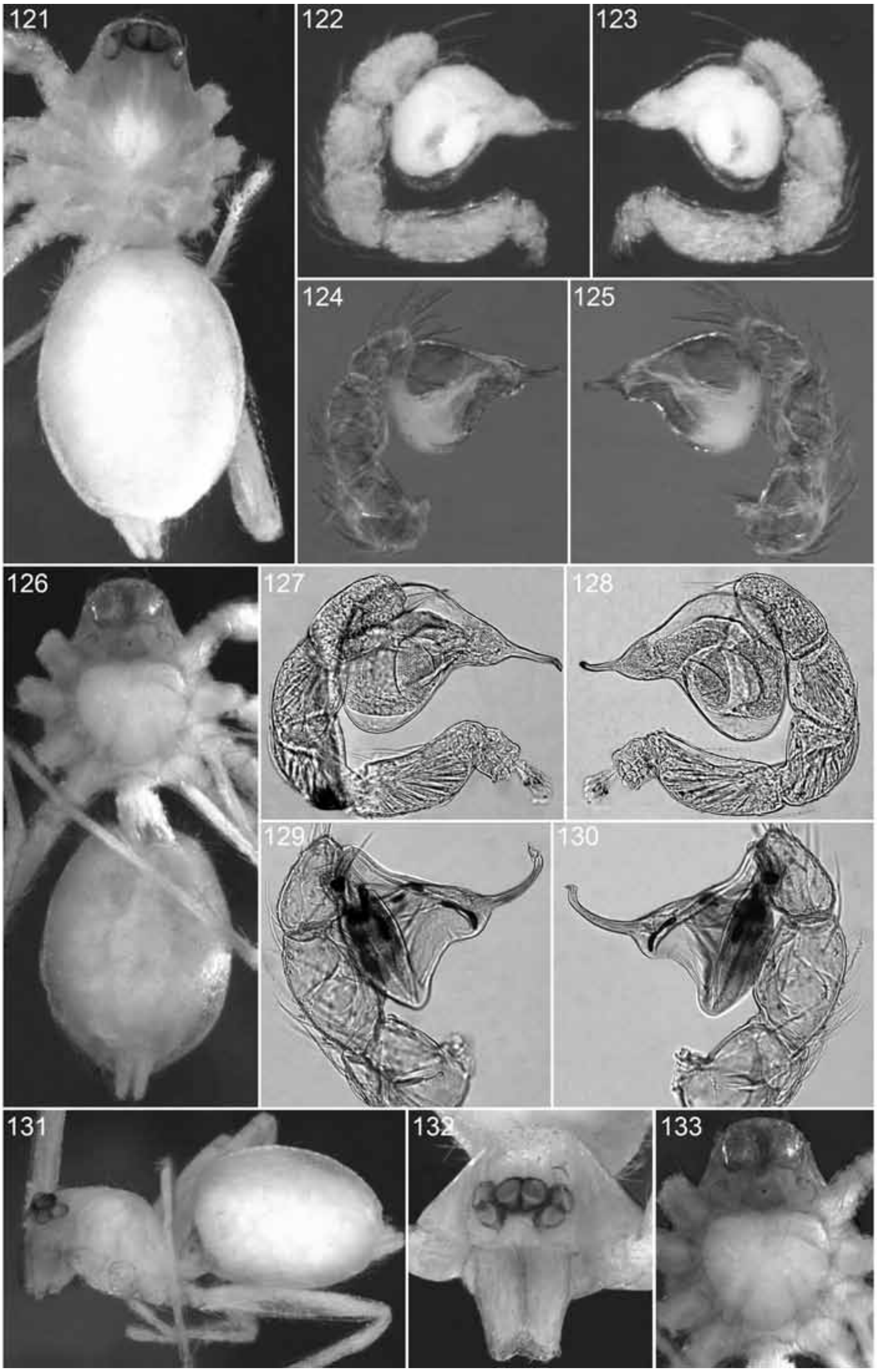
Given that the groundplan for typical oonopids seems well supported by the observations listed above, and clearly different from that of the relevant outgroups, our attention focused on



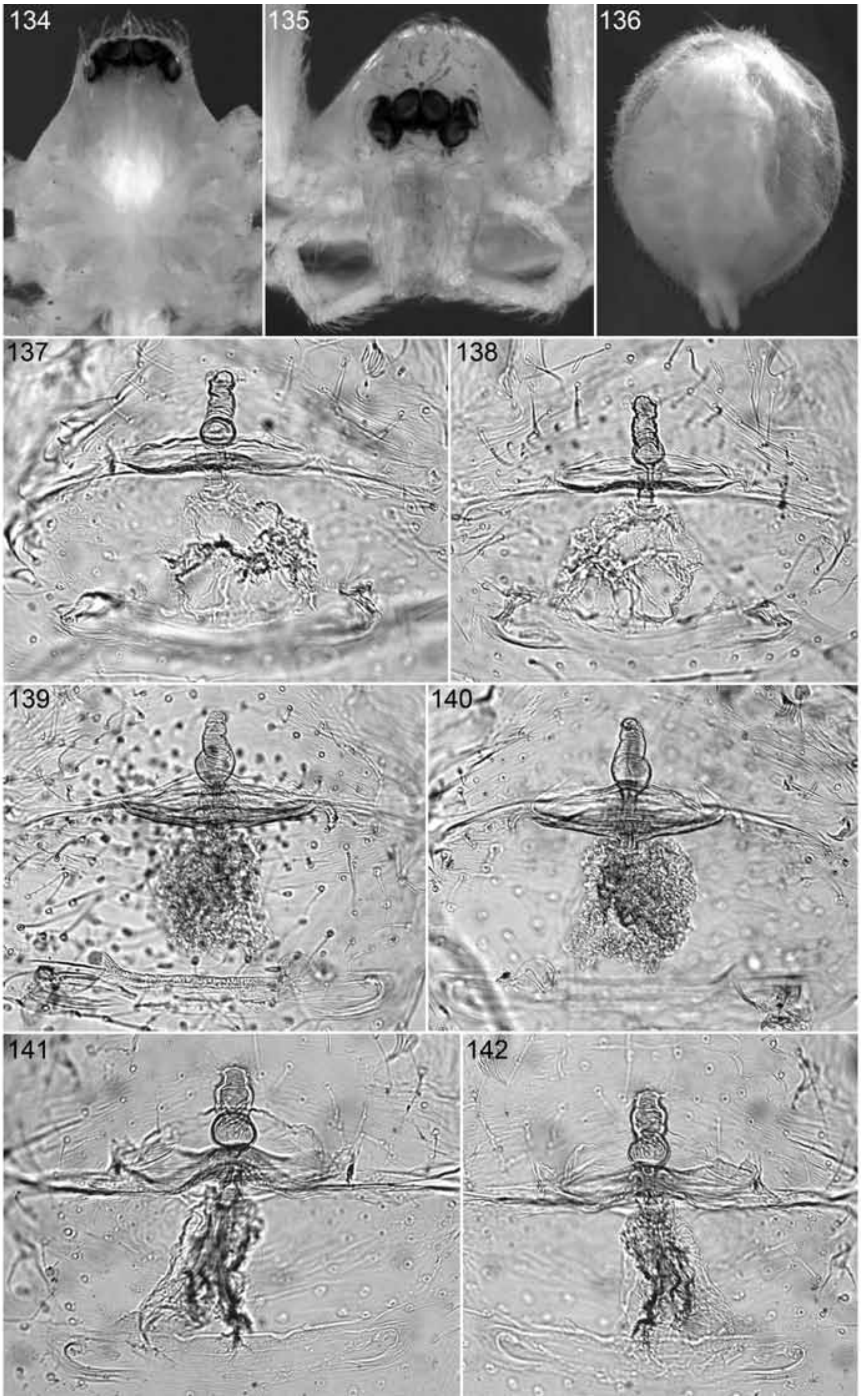
FIGURES 91–105. Tarsal organ, dorsal view, *Orchestina* sp. from Africa, male (91–95), *Orchestina* sp. from South America, female (96–100) and male (101–105). **91, 96, 101.** Leg I. **92, 97, 102.** Leg II. **93, 98, 103.** Leg III. **94, 99, 104.** Leg IV. **95, 100, 105.** Palp.



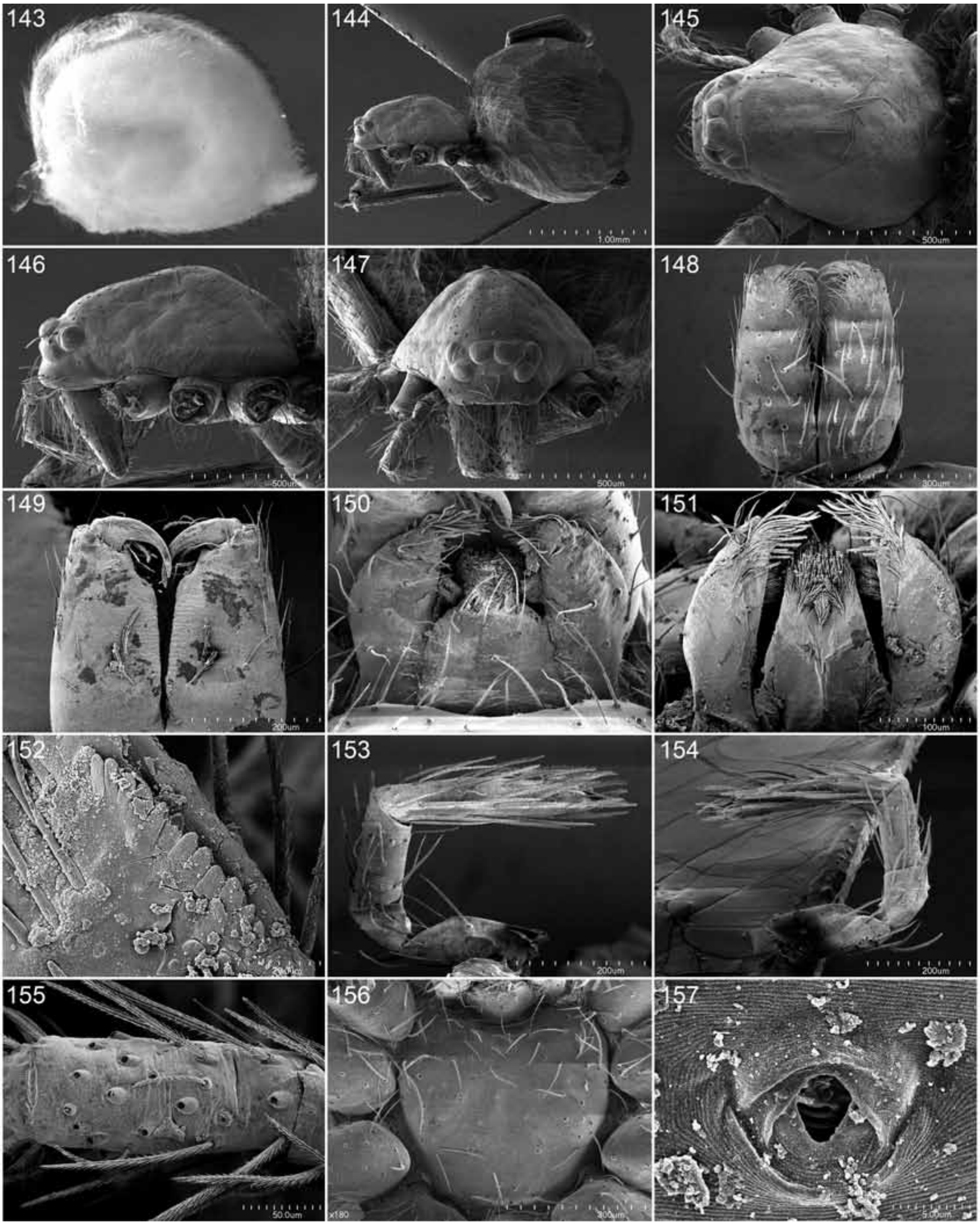
FIGURES 106–120. Tarsal organ, dorsal view, *Cortestina thaleri* Knoflach, male (106–110), *Xiombarg plaumanni* Brignoli, male (111–115), *Unicorn catleyi* Platnick and Brescovit, male (116–120). **106, 111, 116.** Leg I. **107, 112, 117.** Leg II. **108, 113, 118.** Leg III. **109, 114, 119.** Leg IV. **110, 115, 120.** Palp.



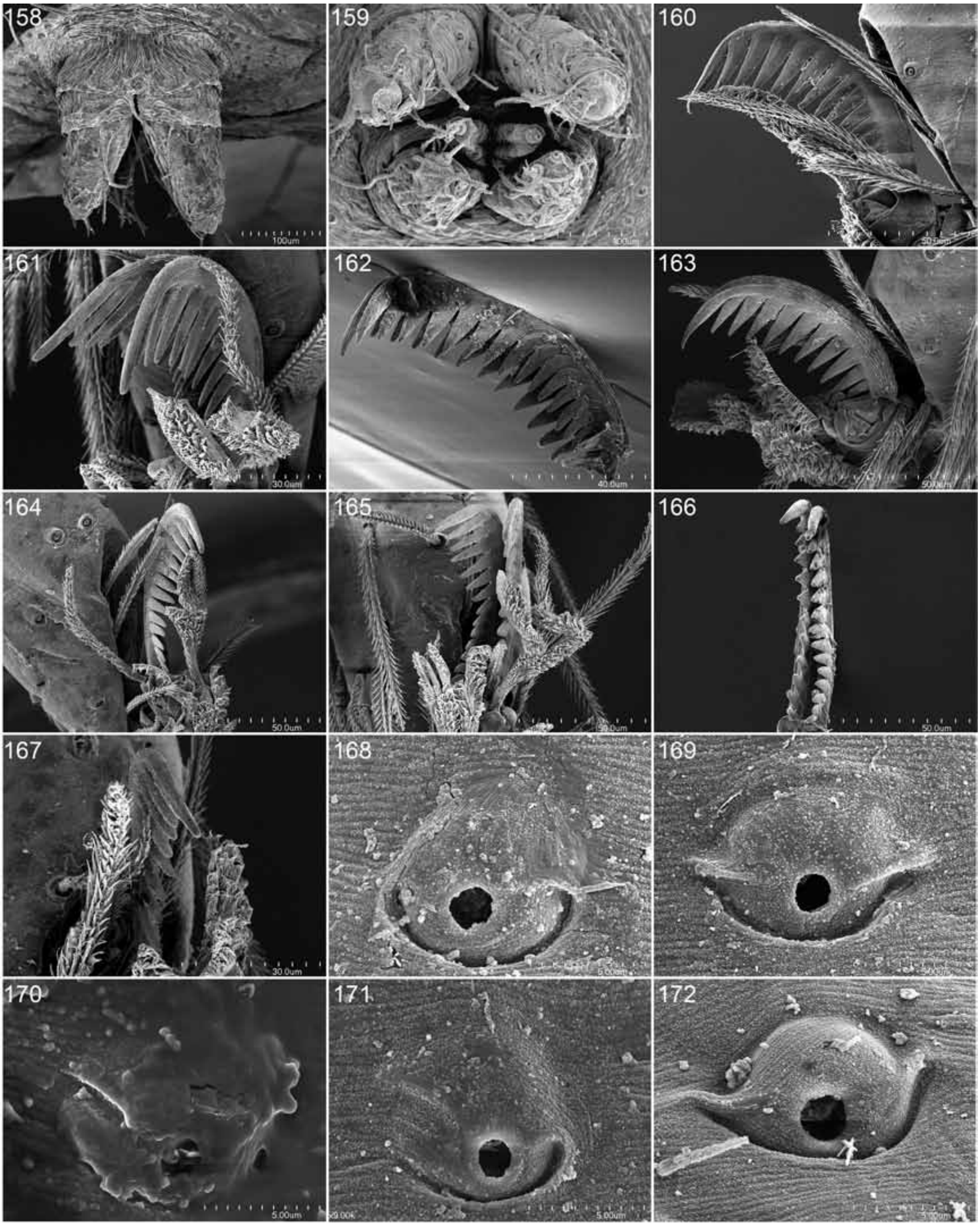
FIGURES 121–133. *Sulsula pauper* (O. P.-Cambridge), male. **121.** Habitus, dorsal view. **122, 127.** Left palp, Algeria, prolateral view. **123, 128.** Same, retrolateral view. **124, 129.** Left palp, Egypt, prolateral view. **125, 130.** Same, retrolateral view. **126.** Habitus, ventral view. **131.** Same, lateral view. **132.** Carapace, anterior view. **133.** Sternum, ventral view.



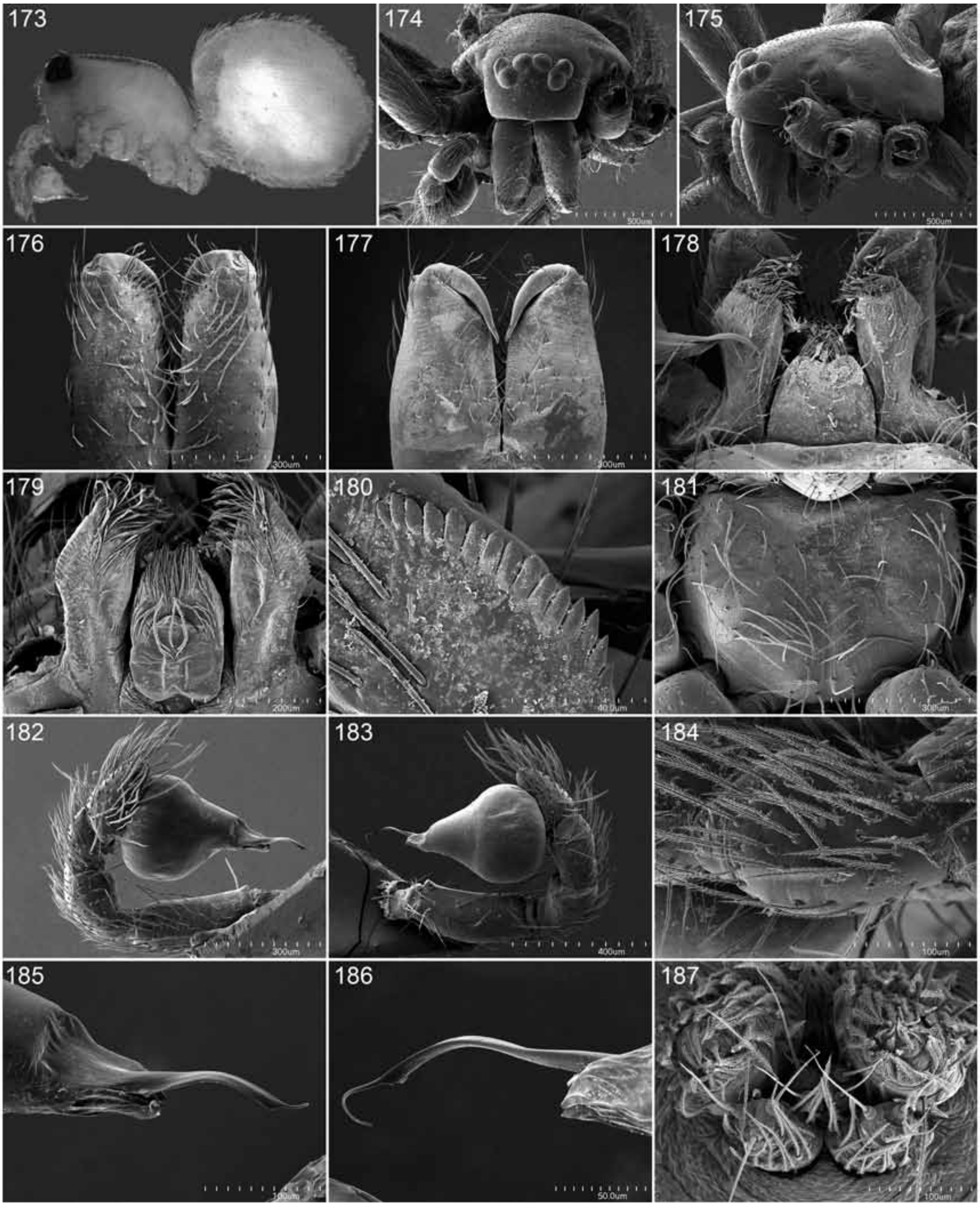
FIGURES 134–142. *Sulsula pauper* (O. P.-Cambridge), females from Algeria (134–138), Egypt (139, 140), and Sudan (141, 142). **134.** Carapace, dorsal view. **135.** Same, anterior view. **136.** Abdomen, ventral view. **137, 139, 141.** Genitalia, ventral view. **138, 140, 142.** Same, dorsal view.



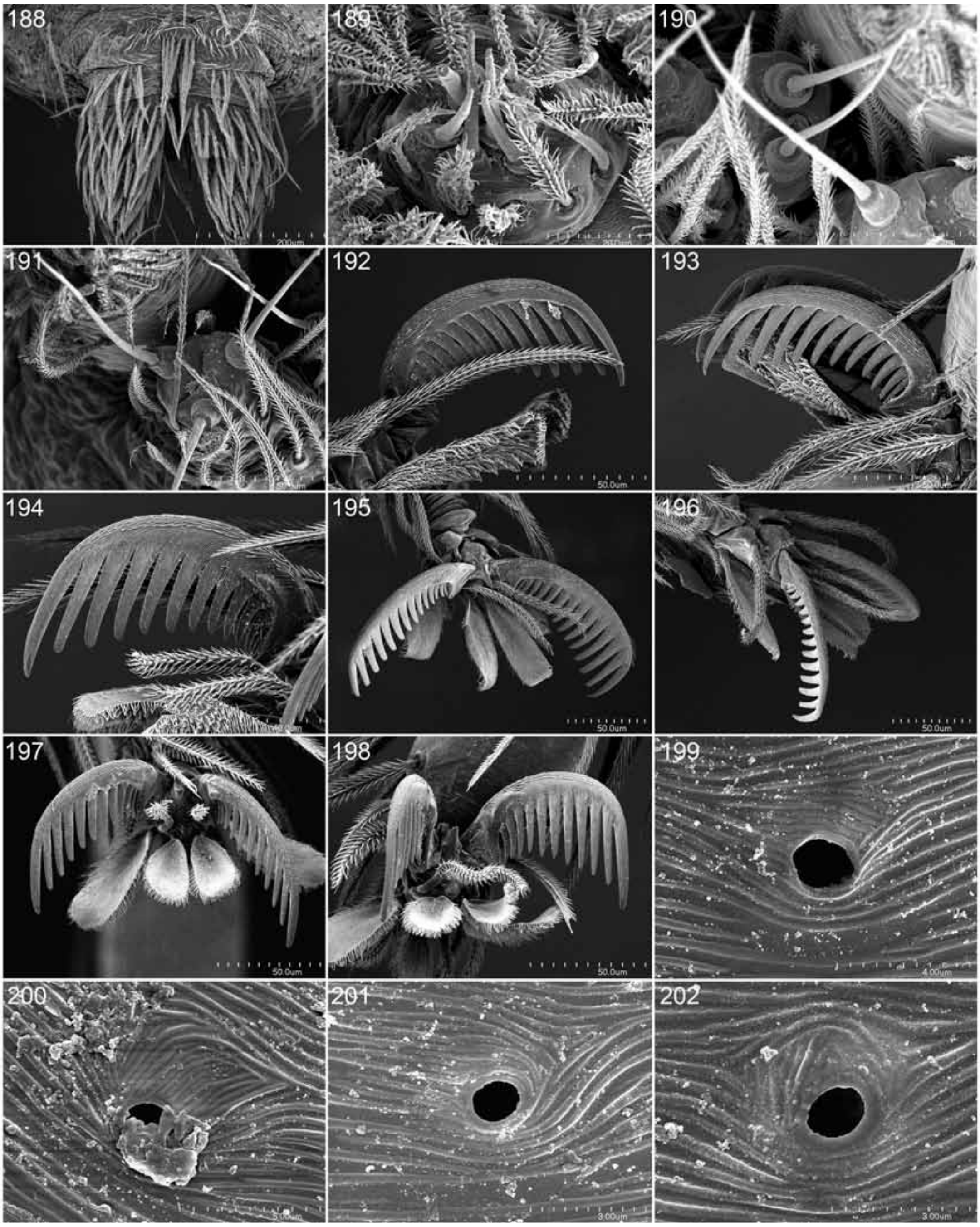
FIGURES 143–157. *Sulsula pauper* (O. P.-Cambridge), female. **143.** Abdomen, lateral view. **144.** Habitus, lateral view. **145.** Carapace, dorsal view. **146.** Same, lateral view. **147.** Same, anterior view. **148.** Chelicerae, anterior view. **149.** Same, posterior view. **150.** Labium and endites, ventral view. **151.** Labrum and endites, dorsal view. **152.** Serrula, dorsal view. **153.** Palp, prolateral view. 154. Same, retrolateral view. **155.** Palpal tibia, dorsal view. **156.** Sternum, ventral view. **157.** Trichobothrial base from tibia IV, dorsal view.



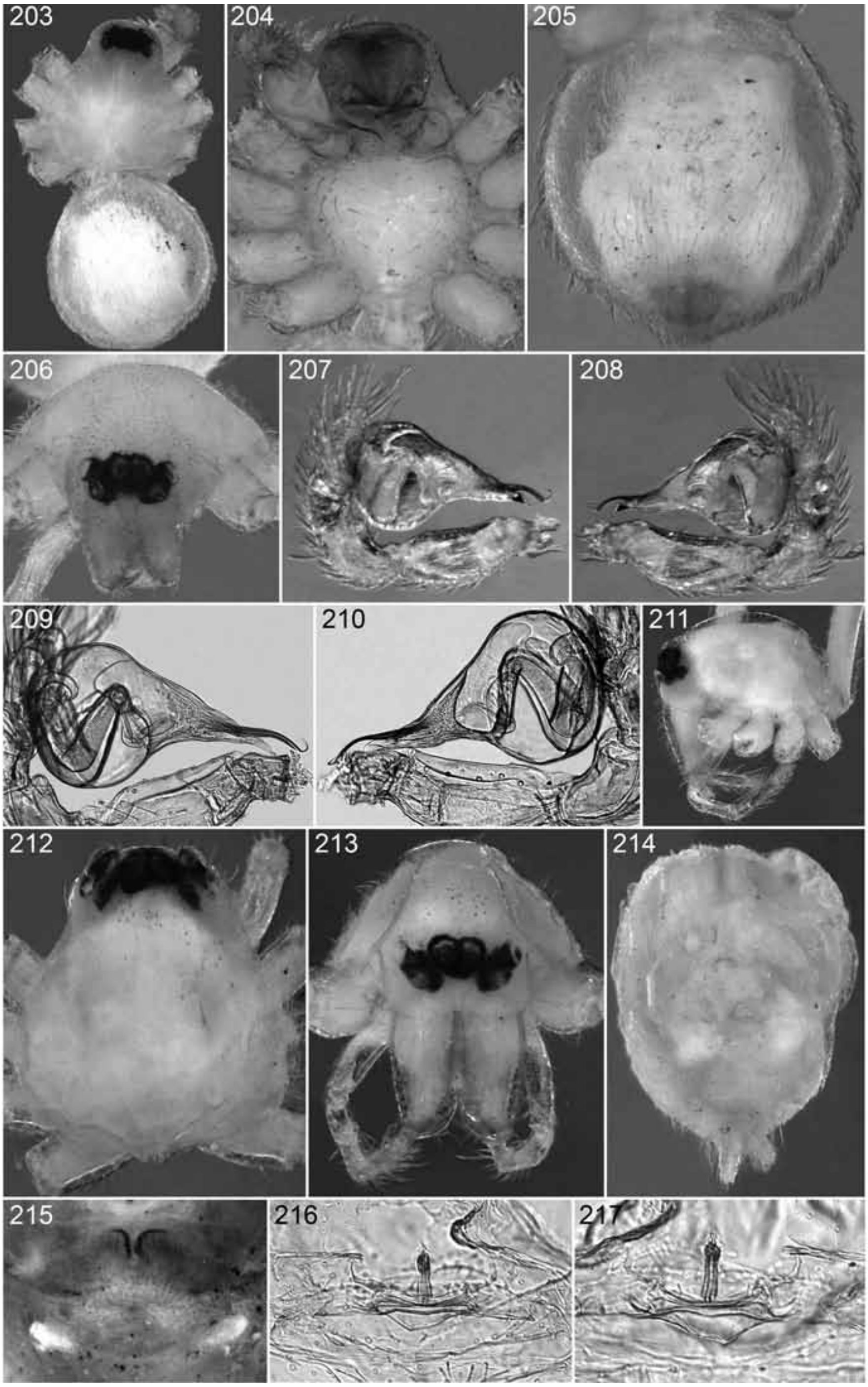
FIGURES 158–172. *Sulsula pauper* (O. P.-Cambridge), female. **158.** Spinnerets, ventral view. **159.** Same, apical view. **160.** Claws of leg I, lateral view. **161.** Same, leg II. **162.** Same, leg III. **163.** Same, leg IV. **164.** Claws of leg I, apical view. **165.** Same, leg II. **166.** Same, leg III. **167.** Same, leg IV. **168.** Tarsal organ from leg I, dorsal view. **169.** Same, leg II. **170.** Same, leg III. **171.** Same, leg IV. **172.** Same, palp.



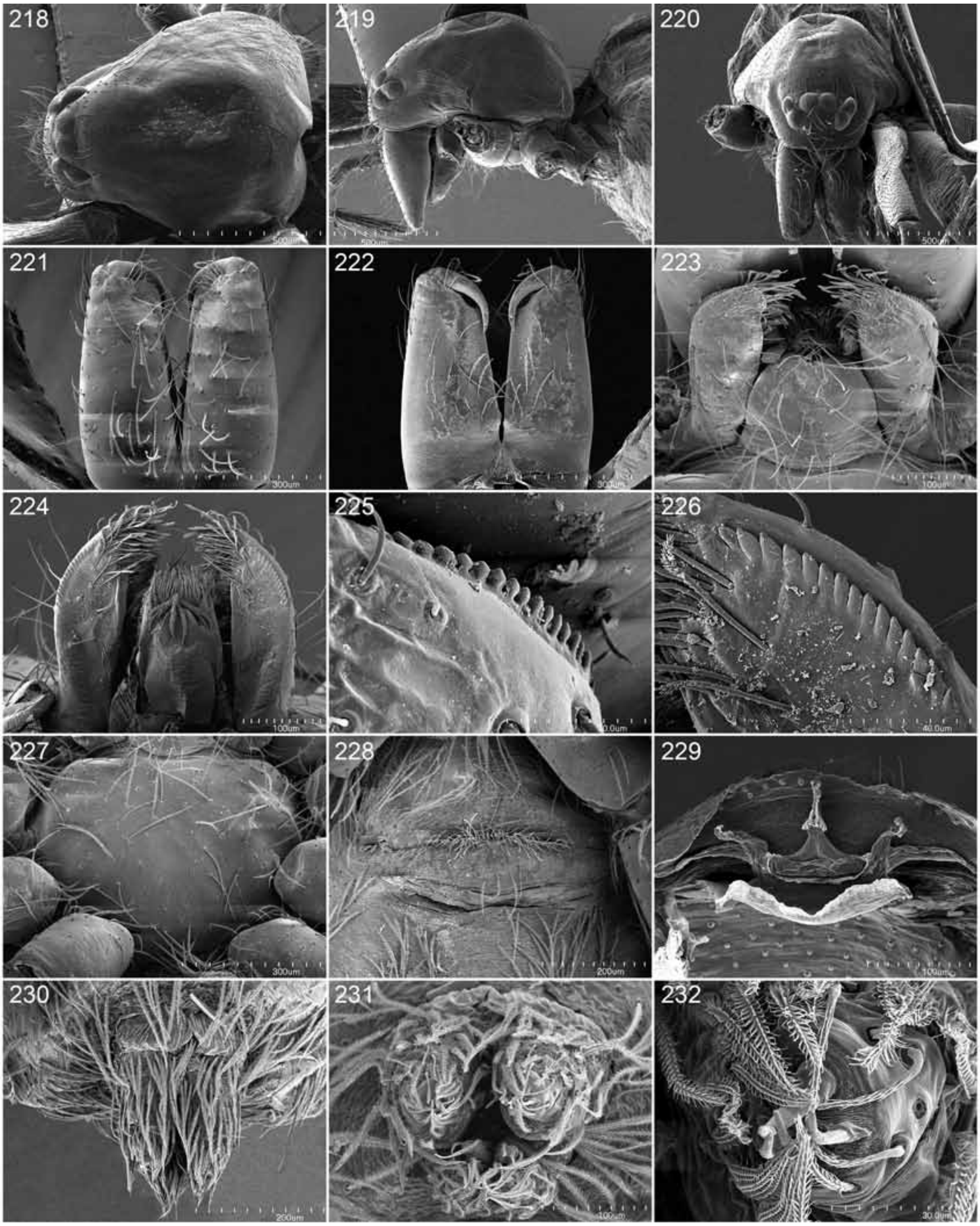
FIGURES 173–187. *Dalmasula lorelei*, new species, male. **173.** Habitus, lateral view. **174.** Carapace, anterior view. **175.** Same, lateral view. **176.** Chelicerae, anterior view. **177.** Same, posterior view. **178.** Labium and endites, ventral view. **179.** Labrum and endites, dorsal view. **180.** Serrula, dorsal view. **181.** Sternum, ventral view. **182.** Left palp, prolateral view. **183.** Same, retrolateral view. **184.** Palpal tibia, dorsal view. **185.** Embolus, prolateral view. **186.** Same, retrolateral view. **187.** Spinnerets, apical view.



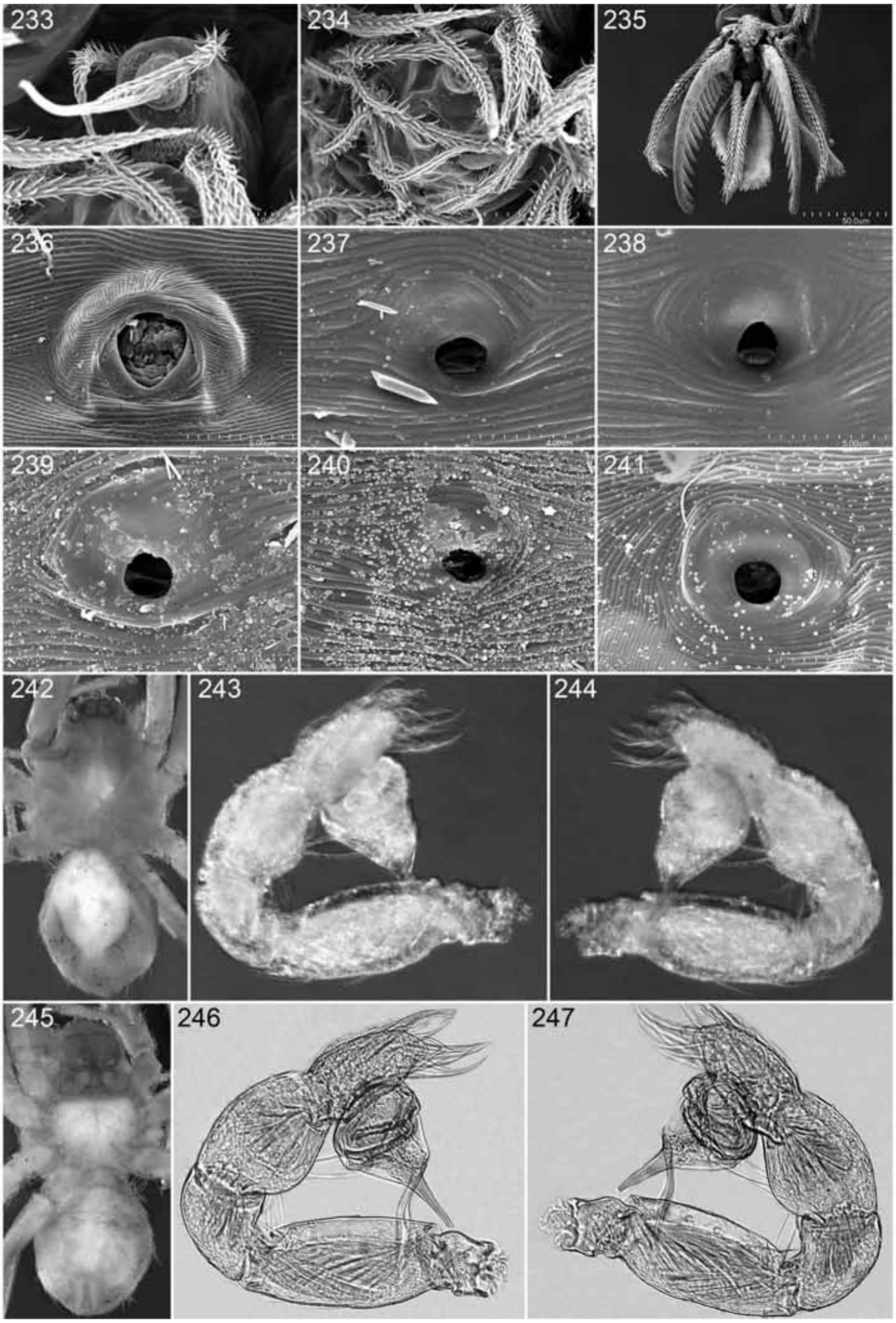
FIGURES 188–202. *Dalmasula lorelei*, new species, male. **188.** Spinnerets, ventral view. **189.** Anterior lateral spinneret, apical view. **190.** Posterior median spinneret, same. **191.** Posterior lateral spinneret, same. **192.** Claws of leg I, lateral view. **193.** Same, leg III. **194.** Same, leg IV. **195.** Claws of leg I, apical view. **196.** Claws of leg II, dorsal view. **197.** Claws of leg III, apical view. **198.** Same, leg IV. **199.** Tarsal organ from leg I, dorsal view. **200.** Same, leg II. **201.** Same, leg III. **202.** Same, leg IV.



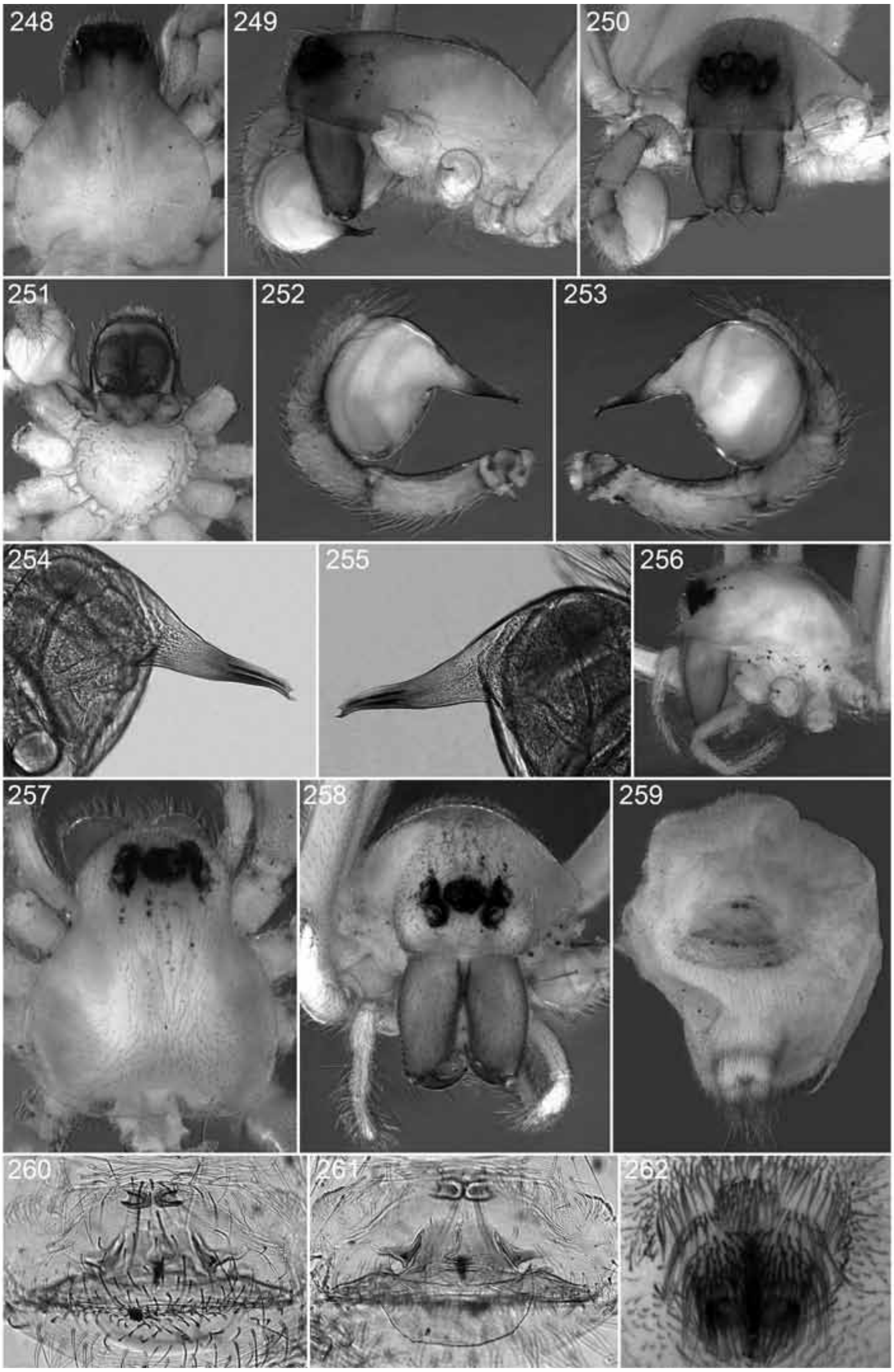
FIGURES 203–217. *Dalmasula lorelei*, new species, male (203–210) and female (211–217). **203.** Habitus, dorsal view. **204.** Sternum, ventral view. **205, 214.** Abdomen, ventral view. **206, 213.** Carapace, anterior view. **207, 209.** Left palp, prolateral view. **208, 210.** Same, retrolateral view. **211.** Carapace, lateral view. **212.** Same, dorsal view. **215, 216.** Genitalia, ventral view. **217.** Same, dorsal view.



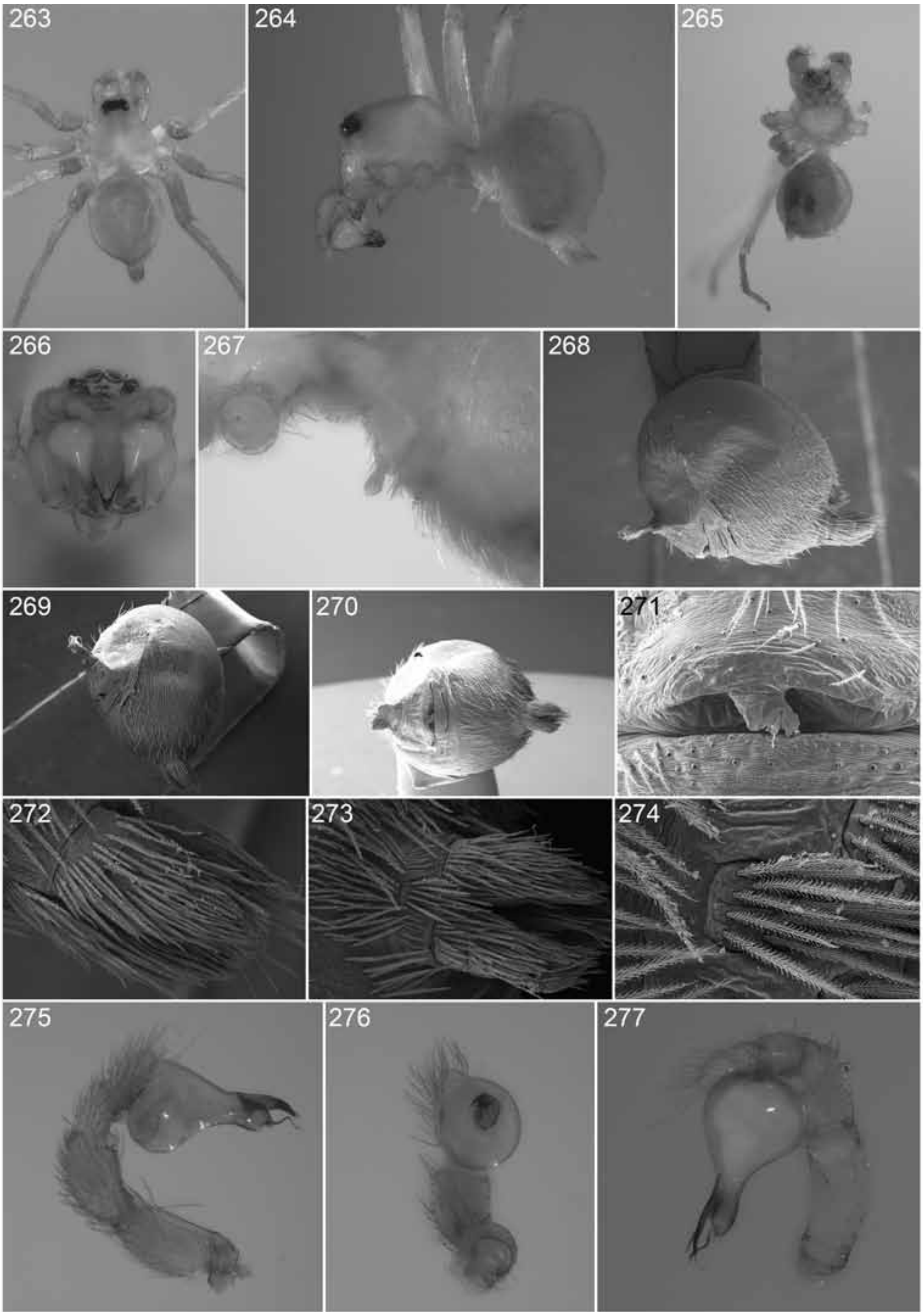
FIGURES 218–232. *Dalmasula lorelei*, new species, female. **218.** Carapace, dorsal view. **219.** Same, lateral view. **220.** Same, anterior view. **221.** Chelicerae, anterior view. **222.** Same, posterior view. **223.** Labium and endites, ventral view. **224.** Labrum and endites, dorsal view. **225.** Serrula, ventral view. **226.** Same, dorsal view. **227.** Sternum, ventral view. **228.** Epigastric region, ventral view. **229.** Genitalia, dorsal view. **230.** Spinnerets, ventral view. **231.** Same, apical view. **232.** Anterior lateral spinneret, apical view.



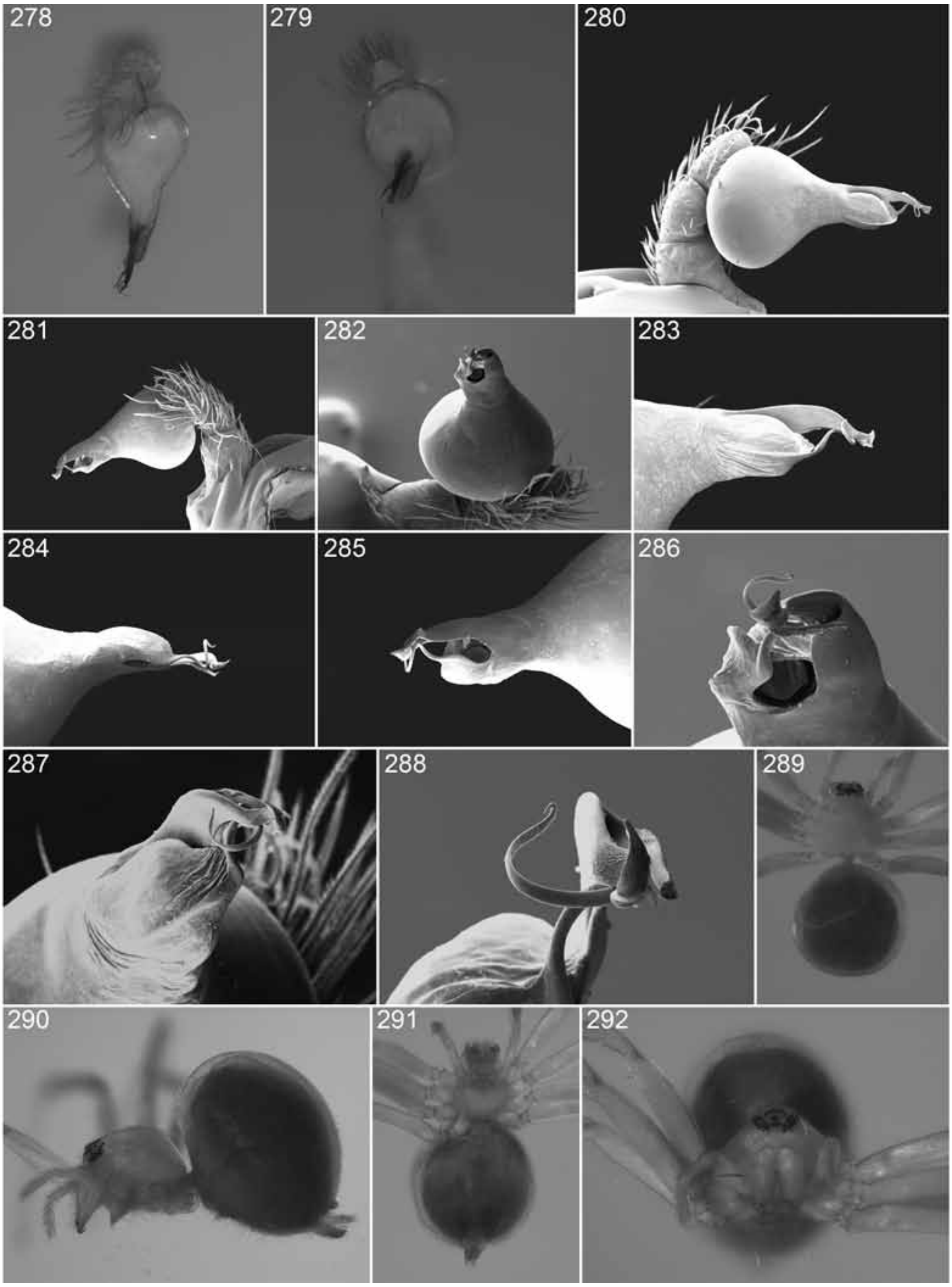
FIGURES 233–247. *Dalmasula lorelei*, new species, female (233–241), *D. parvimana* (Simon), male (242–247). **233.** Posterior median spinneret, apical view. **234.** Posterior lateral spinneret, apical view. **235.** Claws of leg I, anterior view. **236.** Trichobothrial base from tibia III, dorsal view. **237.** Tarsal organ from leg I, dorsal view. **238.** Same, leg II. **239.** Same, leg III. **240.** Same, leg IV. **241.** Same, palp. **242.** Habitus, dorsal view. **243, 246.** Left palp, prolateral view. **244, 247.** Same, retrolateral view. **245.** Habitus, ventral view.



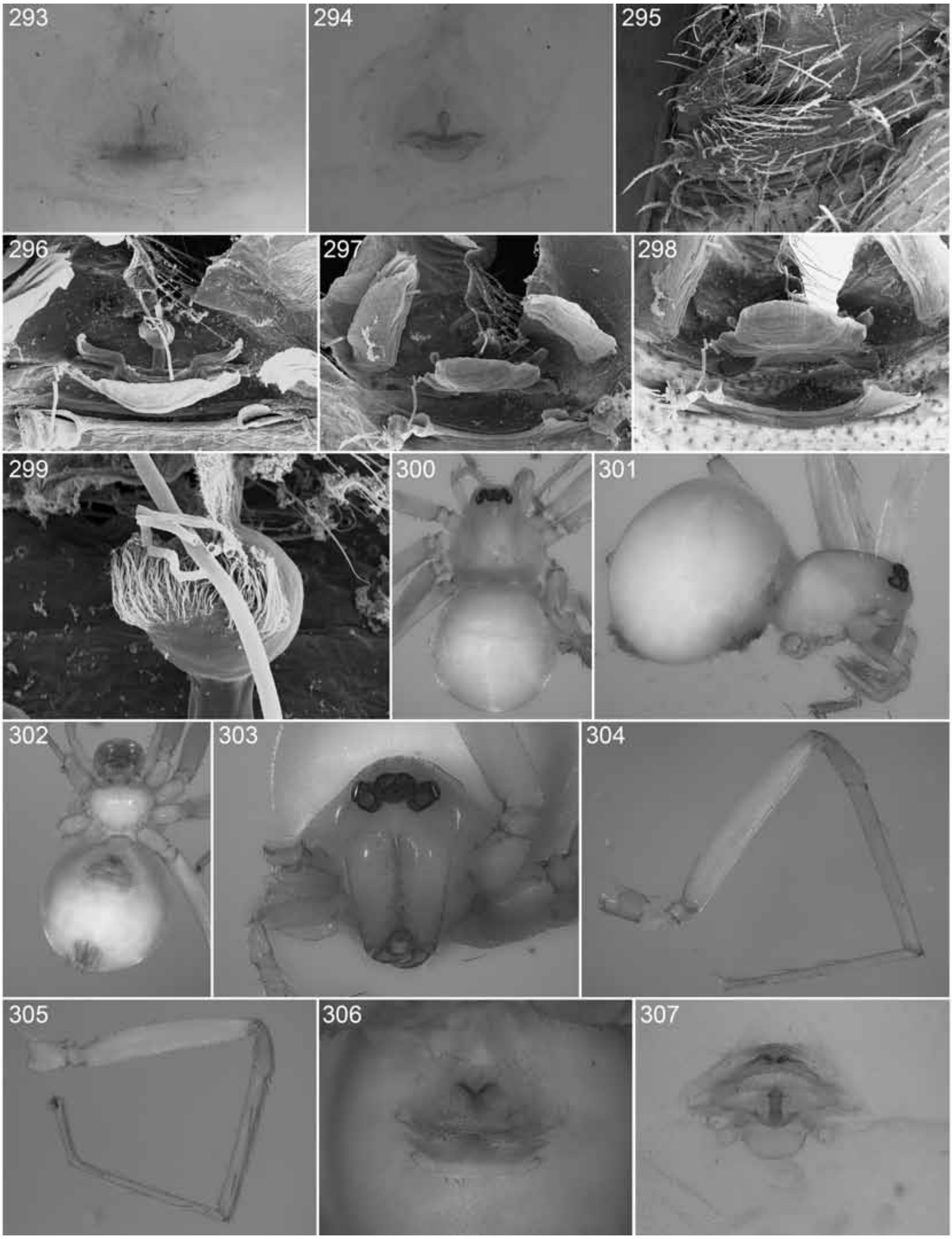
FIGURES 248–262. *Dalmasula tsumkwe*, new species, male (248–255) and female (256–262). **248, 257.** Carapace, dorsal view. **249, 256.** Same, lateral view. **250, 258.** Same, anterior view. **251.** Sternum, ventral view. **252.** Left palp, prolateral view. **253.** Same, retrolateral view. **254.** Embolus, prolateral view. **255.** Same, retrolateral view. **259.** Abdomen, ventral view. **260.** Genitalia, ventral view. **261.** Same, dorsal view. **262.** Spinnerets, ventral view.



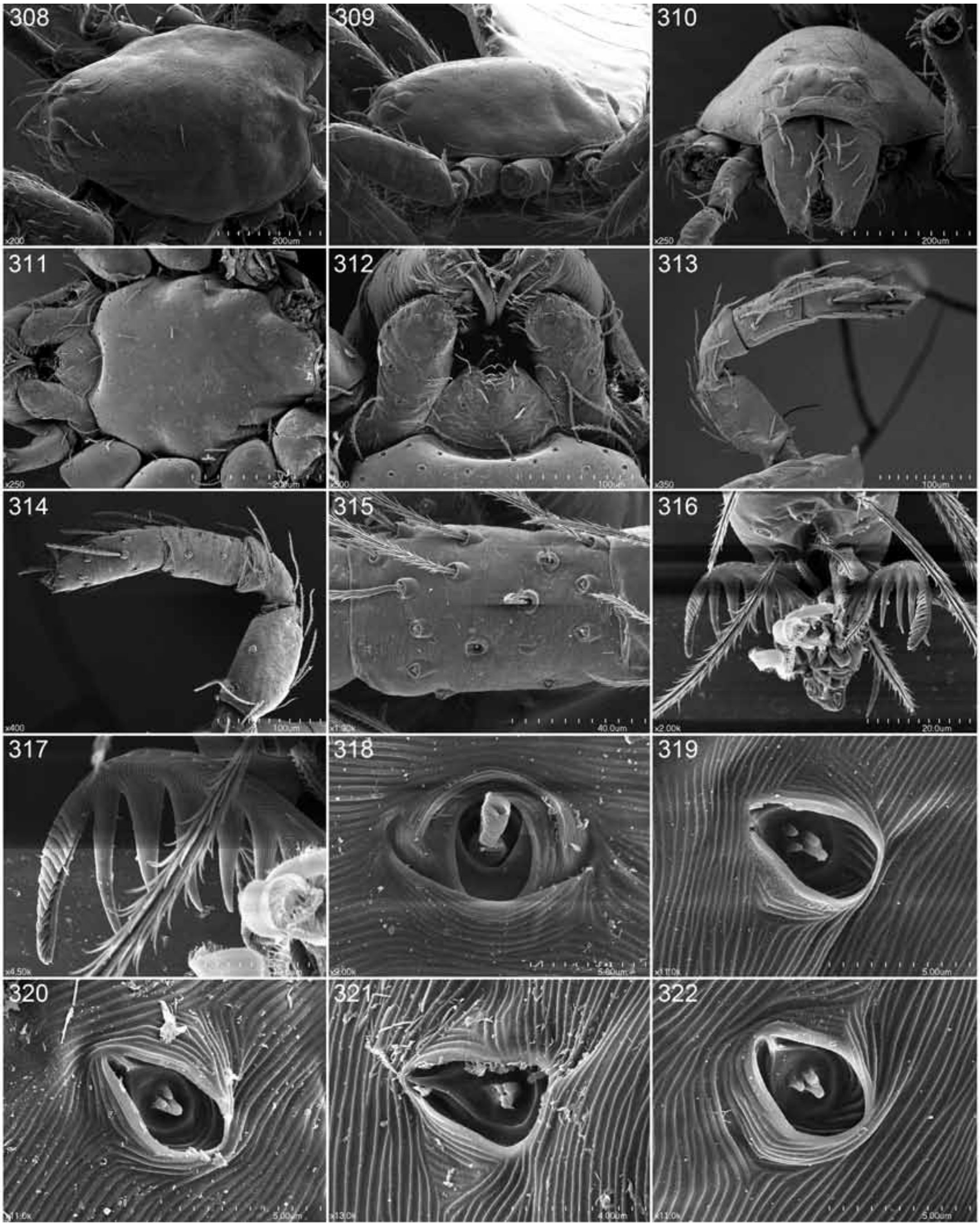
FIGURES 263–277. *Dalmasula griswoldi*, new species, male. **263.** Habitus, dorsal view. **264.** Same, lateral view. **265.** Same, ventral view. **266.** Carapace, anterior view. **267, 268.** Abdomen, lateral view. **269.** Same, oblique lateral view. **270.** Same, ventral view. **271.** Epigastric area, ventral view. **272.** Spinnerets, lateral view. **273.** Same, ventral view. **274.** Colulus, ventral view. **275.** Left palp, prolateral view. **276.** Same, ventral view. **277.** Same, retrolateral view.



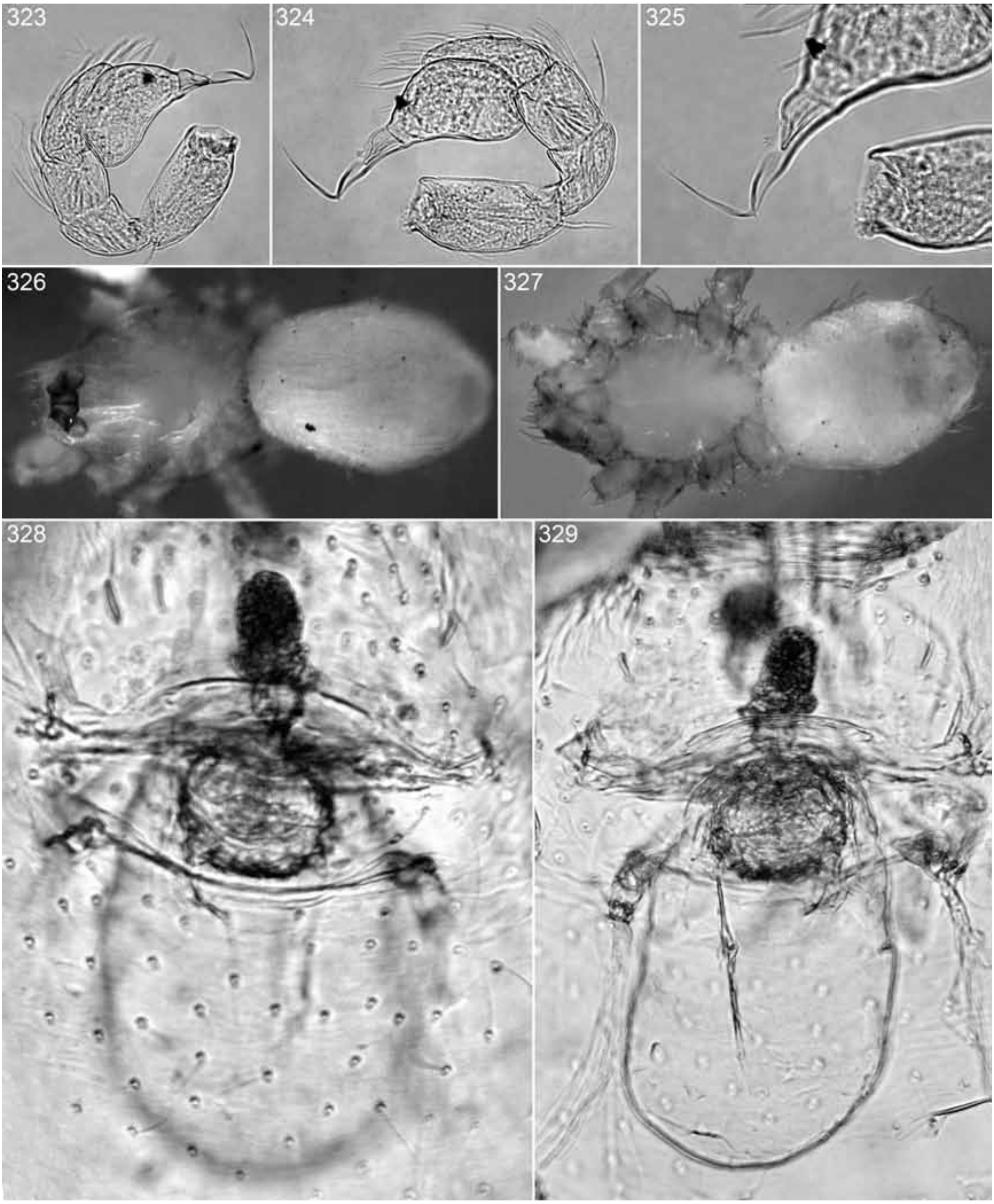
FIGURES 278–292. *Dalmasula griswoldi*, new species, male (278–288) and female (289–292). **278.** Left palp, dorsal view. **279.** Same, apical view. **280.** Left palpal bulb, prolateral view. **281.** Same, retrolateral view. **282.** Same, apical view. **283.** Embolus, prolateral view. **284.** Same, ventral view. **285.** Same, retrolateral view. **286.** Same, apical view. **287.** Conductor, ventral view. **288.** Same, apical view. **289.** Habitus, dorsal view. **290.** Same, lateral view. **291.** Same, ventral view. **292.** Same, anterior view.



FIGURES 293–307. *Dalmasula griswoldi*, new species, female (293–299), *D. dodebai*, new species, female (300–307). **293, 306.** Genitalia, ventral view. **294, 296, 299, 307.** Same, dorsal view. **295.** Epigastric area, ventral view. **297, 298.** Genitalia, oblique dorsal view. **300.** Habitus, dorsal view. **301.** Same, lateral view. **302.** Same, ventral view. **303.** Same, anterior view. **304.** Leg II, prolateral view. **305.** Same, lateral view.



FIGURES 308–322. *Kapitia obscura* Forster, female. **308.** Carapace, dorsal view. **309.** Same, lateral view. **310.** Same, anterior view. **311.** Sternum, ventral view. **312.** Labium and endites, ventral view. **313.** Palp, prolateral view. **314.** Same, retrolateral view. **315.** Palpal tibia, dorsal view. **316.** Claws of leg II, anterior view. **317.** Same, lateral view. **318.** Trichobothrial base from metatarsus II, dorsal view. **319.** Tarsal organ from leg II, dorsal view. **320.** Same, leg III. **321.** Same, leg IV. **322.** Same, palp.



FIGURES 323–329. *Kapitia obscura* Forster, male (323–327) and female (328, 329). **323.** Left palp, prolateral view. **324.** Same, retrolateral view. **325.** Embolus, retrolateral view. **326.** Habitus, dorsal view. **327.** Same, ventral view. **328.** Genitalia, ventral view. **329.** Same, dorsal view.

the types of tarsal organs found among the more basal oonopid genera (i.e., *Orchestina* and similar taxa). *Orchestina* is a highly diverse, nearly worldwide group of species united by the presence of enlarged femora on leg IV; the enlarged femora enable the animals to jump several times their body length. Its members dominate both the oonopid canopy fauna and the oonopid fossil record (including the oldest known oonopids, from Cretaceous amber, Saupe et al., in press; Marusik and Wunderlich, 2008). The tarsal organs of several undescribed species from South America, Africa, and Madagascar have been examined (see figs. 86–105); they resemble those of typical oonopids in having the longitudinal ridge originating from the proximal edge of the organ, and in showing serial dimorphism between the anterior and posterior legs, but differ in having one additional raised receptor (four on the anterior legs and three on the posterior legs), so that their receptor formula is 4-4-3-3, for legs I–IV, rather than 3-3-2-2 (as in typical oonopids).

Forster (1980), based on an extensive survey including most spider families, identified a general trend in tarsal organ evolution: the transformation from an exposed to a capsulate structure. The basal oonopid genera other than *Orchestina* illustrate this trend well. In the genus *Cortestina* Knoflach, the tarsal organ is partly capsulate (figs. 106–110; Knoflach et al., 2009, figs. 50, 51). The receptor-bearing portion of the organ is sunken well below a pair of elevated lateral folds, but one can still see at least some of the raised receptors as well as the longitudinal ridge.

In the remaining basal genera, the tarsal organ has become fully capsulate; in dorsal view, the aperture of the tarsal organ is a tiny circle, and the receptors are situated too far below the opening to be visible in scanning electron microscopy. These fully capsulate structures occur in the North African genus *Sulsula* Simon (figs. 168–172) and the South American genera *Xiombarg* Brignoli (figs. 111–115) and *Unicorn* Platnick and Brescovit (figs. 116–120; Platnick and Brescovit, 1995: figs. 9, 10; González-Reyes et al., 2010: fig. 1c). They also occur in the new genus described below as *Dalmasula*, from Namibia and South Africa, and in an undescribed genus from Argentina (Izquierdo et al., in prep.).

Forster's (1980) view that the transformation from exposed to capsulate tarsal organs has occurred repeatedly in spider evolution is born out also within the Oonopidae. Among the typical oonopids, the genus *Escaphiella* Platnick and Dupérré is notable for having an almost fully capsulate tarsal organ (see Platnick and Dupérré, 2009b: figs. 50–53, 100). The aperture, however, is quite different from that found in the basal genera, forming a long, narrow slit rather than a circle. The structure in *Escaphiella* is clearly modified from that found in the sister group of that genus, *Scaphiella* Simon, where the exposed tarsal organ has become elongated and narrowed (see Platnick and Dupérré, 2010a: figs. 510–514, 560–564). A similarly narrowed tarsal organ shape is found in another member of the *Scaphiella* complex, *Pescennina* Simon (see Platnick and Dupérré, 2011b: figs. 119–123, 164–168), suggesting that *Pescennina* may be the sister group of *Scaphiella* plus *Escaphiella.* A similarly slit-shaped opening occurs also in the more distantly related *Grymeus robertsi* Harvey (see Harvey, 1987: fig. 8), and the tarsal organs of *Longoonops bicolor* Platnick and Dupérré and *L. padiscus* (Chickering) are notably narrowed (see Platnick and Dupérré, 2010b: figs. 598, 599, 623–625, 670, 671, 692, 693), but all the transformations from exposed to capsulate tarsal organs detected to date within the typical oonopids are morphologically easily distinguishable from the character states found in *Cortestina* and the fully capsulate basal genera.

PHYLOGENETIC CONCLUSIONS

We hypothesize that the groundplan of oonopids includes an exposed tarsal organ like that of *Orchestina*, having a distinctive longitudinal ridge originating from the proximal end of the organ, and a serially dimorphic 4-4-3-3 pattern of raised receptors on legs I–IV. So far as we can tell, all oonopids retain the longitudinal ridge, but the ridge (like the receptor nodes) is not visible externally in those taxa that have acquired a fully capsulate tarsal organ morphology. The presence or absence of the ridge (and the number of receptors) in such taxa could be confirmed only by histological sectioning. The majority of oonopid species fit the trend identified within the Orsolobidae by Forster and Platnick (1985: 219), where the number of receptors becomes reduced (from five or six in some species of basal genera such as *Tasmanoonops* Hickman to only two or three). In the vast majority of oonopids, the tarsal organ is exposed and the receptor pattern is reduced from 4-4-3-3 to 3-3-2-2 (i.e., one raised receptor is lost on each tarsal organ).

The reduction to a 3-3-2-2 pattern of raised receptors occurs in the same set of taxa that show a clustered eye arrangement and have lost the heavily sclerotized, thick-walled sperm duct within the male palp, with a single known exception. The only described oonopid species from New Zealand, *Kapitia obscura* Forster, appears to retain the plesiomorphic 4-4-3-3 tarsal organ receptor pattern (figs. 319–322) and an H-shaped shaped eye arrangement (figs. 308, 310, 326), even though its male palp clearly lacks a sclerotized sperm duct (compare figs. 323, 324 with 127, 128, 209, 210). These characters suggest that *Kapitia* Forster is the sister group of the many genera with a 3-3-2-2 tarsal organ receptor pattern and a clustered eye arrangement, and all these taxa, including those previously placed in the Gamasomorphinae, are assigned below to the subfamily Oonopinae. A new subfamily is established below for those more basal genera that share a partly or fully capsulate tarsal organ; that subfamily is here named Sulsulinae, as *Sulsula* appears to be the oldest available name for any of its members. We thus recognize three subfamilies: the Orchestininae Chamberlin and Ivie, the Sulsulinae, and the Oonopinae Simon.

Although the Oonopinae are united by the "loss" of the heavily sclerotized, thick-walled sperm duct that is typical of other araneomorphs, the absence presumably reflects a major transformation in how sperm are stored within the palp, and possibly also changes in the physiological mechanisms involved in the induction of sperm into the palp, and the expulsion of sperm into the female genitalia.

The question of whether sulsulines are more closely related to oonopines or to *Orchestina* remains unanswered. Although the tarsal organ receptor patterns of the fully capsulate sulsuline genera are unknown, our scans of *Cortestina* (figs. 106–110) suggest that in that genus the number of receptors is greatly reduced, probably to 2-2-1-1, so we would expect the fully capsulate basal genera to have a similarly reduced receptor pattern. The apparent retention of a 4-4-3-3 pattern in *Kapitia* suggests, however, that the reduction in the number of tarsal organ receptors has followed different pathways within the sulsuline and oonopine lineages. Unfortunately, without studies of their ultrastructure or innervation, it doesn't seem possible to homologize individual receptors across the three subfamilies. Thus, other characters should be sought to resolve the basal three-taxon statement within the family.

We are far from being able to present a comprehensive, quantitative analysis of oonopid interrelationships. Fully half of the family's generic-level diversity may still be undescribed. Although a few groups of putatively closely related genera have been recognized (e.g., the *Scaphiella*, *Dysderina*, *Gamasomorpha*, *Pelicinus*, and *Stenoonops* groups), we are not yet able to assign many of even the currently described genera to such groups, making the choice of exemplars to be included in any such analysis highly problematic. Although our descriptive database includes a substantial amount of character information on a substantial number of species, those characters were chosen primarily for their efficacy at the species level. Many other characters that are important for higher-level relationships will need to be added before such analyses will become realistic; female genitalic characters, for example, are largely uncoded in the descriptive database. Even though a detailed analysis would therefore be premature at this point, the hypotheses we have presented above can effectively be summarized in the following matrix:

Dysdera	0000000
Orsolobus	0000000
Orchestina	1110000
Cortestina	1101000
Sulsula	1101000
Dalmasula	1101000
Xiombarg	1101000
Unicorn	1101000
Kapitia	1100100
Oonops	1100111
Gamasomorpha, etc.	1100111

where the characters are:

1 tarsal organ with proximal longitudinal ridge
2 tarsal organ with raised receptors only, in serially dimorphic pattern (either 4-4-3-3 or a modified, reduced form of that pattern, i.e., 3-3-2-2 or 2-2-1-1)
3 femur IV enlarged
4 tarsal organ at least partly capsulate
5 male palp without heavily sclerotized sperm duct
6 tarsal organ receptor pattern reduced to 3-3-2-2
7 ocular group clumped

Computer analysis is not needed to discern that these seven characters support the following groups, respectively:

1 Oonopidae (all taxa except *Dysdera* and *Orsolobus*)
2 Oonopidae (all taxa except *Dysdera* and *Orsolobus*)
3 Orchestininae (*Orchestina*)

4 Sulsulinae (*Cortestina, Sulsula, Dalmasula, Xiombarg, Unicorn*)
5 Oonopinae (*Kapitia, Oonops, Gamasomorpha*, etc.)
6 higher Oonopinae (*Oonops, Gamasomorpha*, etc.)
7 higher Oonopinae (*Oonops, Gamasomorpha*, etc.)

Note, however, that (as indicated above) the entries for characters 1 and 2 for the fully capsulate genera (*Sulsula, Dalmasula, Xiombarg, Unicorn*) represent inferences (based on *Cortestina*) rather than direct observations (which would require histological sectioning).

COLLECTIONS EXAMINED

AMNH	American Museum of Natural History, New York, NY
CMC	Canterbury Museum, Christchurch, New Zealand
HDO	Hope Department of Entomology, Oxford University, Oxford, England
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MCTP	Museu de Ciências e Tecnologia de Pontifícia Universidade Católica, Porto Alegre, Brazil
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MPEG	Museu Paraense Emílio Goeldi, Belém, Brazil
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NMNW	National Museum of Namibia, Windhoek, Namibia
OMD	Otago Museum, Dunedin, New Zealand
PPRI	Plant Protection Research Institute, Pretoria, South Africa
QMB	Queensland Museum, Brisbane, Australia
SAM	South African Museum, Cape Town, South Africa
ZMB	Museum für Naturkunde, Humboldt Universität, Berlin, Germany

VOUCHERS

Figs. 1–10, *Oonops pulcher* Templeton: PBI_OON 36412, 36413 (see Platnick and Dupérré, 2009c: 17).

Figs. 11–15, *Triaeris stenaspis* Simon: Trinidad: Simla, Apr. 1964 (A. Chickering, MCZ 71487, PBI_OON 26533).

Figs. 16–25, *Ischnothyreus peltifer* (Simon): Trinidad: University Campus, St. Augustine, Apr. 7–9, 1964 (A. Chickering, MCZ 71345, PBI_OON 27411); Brazil: Amazonas: Base de Operações Geólogo Pedro de Moura, Urucu River, Coari, July 11–20, 2003 (A. Bonaldo, J. Dias, D. Guimarães, MPEG 10214, PBI_OON 40693); Brazil: Pará: Belém, Oct. 2005 (L. Macambira, MPEG 10709, PBI_OON 40692).

Figs. 26–35, *Segestria senoculata* (Linnaeus): Switzerland: Basel (AMNH).

Figs. 36–45, *Ariadna bicolor* (Hentz): United States: Colorado: Fremont Co.: 3 mi E Texas Creek, Aug. 29, 1961 (W. Gertsch, W. Ivie, AMNH).

Figs. 46–55, *Dysdera crocata* C.L. Koch: United States: New Mexico: Grant Co.: Silver City, Apr. 12, 1950 (H. Shantz, AMNH); Pennsylvania: Bucks Co.: E Jamison, Apr.–June 1954 (W. Ivie, AMNH).

Figs. 56–65, *Harpactea lepida* (C.L. Koch): Switzerland: Basel (AMNH).

Figs. 66–75, *Harpactocrates drassoides* (Simon): Switzerland: Basel, July–Aug. (AMNH).

Figs. 76–82, *Tasmanoonops parvus* Forster and Platnick: Australia: Queensland: Lamington National Park, Mar. 20, 2007 (D. Putland, K. Staunton, QMB 22286, PBI_OON 23260).

Fig. 83, *Hickmanolobus* sp.: Australia: Queensland: Lamington National Park, July 27, 2007 (S. Wright, AMNH PBI_OON 31359).

Figs. 84, 85, *Calculus bicolor* Purcell: South Africa: Western Cape: Cape Flats (SAM PBI_OON 2190).

Figs. 86–95, *Orchestina* sp.: Democratic Republic of Congo: Luki Forest Reserve, Sept. 22, 2007, canopy fogging (D. De Bakker, J.-P. Michiels, MRAC 228967, PBI_OON 33693).

Figs. 96–105, *Orchestina* sp.: Argentina: Jujuy: Parque Nacional Calilegua (MACN 17674, 17677, 17678, 18015, 18016, PBI_OON 14896, 14905, 14922, 14924).

Figs. 106–110, *Cortestina thaleri* Knoflach: Austria: Tirol: Innsbruck, May 2006 (F. Stauder, AMNH PBI_OON 43544).

Figs. 111–115, *Xiombarg plaumanni* Brignoli: Brazil: Rio Grande do Sul: Parque Estadual de Itapuã (MCTP 17255, 17274, 17293, PBI_OON 11635, 11636, 43543).

Figs. 116–120, *Unicorn catleyi* Platnick and Brescovit: Chile: Tarapacá: Parinacota, Feb. 3, 1994 (N. Platnick, K. Catley, R. Calderon, R. Allen, AMNH PBI_OON 43542).

SYSTEMATICS

Our methods follow those of Platnick and Dupérré (2009a, 2009b); only differences from the males (beyond the obvious lack of male endite modifications) are mentioned in the descriptions of females. Scans were taken from uncoated right male palps, and the images were flipped for consistency. All measurements are in mm. High-resolution versions of the images, the geocoded locality data, and a distribution map for each species will be available on the goblin spider Planetary Biodiversity Inventory (PBI) project's website (http://research.amnh.org/oonopidae).

Oonopidae Simon

Oonopidae Simon, 1890: 80.

Diagnosis: Oonopids resemble orsolobids but lack the elevated tarsal organs characteristic of that family (figs. 76–85) and have instead a flat, exposed, or capsulate tarsal organ with a distinctive longitudinal ridge originating at the proximal end of the organ (figs. 1, 7, arrows), raised receptors only, and dimorphism between the anterior and posterior legs, with legs I and II having one more receptor than do legs III, IV, and the palpal tarsi (figs. 1–25). Males of representative studied species have a single, fused testis (Burger and Michalik, 2010); females lack a claw on the palpal tarsus (the claw is typically retained in orsolobids).

One other character that has traditionally been used to delimit oonopids is the absence of cheliceral teeth (see, for example, Simon, 1893: 287; Kaston, 1948: 60; Platnick and Brescovit, 1995: 5). However, the presence of cheliceral teeth has now been documented in a wide variety of oonopids (see, for example, Bristowe, 1948: 883; Fannes and Jocqué, 2008: fig. 26; Ubick and Griswold, 2011a: figs. 25, 136).

Included Subfamilies: Orchestininae, Sulsulinae, Oonopinae.

Misplaced Genera: *Calculus* Purcell, here transferred to the Orsolobidae.

Orchestininae Chamberlin and Ivie

Orchestininae Chamberlin and Ivie, 1942: 6.

Diagnosis: Orchestinines are easily recognized by their enlarged femora IV. So far as is known, their 4-4-3-3 tarsal organ receptor pattern is shared only with the basal oonopine genus *Kapitia*. In *Orchestina*, however, the tarsal organs are typically narrowed at the proximal end, producing a neck-shaped appearance (figs. 86–105) that does not occur in *Kapitia*. Most species of *Orchestina* have the posterior median eyes advanced to form a straight row with the anterior lateral eyes (much as in *Segestria*), but at least some undescribed African species have the posterior median eyes situated more posteriorly, in the more H-shaped pattern shared by the sulsulines and *Kapitia*.

Included Genera: Only *Orchestina* Simon; 51 Recent species have been described to date (Platnick, 2012), but as many additional species have already been identified by Matias Izquierdo, Arnaud Henrard, and Natalia Chousou-Polydouri. Saaristo and Marusik (2004) established a monotypic genus, *Ferchestina*, for a single species from the Russian Far East. Those authors noted (2004: 51) that five of the oonopid genera then recognized are each widely distributed and together constitute more than half of the family's then known species diversity, and somehow concluded from those observations that "it is quite safe to postulate that all these five genera are more or less polyphyletic." The argument is nonsensical, as neither the number of included species, nor how widely they occur, are evidence of monophyly or polyphyly; only synapomorphic characters, and their distribution among taxa, are relevant to that question. Saaristo and Marusik (2004: 51) noted that *Orchestina*, in particular, does have at least one putative synapomorphy: "A single key-character used to separate members of *Orchestina* from other non-scutate oonopids is the markedly swollen tibia [sic, lapsus for *femur*] IV."

In our view, there are no convincing characters supporting the placement of *Ferchestina storozhenkoi* Saaristo and Marusik in a genus separate from *Orchestina*; that type species clearly shares the primary synapomorphy of *Orchestina*, the enlarged femur IV. Saaristo and Marusik provided no characters suggesting that their species represents the sister group of all other orchestinines (i.e., that all the other *Orchestina* species form a monophyletic group that excludes *Ferchestina*). The differences they cited in their generic diagnosis, such as the prominent humps on the male carapace, the projection at the tip of the cheliceral paturon, and the details of the male and female genitalia, are all presumably just species-level autapomorphies, and are therefore irrelevant to the question of what the closest relative(s) of the species may be. Saaristo and Marusik commented that compared to *Orchestina pavesii* (Simon), the type species, femur IV is "not so thick" but provided no illustration of that supposed difference. The thickness of the fourth femur varies among the many species of *Orchestina*, possibly in allometric correlation with the total size, which also varies significantly (with some species attaining almost twice the total length of others). The diagnostic character is that the fourth femora are much thicker than femora I–III of the same specimen, not that they are of any particular given thickness (indeed, proportionately much less emphatically enlarged femora IV are also found in some soft-bodied, Neotropical oonopine species currently misplaced in *Oonops*). Both the male and female genitalia of *Ferchestina* fit well within the extensive range of variation shown by *Orchestina* species. We conclude that *Ferchestina* represents just a highly autapomorphic species of *Orchestina*, and that its recognition as a separate genus is positively misleading phylogenetically; we therefore place the name as a junior synonym of *Orchestina* (NEW SYNONYMY).

Although our conclusion is that the recognition of *Ferchestina*, as currently constituted, renders *Orchestina* a paraphyletic group and is therefore unacceptable, it is of course possible that future phylogenetic analyses will be able to discern monophyletic subgroups of orchestinines that are each supported by putatively synapomorphic characters. If, at that time, the type species of *Ferchestina* can be shown to belong to a subgroup that does not also include the type species of *Orchestina*, then it may be possible to resurrect *Ferchestina* as a usable name, but it would have to be on the basis of new evidence, not the insufficient data provided by Saaristo and Marusik (2004).

Sulsulinae Platnick, new subfamily

TYPE GENUS: *Sulsula* Simon (1882).

DIAGNOSIS: This subfamily includes taxa that resemble *Orchestina* in having a transverse, unclumped eye arrangement and a heavily sclerotized sperm duct within the male palp, but have partly or fully capsulate tarsal organs and a normal, rather than expanded, femur IV.

INCLUDED GENERA: *Sulsula* Simon (1882) from North Africa; *Xiombarg* Brignoli (1979) from Brazil and Argentina; *Unicorn* Platnick and Brescovit (1995) from Chile, Bolivia, and Argentina; *Cortestina* Knoflach (see Knoflach et al., 2009) from Austria and Italy, plus two new genera: *Dalmasula*, described below from Namibia and South Africa, and an undescribed genus from Argentina (Izquierdo et al., in prep.). Based on its partly capsulate tarsal organs, the Laurasian genus *Cortestina* probably represents the sister group of the other, fully capsulate, Gondwanan genera. The monophyly of the fully capsulate genera may also be supported by the presence of a single row of teeth on the tarsal claws; most other oonopids, and orsolobids, have two rows of teeth on each claw. However, there are typical oonopids in which one of the tooth rows has been lost in males (as in *Heteroonops* Dalmas; see Platnick and Dupérré. 2009c) or in both sexes (as in *Birabenella* Grismado; see Grismado, 2010).

Sulsula Simon

Sulsula Simon, 1882: 237 (type species by monotypy *Sulsula longipes* Simon).

Salsula: Simon, 1893: 294.

NOTE: Simon (1893) regarded the original spelling of the genus as a printer's error, but the spelling occurs twice in Simon (1882) and his alternate spelling was rejected by Dalmas (1916: 204) and subsequent authors.

DIAGNOSIS: Members of *Sulsula* resemble those of *Dalmasula* in having a globose abdomen (figs. 143, 144), but can be distinguished by the absence of cheliceral teeth, the much smaller colulus (fig. 158; cf. figs. 188, 273, 274), and the uniquely modified tarsal organs, which have a distal, semicircular groove as well as a pair of laterally directed ridges (figs. 168–172). Males have a simple embolus, without a conductor (figs. 127, 128), and the female genital area lacks the anterior sclerotizations found in *Dalmasula* (fig. 136).

Sulsula pauper (O. P.-Cambridge)

Figures 121–172

Oonops pauper O. P.-Cambridge, 1876: 549 (juvenile holotype from Alexandria, Alexandria, Egypt, in HDO; examined).

Sulsula longipes Simon, 1882: 237 (male holotype from Ramleh, Alexandria, Egypt, in MNHN; examined). First synonymized by Simon, 1910: 178.

Salsula longipes: Simon, 1893: 294.

Salsula paupera: Simon, 1910: 178.

Salsula pauper: Simon, 1911: 308.

Sulsula pauper: Dalmas, 1916: 205.

NOTE: Simon (1882) mentioned only a single male specimen, but the vial with that specimen includes also a female, which we suspect Simon erroneously considered to be juvenile.

DIAGNOSIS: With the characters of the genus, a male embolus with a relatively short, terminally curved tip (figs. 127–130), and female genitalia with a tubular, sclerotized anterior receptaculum (figs. 137–142) and an oval, unsclerotized posterior receptaculum (collapsed in those figures).

VARIATION: It is possible that more than one species is represented, but the few available specimens do not provide sufficient evidence to substantiate the description of additional species at this time. Females are available from three sites, but the one from Sudan (figs. 141, 142) has genitalia that seem more similar to that of a female from Algeria (figs. 137, 138) than to the geographically much closer one from Egypt (figs. 139, 140). Only two males are available, from Algeria and Egypt. Under a dissecting microscope, the Algerian male appears to have a bulb that extends farther toward the palpal patella (figs. 122–125), but under a compound microscope, that difference is not obvious (figs. 127–130; unfortunately, the bulb of the Egyptian male collapsed in clove oil under the compound microscope). The embolus shows differences under the compound microscope, but at least some of those differences reflect different positioning of the palps and consequent foreshortening in the photographs of the Algerian male.

MALE (PBI_OON 813, figs. 121–133, images of nonsexual characters based on female): Total length 2.16. **Cephalothorax:** Carapace white, without any pattern, piriform in dorsal view (figs. 134, 145), pars cephalica flat in lateral view (fig. 131), anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, pars thoracica without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent; marginal and nonmarginal pars cephalica and pars thoracica setae dark, needlelike. Clypeus margin unmodified, straight in front view (fig. 147), vertical in lateral view (fig. 146), high, ALE separated from edge of carapace by their radius or more, median projection absent; setae dark, needlelike. Chilum absent. Eyes six, well developed, PME largest, ALE oval, PME squared, PLE oval; posterior eye row recurved from above, straight from front; ALE separated by more than their diameter, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separated by PME radius to PME diameter (figs. 121, 132, 135, 145). Sternum wider than long (fig. 156), white, uniform in coloration, not fused to carapace, median concavity absent, without radial furrows between coxae I–II, II–III, III–IV, radial furrow opposite coxae III absent, surface smooth, without pits, microsculpture absent, sickle-shaped structures absent, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles absent, lateral margins unmodified, without posterior hump; setae sparse, dark, needlelike, densest laterally, originating from surface, hair tufts absent (figs. 126, 133). Mouthparts yellow. Chelicerae straight, anterior face unmodified; without teeth on promargin or retromargin (figs. 148, 149); fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified; setae dark, needlelike, evenly scattered; paturon inner margin with scattered setae, distal region unmodified, posterior surface unmodified, promargin unmodified, inner margin unmodified, laminate groove absent. Labium triangular, not fused to sternum, anterior margin not indented at middle, same as sternum in sclerotization; with six or more setae on anterior margin, subdistal portion with unmodified setae (fig. 150). Endites distally not excavated, serrula present in single row (figs. 151, 152), anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. **Abdomen:** White, without scuta or color pattern, globular (figs. 136, 143, 144), without long posterior extension, rounded posteriorly; book lung covers large, ovoid, without setae, anterolateral edge unmodified; posterior spiracles connected by groove; pedicel tube short, unmodified, scutopedicel region unmodified, abdomen extending anteriad of pedicel, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent; dorsal, epigastric, and postepigastric setae light, needlelike; dense patch of setae anterior to spinnerets absent. Spinnerets probably with unsclerotized strip crossing base of anterior lateral pair (fig. 158), all spinnerets with few spigots (fig. 159). Colulus small, with two setae. **Legs:** White, without color pattern; femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace, tibia I unmodified, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I, II mesoapical comb absent, metatarsi III, IV weak ventral scopula absent. Leg spination (only surfaces bearing spines listed, legs in poor condition, most spines lost, their bases not detectable without scanning): tibia IV r1-0-0. Tarsi without inferior claw, superior claws with single row of teeth (figs. 160–167). Trichobothrial bases with arched ridge (fig. 157). Tarsal organ capsulate, with distal, semicircular groove and pair of laterally directed ridges (figs. 168–172). **Genitalia:** Epigastric region with sperm pore not visible; furrow without Ω-shaped insertions, without setae. Palp of normal size, not strongly sclerotized, proximal segments yellow; trochanter of normal size, unmodified; femur of normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, slightly widened, without prolateral row of ridges, setae unmodified; cymbium yellow, narrow in dorsal view, not fused with bulb, not extending beyond distal tip of bulb, plumose setae, stout setae, distal patch of setae all absent; bulb yellow, more than 2 times as long as cymbium, stout, tapering apically; embolus dark, curved distally, without prolateral excavation; conductor absent (figs. 122–125, 127–130).

FEMALE (PBI_OON 813, figs. 134–172): Total length 3.19. Palpal tarsus without claws (figs. 153, 154); tibia with trichobothria (fig. 155); spines present, tibia p1-0-0; patella without prolateral row of ridges. Leg spination (only surfaces bearing spines listed, all spines longer than segment width): femora: I d0-0-2, p0-1-1; II d0-0-2; III, IV d0-0-1; patellae: III d1-0-0, p1-0-0, r1-0-0; tibiae: I p0-0-1, v0-0-1, r0-0-1; II p0-0-1, v0-0-1; III d1-1-0, p1-1-1, r1-0-1; IV d1-1-0, p1-1-1, v1-0-0, r1-1-1; metatarsi: I p1-1-0, r1-0-0; II p1-0-0, r1-0-0; III r1-0-0; IV d0-1-0, p1-1-0, r1-0-1. Anterior receptaculum sclerotized, short, tubular, narrowed at about one-third its length; posterior receptaculum unsclerotized, oval (figs. 137–142).

MATERIAL EXAMINED: **Algeria:** *Biskra:* Biskra (MNHN 12281, PBI_OON 814), 1♂, 2♀. **Egypt:** *Alexandria:* Alexandria, Apr. 1864, under stone (O. P.-Cambridge, HDO PBI_OON 3012), 1 juv. (holotype); Ramleh (M. Letourneux, MNHN 3230, PBI_OON 813), 1♂ (holotype), 1♀. **Sudan:** *Red Sea:* Port Sudan, July 1962 (J. Cloudsley-Thompson, MRAC 127163, PBI_OON 815), 1♀.

DISTRIBUTION: North Africa (Algeria, Egypt, Sudan).

SYNONYMY: It appears that Simon (1910, 1911) was able to borrow the holotype of *Oonops pauper*, compared it directly to his material of *Sulsula longipes*, and concluded that the specimens are conspecific. Although the holotype of *O. pauper* is a juvenile, there is no evidence that disputes Simon's conclusion. The specimens came from the same area (Ramleh is one of the beaches of Alexandria) and are clearly congeneric; it is unlikely that multiple species of *Sulsula* occur within Alexandria.

Dalmasula Platnick, Szüts, and Ubick, new genus

TYPE SPECIES: *Dalmasula lorelei*, new species.

ETYMOLOGY: The generic name is a contraction of "Dalmas' *Sulsula*" and is feminine in gender. It honors Raymond de Dalmas and his pioneering study of *Orchestina*, in which (after discussing the similarities of *Sulsula* and *Calculus* with that genus) he commented (1916: 205) that: "On peut ajouter que *Sulsula parvimanus* E. Simon (1910: 178), décrit du pays des Namaquas, dans le Sud-Ouest Africain, et dont le *type* unique est en Allemagne, deviendra peut-être le type d'un quatrième genre de cette série." The existence of this genus in South Africa was discovered independently by Charles Griswold (in Platnick and Brescovit, 1995: 6).

Diagnosis: Members of this genus resemble those of *Sulsula* in having a globose abdomen (fig. 173), but can be distinguished by the presence of a promarginal cheliceral tooth (fig. 176) and a very wide, hirsute colulus (fig. 274), and the absence of a distal, semicircular groove and laterally directed ridges on the tarsal organ (figs. 199–202, 237–241). Males typically have both an embolus and a conductor (figs. 275, 277), although they appear to have fused in *D. tsumkwe*, new species (figs. 254, 255); the female genital area has peculiar, distinctive anterior sclerotizations that probably function as coupling ridges (figs. 215, 259–261, 293, 306). Males also have unusual modifications of the mouthparts; in those of *D. lorelei*, *D. parvimana*, and *D. griswoldi*, the base of the endites bears a triangular projection directed toward the chelicerae (fig. 175). Males of *D. tsumkwe* apparently lack those projections, but have a similar spur situated distally on the cheliceral paturon (figs. 250, 251).

Description: Total length of males 1.7–2.8, of females 2.2–3.1. **Cephalothorax:** Carapace yellow or pale orange, without any pattern, ovoid to piriform in dorsal view (fig. 218), pars cephalica usually flat or slightly elevated in lateral view in males (fig. 175), slightly elevated in females (fig. 219), anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, pars thoracica without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent; pars cephalica and pars thoracica setae dark, needlelike. Clypeus margin unmodified, curved downwards in front view, vertical in lateral view, high, ALE separated from edge of carapace by their radius or more (figs. 174, 220), median projection absent; setae dark, needlelike. Chilum absent. Eyes six, well developed, PME largest, ALE oval, PME squared, PLE oval; posterior eye row recurved from above, straight or slightly procurved from front; ALE separated by more than their diameter, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separated by PME radius to PME diameter. Sternum yellow, wider than long (figs. 181, 227), uniform, not fused to carapace, median concavity absent, without radial furrows between coxae I-II, II-III, III-IV, radial furrow opposite coxae III absent, surface smooth, without pits, microsculpture absent, sickle-shaped structures absent, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles present, lateral margins unmodified, without posterior hump; setae sparse, dark, needlelike, densest laterally, originating from surface; hair tufts absent. Mouthparts yellow. Chelicerae straight; promargin with one tooth (figs. 176, 221), retromargin without teeth; fangs without toothlike projections, directed medially, slightly sinuous at tip (figs. 177, 222), without prominent basal process, tip unmodified; setae dark, needlelike, evenly scattered; paturon inner margin with scattered setae, distal region unmodified (except in males of *D. tsumkwe*, figs. 250, 251), posterior surface unmodified, promargin unmodified, inner margin unmodified, laminate groove absent. Labium not fused to sternum, slightly narrowed in front, anterior margin, slightly indented at middle (figs.

178, 223), with six or more setae, same as sternum in sclerotization, subdistal portion with unmodified setae. Endites distally not excavated, serrula present in single row (figs. 179, 180, 224–226), anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization; males (except in *D. tsumkwe*) with triangular process situated at base of dorsal surface, directed toward chelicerae (fig. 175). Female palp without claw, sometimes with spines; patella without prolateral row of ridges; tarsus unmodified. **Abdomen:** White, globular, without long posterior extension, rounded posteriorly, interscutal membrane without rows of small sclerotized platelets; dorsum soft portions without color pattern; book lung covers large, ovoid, without setae, anterolateral edge unmodified; posterior spiracles connected by groove; pedicel tube short, unmodified, scutopedicel region unmodified, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent; dorsal, epigastric, postepigastric, and spinneret scuta absent; dorsal, epigastric, and postepigastric setae light, needlelike, epigastric setae not basally enlarged; dense patch of setae anterior to spinnerets absent. Spinnerets (scanned only in *D. lorelei*) with conspicuous unsclerotized strip crossing base of anterior lateral pair (figs. 188, 230, 262, 272); anterior laterals large (figs. 187, 231), with one major ampullate gland spigot and five piriform gland spigots in male (fig. 189), three in female (fig. 232); posterior medians with two long spigots in males (fig. 190), one in females (fig. 233); posterior laterals with three long spigots in males (fig. 191) and females (fig. 234). Colulus extremely wide, hirsute (figs. 188, 273, 274). **Legs:** Yellow or pale orange, without color pattern; femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace, tibia I unmodified, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I, II mesoapical comb absent, metatarsi III, IV weak ventral scopula absent. Leg spines present, longer than segment width. Tarsal proclaws and retroclaws with inner face striate, with single row of nine or more teeth; inferior claw absent (figs. 192–198, 235). Trichobothria base rounded, aperture internal texture not gratelike, hood covered by numerous low, closely spaced ridges (fig. 236). Tarsal organ capsulate (figs. 199–202, 237–241). **Genitalia:** Male epigastric region with sperm pore not visible; furrow without Ω-shaped insertions, without setae. Male palp yellow or pale orange, of normal size, not strongly sclerotized, right and left palps symmetrical; embolus dark, prolateral excavation absent; trochanter of normal size, unmodified; femur of normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae unmodified; tibia with trichobothria (fig. 184); cymbium not fused with bulb, not extending beyond distal tip of bulb, narrow to ovoid in dorsal view, without plumose setae, stout setae, or distal patch of setae; bulb more than twice as long as cymbium, stout, tapering apically; embolus accompanied by conductor, conductor sometimes partially fused with embolus (figs. 182, 183, 185, 186). Female genitalia with gonopore region swollen (fig. 228), bearing distinctive sclerotizations, probably functioning as coupling ridges, situated anteriorly on epigastric area (figs. 215, 259–261, 293, 306); internal genitalia with long anterior projection (fig. 229).

Distribution: Known only from Namibia and South Africa.

Dalmasula lorelei Platnick and Dupérré, new species

Figures 173–241

Types: Male holotype and female allotype taken in pitfall traps at a site 10 km east of Lorelei Mine, Lüderitz District, Karas, Namibia (Aug. 9–22, 1990; C. Roberts, E. Marais), deposited in NMNW (ex 41492, PBI_OON 33774).

Etymology: The specific name is a noun in apposition taken from the type locality.

Diagnosis: Males differ from those of *D. parvimana* in having a longer embolus (figs. 185, 186), from those of *D. tsumkwe* in lacking cheliceral apophyses and having an unsclerotized palpal conductor (figs. 209, 210), and from those of *D. griswoldi* in having a narrow embolus (figs. 185, 186); females have much larger ridges at the anterior end of the genital area (fig. 215) than do those of the other known females.

Male (PBI_OON 33774, figs. 173–210): Total length 2.13. Posterior eye row straight from front. Chelicerae anterior face unmodified. Epigastric furrow unmodified. Leg spination: tibiae: I d0-1-1, p1-0-1, v0-0-2, r1-0-1; II d0-0-1, p1-0-1, v0-0-2, r1-0-0; III d0-0-1, p0-0-1, v1p-1p-2, r0-0-1; IV d0-0-1, p0-0-1; metatarsi: I p1-0-0, v0-0-1p, r1-0-0; II p0-0-1, v0-0-1p; III v0-1p-1p; IV p0-1-0, v0-1p-1p, r0-1-0. Palp with embolus long, thin, basally sinuous, accompanied by long, thin, parallel, translucent conductor.

Female (PBI_OON 33774, figs. 211–241): Total length 2.24. Palpal spines absent. Leg spination: tibiae: I p1-0-1, v0-0-1r, r1-0-1; II p1-0-1, v0-1p-1r, r1-0-1; III, IV d0-0-1, p1-0-1, v0-1p-1p, r1-0-1; metatarsi: I, II d1-0-0, p1-0-0, r1-0-0; III d1-0-0, v2-0-1p, r1-1-0; IV d1-1-0, p1-1-0, v1p-0-1p, r1-1-0. Epigastric area with pair of elevated, anteriorly and medially sclerotized paramedian ridges, anterior genitalic projection with narrow anterior extension.

Other Material Examined: **Namibia:** *Erongo:* Lower Ostrich Gorge, 22°20′S, 14°58′E, Rössing Mine Survey, June 6, 1984, in web at base of tree trunk (E. Griffin, NMNW 38953, PBI_OON 33761), 1♀; 3.5 km N Okondeka, 18°57′S, 15°50′E, May 16–June 15, 1986, pitfall trap (E. Griffin, NMNW 39382, PBI_OON 33776), 1♀. *Karas:* Lüderitz District: 10 km E Lorelei Mine, Aug. 9–22, 1990, pitfalls (C. Roberts, E. Marais, NMNW 41492, PBI_OON 33774), 7♂.

Distribution: Namibia (Erongo, Karas).

Dalmasula parvimana (Simon), new combination

Figures 242–247

Salsula parvimanus Simon, 1910: 178 (male holotype from Rooibank, Erongo, Namibia, in ZMB; examined).

Sulsula parvimana: Roewer, 1942: 281.

Diagnosis: Males resemble those of *D. lorelei* but have a much shorter embolus, which extends only about half as far as the conductor (figs. 246, 247).

Male (PBI_OON 822, figs. 242–247): Total length 1.77. Posterior eye row straight from front. Chelicerae anterior face unmodified. Epigastric furrow unmodified. Leg spination: tibia

IV p1-0-0, v1p-0-2; metatarsus IV v0-1p-0. Embolus extending only about half as far as divergent, translucent conductor.

Female: Unknown.

Material Examined: Only the male holotype (ZMB 32720, PBI_OON 822).

Distribution: Namibia (Erongo).

Dalmasula tsumkwe Platnick and Dupérré, new species

Figures 248–262

Types: Male holotype, female allotype, and female paratype from the CDM Camp at Tsumkwe, Bushmanland, Otjozondjupa, Namibia (May 1993; S. Green), deposited in NMNW (43119, PBI_OON 33771).

Etymology: The specific name is a noun in apposition taken from the type locality.

Diagnosis: Males can easily be distinguished by the cheliceral apophysis near the fang (figs. 250, 251), females by the very small ridges at the front of the genital area (figs. 260, 261).

Male (PBI_OON 33771, figs. 248–255): Total length 2.68. Posterior eye row straight from front. Chelicerae anterior face with conical apophysis. Epigastric furrow unmodified. Leg spination: tibia IV p0-0-1, v0-0-1p, r0-0-1; metatarsi: I, II v0-0-2; III v0-0-2; IV p1-2-1. v1p-2-2. r0-0-1. Embolus only slightly longer than conductor; conductor apparently fused with embolus.

Female (PBI_OON 33771, figs. 256–262): Total length 3.18. Chelicerae without apophyses. Palpal spination: tibia p0-1-2; tarsus p0-1-2, v0-1-2, r0-2-2. Leg spination: tibiae: III p0-1-1; IV p0-1-1, v0-0-2, r0-0-1; metatarsi: I v0-0-1p; II p0-0-1, v0-0-2; III v0-0-2; IV p0-2-2, v1p-1p-2, r0-1-1. Anterior edge of weak epigastric scutum with pair of paramedian, sharply recurved ridges.

Other Material Examined: None.

Distribution: Namibia (Otjozondjupa).

Dalmasula griswoldi Szüts and Ubick, new species

Figures 263–299

Types: Male holotype, female allotype, and three male and one female paratypes taken from dunes to the north of Muizenberg, 34°06′S, 18°27′E, Western Cape, South Africa (June 16–30, 1991; R. Legg), deposited in MRAC (173912, PBI_OON 36053).

Etymology: The specific name is a patronym in honor of Charles Griswold, who first discovered the South African members of this genus.

Diagnosis: Males differ from those of the other *Dalmasula* species in having a more complex embolar region with a dorsal lobe terminating in two ribbonlike lamellae and a broad ventral lobe terminating in a slender spiral prong (figs. 275–288); females differ in having an epigynum with the anteromedian coupling ridges C-shaped and widely separated, and an internal median process with a slender stalk and a rounded head (figs. 293–299).

Male (PBI_OON 36091, figs. 263–288): Total length 2.33. Posterior eye row procurved from front. Chelicerae anterior face unmodified. Epigastric furrow with anterior margin swollen, glabrous, with median projection (extrusion through torn cuticle?). Leg spination: tibiae:

I, II p1-1-0; III p1-1-0, r1-1-0; IV d1-0-0, v0-0-2, r1-0-1; metatarsi: I, II p1-1-1; IV d1-1-2, p1-1-0, r1-1-1. Embolar opening apparently between bases of dorsal lamellae; distal portion of bulb terminating in two main divisions: dorsal lobe, with two distal lamellae, and ventral lobe, broad basally with distal attenuation, thin, twisted, in contact with dorsal lamellae.

Female (PBI_OON 36091, figs. 289–299): Total length 3.05. Palpal spines absent. Leg spination: tibiae: I p1-1-0, v1-1-2, r1-1-0; II d1-1-1, p1-1-0, v1-1-2;,r1-1-0; III d1-1-1, p1-1-1, v1-1-1, r1-1-0; IV d1-1-1, p1-1-0, v1-1-1, r1-1-0; metatarsi: I p1-1-1, v1-1-1, r1-1-1; II d1-1-1, p1-1-1, v1-1-1, r1-1-1; III d1-1-1, v1-1-0, r1-1-1; IV d1-1-1, p1-1-1, v1-1-2, r1-1-1. Gonopore margins swollen, densely setose, anteriorly with pair of median pockets, evenly curved, separated; dorsally, anterior margin with median process, stalked, with round head bearing pores and strands; posterior margin with pair of lateral apodemes and oval posterior receptaculum.

Other Material Examined: **South Africa**: *Western Cape*: dunes to N of Muizenberg, 34°06′S, 18°27′E, May 19–June 2, 1991 (R. Legg, MRAC 173909, PBI_OON 36091), 3♂, 4♀.

Distribution: South Africa (Western Cape).

Dalmasula dodebai Szüts and Ubick, new species

Figures 300–307

Type: Female holotype taken in pitfall trap at Koiingnaas, 30°21.357′S, 17°19.664′E, Northern Cape, South Africa (July 13, 2007; C. Lyons, J. Mingo), deposited in PPRI (PBI_OON 36069).

Etymology: The specific name is a patronym in honor of the Belgian arachnologist Domir De Bakker, in recognition of his assistance at the MRAC throughout the visit there during which Tamás Szüts found the specimen described here, formed by combining the first two letters of each of his names.

Diagnosis: Females differ from those of the other *Dalmasula* species in having an epigynum with the anteromedian coupling ridges straight and posteriorly contiguous, and an internal median process with a thick stalk and an angular head (figs. 306, 307).

Male: Unknown.

Female (PBI_OON 36069, figs. 300–307): Total length 2.69. Posterior eye row procurved from front. Palpal spines absent. Leg spination: tibiae: I, II d1-1-0, p1-1-0, v1-1-2, r1-1-0; III, IV d1-1-0, p1-1-0, v1-1-2, r1-1-0; metatarsi: I p1-1-1, v1-1-1, r1-1-1; II d1-1-1, p1-1-1, v1-1-1, r1-1-1; III d1-1-1, v1-1-1, r1-1-1; IV d1-1-0, p1-1-1, v1-1-2, r1-1-1. Gonopore with margins swollen, setose, anteriorly with pair of curved, median, posteriorly contiguous pockets; dorsally with anterior stalked process, shaft thick, as broad as head, posterior part with foliate lateral apodemes and large rounded receptaculum.

Other Material Examined: None.

Distribution: South Africa (Northern Cape).

Oonopinae Simon

Oonopidae Simon, 1890: 80.

Gamasomorphinae Petrunkevitch, 1923: 172.

“Pseudogamasomorphinae” (nomen nudum): Dumitresco and Georgesco, 1983: 103.

Diagnosis: The bulk of the currently recognized oonopid genera (i.e., all those except *Orchestina*, *Sulsula*, *Dalmasula*, *Xiombarg*, *Unicorn*, and *Cortestina*) are here assigned to the Oonopinae, and are characterized by the absence of a heavily sclerotized, thick-walled sperm duct in the male palp. This absence presumably reflects a major transformation in palpal mechanics. With the exception of the New Zealand genus *Kapitia*, all known oonopines have a distinctively clumped eye arrangement and a 3-3-2-2 tarsal organ receptor pattern.

Relationships: So far as is known, a 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement are retained only in *Kapitia*, suggesting that this enigmatic, seldom collected New Zealand genus is the sister group of all the other oonopines. Aside from the original description by Forster (1956), information on *Kapitia* has been supplied only by Paquin et al. (2010), so we present below a redescription of the species. Of particular interest are the teeth on the tarsal claws (figs. 316, 317); it appears that the inner tooth row has been displaced entirely to the tip of the claw, presumably representing a stage in the loss of that tooth row.

Within the massive assemblage of remaining oonopine species united by the reduction to a 3-3-2-2 tarsal organ receptor pattern and a clustered eye arrangement, we can recognize only a few large groupings at this point. Platnick and Dupérré (2010b) suggested that those genera with a distinctly sclerotized cephalothorax might form a monophyletic group; if so, then several genera that were classically placed in the Oonopinae are actually more closely related to the classical gamasomorphines than to *Oonops* and such similarly soft-bodied taxa as *Heteroonops* and *Oonopoides* Bryant. These anteriorly hard-bodied genera include at least *Stenoonops* Simon, *Australoonops* Hewitt, *Scaphioides* Bryant, *Khamisia* Saaristo and van Harten, and *Longoonops* Platnick and Dupérré. The classical gamasomorphines might also represent a monophyletic subgroup of this enlarged group. It remains to be seen, for example, whether taxa in the *Scaphiella* complex, where males have dorsal abdominal scuta that are lacking in females, or the similarly sexually dimorphic taxa in the *Dysderina* complex, represent independent gains of dorsal scuta in males, or independent losses of dorsal scuta in females. However, even if the presence of a dorsal scutum does not turn out to be a synapomorphy of the classical gamasomorphines, the movement of the male gonopore onto the epigastric scutum may well be synapomorphic for that group. Nevertheless, neither the classical nor the enlarged group could be recognized as a subfamily unless a separate subfamily were to be established for *Kapitia* and the many other genera that (like *Oonops*) have both a soft-bodied cephalothorax and a soft-bodied abdomen can also be shown to constitute a monophyletic group (i.e., a smaller Oonopinae). At present, we know of no potentially synapomorphic characters supporting that smaller group.

Kapitia Forster

Kapitia Forster, 1956: 166 (type species by original designation *Kapitia obscura* Forster).

Diagnosis: The lack of a heavily sclerotized sperm duct within the male palp, combined with the presence of a 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement, is diagnostic for the genus.

Kapitia obscura Forster

Figures 308–329

Kapitia obscura Forster, 1956: 166, figs. 140–144 (male holotype and female allotype from Kapiti Island, New Zealand, in CMC; examined). – Paquin et al., 2010: 32, figs. 10.1–10.4.

Diagnosis: With the characters of the genus, an abruptly bent embolus (figs. 323–325), and receptacula as in figures 328, 329.

Male (PBI_OON 26044, figs. 323–327, images of nonsexual characters based on female): Total length 1.26. **Cephalothorax:** Carapace yellow, without any pattern, ovoid in dorsal view, pars cephalica flat in lateral view (fig. 309), anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, pars thoracica without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent (fig. 308). Clypeus margin unmodified, straight in front view, vertical in lateral view, low, ALE separated from edge of carapace by less than their radius, median projection absent. Eyes six, well developed, all subequal, ALE oval, PME oval, PLE circular; posterior eye row recurved from above; ALE separated by their radius to diameter, ALE-PLE touching, PME touching throughout most of their length, PLE-PME touching (fig. 310). Sternum longer than wide, white, uniform in coloration, not fused to carapace, median concavity absent, without radial furrows between coxae I–II, II–III, III–IV, radial furrow opposite coxae III absent, surface smooth, without pits, microsculpture absent, sickle-shaped structures absent, anterior margin unmodified, posterior margin extending posteriorly beyond anterior edges of coxae IV as single extension, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles absent, lateral margins unmodified, without posterior hump; setae sparse, light, needlelike, evenly scattered, originating from surface, without hair tufts (fig. 311). Mouthparts white. Chelicerae slightly divergent, without teeth, anterior face unmodified; fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified; setae light, needlelike, evenly scattered. Labium rectangular, not fused to sternum, anterior margin indented at middle, same as sternum in sclerotization; with one or two setae on anterior margin, subdistal portion with unmodified setae (fig. 312). Endites distally not excavated, serrula present as single row of teeth, anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. **Abdomen:** Ovoid, without long posterior extension, rounded posteriorly, interscutal membrane rows of small sclerotized platelets absent posteriorly; dorsum soft portions yellow, without color pattern; book lung covers small; pedicel tube short, unmodified, scutopedicel region unmodified, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent; dorsal, epigastric, postepigastric and spinneret scuta absent; setae light, needlelike, epigastric area setae not enlarged at base; dense patch of setae anterior to spinnerets absent. Colulus absent. **Legs:** Yellow, without color pattern; femur IV not thickened, same size as femora I–III, tibia I unmodified, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I, II mesoapical comb absent, metatarsi III, IV weak ventral scopula absent. Leg spines absent. Tarsal claws with inner tooth row displaced to tip of claw, inner faces striated, inferior claw absent (figs. 316, 317). Trichobothrial base with arched ridge (fig. 318). Tarsal organs apparently with four receptors on anterior legs, three on posterior legs and palps (figs. 319–322). **Genitalia:** Epigastric region with sperm pore not visible; furrow without Ω-shaped insertions, without setae. Palp of normal size, not strongly sclerotized, right and left palps symmetrical, proximal segments white; embolus light, prolateral excavation absent; trochanter of normal size, unmodified; femur of normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae unmodified; tibia with trichobothria; cymbium white, ovoid in dorsal view, not fused with bulb, not extending beyond distal tip of bulb, without stout setae, without distal patch of setae; bulb white, without sclerotized sperm duct (figs. 323, 324), embolus abruptly bent (fig. 325).

Female (PBI_OON 26045, figs. 308–322, 328, 329): Total length 1.63. Palpal tarsus without claw or spines, unmodified, patella without prolateral row of ridges (figs. 313, 314), tibia with three trichobothria (fig. 315). Anterior receptaculum with ventral expansion at base, tip microphone-shaped, posterior receptaculum long, ovoid (figs. 328, 329).

Material Examined: **New Zealand:** *North Island:* Cook Strait: Kapiti Island, May 1947, leaf litter (R. Forster, CMC 1192, 1193, PBI_OON 26044, 26045), 1♂, 1♀ (holotype, allotype); Nigger Head, Apiti-Utawai, Sept. 28, 1972, roadside (C. Wilton, OMD PBI_OON 26512), 2♀; summit, Three Kings, Nov. 28, 1970 (G. Ramsay, OMD PBI_OON 26508), 1♂.

Distribution: The few available records span the full length of the North Island of New Zealand.

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REFERENCES

Abrahim, N., et al. In press. A revision of the Neotropical goblin spider genus *Neoxyphinus* Birabén, 1953, (Araneae, Oonopidae). American Museum Novitates.

Álvarez-Padilla, F., D. Ubick, and C.E. Griswold. In press. *Noideattella* and *Tolegnaro*, two new genera of goblin spiders from Madagascar, with comments on the gamasomorphoid and silhouetteloid oonopids (Araneae, Oonopidae). Bulletin of the American Museum of Natural History.

Baehr, B.C., and H.M. Smith. 2008. Three new species of the Australian orsolobid spider genus *Hickmanolobus* (Araneae: Orsolobidae). Records of the Western Australian Museum 24: 325–336.

Baehr, B.C., and D. Ubick. 2010. A review of the Asian goblin spider genus *Camptoscaphiella* (Araneae: Oonopidae). American Museum Novitates 3697: 1–65.

Baehr, B.C., M.S. Harvey, M. Burger, and M. Thoma. In press. The new Australasian goblin spider genus *Prethopalpus* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History.

Baehr, B.C., M.S. Harvey, and H.M. Smith. 2010. The goblin spiders of the new endemic Australian genus *Cavisternum* (Araneae: Oonopidae). American Museum Novitates 3684: 1–40.

Blumenthal, H. 1935. Untersuchungen über das "Tarsalorgan" der Spinnen. Zeitschrift für Morphologie und Ökologie der Tiere 29: 667–719.

Brescovit, A.D., L.A. Bertoncello, R. Ott, and A.A. Lise. 2004. Description and ecology of two new species of the Brazilian spider genus *Losdolobus* Platnick & Brescovit (Araneae, Dysderoidea, Orsolobidae). Revista Ibérica de Arachnología 9: 249–257.

Brescovit, A.D., C.A. Rheims, A.B. Bonaldo, A.J. Santos, and R. Ott. In press. The Brazilian goblin spiders of the new genus *Predatoroonops* (Araneae: Oonopidae). American Museum Novitates.

Brignoli, P.M. 1979. Ragni del Brasile V. Due nuovi generi e quattro nuove specie dello stato di Santa Catarina (Araneae). Revue Suisse de Zoologie 86: 913–924.

Bristowe, W.S. 1948. Notes on the structure and systematic position of oonopid spiders based on an examination of the British species. Proceedings of the Zoological Society of London 118: 878–891.

Burger, M., and P. Michalik. 2010. The male genital system of goblin spiders: evidence for the monophyly of Oonopidae (Arachnida: Araneae). American Museum Novitates 3675: 1–13.

Cambridge, O. P.-. 1876. Catalogue of a collection of spiders made in Egypt, with descriptions of new species and characters of a new genus. Proceedings of the Zoological Society of London 1876: 541–630.

Chamberlin, R.V., and W. Ivie. 1942. A hundred new species of American spiders. Bulletin of the University of Utah 32 (13): 1–117.

Chickering, A.M. 1951. The Oonopidae of Panama. Bulletin of the Museum of Comparative Zoology 106: 207–245.

Dalmas, R. de. 1916. Révision du genre *Orchestina* E.S. [Arachn. Oonopidae], suivie de la description de nouvelles espèces du genre *Oonops* et d'une étude sur les Dictynidae du genre *Scotolathys*. Annales de la Société Entomologique de France 85: 203–258.

Dumitresco, M., and M. Georgesco. 1983. Sur les Oonopidae (Araneae) de Cuba. Résultats des Expéditions Biospéologiques Cubano-Roumaines à Cuba 4: 65–114.

Eichenberger, B., et al. In press. Morphology of new Indian/Indonesian *Gamasomorpha* and *Xestaspis* species (Araneae: Oonopidae). Zootaxa.

Fannes, W. 2010. On *Melchisedec*, a new genus of the spider family Oonopidae (Araneae, Dysderoidea). American Museum Novitates 3702: 1–28.

Fannes, W., and R. Jocqué. 2008. Ultrastructure of *Antoonops*, a new, ant-mimicking genus of Afrotropical Oonopidae (Araneae) with complex internal genitalia. American Museum Novitates 3614: 1–30.

Forster, R.R. 1956. New Zealand spiders of the family Oonopidae. Records of the Canterbury Museum 7: 89–169.

Forster, R.R. 1980. Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. *In* J. Gruber (editor), Verhandlungen 8. Internationaler Arachnologen-Kongress: 269–284. Vienna: Verlag H. Egermann.

Forster, R.R., and N.I. Platnick. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. Bulletin of the American Museum of Natural History 181 (1): 1–230.

Giroti, A.M., and A.D. Brescovit. 2011. The spider genus *Segestria* Latreille, 1804 in South America (Araneae: Segestriidae). Zootaxa 3046: 59–66.

González Reyes, A.X., J.A. Corronca, and M.B. Cava. 2010. New species of *Unicorn* Platnick & Brescovit (Araneae, Oonopidae) from north-west Argentina. Munis Entomology & Zoology 5: 374–379.

Grismado, C.J. 2010. Description of *Birabenella*, a new genus of goblin spiders from Argentina and Chile (Araneae: Oonopidae). American Museum Novitates 3693: 1–21.

Griswold, C.E., and N.I. Platnick. 1987. On the first African spiders of the family Orsolobidae (Araneae, Dysderoidea). American Museum Novitates 2892: 1–14.

Harvey, M.S. 1987. *Grymeus*, a new genus of pouched oonopid spider from Australia (Chelicerata: Araneae). Memoirs of the Museum of Victoria 48: 123–130.

Hickman, V.V. 1979. Some Tasmanian spiders of the family Oonopidae, Anapidae and Mysmenidae. Papers and Proceedings of the Royal Society of Tasmania 113: 53–79.

Jiménez, M.L., N.I. Platnick, and N. Dupérré. 2011. The haplogyne spider genus *Nopsides* (Araneae, Caponiidae), with notes on *Amrishoonops*. American Museum Novitates 3708: 1–18.

Kaston, B.J. 1948. Spiders of Connecticut. Bulletin of the State Geological and Natural History Survey of Connecticut 70: 1–874.

Knoflach, B., K. Pfaller, and F. Stauder. 2009. *Cortestina thaleri*–a new dwarf six-eyed spider from Austria and Italy (Araneae: Oonopidae: Oonopinae). Contributions to Natural History: Scientific Papers from the Natural History Museum Bern 12: 743–771.

Lise, A.A., and L. Almeida. 2006. A new species of *Losdolobus* Platnick & Brescovit, 1994 (Araneae: Dysderoidea: Orsolobidae) from southern Brazil. Zootaxa 1277: 23–27.

Marusik, Y.M., and J. Wunderlich. 2008. A survey of fossil Oonopidae (Arachnida: Aranei). Arthropoda Selecta 17: 65–79.

Michalik, P. 2009. The male genital system of spiders (Arachnida: Araneae) with notes on the fine structure of seminal secretions. Contributions to Natural History: Scientific Papers from the Natural History Museum Bern 12: 959–972.

Ott, R., and A.D. Brescovit. 2004. Three new species of the haplogyne spider genus *Coxapopha* Platnick from the Amazon region (Araneae, Oonopidae). Revista Ibérica de Aracnología 9: 127–135.

Paquin, P., C.J. Vink, and N. Dupérré. 2010. Spiders of New Zealand: annotated family key & species list. Lincoln, New Zealand: Manaaki Whenua Press, vii + 118 pp.

Petrunkevitch, A. 1923. On families of spiders. Annals of the New York Academy of Sciences 29: 145–180.

Platnick, N.I. 2012. The world spider catalog, version 12.5. New York: American Museum of Natural History, Internet resource (http://research.amnh.org/iz/spiders/catalog). [doi: 10.5531/db.iz.0001]

Platnick, N.I., and A.D. Brescovit. 1995. On *Unicorn*, a new genus of the spider family Oonopidae (Araneae, Dysderoidea). American Museum Novitates 3152: 1–12.

Platnick, N.I., and N. Dupérré. 2009a. The goblin spider genera *Opopaea* and *Epectris* (Araneae, Oonopidae) in the New World. American Museum Novitates 3649: 1–43.

Platnick, N.I., and N. Dupérré. 2009b. The American goblin spiders of the new genus *Escaphiella* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 328: 1–151.

Platnick, N.I., and N. Dupérré. 2009c. The goblin spider genus *Heteroonops* (Araneae, Oonopidae), with notes on *Oonops*. American Museum Novitates 3672: 1–72.

Platnick, N.I., and N. Dupérré. 2010a. The goblin spider genus *Scaphiella* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 332: 1–156.

Platnick, N.I., and N. Dupérré. 2010b. The goblin spider genera *Stenoonops* and *Australoonops* (Araneae, Oonopidae), with notes on related taxa. Bulletin of the American Museum of Natural History 340: 1–111.

Platnick, N.I., and N. Dupérré. 2010c. The Andean goblin spiders of the new genera *Niarchos* and *Scaphios* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 345: 1–120.

Platnick, N.I., and N. Dupérré. 2011a. The Andean goblin spiders of the new genus *Scaphidysderina* (Araneae, Oonopidae), with notes on *Dysderina*. American Museum Novitates 3712: 1–51.

Platnick, N.I., and N. Dupérré. 2011b. The goblin spider genus *Pescennina* (Araneae, Oonopidae). American Museum Novitates 3716: 1–64.

Platnick, N.I., and N. Dupérré. 2011c. The goblin spider genus *Simonoonops* (Araneae, Oonopidae). American Museum Novitates 3724: 1–30.

Platnick, N.I., and N. Dupérré. 2011d. The Andean goblin spiders of the new genera *Paradysderina* and *Semidysderina* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 364: 1–121.

Platnick, N.I., and N. Dupérré. 2012. The goblin spider genus *Costarina* (Araneae, Oonopidae), part 1. American Museum Novitates 3730: 1–64.

Platnick, N.I., J.A. Coddington, R.R. Forster, and C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1–73.

Platnick, N.I., N. Dupérré, R. Ott, and Y. Kranz-Baltensperger. 2011. The goblin spider genus *Brignolia* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 349: 1–131.

Purcell, W.F. 1910. The phylogeny of the tracheae in Araneae. Quarterly Journal of Microscopical Science 54: 519–564.

Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Journal of Arachnology 28: 149–157.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Budy, Bremen, 1: 1–1040.

Saaristo, M.I., and Y.M. Marusik. 2004. *Ferchestina*, a new genus of oonopid spiders from Russian Far East (Aranei: Oonopidae). Arthropoda Selecta 13: 51–54.

Sánchez-Ruiz, A., N.I. Platnick, and N. Dupérré. 2010. A new genus of the spider family Caponiidae (Araneae, Haplogynae) from the West Indies. American Museum Novitates 3705: 1–44.

Saupe, E.E., et al. In press. New *Orchestina* (Simon, 1882) (Araneae: Oonopidae) from Cretaceous ambers of Spain and France: first spiders described using phase-contrast x-ray synchrotron microtomography. Palaeontology.

Simon, E. 1882. Études arachnologiques. 13^{e} Mémoire. XX. Descriptions d'espèces et de genres nouveaux de la famille des Dysderidae. Annales de la Société Entomologique de France (ser. 6) 2: 201–240.

Simon, E. 1890. Études arachnologiques. 22^{e} Mémoire (I). XXXIV. Étude sur les arachnids de l'Yemen. Annales de la Société Entomologique de France (ser. 6) 10: 77–124.

Simon, E. 1893. Histoire naturelle des araignées: 1: 257–488. Paris: Roret.

Simon, E. 1910. Arachnoidea. Araneae (ii). *In* L. Schultze, Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika. Denkschriften Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena 16: 175–218.

Simon, E. 1911. Catalogue raisonné des arachnids du nord de l'Afrique (1re partie). Annales de la Société Entomologique de France 79: 265–332.

Ubick, D., and C.E. Griswold. 2011a. The Malagasy goblin spiders of the new genus *Malagiella* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 356: 1–86.

Ubick, D., and C.E. Griswold. 2011b. The Malagasy goblin spiders of the new genus *Molotra* (Araneae, Oonopidae). American Museum Novitates 3729: 1–69.

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On *Puan*, a new genus of goblin spiders from Argentina (Araneae, Dysderoidea, Oonopidae)

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ABSTRACT

A new genus of Oonopidae, *Puan*, is described from Argentina. The genus exhibits several features also found in orsolobids, including a well-sclerotized sperm duct and an H-shaped eye pattern. *Puan* resembles the oonopid genus *Unicorn* Platnick and Brescovit but differs in male palpal morphology. In addition, males lack the clypeal horn characteristic of *Unicorn*. Two new species, *P. chechehet* and *P. nair*, are described from the southwestern mountains of Buenos Aires province. Complex copulatory bulbs are the principal characteristic of these species and could be a synapomorphy for the genus.

INTRODUCTION

Oonopidae (goblin spiders) are members of the Dysderoidea, a superfamily that also includes the families Segestriidae, Dysderidae, and Orsolobidae. The four families have similar internal female genitalia (Forster and Platnick, 1985; see also Izquierdo and Labarque, 2010). The Oonopidae are the sister group of the Orsolobidae (see, e.g., Ramírez, 2000).

Since the start of the PBI project (http://research.amnh.org/oonopidae/), the spider family Oonopidae has experienced substantial growth in the number of described species. In 2006 the

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family contained 459 described species (Platnick, 2006); currently, the family includes 1016 species (Platnick, 2012), an increase of 121%.

Traditionally, the family was divided into two informal subfamilies (see, for example, Roewer, 1942) with the Oonopinae including the soft-bodied spiders and the Gamasomorphinae for those spiders with hard bodies. However, the monophyly of these groups has not been tested (Platnick, 2000). More recently, Platnick et al. (2012) recognize three subfamilies based on tarsal organ morphology and additional characters: Orchestininae Chamberlin and Ivie (containing only *Orchestina* Simon, 1882), Sulsulinae (containing *Sulsula* Simon, 1882, *Xiombarg* Brignoli,1979, *Unicorn* Platnick and Brescovit, 1995, *Cortestina* Knoflach, 2009, and *Dalmasula* Platnick et al., 2012, a new genus from Namibia and South Africa), and Oonopinae Simon (containing all the remaining genera, including those previously placed in the Gamasomorphinae). Here, a new genus, *Puan*, is described from the southwestern mountains of Buenos Aires province. We discuss the relationships of this new genus in light of this new evidence.

MATERIAL AND METHODS

Specimens are deposited in the arachnid collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ar), Buenos Aires. Female genitalia were observed in temporary preparations in clove oil under an Olympus BH-2 compound microscope and illustrated using a camera lucida. Photographs were taken with a Leica digital camera mounted on a Leica compound microscope and focal planes combined with Helicon Focus 3.10.3 software (http://helicon.com.ua/heliconfocus/). For scanning electron microscope (SEM) preparations male and female specimens were dissected, dehydrated in a graded ethanol series (80%–100%), critical point dried, and coated with a gold-palladium alloy. One female's genitalia (PBI_OON 43388) were dissected and prepared for SEM according to Álvarez-Padilla and Hormiga (2008). Images were taken under high vacuum with a Philips FEI XL30 TMP. High-resolution versions of all images will be available on the PBI website (http://research.amnh.org/oonopidae). SEM images are provided only for males and females of *Puan chechehet*, new species.

In addition to the collection number, vials contain PBI codes as well as preparation codes, formed by initials of the name and surname of the first author plus a five-digit number (for example, MAI 00354). Preparation codes refer to a Microsoft Access database that contains all the information of the specimen (locality, collector, depository, etc.) as well as relevant information on the preparations performed (SEM, temporary mount on alcohol, part mounted, author of preparation, etc.). Holotype and paratypes are separated in microvials with their respective labels.

Descriptions were generated with the aid of the PBI descriptive database and shortened when possible. The species descriptions contain only the differences from the generic description. The description of the females includes only differences from the male. In describing the female genitalia we follow Forster and Platnick (1985), Burger et al. (2010), and Henrard and Jocqué (2011) with some minor modifications. All measurements are in millimeters.

MORPHOLOGY

CHELICERAE: Platnick and Brescovit (1995) mentioned that the chelicerae of *Unicorn* are sexually dimorphic; those of males are long, slender, and anteriorly more excavated that those of females, although there are no images in that paper documenting this character feature. Chelicerae can be similarly characterized in *Puan*: In females, the anterior face of the paturon is not excavated (fig. 17). Males, however, have excavated chelicerae with a prominent basal swelling. The swelling carries a group of long setae (figs. 8, 24, 60). These are lacking in some specimens, but their sockets are still detectable (fig. 61). This character is present in a variety of hard-bodied oonopids but with varying degrees of expression.

STERNUM: Males and females possess a sternum with a sclerotized border and precoxal triangles (fig. 10). Posterior to the sternum there is a sclerotized band. The band is separated from the sternum by a narrow nonsclerotized region (fig. 12). This character is described here as "pedicel with ventral sclerotization." It may also be present in *Predatoroonops* Brescovit et al., from Brazil (Brescovit et al., 2012) and in females of *Niarchos* Platnick and Dupérré and *Scaphios* Platnick and Dupérré. However, in *Puan* this sclerotized band is closer to the sternum than the pedicel and with lateral projections longer than in any of these other genera.

LEGS: All legs have spines. As in *Unicorn*, *Xiombarg*, *Sulsula,* and *Dalmasula,* the tarsal claws have only one row of teeth (figs. 37, 38, 43–45). As in all Oonopidae, the tarsi are provided with an onychium (figs. 43–45). There are at least four claw tuft setae (fig. 45), with normal bases and the adherent surface facing downward (fig. 45, 46, 48). Also, near the base of each claw is a long seta with a modified socket that has a long projection that touches the base of the claw (fig. 47: arrow). This projection was also observed in some undescribed species of *Orchestina* (Izquierdo, personal obs.).

MALE PALP: The male bulb of *Puan* resembles that of Orsolobidae (figs. 25–32, 70–76). The basal part of the bulb is spherical and there are several terminal apophyses (figs. 70–75). The ventral lobe (fig. 72) resembles a similar structure found in *Orsolobus* Simon (see Forster and Platnick, 1985: figs. 24–29, Izquierdo and Labarque, 2010: figs. 6A, "DSL"). The embolus is dark

FIGS. 1–2. Habitat of *Puan*, n. gen., at the Ernesto Tornquist Provincial Park.

and long with a subterminal sperm outlet (fig. 76, scanned only in *P. chechehet*). An excavated apophysis is in close connection with the embolus; the excavation seems to be the groove into which the embolus fits (figs. 74–75). Two additional apophyses are present (fig. 75), the morphology of which is species specific. The sperm duct is a well-sclerotized structure (figs. 25–32), as in Segestriidae, Dysderidae, Orsolobidae, and in the oonopids *Xiombarg*, *Unicorn*, *Orchestina,* and *Cortestina*.

Female Genitalia: The female genitalia resemble that of Orsolobidae (in particular *Orsolobus*), *Unicorn*, *Xiombarg,* and *Orchestina* (figs. 33–36, 77–82). In these genera, the anterior part of the female genitalia is a sclerotized structure (here called *anterior sclerite,* equivalent to the *median rod* of Forster and Platnick, 1985). Izquierdo and Labarque (2010) hypothesized that the anterior sclerite may be homologous to the anterior receptaculum present in other Dysderoidea, judging by its position and the presence of gland ducts (figs. 79, 80) that suggest a sperm-storage function. However, this structure is highly sclerotized and its storage function seems to have been lost in some genera or at least reduced (Izquierdo and Labarque, 2010). The transformation of the anterior receptaculum into a sclerotized structure may be a consequence of another function attributed to the genitalia, possibly related to sexual selection or control of sperm destiny by the female. In *Puan*, a group of muscles (M2, fig. 36) is attached to the tip of the anterior sclerite and are directed to posterior sclerotized plates. For other oonopids it has been suggested that these plates can be moved back and forth by contraction and relaxation of the M2 muscles, suggesting that the uterus externus can be locked, which might prevent sperm from entering during copulation (Burger et al., 2010). The M2 muscles are present in *Orchestina*, *Unicorn,* and *Orsolobus* (Izquierdo, personal obs.). Thus, the sclerotization of the anterior receptaculum may be necessary for the attachment of these muscles. The posterior receptaculum is similar to that of Dysderoidea (figs. 77, 82).

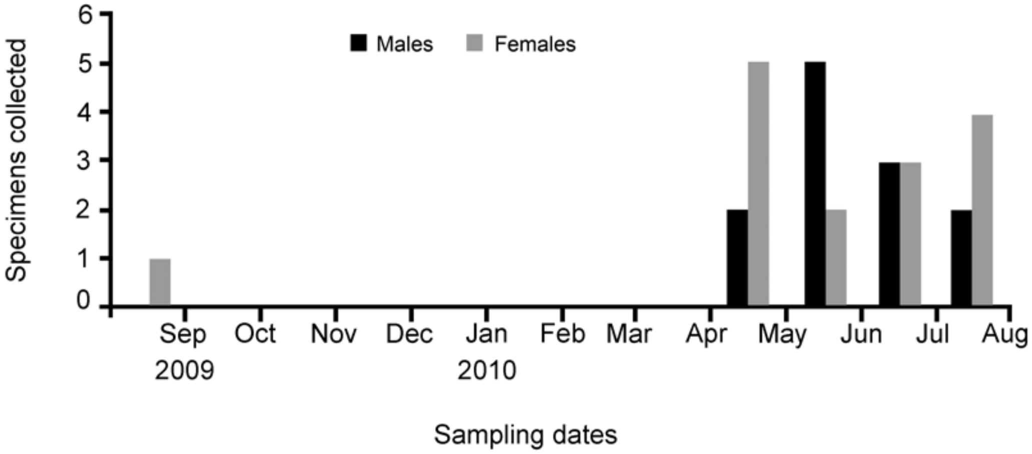
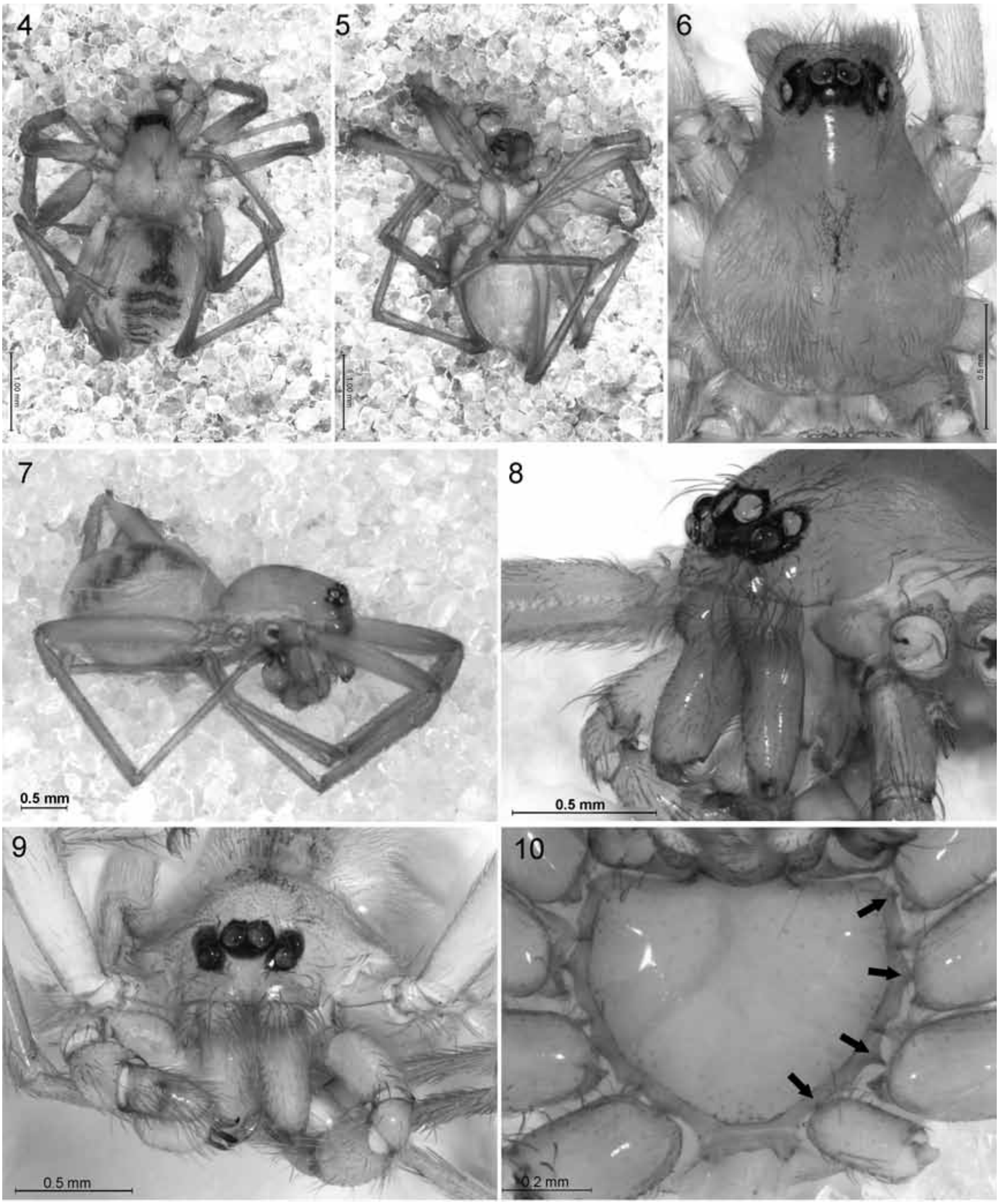
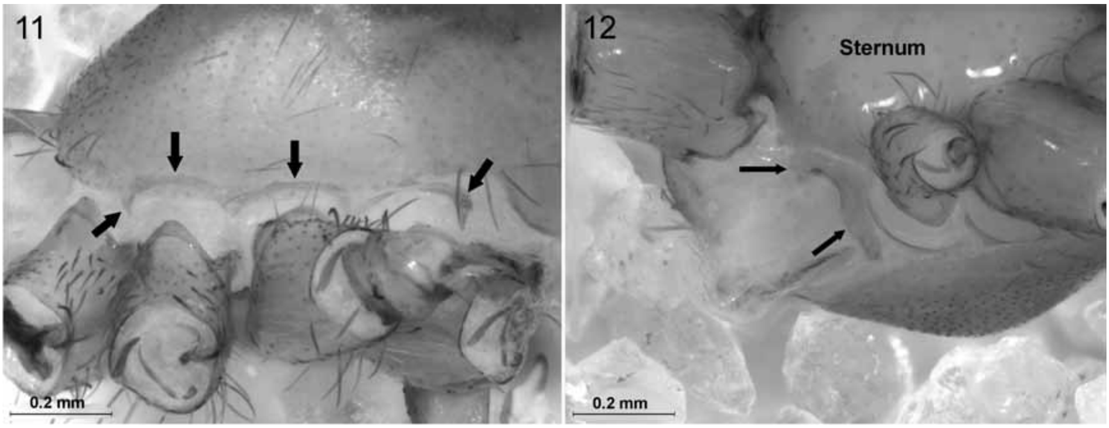


FIG. 3. Phenology of *Puan*, n. gen., based on specimens collected (individuals/month).



FIGS. 4–10. *Puan chechehet*, n. sp., male. **4.** Holotype, habitus, dorsal view (PBI_OON 43344). **5.** Same, ventral view. **6.** Carapace, dorsal view (PBI_OON 00043350). **7.** Habitus, lateral view (PBI_OON 00043350). **8.** Clypeus and chelicerae, lateral view (PBI_OON 00043350). **9.** Same, anterior view. **10.** Sternum, arrows at precoxal triangles.



FIGS. 11–12. *Puan chechehet*, n. sp., male. **11.** Cephalothorax, lateral view, arrows at supracoxal sclerites. **12.** Pedicel, ventral view, arrows at ventral sclerotization.

SYSTEMATICS

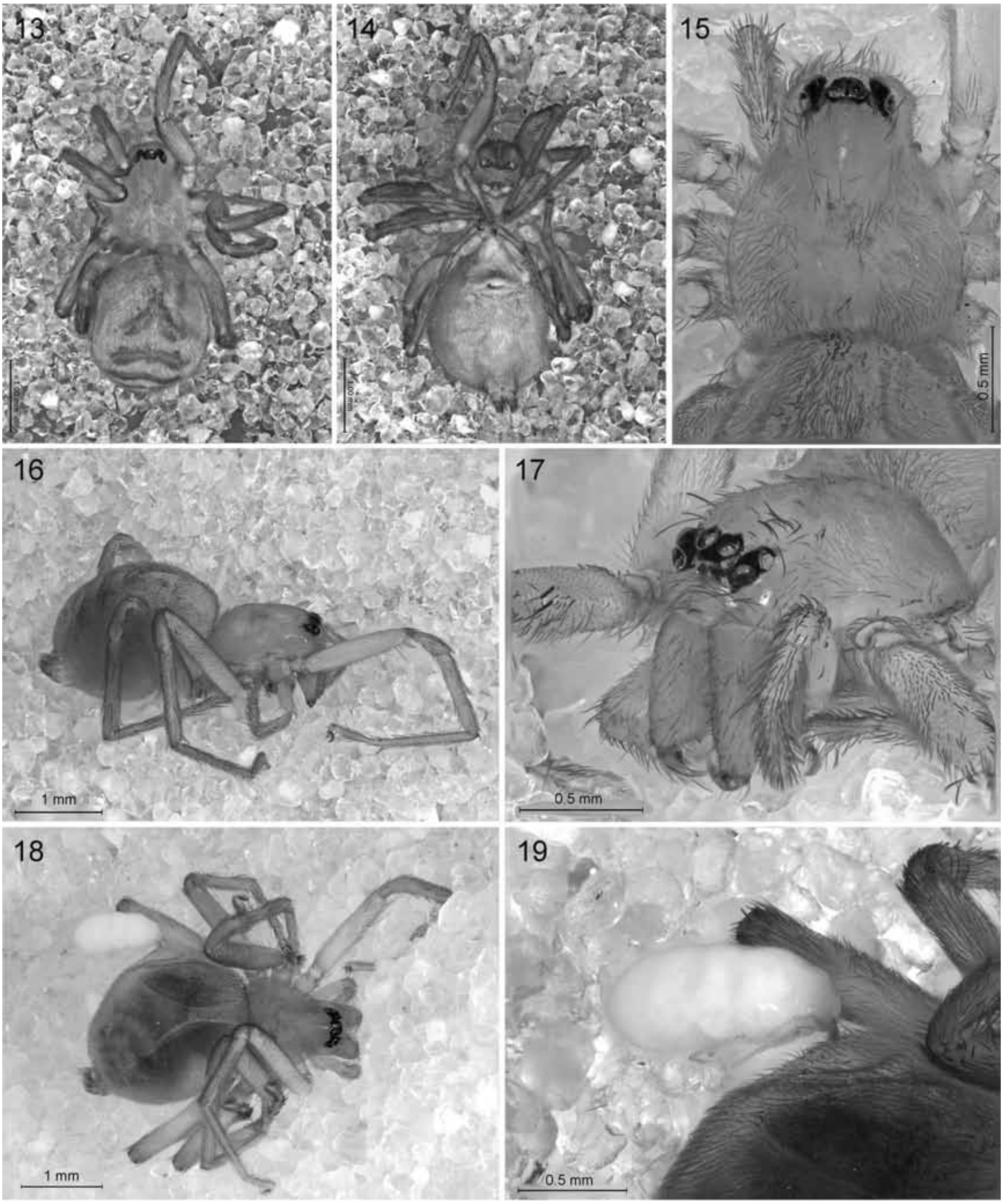
Puan Izquierdo, new genus

Type Species: *Puan chechehet*, new species.

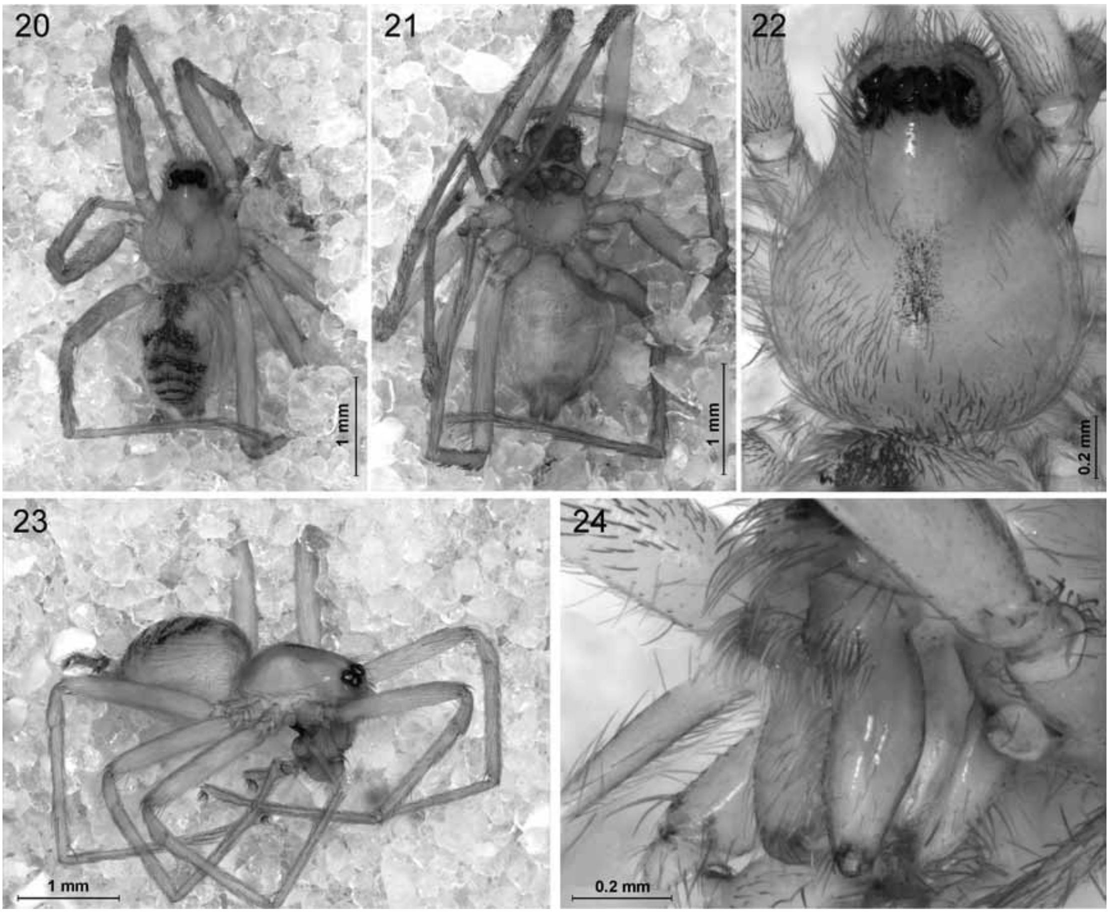
Etymology: The generic name is taken from one of the ranges of the Ventania system, Puan. Gender is feminine.

Diagnosis: The presence of a nonelevated and fully capsulate tarsal organ (figs. 49–52) separates this genus from the Orsolobidae, *Orchestina,* and *Cortestina*. This fully capsulated tarsal organ is also present in *Xiombarg*, *Unicorn*, *Sulsula,* and *Dalmasula*. The presence of leg spines separates *Puan* from *Xiombarg*; it lacks the clypeal horn that typifies the males of *Unicorn*; the presence of cheliceral teeth and wide, and hirsute colulus distinguish it from *Sulsula;* and the absence of copulatory ridges in the female epigastric region separates it from *Dalmasula*.

Description: *Male:* **Cephalothorax**: Carapace with *Xiombarg*-type color pattern, broadly oval in dorsal view (fig. 6), pars cephalica slightly elevated in lateral view (fig. 7), anteriorly narrowed to between 0.5 and 0.75 times its maximum width, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, thorax without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent; nonmarginal pars cephalica setae dark, needlelike, scattered; nonmarginal pars thoracica setae dark, needlelike; marginal setae dark, needlelike. Clypeus margin unmodified, curved downward in front view, vertical in lateral view, high, ALE separated from edge of carapace by their radius or more, median projection absent; setae present, dark, needlelike (figs. 8, 9). Chilum absent. Eyes six, well developed, all subequal, all eyes circular; posterior eye row recurved from above, straight from front; ALE separated by more than their diameter, ALE-PLE touching, PME touching for less than half

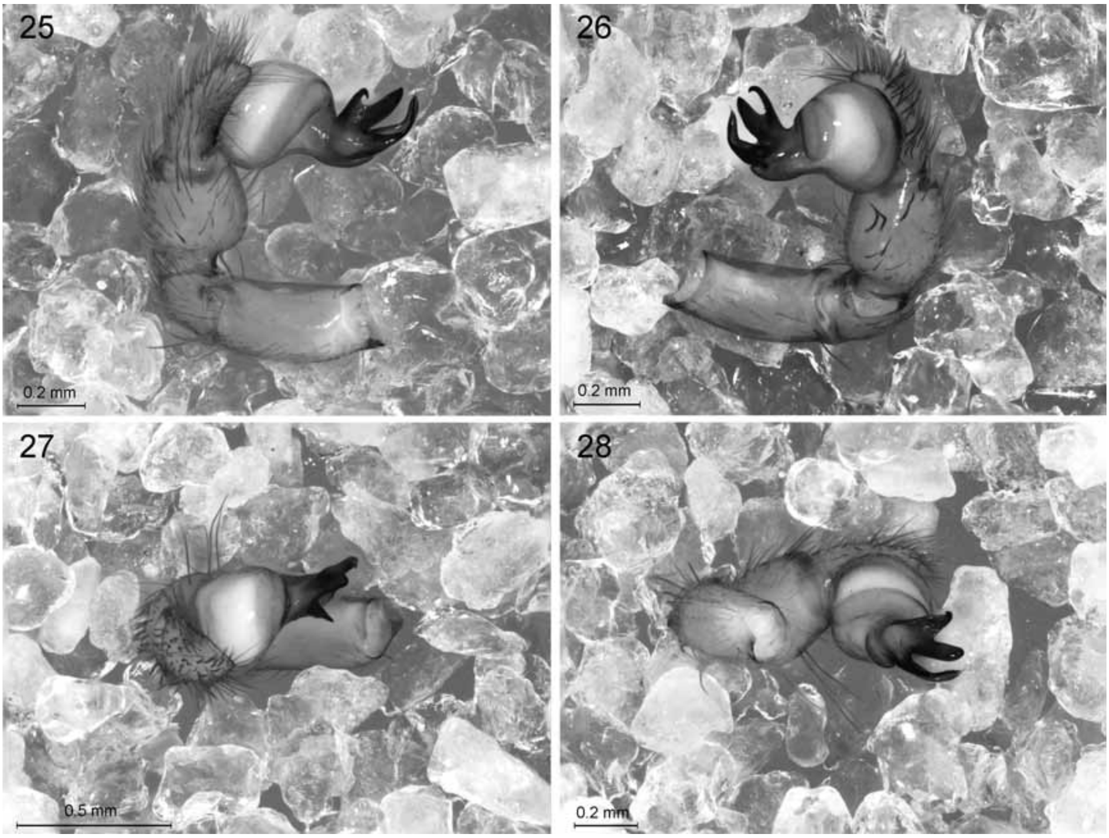


FIGS. 13–19. *Puan chechehet*, n. sp., female. **13.** Paratype, habitus, dorsal view (PBI_OON 43344). **14.** Same, ventral view. **15.** Carapace, dorsal view (PBI_OON 43360). **16.** Same, habitus, lateral view. **17.** Same, clypeus and chelicerae, lateral view. **18.** Female with acari (PBI_OON 43352). **19.** Same, detail.



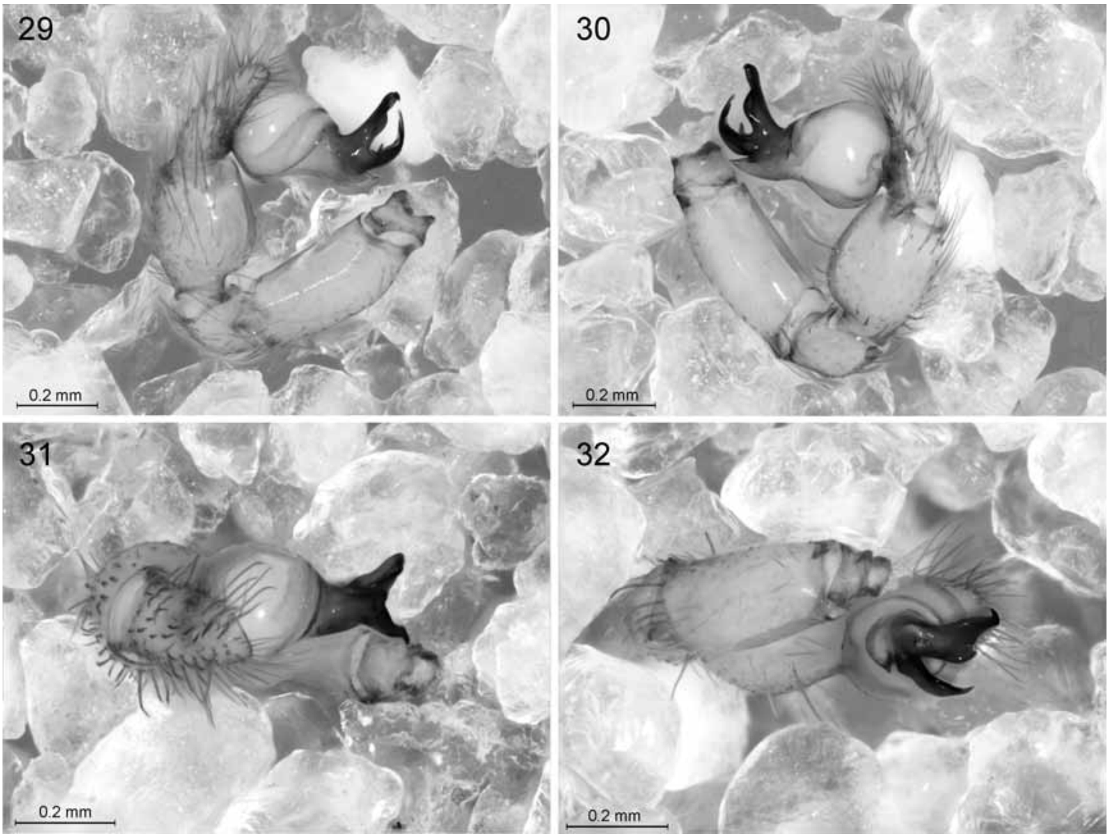
FIGS. 20–24. *Puan nair*, n. sp., holotype male. **20.** Habitus, dorsal view. **21.** Same, ventral view. **22.** Carapace, dorsal view. **23.** Habitus, lateral view. **24.** Clypeus and chelicerae, lateral view.

their length, PLE-PME separated by PME radius to PME diameter (figs. 6, 8, 9, 22). Sternum wider than long (fig. 10), pale orange, uniform, not fused to carapace, with a sclerotized border (fig. 10), median concavity absent, without radial furrows between coxae I–II, II–III, III–IV, radial furrow opposite coxae III absent, surface smooth, without pits, sickle-shaped structures absent, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles present (fig. 10: arrows), without posterior hump; setae sparse, dark, needlelike, evenly scattered, originating from surface, without hair tufts. Mouthparts: Chelicerae (figs. 59–63), endites, and labium pale orange. Chelicerae straight, anterior face with swelling and long setae (figs. 8, 24); without teeth on both promargin and retromargin; fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified; setae dark, evenly scattered; paturon inner margin with scattered setae, distal region unmodified, posterior surface unmodified, promargin unmodified, inner margin unmodified, laminate groove absent. Labium elongated hexagon,



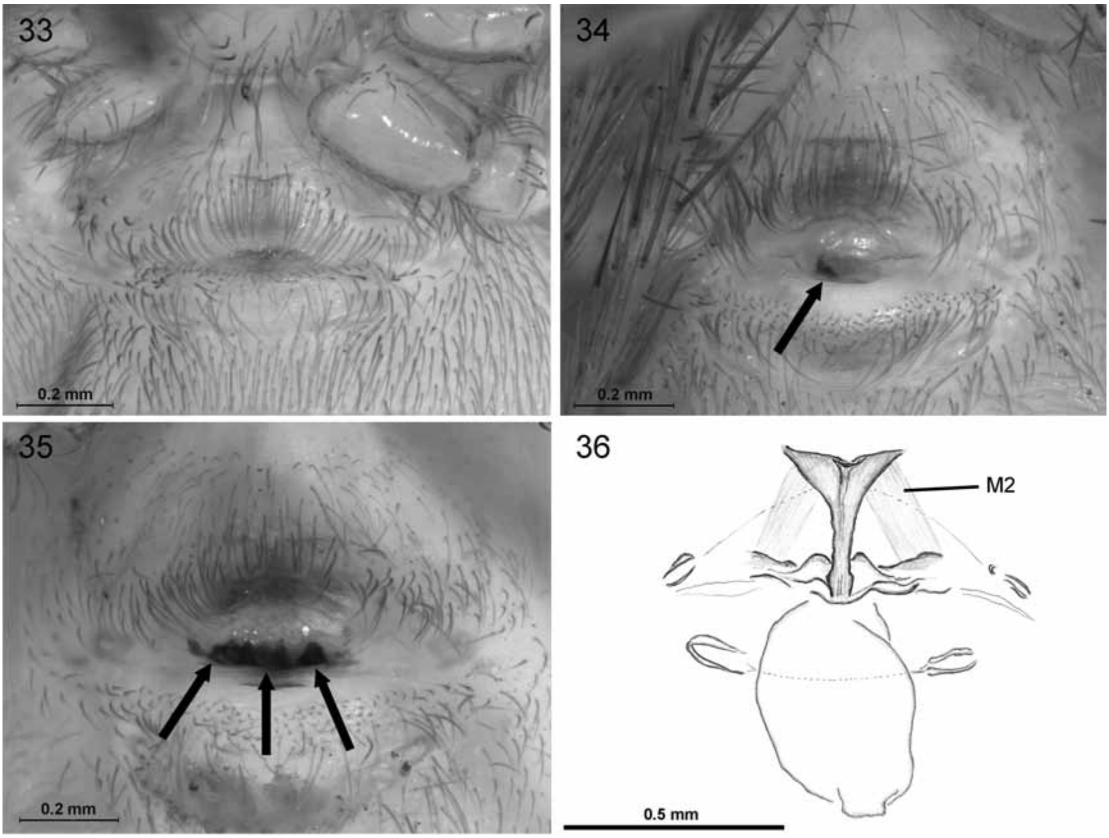
FIGS. 25–28. *Puan chechehet*, n. sp., male left palp (PBI_OON 43343). **25.** Prolateral view. **26.** Retrolateral view. **27.** Dorsal view. **28.** Ventral view.

fused to sternum, anterior margin not indented at middle, same as sternum in sclerotization; with six or more setae on anterior margin, subdistal portion with unmodified setae. Endites distally not excavated, serrula present in single row (fig. 58), anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. **Abdomen**: Ovoid, without long posterior extension, rounded posteriorly, interscutal membrane rows of small sclerotized platelets absent posteriorly; dorsum white, with median chevrons. Book lung covers large, round, without setae, anterolateral edge unmodified. Posterior spiracles connected by groove. Pedicel with ventral sclerotization (fig. 12). Pedicel tube medium, scutopedicel region unmodified, abdomen extending anteriad of pedicel, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent. Dorsal scutum absent. Epigastric scutum weakly sclerotized, not surrounding pedicel, not protruding, small lateral sclerites absent. Postepigastric scutum absent. Spinneret scutum absent. Supraanal scutum absent. Dorsum setae present, dark, needlelike. Epigastric area setae uniform, dark, needlelike. Postepigastric area setae present, dark, needlelike. Dense patch of setae anterior to spinnerets absent. Spinnerets (figs. 64–69*)*: ALS with one major ampullate gland spigot and four piriform gland spigots; PMS with two minor ampullate gland spigots; PLS with five acini-



FIGS. 29–32. *Puan nair*, n. sp., male left palp (PBI_OON 43373). **29.** Prolateral view. **30.** Retrolateral view. **31.** Dorsal view. **32.** Ventral view.

form gland spigots. Colulus present with at least six setae (fig. 66). **Legs**: Orange, without color pattern; supracoxal sclerites present (fig. 11: arrows), femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace, tibia I unmodified, tibia I Emerit's glands absent, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I and II mesoapical comb absent, metatarsi III and IV weak ventral scopula absent. Leg spines present. Tarsal proclaws and retroclaws inner face smooth; tarsus I–IV superior claws with nine or more teeth on lateral surface of proclaw, nine or more teeth on lateral surface of retroclaw (figs. 43–45). Tarsi I to IV without inferior claw. Trichobothria metatarsus: each with one; base rounded, aperture internal texture not gratelike, hood smooth (figs. 53–56). Tarsal organ fully capsulate (figs. 49–52). **Genitalia**: Epigastric region with sperm pore not visible; furrow without Ω-shaped insertions, without setae. Palp normal size (figs. 25–32), not strongly sclerotized, right and left palps symmetrical, proximal segments pale orange; embolus dark, prolateral excavation absent; trochanter normal size, unmodified; femur normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae

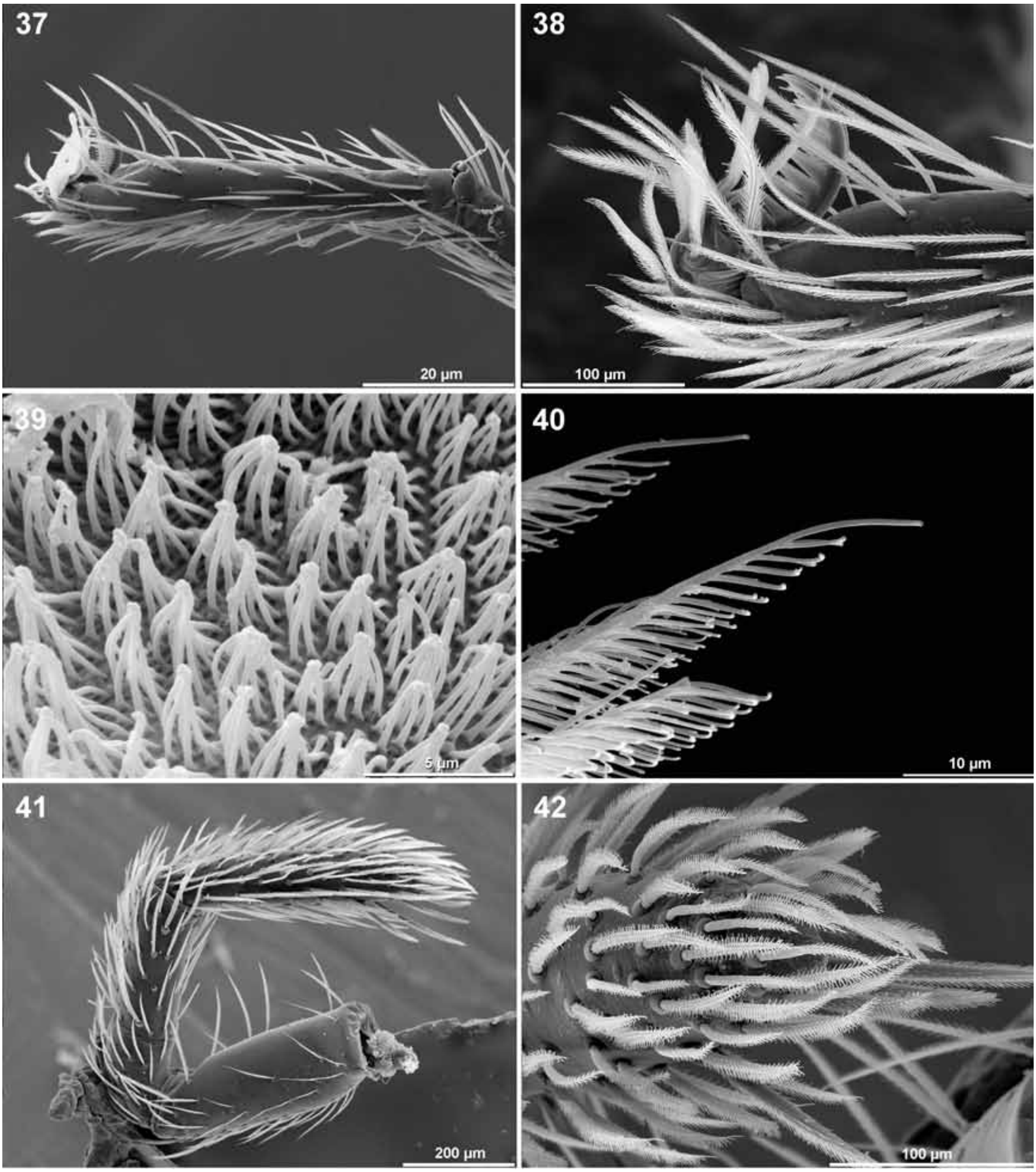


FIGS. 33–36. *Puan chechehet*, n. sp., female genitalia, ventral views. **33.** Paratype. **34, 35.** Dark marks in the epigastric region (arrows) (PBI_OON 43360, PBI_OON 43346 respectively). **36.** Drawing, in clove oil temporary mount (PBI_OON 43342).

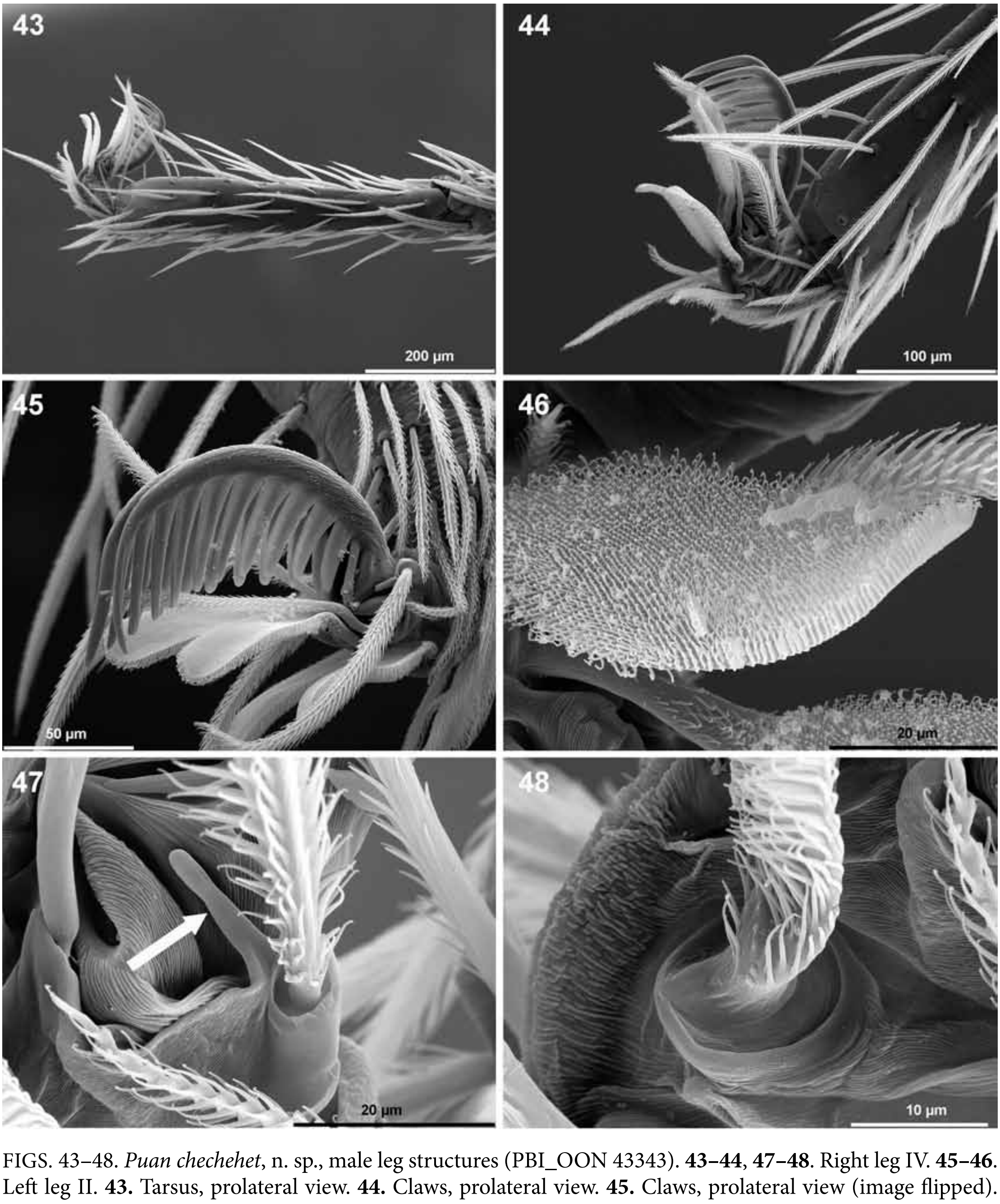
unmodified; tibia enlarged, trichobothria not examined; cymbium pale orange, ovoid in dorsal view, not fused with bulb, not extending beyond distal tip of bulb, plumose setae absent, without stout setae, without distal patch of setae; bulb 1 to 1.5 times as long as cymbium, stout, tapering apically.

Female: As in male except as noted. **Cephalothorax**: Carapace orange. Mouthparts: Chelicerae anterior face unmodified. Female palp claws absent (figs. 41, 42); spines absent; tarsus unmodified, patella without prolateral row of ridges. **Abdomen**: Epigastric scutum slightly protuding, without lateral joints. Epigastric area frontal setae thickened.

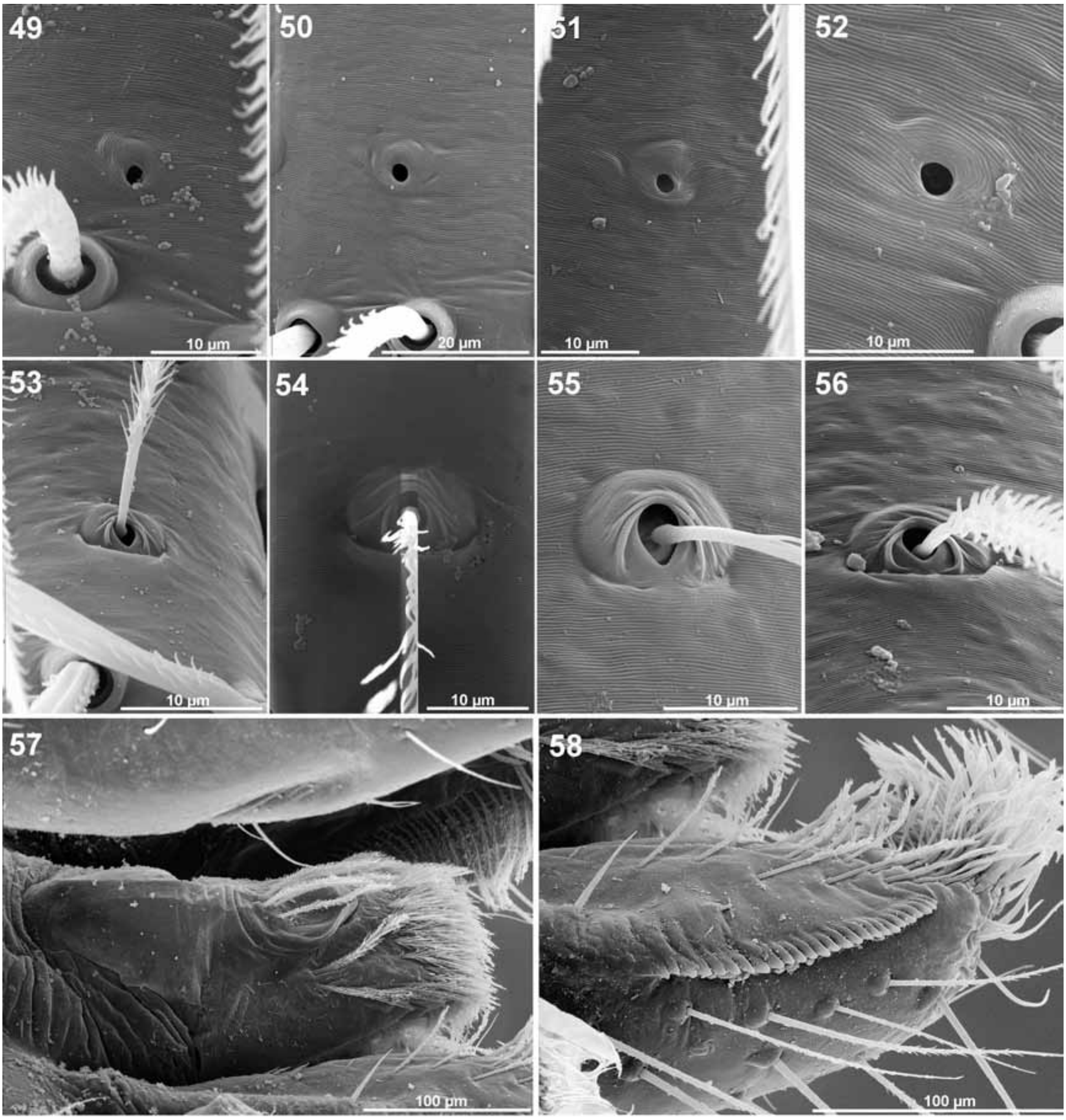
Natural History: The specimens were collected during ecological studies in the Ernesto Tornquist Provincial Park (figs. 1, 2) (Ferretti et al., 2012). This park has a surface area of 6718 ha and is located in the Ventania system, a group of mountain ranges (Lizzi et al., 2007). The protected area is one of the few places where the pampean grasslands are conserved (Lizzi et al., 2007). The climate is humid and temperate, with an annual mean temperature of 14.5° C; average annual rainfall is 850 mm (Pérez and Frangi, 2000). Additional information on the



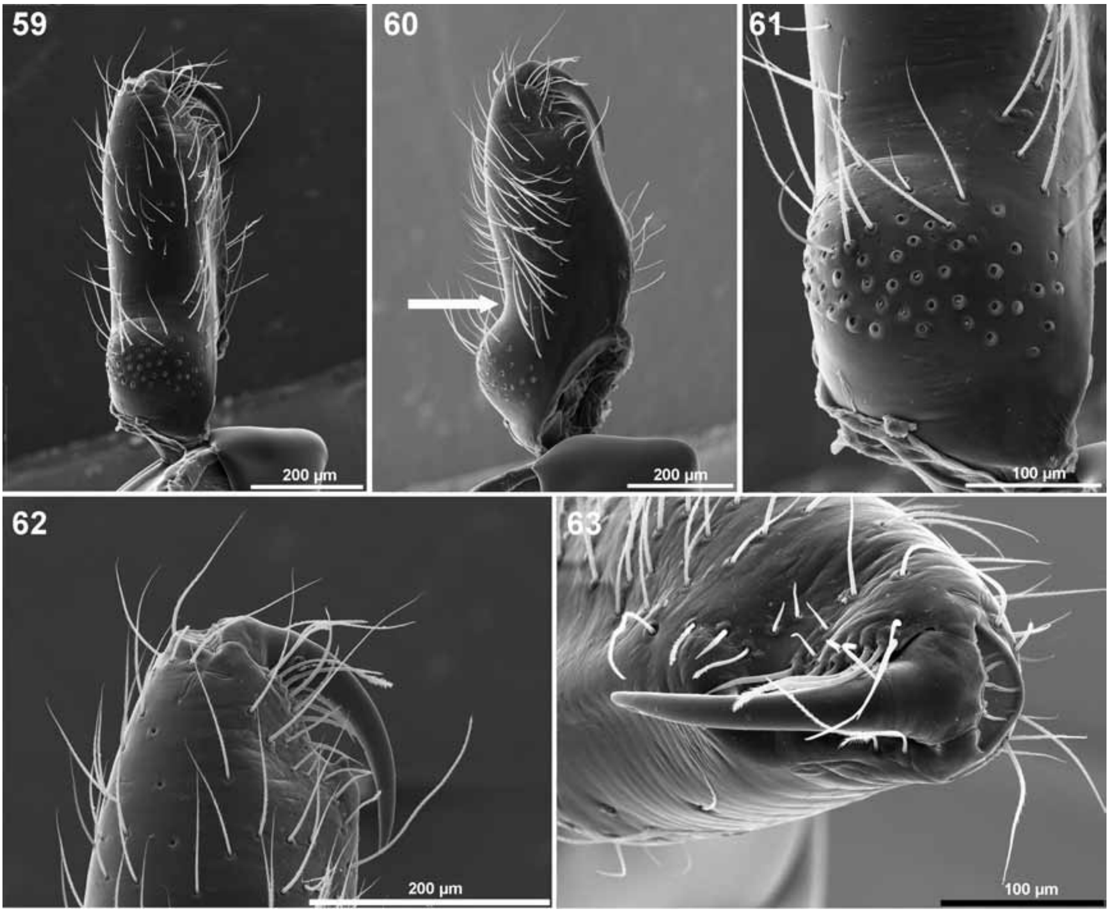
FIGS. 37–42. *Puan chechehet*, n. sp., female leg structures and palp. **37.** Left tarsus II, retrolateral view (PBI_OON 43388). **38.** Claws IV, prolateral view (PBI_OON 43342). **39.** Leg II, claw tuft setae, tenent surface (PBI_OON 43388). **40.** Left leg IV, detail of chemosensory setae (PBI_OON 43342). **41–42.** Left palp (PBI_OON 43342). **41.** Prolateral view. **42.** Prolateral-apical view.



FIGS. 43–48. *Puan chechehet*, n. sp., male leg structures (PBI_OON 43343). **43–44**, **47–48**. Right leg IV. **45–46**. Left leg II. **43.** Tarsus, prolateral view. **44.** Claws, prolateral view. **45.** Claws, prolateral view (image flipped). **46.** Claw tuft, tenent surface. **47.** Onychium, detail of a seta base. **48.** Same, detail of a claw tuft seta base.



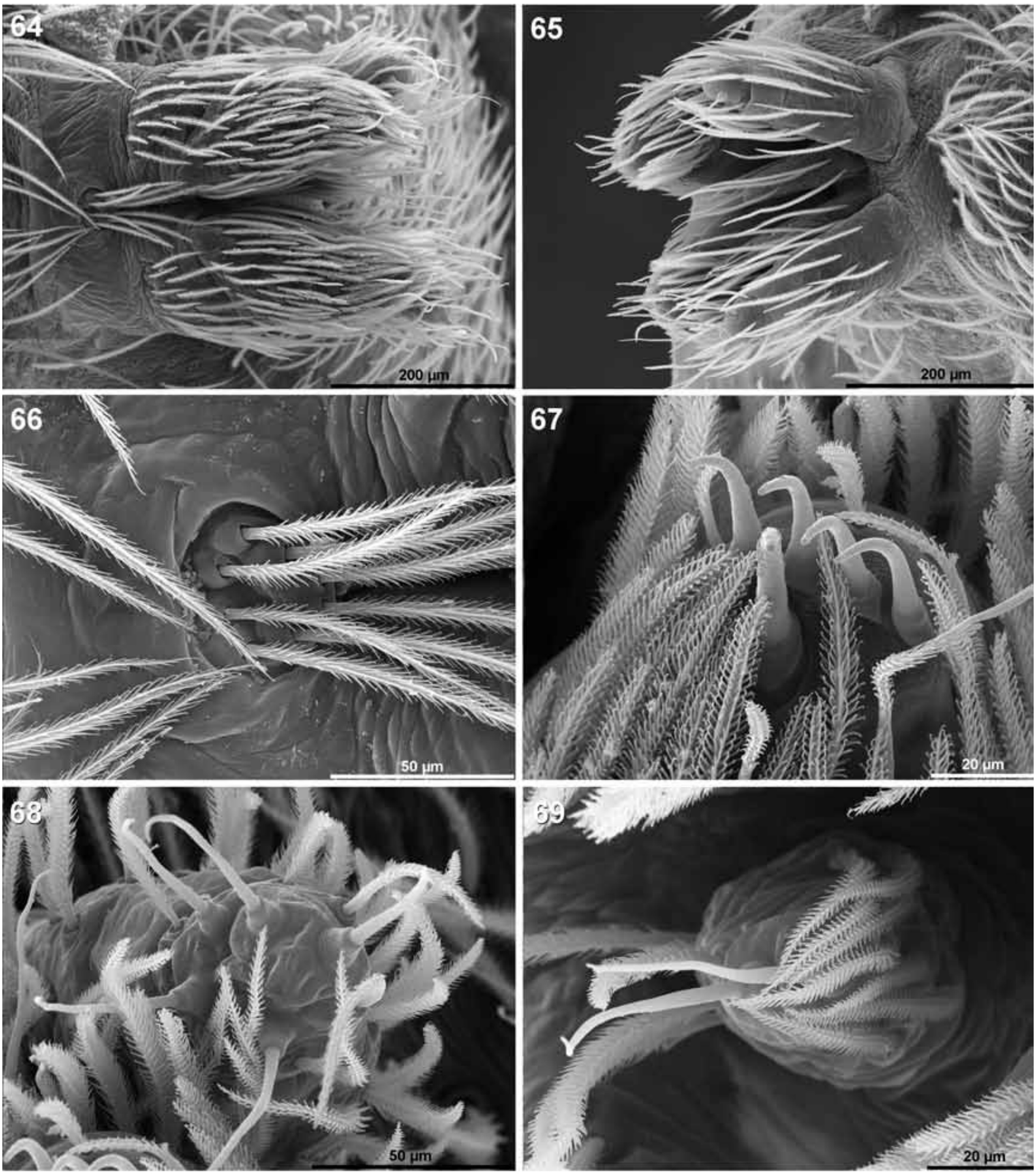
FIGS. 49–58. *Puan chechehet*, n. sp., female and male leg structures and endites. **49–52.** Tarsal organs. **53–56.** Metatarsal trichobothria sockets. **57–58.** Male mouthparts. **49.** Female left leg IV (PBI_OON 43342). **50.** Same, leg II (PBI_OON 43388). **51.** Male, right leg IV (PBI_OON 43343). **52.** Same, left leg I. **53.** Female, left leg IV (PBI_OON 43342). **54.** Same, leg II (PBI_OON 43388). **55.** Male, right leg IV (PBI_OON 43343). **56.** Same, left leg I. **57.** Labrum, lateral view (PBI_OON 43350). **58.** Serrula, lateral view.



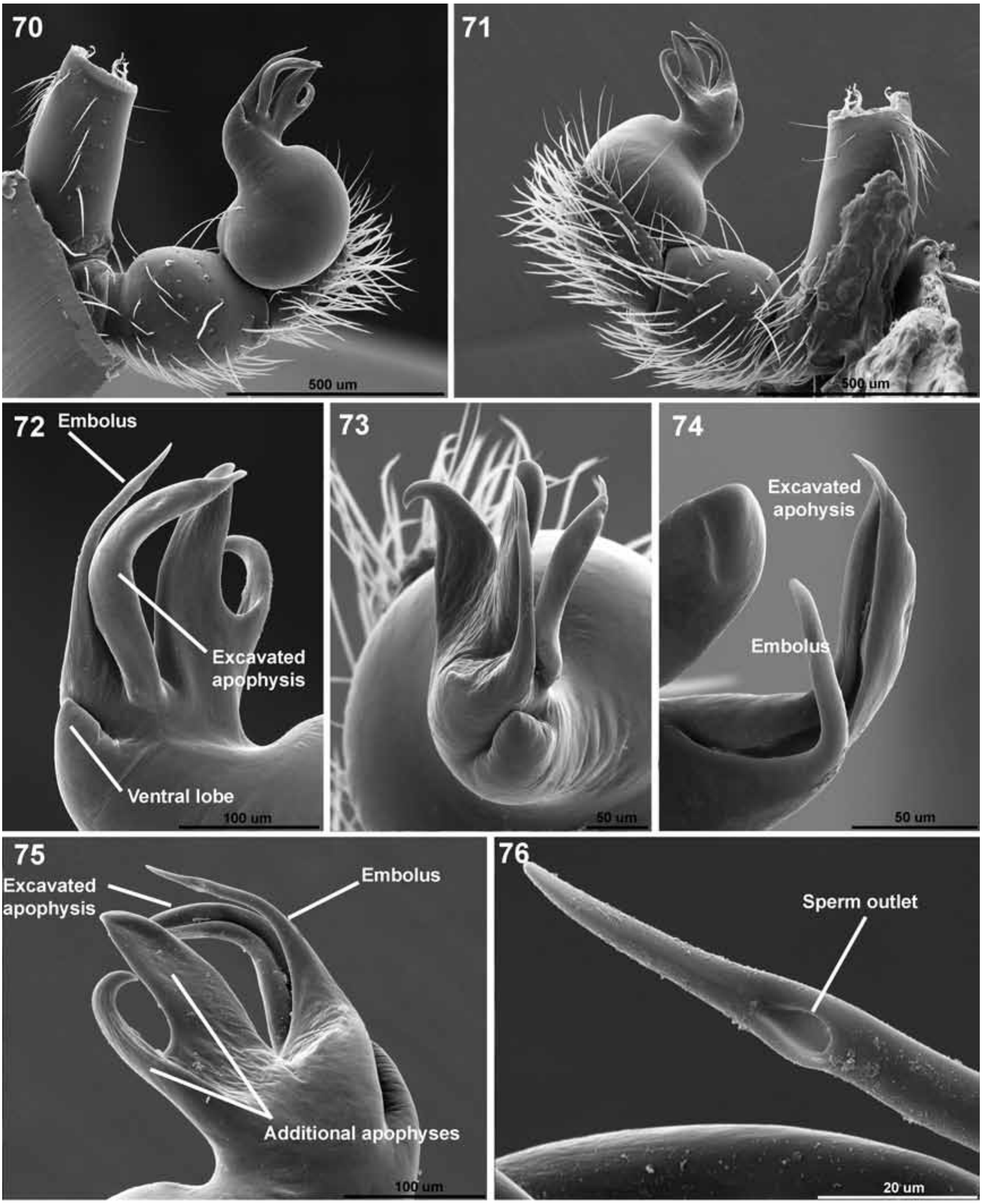
FIGS. 59–63. *Puan chechehet*, n. sp., male left chelicerae (PBI_OON 43343). **59.** Anterior view. **60.** Anterior-mesal view, arrow to the excavation. **61.** Detail of cheliceral boss region. **62.** Fang, promarginal view. **63.** Apical view.

geography, geology, flora, and fauna of the park can be found in Gregori et al. (2005), Sellés-Martínez (2001), and Frangi and Bottino (1995).

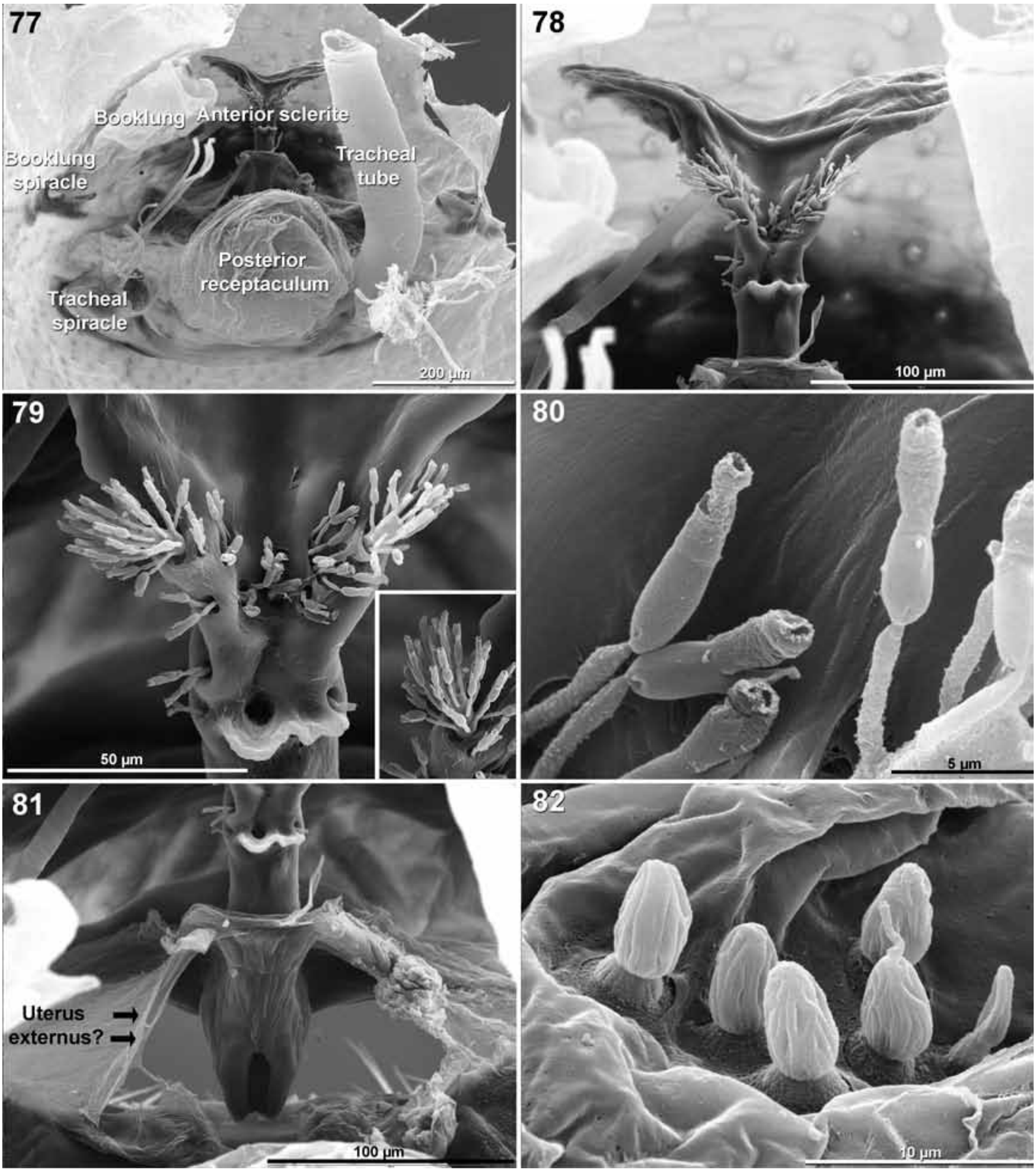
The spiders were found on the eastern slope of a hill near the Cerro de la Ventana at altitudes ~520 m. The specimens were collected during a pitfall campaign that ran from September 2009 to August 2010. Males were observed from May to August (winter season) with a maximum number of captured specimens in June (fig. 3). The temperatures during these months are low, ranging from 5° C to 10° C. Females were more abundant and were captured during the same period with the exception of one recorded in September (spring). The abundance in the winter compared with other months suggests that the spiders' biological cycle may be displaced to this season in order to avoid predation or competition. It is interesting to note that juveniles were not found in any month of sampling.



FIGS. 64–69. *Puan chechehet*, n. sp., female spinnerets and colulus (PBI_OON 43342). **64.** ALS, ventral view. **65.** PLS, dorsal view. **66.** Colulus. **67.** ALS spigots. **68.** PLS spigots. **69.** PMS spigots.



FIGS. 70–76. *Puan chechehet*, n. sp., male left palp (PBI_OON 43343). **70.** Retrolateral view. **71.** Prolateral view. **72.** Bulb, terminal elements, retrolateral view. **73.** Same, apical view. **74.** Embolus and excavated apophysis, prolateral view. **75.** Terminal elements, prolateral view. **76.** Embolus, sperm outlet.



FIGS. 77–82. *Puan chechehet*, n. sp., female digested vulva (PBI_OON 43388). **77.** Dorsal view. **78.** Anterior sclerite, detail of tip. **79.** Glands of the anterior sclerite (detail in the right square). **80.** Detail of glands. **81.** Anterior sclerite, detail of base. **82.** Glands of posterior receptaculum.

One female of *P. chechehet* had a mite attached to its abdomen, probably a larva of Parasitengona (Trombidiformes: Prostigmata) (Andrés Porta, personal commun.; figs. 18, 19). Some females have dark marks on the epigastric region (figs. 34, 35). These marks may be the result of copulatory maneuvers by the male; the bulbal structures could injure the female tissues. Similar scars have been observed in females of *Physocyclus globosus* (Taczanowski) after a second copulation event (Alfredo Peretti, personal commun.). Recently, Izquierdo and Rubio (2011) found embolus fragments inside the posterior receptaculum of females of *Unicorn catleyi* Platnick and Brescovit. We did not find bulbal structures in the female genital tract of *P. chechehet.*

Distribution: Known only from the Ernesto Tornquist Provincial Park at Buenos Aires province.

Puan chechehet Izquierdo, new species

Figures 4–19, 25–28, 33–82

Types: Male holotype and female paratype from Buenos Aires, Tornquist, Ernesto Tornquist Provincial Park: 300 m from the seismograph of the forest, grasses, 525 m, -38.05611°, -61.96666°, Argentina, May 2010, N. Ferretti (MACN 27623 PBI_OON 43344).

Etymology: The *chechehet* were one of the three principal divisions of the *het,* or native pampas, according to the classification of the English Jesuit Thomas Falkner in 1774.

Diagnosis: Males can be distinguished by the shape of the additional apophyses, which are clearly separated (figs. 26, 75). *Male* (PBI_OON 43344): Total length 3.03. **Cephalothorax**: Carapace orange. Eyes surrounded with dark pigment (figs. 6, 8, 9). Labrum as in figure 57. **Legs**: Leg spination (only surfaces bearing spines listed; all spines longer than segment width): tibiae: I p1-1-0; v0-0-2; r0-1-0; II p1-1-1; r1-1-0; III p1-1-0; v0-p1-2; r1-1-0; IV d0-1-0; p1-1-1; vp1-p1-2; r1-1-1; metatarsi: I v0-0-2; II p0-1-0; v0-0-2; r0-1-0; III d1-1-1; vp1-p1-2; r1-1-1. Teeth of tarsi I–IV superior claws examined in detail. Trichobothria examined with SEM (figs. 55, 56). **Genitalia**: Palpal bulb pale orange. Additional apophyses clearly separated.

Variation: Spination, tibia II: p1-1, metatarsus IV: d1-1-1-1; p1-1-1-1; r1-1-1-1; v p1-p1-p1-2.

Female (PBI_OON 43344): Total length 3.49. As in male except as noted. **Cephalothorax**: Female palp spines absent (fig. 41). **Abdomen**: Colulus with at least six setae. Spinnerets: ALS with one major ampullate gland spigot and four piriform gland spigots (fig. 67); PMS with two spigots (fig. 69); PLS with five aciniform gland spigots (fig. 68). **Legs**: Leg spination (only surfaces bearing spines listed, all spines longer than segment width): tibiae: I, II p0-1-1; vp1-p1-2; r0-1-1; III, IV d0-1-0; p0-1-1; vp1-p1-2; r1-1-1; metatarsi: I p0-1-1; vp1-p1-2; r0-1-1; II p0-1-1; vp1-p1-2; r0-1-0; III d1-1-1; vp1-p1-2; r1-1-1; IV d1-1-1; p1-1-1; vp1-p1-2; r1-1-1. Teeth of tarsi I–IV superior claws examined in detail. Trichobothria examined with SEM (figs. 53, 54).

Variation: Spination, tibia III: p1-1-1.

Other Material Examined: **ARGENTINA: Buenos Aires:** Tornquist: Parque Provincial Ernesto Tornquist: 300 m del bosque del sismógrafo, grasses, 525 m, -38.05611°, -61.96666°, May 2010, N. Ferretti, 2 males, 1 female (MACN 27620 PBI_OON 43342); same, 1 female, 1 male (MACN 27628 PBI_OON 43343);; same, 520 m, -38.05583°, -61.96666°, Aug. 2010, N.

Ferretti, 2 females (MACN 27615 PBI_OON 43346); same, 1 male (MACN 27624 PBI_OON 43347); same, 530 m, -38.05638°, -61.96666°, Aug. 2010, N. Ferretti, 2 males (MACN 27622 PBI_OON 43348); same, 528 m, -38.05638°, -61.96666°, May 2010, N. Ferretti, 1 male, 1 female (MACN 27616 PBI_OON 43349); same, July 2010, N. Ferretti, 1 male (MACN 27626 PBI_OON 43350); same, 525 m, -38.05611°, -61.96666°, Jul. 2010, N. Ferretti, 1 female (MACN 27617 PBI_OON 43351); same, 527 m, -38.05638°, -61.96666°, Jul. 2010, N. Ferretti, 2 females (MACN 27618 PBI_OON 43352); same, 520 m, -38.05583°, -61.96666°, Sep. 2009, N. Ferretti, 1 female (MACN 27614 PBI_OON 43356); same, 527 m, -38.05638°, -61.96666°, Aug. 2010, N. Ferretti, 2 females (MACN 27629 PBI_OON 43360); same, 530 m, -38.05638°, -61.96666°, Aug. 2010, N. Ferretti, 1 female (MACN 27625 PBI_OON 43361); same, 525 m, -38.05611°, -61.96666°, May 2010, N. Ferretti, 1 female (MACN 27619 PBI_OON 43374); same, 1 female (MACN 27621 PBI_OON 43387); same, 2 females, 1 male (MACN 27627 PBI_OON 43388).

Distribution: Known only from the type locality.

Puan nair Izquierdo, new species

Figures 20–24, 29–32

Type: Male holotype from Buenos Aires, Tornquist, Parque Provincial Ernesto Tornquist: 300 m from the seismograph of the forest, grasses, 530 m, -38.05638°, -61.96666°, Argentina, Jul. 2010, N. Ferretti (MACN 27630 PBI_OON 43373).

Etymology: The species name is an arbitrary combination of letters.

Diagnosis: The different male palpal morphology, with a small apophysis near the base of the embolus and the additional apophyses almost united, separates this species from *P. chechehet* (figs. 29–32). *Male:* **Cephalothorax**: Carapace pale orange. **Legs**: Leg spination (only surfaces bearing spines listed; all spines longer than segment width): femora: I, II d0-0-1; p0-0-1; tibiae: I, II p1-1-0; vp1-p1-2; r1-1-0; III d0-1-0; p1-1-0; vp1-p1-2; r1-1-0; IV d0-1-0; p1-1-0; vp1-p1-2; r1-1-1; metatarsi: I p0-1-1; vp1-p1-2; r1-1-0; II p0-1-0; vp1-p1-2; r0-1-0; III d1-1-1; vp1-p1-2; r1-1-0; IV d1-1-1; p1-1-1; vp1-p1-2; r1-1-1. Tarsi I to IV superior claws teeth not examined in detail. Trichobothria examined with stereo microscope. **Genitalia**: Palpal bulb yellow. A small, dark, pointed apophysis near the base of the embolus (figs. 29, 30). Additional apophyses almost completely fused.

Variation: Spination, right femora I: p0-0-2, leg II: femora d0-0-0; p0-0-0; metatarsus r1-1-0.

Female: Unknown.

Other Material Examined: None.

Distribution: Known only from the type locality.

DISCUSSION

The studies of the family Oonopidae in the past few years has led to the elucidation of morphological patterns and phylogenetic relationships at various levels. One example of this improvement is in the analysis of the tarsal organ, eye arrangement, and genitalia that recently allowed the delimitation of three subfamilies (Platnick et al., 2012): The Orchestininae are distinguished by the presence of an exposed tarsal organ with a longitudinal ridge originating from the proximal end of the organ and a serially dimorphic 4-4-3-3 pattern of raised receptors on legs I–IV. The Sulsulinae are united by having tarsal organs that are partially (in the case of *Cortestina*) or fully capsulated (in the case of *Sulsula*, *Xiombarg*, *Unicorn,* and *Dalmasula;* Platnick et al., 2012). The members of this subfamily resembles to Orchestininae in retaining two plesiomorphic features, an H-shaped, transverse eye arrangement and a heavily sclerotized, thick-walled sperm duct within the male palp. The Oonopinae (the remaining higher oonopids) are united by the loss of the heavily sclerotized palpal sperm duct, the reduction in the tarsal organ pattern to 3-3-2-2 raised receptors on legs I–IV and by the acquisition of a clumped eye arrangement. A 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement seem to be retained only in the New Zealand genus *Kapitia* Forster.

In this context, *Puan* belong to the Sulsulinae because of the presence of fully capsulated tarsal organs (figs. 49–52). The H-shaped eye arrangement and the heavily sclerotized sperm duct are additional characters shared with this subfamily and the Orchestininae.

The complex male copulatory bulb is perhaps one of the main characteristics of *Puan* and a probable synapomorphy for the genus; its general shape resembles the palps of Orsolobidae. As far as we know this complexity is unique for this genus. Complex copulatory bulbs are also found in *Dalmasula,* although they are simpler than in *Puan* (see Platnick et al., 2012). As in *Puan,* large size, color pattern, the tarsal claws with one row of teeth and the enlarged tibia of the male palp are also present in *Xiombarg* and *Unicorn*. Additional support for grouping *Puan* with these genera is their shared geographic distribution (they are all present only in the southern part of South America). However, the presence in *Puan* of a hirsute colulus could indicate the genus should be grouped with *Dalmasula*. The evidence provides a good opportunity for further explor biogeographic aspects and speciation processes of these spiders.

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REFERENCES

Álvarez-Padilla, F., and G. Hormiga. 2008. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. Journal of Arachnology 35: 538–542.

Brescovit, A.D, C.A. Rheims, A.B. Bonaldo, A.J. Santos, and R. Ott. 2012. The Brazilian goblin spiders of the new genus *Predatoroonops* (Araneae: Oonopidae). Bulletin of the American Museum of Natural History 370: 1–68.

Burger, M., M. Izquierdo, and P. Carrera. 2010. Female genital morphology and mating behavior of *Orchestina* (Arachnida: Araneae: Oonopidae). Zoology 113: 100–109.

Ferretti, N., G. Pompozzi, S. Copperi, F. Pérez-Miles, and A. González. 2012. Mygalomorph spider (Araneae) community of a natural reserve in a hilly system from central Argentina. Journal of Insect Science 12 (31): 1–16.

Forster, R.R., and N.I. Platnick. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. Bulletin of the American Museum of Natural History 181: 1–230.

Frangi, J.L., and O.J. Bottino. 1995. Comunidades vegetales de la Sierra de la Ventana, Provincia de Buenos Aires. Revista de la Facultad de Agronomía (La Plata) 71: 93–133.

Gregori, D.A., V.L. López, and L.E. Grecco. 2005. A late Proterozoic–Early Paleozoic magmatic cycle in Sierra de la Ventana, Argentina. Journal of South American Earth Sciences 19: 155–171.

Henrard, A., and R. Jocqué. 2012. An overview of Afrotropical canopy-dwelling *Orchestina* (Araneae, Oonopidae), with a wealth of remarkable sexual dimorphic characters. Zootaxa 3284: 1–104.

Izquierdo, M.A., and F.M. Labarque. 2010. Description of the female of *Orsolobus pucara* Forster and Platnick 1985, with comments on the functional morphology of the female genitalia in Dysderoidea (Araneae: Dysderoidea: Orsolobidae). Journal of Arachnology 38: 511–520.

Izquierdo, M.A., and G.D. Rubio. 2011. Male genital mutilation in the high-mountain goblin spider, *Unicorn catleyi*. Journal of Insect Science 11: 118.

Knoflach, B., K. Pfaller, and F. Stauder. 2009. *Cortestina thaleri* – a new dwarf six-eyed spider from Austria and Italy (Araneae: Oonopidae: Oonopinae). Contributions to Natural History 12: 743–771.

Lizzi, J., M.F. Garbulsky, R.A. Golluscio, and A.V. Deregibus. 2007. Mapeo indirecto de la vegetación de la Ventana, provincia de Buenos Aires. Ecología Austral 17: 217–230.

Pérez, C.A., and J.L. Frangi. 2000. Grassland biomass dynamics along an altitudinal gradient in the Pampa. Journal of Range Management 53: 518–528.

Platnick, N.I., and A.D. Brescovit. 1995. On *Unicorn*, a new genus of the spider family Oonopidae (Araneae, Dysderoidea). American Museum Novitates 3152: 1–12.

Platnick, N.I. 2000. On *Coxapopha*, a new genus of the spider family Oonopidae from Panama (Araneae, Haplogynae). Memorie della Società Entomologica Italiana 78: 403–410.

Platnick, N.I. 2006. The Oonopid spider PBI. Available online (http://research.amnh.org/oonopidae/projectdescription/projectdescription.php).

Platnick, N.I. 2012. The world spider catalog, version 12.5. New York: American Museum of Natural History. Available online (http://research.amnh.org/iz/spiders/catalog). [DOI: 10.5531/db.iz.0001]

Platnick, N.I., et al. 2012. Tarsal organ morphology and the phylogeny of goblin spiders (Araneae, Oonopidae) with notes on basal genera. American Museum Novitates 3736: 1–52.

Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Journal of Arachnology 28: 149–157.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940: 1: 1–1040. Bremen: Natura.

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