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Cover photo: Spiderlings emerging from egg sac guarded by female southern crevice spider, *Kukulcania hibernalis*. Photo by Jim Carrel.

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THE WOLF SPIDERS OF ARTESIAN SPRINGS IN ARID SOUTH AUSTRALIA, WITH A REVALIDATION OF *TETRALYCOSA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Artesian springs, commonly referred to as mound springs, are isolated unique threatened wetlands in arid central Australia that harbor a large number of endemic and relict species. Wolf spiders (Lycosidae) are the dominant invertebrate predators in mound springs and are the most abundant spider family present. Nine species are common, five of which are known to occur in other Australian wetland habitats, such as river floodplains and lakeshores: *Artoria howquaensis* Framenau 2002, *Hogna crispipes* (L. Koch 1877) new combination (= *Trochosa pulveresparsa* (L. Koch 1877) new synonymy; = *Geolycosa tongatabuensis* (Strand 1911) new synonymy; = *Tarentula tanna* Strand 1913 new synonymy; = *Lycosa waitei* Rainbow 1917 new synonymy; = *Lycosa strenua* Rainbow 1920 new synonymy; = *Lycosa rainbowi* (Roewer 1951) new synonymy), *Venatrix arenaris* (Hogg 1905), *V. fontis* Framenau & Vink 2001, and *V. goyderi* (Hickman 1944). Four species commonly found in mound springs are described as new: *Artoria victoriensis* new species, *Hogna diyari* new species, *H. kuyani* new species, and *Tetralycosa arabanae* new species. *Venatrix fontis* and *T. arabanae* are mainly found at mound springs and have only rarely been recorded from other wetland habitats. *Tetralycosa* Roewer 1960 is revalidated with *Lycosa meracula* Simon 1909 as type species. The genus is defined by its unique male pedipalp morphology with a deeply divided tegulum that carries a mesally directed spur on its retrolateral section opposing the hook-shaped median apophysis. Three Australian species are transferred to *Tetralycosa*: *T. alteripa* (McKay 1976) new combination, *T. eyrei* (Hickman 1944) new combination and *T. oraria* (L. Koch 1876) new combination (= *Trochosa candicans* (L. Koch 1877) new synonymy; = *Lycosa meracula* Simon 1909 new synonymy). *Hogna pexa* (Hickman 1944) new combination, an Australian wolf spider closely related to *Hogna kuyani* new species, is transferred from *Pardosa*.

Keywords: *Artoria*, *Venatrix*, *Hogna*, systematics, new species, mound springs

Central Australia is one of the driest places on earth. In the northern regions of South Australia the mean annual rainfall is between 100–150 mm and has an annual evaporation rate in excess of 3600 mm (Kotwicki 1987). The largest single source of water in this region is located below the surface in an enormous aquifer known as the Great Artesian Basin. This basin is a single continuous aquifer spanning 1.76 million km^2 across the states of Queensland, New South Wales, South Australia and the Northern Territory (Habermehl 1980, 1982; Harris 1992). The water from this basin discharges naturally from artesian springs (referred to as mound springs in South Australia) and artificially from free flowing bores (known locally as bore drains) (Fig. 1). These springs and bores form habitats that are analogous to islands in an otherwise desert environment for species that are dependent on permanent water for their survival (Harris 1981).

Artesian springs in this region form at fractures and fault lines along the margin of the basin creating wetlands of varying sizes. The typical artesian spring in South Australia is a low mound with water flowing from the top and forming a wetland around the base (Fig. 2). The mound is formed as water with high mineral and bicarbonate content precipitates minerals on the surface that over time create a raised area. Additionally, vegetation around

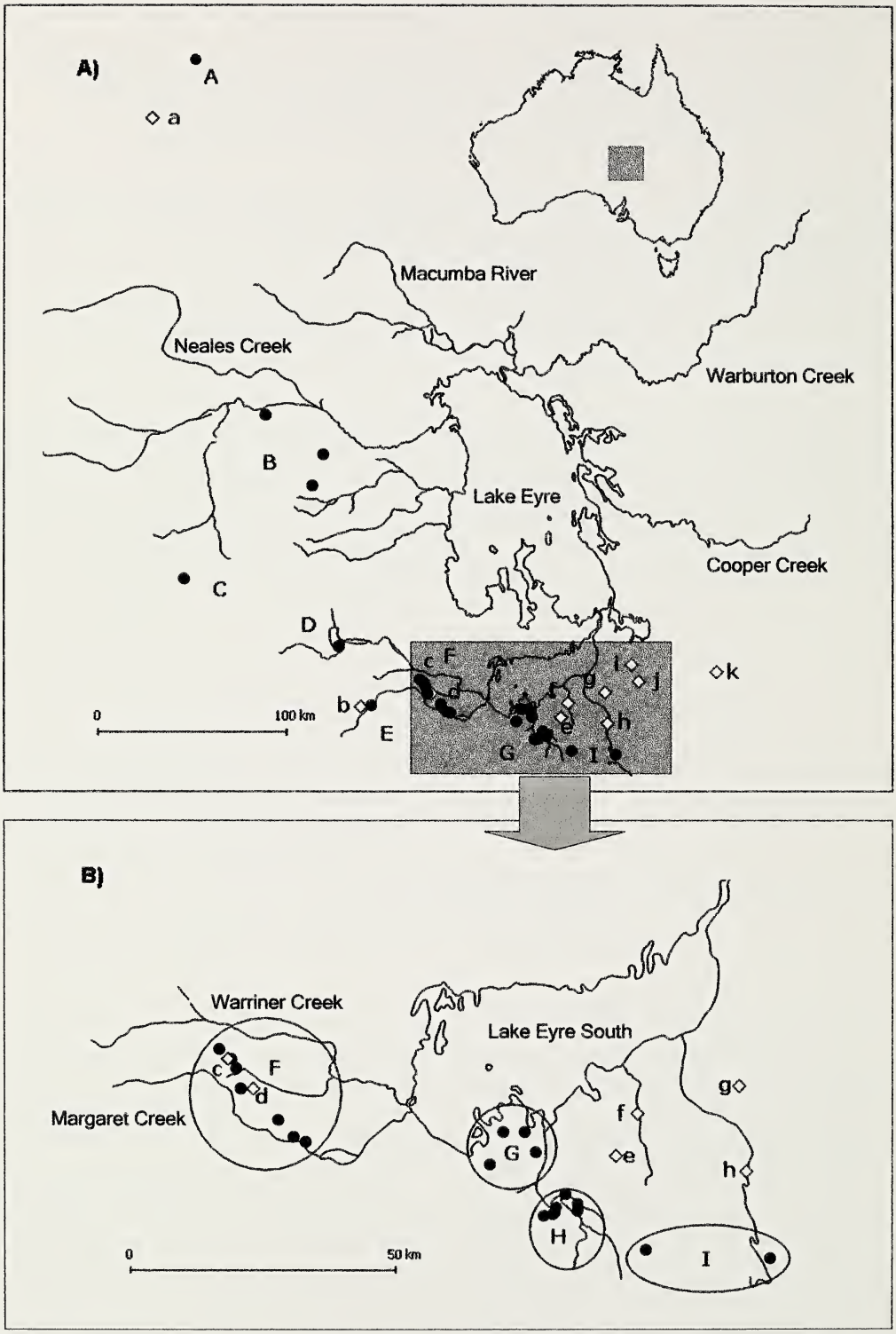

Figure 1.—Geographical locations of the South Australian artesian springs and bore drains. (A) shows the distribution of artesian spring complexes (●, capital letters) and flowing bore brains (◇, lower case letters) included in this study; (B) is an expanded view of the spring complexes and bore drains around Lake Eyre South. Artesian spring complexes: A = Dalhousie, B = Neales River, C = Lake Cadibarrawirracanna, D = Francis Swamp, E = Billa Kalina, F = Margaret River, G = Lake Eyre South, H =

the discharge region traps and collects windblown sand (Habermehl 1982). The flow rate from these artesian springs ranges from almost insignificant for small soaks to greater than 50 million litres per day such as at Dalhousie Springs (Sibenaler 1996). The wetland area is dependent on water flow and is categorized into two areas. The vent is the area where water issues from the ground and can vary in form from an active spring with a pool of open water to a damp soak, and there can be one to a number of vents associated with a particular mound. The tail is the part of the spring that results from the outflow of water away from the vent. It can be a channel or a uniform flow radiating out from the vent, and can range in area from less than 1 m^2 to greater than 70 ha and over 16 km in length (Sibenaler 1996). These areas support substantial water dependent vegetation that is usually dominated by only one or two species (Symon 1985; Fatchen & Fatchen 1993).

Artesian springs in South Australia host numerous endemic species of high conservation status due to their very restricted distribution and potential threats to the integrity of their fragile habitats. They include endemic gastropods, crustaceans and fish (Ferguson 1985; Ponder 1985; Boyd 1990; Kinhill Engineers 1997). Artesian springs are threatened by a number of human impacts, most importantly excessive water consumption by cattle, mining companies and gas abstraction operations. This may result in a localized reduction of water pressure in the Great Artesian Basin followed by reduced flows and, in rare instances, spring extinction (Kinhill Engineers 1997).

Recent studies of artesian springs and bore drains in South Australia have shown that wolf spiders (Lycosidae) are the most abundant predatory group. They include a number of undescribed taxa and are associated with vegetated areas of *Cyperus laevigatus*, *Phragmites australis* and *Typha domingensis* both at the vent and on the tail (Lamb 1998; Gotch 2000). Other spider families have been reported from artesian springs and bore drains in lower numbers, including Hahniidae, Pisauridae, Linyphiidae, Clubionidae, Salticidae, Zodariidae, Oxyopidae, Gnaphosidae, Desidae, Corinnidae, Araneidae, Tetragnathidae and Prodidomidae (Lamb 1998; Gotch 2000; D. Niejalke & D. Hirst, pers. comm.).

Here we provide a complete taxonomic treatment of wolf spiders of artesian springs in South Australia to facilitate their identification as part of on-going research to develop procedures for environmental monitoring of these unique habitats.

METHODS

Typical artesian spring lycosids as defined for this study are species which are facultatively dependent on the occurrence of open spring or bore water and will only be found in the confined space where it is available. These do not include the mostly burrowing species of the arid environment surrounding the springs, which on rare occasions can be found at the springs (for example *Lycosa woonda* McKay 1979; VWF, TBG pers. obs.).

This study is mainly based on material collected during three studies on the arthropod communities of South Australian artesian springs (Lamb 1998; Gotch 2000) lodged at the South Australian Museum. In addition, the collections of all other major museums in Australia were examined thoroughly for conspecifics of the artesian spring species as part of an ongoing revision of the Lycosidae of Australia.

Descriptions are based on specimens preserved in 70% EtOH. Internal female genitalia were prepared for examination by submersion in 10% KOH overnight at room temperature. For clarity, the illustrations of epigyna and male pedipalps omit the setae. The morphological nomenclature follows Framenau & Vink (2001) and Framenau (2002). All type material was examined unless otherwise stated. All measurements are in millimeters (mm).

Abbreviations.—*Eyes:* anterior (AE), anterior median (AME), anterior lateral (ALE), posterior (PE), posterior median (PME), posterior lateral (PLE). *Measurements (adult spiders, if not otherwise stated):* total length

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Hermit Hill, I = Davenport/Wangianna. Bore drains: a = Hamilton, b = Welcome, c = Elizabeth, d = Coward, e = Charles Angus, f = Morris Creek, g = Crows Nest, h = Coranna, i = Muloorina, j = Lake Letty no. 3, k = Clayton.

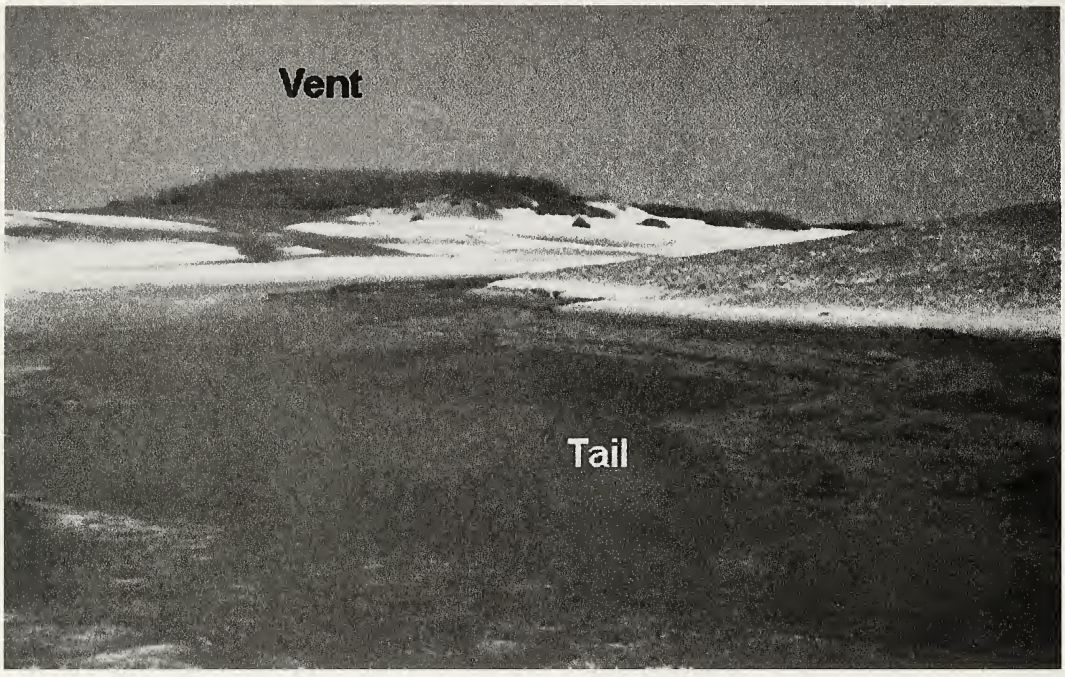


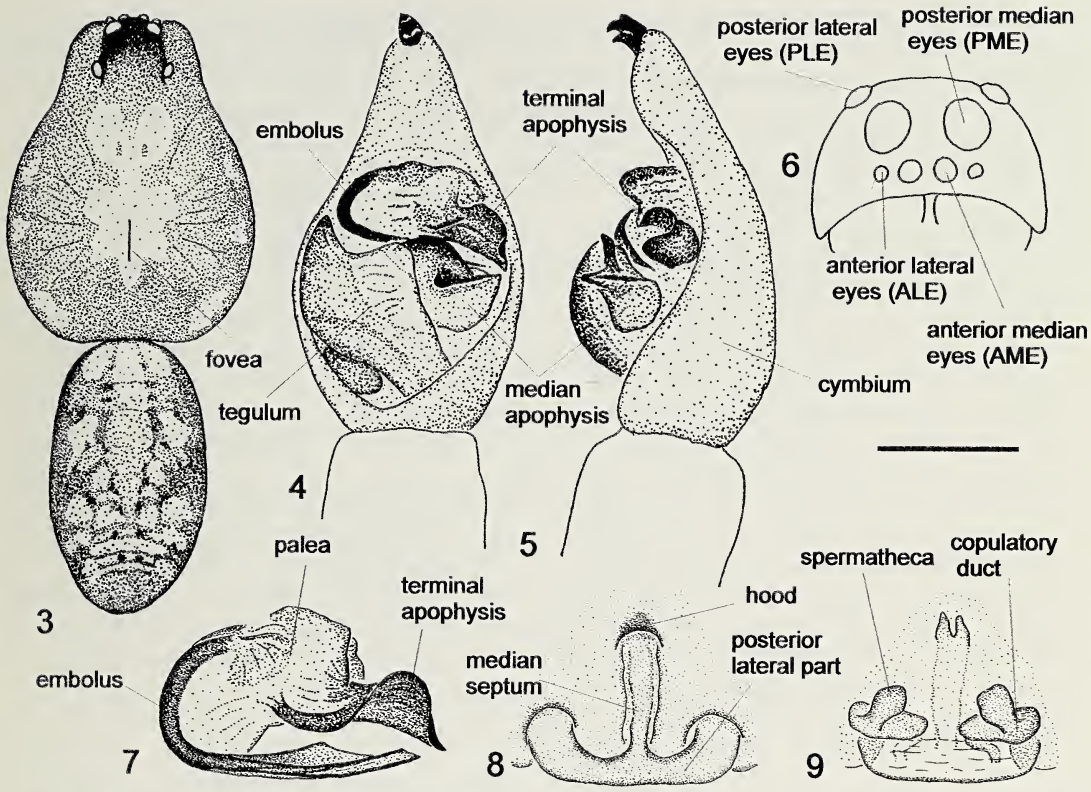
Figure 2.—McLachlan Springs, a typical artesian spring in South Australia showing the vent and tail microhabitats.

(TL), carapace length (CL) and width (CW), abdomen length (AL) and width (AW). *Australian States and Territories*: Australian Capital Territory (ACT), New South Wales (NSW), Northern Territory (NT), Queensland (Qld), South Australia (SA), Tasmania (Tas), Victoria (Vic), Western Australia (WA).

Collections: AM = Australian Museum, Sydney; ANIC = Australian National Insect Collection, Canberra; BMNH = Natural History Museum, London; CVIC = Central Victorian Insect Collection, LaTrobe University, Bendigo; MNHP = Museum National d'Histoire Naturelle, Paris; MV = Museum Victoria, Melbourne; QM = Queensland Museum, Brisbane; QVMAG = Queen Victoria Museum and Art Gallery, Launceston; SAM = South Australian Museum, Adelaide; SMF = Senckenberg Museum, Frankfurt; TMAG = Tasmanian Museum and Art Gallery, Hobart; WAM = Western Australian Museum, Perth; ZMB = Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin; ZMH = Zoologisches Institut und Zoologisches Museum, Universität Hamburg.

KEY TO LYCOSIDAE OF SOUTH AUSTRALIAN ARTESIAN SPRINGS

1. Male pedipalp with basoembolic apophysis that reaches around the base of the median apophysis; median apophysis with a long narrow base, originating apically at tegulum (Figs. 59, 65, 67); epigynum a simple posterior atrium that is sclerotized laterally (Fig. 61), or with a posterior sclerotized rim that reaches anteriorly into a white, oval center (Fig. 68) Genus *Artoria* Thorell 1877 8
   Male pedipalp without basoembolic apophysis, median apophysis originating laterally at tegulum (Figs. 4, 11, 15, 20, 35, 42), or a basally directed broad hook (Fig. 49); epigynum inverted T-shaped (Figs. 8, 13, 25, 27–31, 38, 45), or a triangular atrium (Figs. 17, 54, 55) 2
2. Tegulum of male pedipalp with deep and wide longitudinal division in retrolateral half, median apophysis forms a basally directed hook opposing a distinct tip on the retrolateral part of the tegulum (Fig. 49); female epigynum forms a triangular atrium, hoods clearly



Figures 3–9.—*Venatrix arenaris* (Hogg 1905): Male from Horse Springs, SA (WAM T47290): 3. habitus; 4. left pedipalp, ventral; 5. left pedipalp, retrolateral; 6. eye arrangement; 7. apical part of bulb. Female from Fred Springs, SA (WAM T47292): 8. ventral view of epigynum; 9. dorsal view of epigynum. Scale bar: (3) 2.07 mm, (4, 5) 0.58 mm, (6) 0.98 mm, (7) 0.36 mm, (8, 9) 0.46 mm.

separated (Figs. 54, 55); carapace and abdomen light yellowish-brown, carapace with indistinct dark radial pattern, abdomen with indistinct white patches (Fig. 48); small spiders; TL 4.8–11.5 mm. Main distribution at artesian springs, occasionally near salt lakes (only recorded from SA) ..... ***Tetralycosa arabanae*** new species

Tegulum not divided, median apophysis directed retrolaterally, much broader at the base than tip and with a ventrally directed process (e. g. Figs. 4, 11, 15, 20, 35, 42); epigynum inverted T-shaped (e. g. Figs. 8, 13, 25, 27–31, 38, 45), or a triangular atrium with distinct anterior hoods separated from atrium (Fig. 17); carapace brown with light median band or uniformly dark grey to black; small to medium-sized spiders; TL 5.5–20.0 Subfamily Lycosinae 3

3. Tip of male cymbium with large, claw-like setae (Figs. 4–5, 11, 15), outer edge of fangs in males with tubercle (Fig. 16); posterior lateral edges of epigynum bulging anteriorly (Figs. 8, 13), or epigynum a triangular atrium with distinct anterior hoods separated from atrium (Fig. 17) Genus *Venatrix* Roewer 1960 4

Tip of male cymbium without claw-like setae, but with a variable number of macrosetae (Figs. 20, 21, 35, 36, 42, 43); posterior lateral edges of epigynum not bulging anteriorly, i.e. posterior lateral parts thickest at their base near the median septum (Figs. 25, 27–31, 38, 45) Genus *Hogna* Simon 1885 6

4. Carapace brown with a wide median band that constricts anteriorly of fovea and forms a star-like pattern around the fovea (Fig. 3); terminal apophysis of the male pedipalp forms a large roof over the tip of the embolus (Figs. 4, 7); bulging posterior lateral ends of epigynum whitish, median septum of equal width along its whole length (Fig. 8). TL 8.0–15.0. Aus-

tralia-wide on sand and small gravel near rivers, ponds and springs (Fig. 10) ..... *Venatrix arenaris* (Hogg 1905)

Carapace brown to dark brown with a narrow light brown median band 5

5. Terminal apophysis of male pedipalp sickle-shaped (Figs. 11, 12); epigynum inverted T-shaped, the median septum widening anteriorly (Figs. 13); TL 8.0–17.0 mm. Mainly at artesian springs, rarely found near rivers (NSW, SA, Vic) (Fig. 14) ..... *Venatrix fontis* Framenau & Vink 2001

Terminal apophysis of male pedipalp forms a roof over the tip of the embolus (Figs. 15); female epigynum a triangular atrium (Fig. 17); TL 5.0–11.0 mm. Open, vegetated areas near water, Australia-wide (Fig. 18), also in New Zealand and New Caledonia ..... *Venatrix goyderi* (Hickman 1944)

6. Carapace dark reddish-brown, appears dark grey to black due to a dense cover of silver-grey setae (in particular in fresh material); no light median band; abdomen dark grey with indistinct light and dark patches (Fig. 41); pedipalp Figs. 42–44; epigynum Figs. 45, 46; TL 8.5–20.0 mm. Near water (SA, Qld, NSW, WA) (Fig. 47) ... ***Hogna kuyani*** new species

Carapace brown with a distinct light median band 7

7. Light median band on carapace wide, covering approx. one third of carapace width (Fig. 33); venter yellow with two black spots behind epigastric furrow and a variable number of black spots laterally (Fig. 34); pedipalp Figs. 35–37; epigynum Figs. 38, 39; TL 9.5–18.0 mm. Near water (SA, Qld, NSW, Vic) (Fig. 40) ..... ***Hogna diyari*** new species

Light median band on carapace narrow, covering less than a quarter of carapace width (Fig. 19), submarginal band with three dark blotches (sometimes not very distinct); venter uniformly yellow-brown; pedipalp Figs. 20, 21, 24; epigynum Figs. 25–31; TL 7.0–20.0 mm. Open areas near water on sand or grass, inland and coastal (Australia-wide, including offshore islands and reefs (Fig. 32); also in New Zealand and Pacific islands) ..... *Hogna crispipes* (L. Koch 1877)

8. Median apophysis of male pedipalp with triangular apical process and a broad, ventrally bent tip (Figs. 59); pedipalp patella and tibia bright yellow; pedipalp tibia and basal half of cymbium with dense cover of white setae (very conspicuous in unpreserved specimens); epigynum forms an indistinct, lightly sclerotized posterior atrium (Fig. 61); carapace black with light marginal bands due to a dense cover of white setae; TL 3.5–6.0 mm. Open, but shaded areas near water, mound springs and lowland river floodplains (SA, Vic) (Fig. 62) ..... *Artoria howquaensis* Framenau 2002

Median apophysis of male pedipalp in ventral view shaped like an upside-down sock (Fig. 65), pedipalp patella light brown, cymbium without white setae; epigynum forms an oval atrium with a sclerotized posterior rim that reaches into the center of the atrium (Fig. 68); carapace brown with light median and submarginal bands and dark radial pattern (Fig. 63); femora of all legs with dark annulations (particularly distinct on ventral side of leg III and IV); TL 3.5–8.5 mm. Rare at artesian Springs, but very common in open, moderately moist cultural landscapes and suburban areas (NSW, SA, Tas, Vic) (Fig. 70) ..... ***Artoria victoriensis*** new species

TAXONOMY

Subfamily Lycosinae Simon 1898

Remarks.—The Lycosinae appear to be well-defined since Dondale (1986) established synapomorphic characters for the male pedipalp (p. 331): "median apophysis transverse, with ventrally directed spur" and "median apophysis with sinuous channel on dorsal surface". However, there are difficulties in establishing monophyletic taxa below the subfamily level. Molecular analysis suggests that Dondale's (1986) '*Trochosa*-' and '*Lycosa*-groups' within the Lycosinae, based on the shape of the terminal apophysis, are paraphyletic (Vink et al. 2002). Alternatively, Zyuzin (1993) distinguished his tribes Trochosini and Lycosini based on the shape of the median apophyis ('tegular apophysis, TA' sensu Zyuzin 1993) and the female epigynum.

Genus *Venatrix* Roewer 1960

Venatrix Roewer 1960: 745 (name first listed as a *nomen nudum* in Roewer 1955: 307).

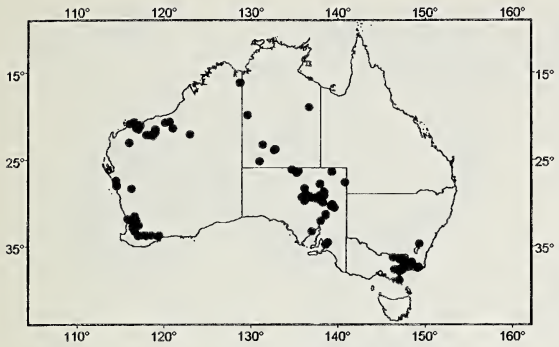


Figure 10.—Records of *Venatrix arenaris* (Hogg 1905) in Australia.

Remarks.—*Venatrix* was established by Roewer (1960) and recently revised to include 22 Australian species, of which one, *V. goyderi*, is also found in New Zealand and New Caledonia (Framenau & Vink 2001; Vink 2002; C.J. Vink, pers. comm.). Males of *Venatrix* have a tubercle on the outer edge of the fangs (Fig. 16) and large, claw-like setae at the tip of the cymbium (Figs. 4, 5, 11, 15). Three species of *Venatrix* are present at artesian springs and bore drains of South Australia, *V. arenaris*, *V. fontis* and *V. goyderi*. Full taxonomic bibliographies for these species can be found in Framenau & Vink (2001), but updated distribution maps are provided here.

Venatrix arenaris Hogg 1905
Figs. 3–10

Lycosa arenaris Hogg 1905: 586–588, fig. 88; McKay, 1974: 1–6, figs. 1a–m.

Lycosa celaenica Rainbow 1917: 488–489, plate 32, figs. 10, 11.

Venatrix arenaris (Hogg 1905): Framenau and Vink 2001: 960–962, figs. 40a–f, 41.

Diagnosis.—*Venatrix arenaris* is a medium-sized spider (TL 8.0–15.0). Its mottled, indistinct coloration varies from very dark to light beige (Fig. 3) and blends very easily with its preferred sandy habitat. Most specimens, except very dark spiders, have a light narrow band on the anterior half of the sternum. Males are distinguished by their broad terminal apophysis, which bends ventrally forming a roof over the tip of the embolus (Figs. 4, 5, 7). The female epigynum forms an inverted 'T', with a narrow median septum. The lateral tips of the posterior transverse part bulge anteriorly (Fig. 8).

Distribution and habitat preferences.—*Venatrix arenaris* is found Australia-wide (Fig. 10). It is present in most artesian springs and bore drains in South Australia, and is the dominant species in the south-eastern springs from the Blanche Cup in the west to Mulligan Springs in the east (Table 1). Within springs *V. arenaris* typically resides next to the edges of open wet spaces and small open water pools. It is rarely active during the day and usually conceals itself under *C. laevigatus*. At night this species can be observed foraging on the surface of still water.

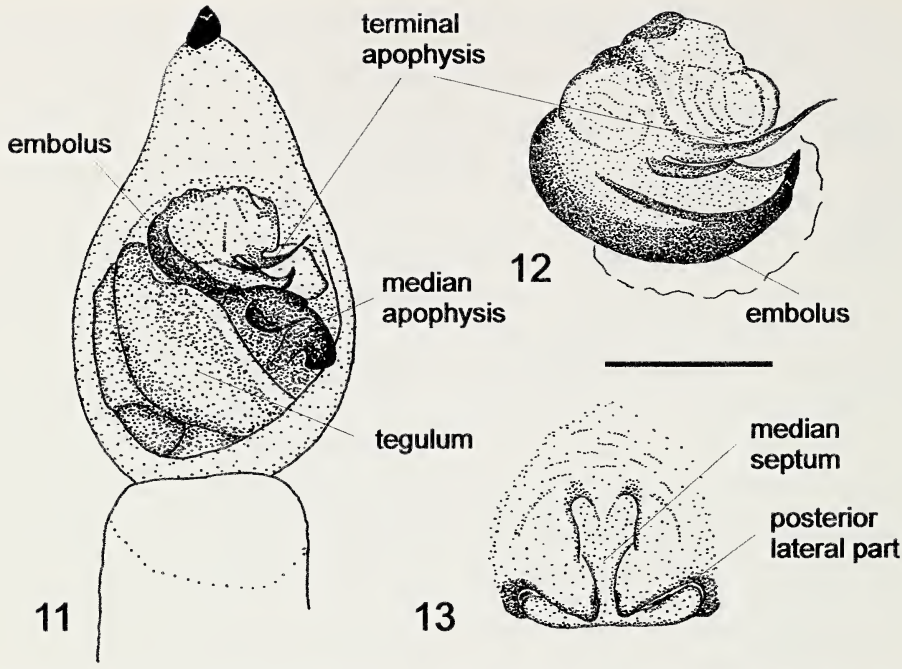
Remarks.—Recent preliminary allozyme studies indicate that *V. arenaris* populations from the South Australia and those inhabiting lowland floodplains of the Great Dividing Range in south-eastern Australia (illustrated in Framenau & Vink 2001) possibly represent two different species (Gotch 2003; M. Adams pers. comm.). Thus, the status and distribution of *V. arenaris* as presently defined on morphological grounds needs to be reassessed in conjunction with more detailed allozyme studies. Representative male and female specimens from South Australia are illustrated here (Figs. 3–9).

Venatrix fontis Framenau & Vink 2001
Figs. 11–14

Venatrix fontis Framenau & Vink 2001: 959–960, figs. 38–f, 39.

Diagnosis.—This is a medium-sized wolf spider (TL 8.0–17.0 mm). The carapace varies from nearly black to a light olive-grey and a narrow, yellow median band is always present. The abdomen is dark grey and has a lanceolate yellow heart mark in its anterior half. The body coloration resembles *V. goyderi*, however, *V. fontis* is generally larger. In contrast to *V. arenaris* and *V. goyderi*, the terminal apophysis of the male pedipalp of *V. fontis* is sickle-shaped (Figs. 11, 12). The female epigynum is inverted T-shaped, but in contrast to *V. arenaris*, its median guide widens anteriorly (Figs. 13).

Distribution and habitat preferences.—*Venatrix fontis* appears to have its main distribution at the South Australian artesian springs; however, single specimens have been found in Victoria and New South Wales (Fig. 14). It is the dominant species in the western and northern springs, from Coward Springs in the south to the Mt. Dutton spring complex in the north (Table 1). *Venatrix fontis* is a noc-



Figures 11–13.—*Venatrix fontis* Framenau & Vink 2001: Male from Freeling Springs, SA (SAM NN9908): 11. left pedipalp, ventral; 12. apical part of bulb. Females from Freeling Springs, SA (SAM NN9910): 13. ventral view of epigynum. Scale bar: (11) 0.59 mm, (12) 0.29 mm, (13) 0.57 mm.

turnal species that is associated with less densely vegetated springs, especially those with gravel or travertine substrates. During the day large adult *V. fontis* can be found under sheets of travertine and rocks while juveniles shelter in clumps of *C. laevigatus* at the spring margins.

Venatrix goyderi (Hickman 1944)
Figs. 15–18

Lycosa goyderi Hickman 1944: 33–34: plate 2, fig. 20.

Lycosa howensis McKay 1979b: 237–238, figs. 1a–e.

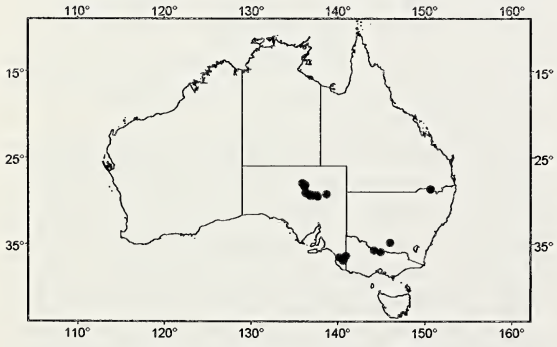
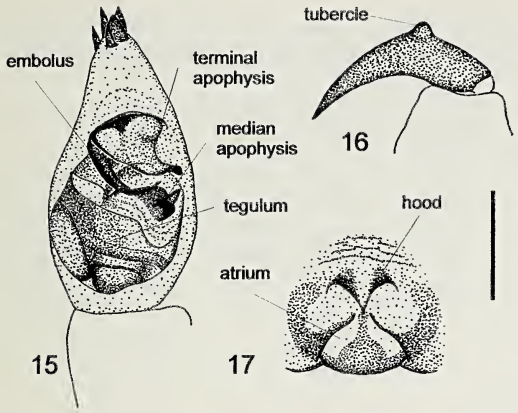


Figure 14.—Records of *Venatrix fontis* Framenau & Vink 2001 in Australia.

Venatrix goyderi (Hickman 1944): Framenau & Vink, 2001: 963–965, figs. 44a–e, 45.

Diagnosis.—This is the smallest (TL 5.0–11.0 mm) of the three *Venatrix* species found regularly at South Australian artesian springs and bore drains. This species is brown to dark brown. The carapace has a narrow, light median band. The abdomen bears a light median heart mark and pairs of light brown patches. The terminal apophysis of the male pedipalp forms a roof-like structure over the embolus (Fig. 15). The female of *V. goyderi* is the only member of the subfamily Lycosinae at the artesian springs that does not have an inverted T-shaped epigynum (Fig. 17).

Distribution and habitat preferences.—*Venatrix goyderi* has been found in all states of mainland Australia as well as Lord Howe Island (Fig. 18), the North Island of New Zealand (Framenau & Vink 2001) and recently in New Caledonia (C.J. Vink pers. comm.). In the arid zone of South Australia it is found associated with wetlands across the north-east of the state, particularly the Coopers Creek and Diamantina River systems, and with artificial wetlands such as bore drains where it is the dominant wolf spider. This species is



Figures 15–17.—*Venatrix goyderi* (Hickman 1944): Male from Howqua River, Vic (AM KS58209): 15. left pedipalp, ventral; 16. fang with tubercle. Female from Howqua River, Vic (AM KS58206): 17. ventral view of epigynum. Scale bar: (15) 0.43 mm, (16) 0.41 mm, (17) 0.31 mm.

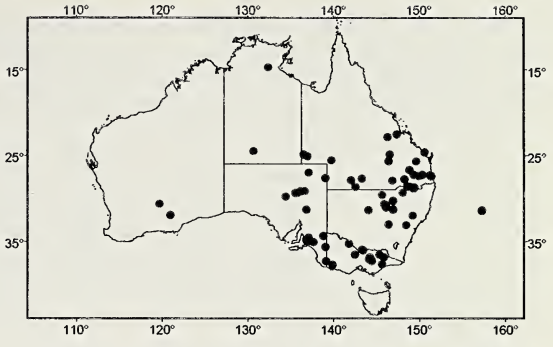


Figure 18.—Records of *Venatrix goyderi* Hickman in 1944 Australia.

also found in large numbers at springs that have been exposed to significant disturbance from over grazing, dredging or from severe floods such as at Buttercup Springs (Table 1).

Remarks.—The holotype female of *V. goyderi* had been reported lost (McKay 1985; Framenau & Vink 2001), however, it was recently discovered at the Australian Museum in Sydney (AM KS49705, VWF, examined) confirming the identity of this species.

Genus *Hogna* Simon 1885

Remarks.—*Hogna* was first listed by Simon (1885), and subsequently (Simon 1898: 347) defined mainly based on somatic characters, in particular the arrangement of the eyes and the correlation of the length of leg segments of the fourth leg. The type species is *H. radiata* (Latreille 1817), a common species in the Mediterranean region, that is found across Central Asia and Central Africa (Platnick 2004).

Currently, *Hogna* includes more than 200 species (Platnick 2005), however, the genus is in need of revision (Dondale & Redner 1990). Here we place three lycosids from South Australian artesian springs in this genus due to the similarity of their male and female genitalia with those of *H. radiata* as illustrated by Fuhn & Niculescu-Burlacu (1971) and Miller (1971). One of the artesian spring species, *H. crispipes*, is transferred from *Lycosa* Latreille 1804, the two other species are new to science, *H. diyari* new species and *H. kuyani* new species.

The examination of type material of Australian wolf spiders to establish the identity of the artesian spring species revealed that the genitalic morphology of *Pardosa pexa* Hickman 1944 (holotype male, AM KS17123, from 'Burts Waterhole' (SA), examined by VWF) is very similar to the species here placed in *Hogna*. Consequently, we transfer *Pardosa pexa* to *Hogna*: *Hogna pexa* (Hickman 1944) new combination. This new generic placement also reflects the true subfamily status of this species, as it clearly belongs to the Lycosinae and not Pardosinae (*sensu* Dondale 1986).

Hogna crispipes (L. Koch 1877) new combination
Figs. 19–32

Lycosa crispipes L. Koch 1877: 923–925, plate 79, figs. 8, 8a, plate 80, figs. 1, 1a; Rainbow 1911: 266; McKay 1979a: 253, figs. 4e–f, m; McKay 1985: 76; Platnick 1989: 370.

not *Lycosa crispipes* L. Koch 1877 sensu McKay 1979a 252–255, figs. 4a–d, g–l (misidentification, not *L. crispipes* but two undescribed species).

Lycosa pulvere-sparsa L. Koch 1877: 941–942, plate 79, fig. 2; Rainbow 1911: 272. NEW SYNONYMY.

Tarentula tongatabuensis Strand 1911: 207; Strand 1915: 258, plate 14, fig. 21, plate 19, fig. 99. NEW SYNONYMY.

Tarentula tanna Strand 1913: 121–122; Strand 1915: 260, plate 19, fig. 96a–b; Ledoux & Hallé 1995: 7. NEW SYNONYMY.

Lycosa waitei Rainbow 1917: 487–788, plate 32, figs. 7–9; Roewer 1955: 272; McKay 1973: 380; Bonnet 1957: 2669; McKay 1985: 84. NEW SYNONYMY.

Table 1.—Distribution and relative abundance of lycosid species at a selection of artesian springs and bore drains in South Australia (+++ dominant species, ++ subordinate species, + rare species); see Fig. 1 for geographical location for each site.

	Species								
Sample Locations	*Artoria howquaensis* Framenau 2002	*Artoria victoriensis* new species	*Hogna crispipes* (L. Koch 1877)	*Hogna diyari* new species	*Hogna kuyani* new species	*Tetralycosa arabanae* new species	*Venatrix arenaris* (Hogg 1905)	*Venatrix fontis* Fr. & V. 2001	*Venatrix goyderi* (Hickman 1944)
ARTESIAN SPRINGS									
Dalhousie (A)									
Dalhousie							++		
Kingfisher		+						++	
Neales River (B)									
Freeling			++					+++	
Hawker							+	+++	
Outside	++							+++	
Lake Cadibarrawirracanna (C)									
Lake Cadi				++					
Francis Swamp (D)									
Big Depot							++	+++	
Francis Swamp		+		++		++	+	+++	
Billa Kalina (E)									
Billa Kalina							+++		++
Margaret River (F)									
Blanche Cup	+++			+		+	+++		
Bubbler	++						++	+++	
Buttercup	++					++	++	+	
Coward			+					+++	
Elizabeth	++		+			+	+	+++	
Horse	+++					++	+++	++	
Jersey	+++			+		++	++	+++	
Kewson Hill							++		
Little Bubbler	++						++		
Lake Eyre South (G)									
Fred	+++		++	++			+++		++
Gosse	+++		+			++	++	++	++
McLachlan	+++					+	++		
Smith						++		+	
Hermit Hill (H)									
Bopeechee	++						+++		
Dead Boy	+++						++		
Hermit Hill	+++			+	++	+	+++		
Old Finniss	++		+		++	++	++		
Old Woman	++				+		++		
Sulphuric	+++						+++		
West Finniss	++						+++	++	
Wangianna/Davenport (I)									
Davenport							+++		
Welcome							+++		

Table 1.—Continued.

Sample Locations	Species								
	Artoria howquaensis Framenau 2002	*Artoria victoriensis* new species	*Hogna crispipes* (L. Koch 1877)	*Hogna diyari* new species	*Hogna kuyani* new species	*Tetralycosa arabanae* new species	*Venatrix arenaris* (Hogg 1905)	*Venatrix fontis* Fr. & V. 2001	*Venatrix goyderi* (Hickman 1944)
BORE DRAINS									
Hamilton (a)							+++		
Welcome (b)							+++		
Elizabeth (c)	++					++			
Coward (d)	++			+			+++		
Charles Angus (e)	+++		++				+++		
Morris Creek (f)	+++		++		++	++	++	+	+++
Crows Nest (g)							++		
Coranna (h)			++						
Muloorina (i)							+++		++
Lake Letty #3 (j)									++
Clayton (k)				+	++		+		+++

Lycosa (?) immansueta Simon 1909: Rainbow 1915: 787 (misidentification).

Lycosa strenua Rainbow 1920: 260–261, plate 30, figs. 92–93 (preoccupied by *Lycosa strenua* Nicolet 1849 and *Lycosa strenua* Thorell 1872). NEW SYNONYMY.

Lycosa tanna (Strand 1913): Berland 1938: 182–183, figs. 147–149; Bonnet 1957: 2666.

Tarentula rainbowi Roewer 1951: 442 (replacement name for *Lycosa strenua* Rainbow 1920). NEW SYNONYMY.

Hygrolycosa crispipes (L. Koch 1877): Roewer 1955: 261; Rack 1961: 37; McKay 1973: 380.

Lycosa rainbowi (Roewer 1951): Roewer 1955: 272; McKay 1985: 82.

Scaptocosa tongatabuensis (Strand 1911): Roewer 1955: 291.

Varacosa pulveresparsa (L. Koch 1877): Roewer 1955: 305; Rack 1961: 38; McKay 1973: 381.

Varacosa tanna (Strand 1913): Roewer 1955: 305; Chrysanthus 1967: 424, figs. 73, 78–79.

Lycosa tongatabuensis (Strand 1911): Bonnet 1957: 2667.

Lycosa pulveresparsa L. Koch 1877: McKay, 1985: 82.

"*Lycosa*" *tongatabuensis* (Strand 1911): Ledoux & Hallé 1995: 7, figs. 5a–c.

Geolycosa tongatabuensis (Strand 1911): Platnick 1998: 554; Vink 2002: 36–37, figs. 31, 38, 65, 92.

Types examined.—Lectotype (designated here) of *Lycosa crispipes*, 1 female, Queensland, Bowen, 20°00′S, 148°14′E, BMNH, 1919.9.18.222. Paralectotype of *Lycosa crispipes*, 1 female, Queensland, Bowen, 20°00′S, 148°14′E, Museum Godeffroy 14572, Rack (1961)-catalogue 450 (ZMH).

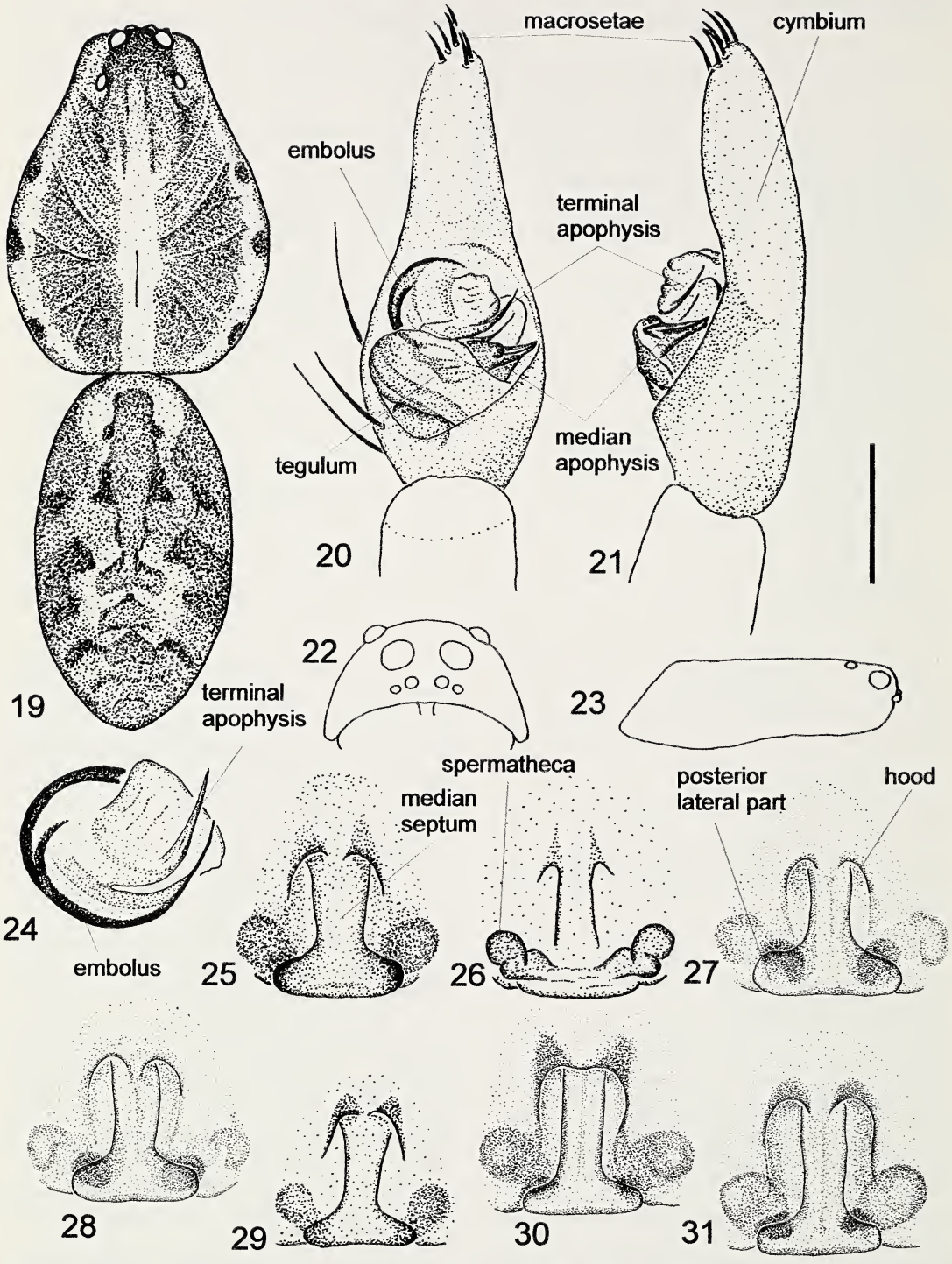
Syntype of *Lycosa pulvere-sparsa*, 1 female, Rockhampton 23°22′S, 150°30′E, Museum Godeffroy 14554, Rack (1961)-catalogue 476 (ZMH). The whereabouts of a second syntype of *Lycosa pulvere-sparsa* from 'Bradley's Collection' listed by L. Koch (1877) is unknown to VWF.

Lectotype (designated by Vink 2002) of *Tarentula tongatabuensis*, 1 female, Tonga, Tongatupu Nuku'alofa, 21°07′S, 175°12′W, 4.vi.1909, E Wolf, 1909 (SMF 2199). Paralectotype of *Tarentula tongatabuensis*, 1 juvenile, same data as lectotype (SMF).

Holotype of *Tarentula tanna*, 1 female, Vanuatu, Tanna, 19°30′S, 169°20′E, 23.v.1909, E. Wolf (SMF 2167).

Holotype of *Lycosa waitei* Rainbow 1917, 1 female, South Australia, Coopers Creek, ca. 28°23′S 137°41′E, September/October 1916, South Australian Museum Expedition to the Interior (SAM NN380).

Holotype of *Lycosa strenua* Rainbow 1920,



Figures 19–31.—*Hogna crispipes* (L. Koch 1877): Male from Cullyamurra Waterhole, SA (SAM NN13955): 19. habitus; 20. left pedipalp, ventral; 21. left pedipalp, retrolateral; 22. eye arrangement; 23. lateral view of carapace; 24. apical part of bulb. Female: 25. ventral view of epigynum (WAM T47310, from Fred Springs, SA); 26. dorsal view of epigynum (WAM T47310); 27. ventral view of epigynum (lectotype from Bowen, Qld; BMNH 1919.9.18.222); 28. ventral view of epigynum (paralectotype from Bowen, Qld; ZMH 450); 29. ventral view of epigynum (lectotype of *Tarentula tongatabuensis* Strand

1 female, New South Wales, Norfolk Island, 29°02′S, 167°57′E, A.M. Lea, December 1915–January 1916 (SAM NN277).

All types examined.

Other material examined.—AUSTRALIA: *South Australia*: 1 ♂, Bakers Creek, N of Wilpena (QM S21408); 1 ♂, 1 ♀, 1 juv. Charles Angus Bore (SAM NN13945–6); 22 ♂, 8 ♀, 1 ♀ with eggsac, 39 juv., Coongie Lake (SAM NN13979–82, NN13983–4006, NN14108–10); 1 ♂, 1 ♀, Coongie Lake, 1.77 km W (SAM NN13977, NN20979); 1 ♀, Coongie Lake, 50 m SSW (SAM NN13976); 1 ♀, Coongie Lake, 700m E (SAM NN13978); 1 ♀, Coongie Lake, 7 km SE (SAM NN13975); 6 ♂, 8 juv., Coranna Bore (WAM T47304, T47308–9); 1 ♀ with 116 spiderlings, Coward Springs (SAM NN13948); 3 ♀, 1 juv., Culburra (QM S61110); 15 ♂, 5 ♀, 1 juv. (SAM NN13955–74); 1 ♂, Dickinna Hill, 9.5 km SW (SAM NN13954); 1 ♀, Elizabeth Springs (Nth B) (SAM NN13938); 5 ♀, Finnis Springs (SAM NN13139–40); 6 ♂, 2 ♀, Fred Springs (SAM NN13941–2, WAM T47302–3, T47305, T47307, T47310); 1 ♂, Freeling Spring (SAM NN13947); 1 ♂, Gosse East Spring (SAM NN13937); 1 ♂, 1 juv., Greenfields Wetlands, Dry Creek, Salisbury (SAM NN14010); 1 ♀, Johnsons Dam, Granite Downs Station (SAM NN13953); 1 ♂, 1 juv., Karroongooloo Station, via Adelaide (MV K8147); 1 ♂, Lake Hope channel, 3.9 km S Lake Appadare (SAM NN13949); 1 ♂, Lake S Siccus River (Koonamoore Station?) (SAM NN14007); 1 ♂, Maslins Beach (SAM NN14012); 1 ♂, 2 ♀, Morris Creek Bore (SAM NN13943–4; WAM T47306); 1 ♂, Mt Fairview, Paney Station (SAM NN14008); 1 ♀, Scott Creek Weir (AM KS32122); 1 ♀, Todmordon, 90 miles W Oodnadatta, Capt. SA White Expedition, published in Rainbow (1915) as *Lycosa (?) immansueta* (SAM NN411); 1 ♂, Twin Hill (SAM NN13951); 1 ♀, Windsor Gardens, Adelaide (SAM NN14011). *New South Wales*: 2 ♀, no location (NSW?), W.J. Rainbow manuscript no. 115 (AM KS84107); 1 ♀, no location (NSW?), W.J. Rainbow manuscript no. 78 (AM KS84109); 1 ♀, Armidale (AM KS84106); 15 ♂, 17 ♀, Bowra Station, 350 m past entrance, N of Carinda (AM KS76337–40, KS76743); 1 ♀, Broken Hill (SAM NN14123); 1 ♂, Clarence River, Copmanhurst (SAM NN14013); 1 ♀, Coolaba Ramsey Park (AM KS42374); 1 ♂, Cootamundra (AM KS84103); 1 ♂, 1 ♀, Darling River, 1.5 km South of Trilby Station (AM KS76557, KS76562); 3 ♂, 1 ♀, Gwydir Highway, 300 m N of Minnamurra Station turnoff (AM KS76554, KS76561, KS76564); 2 ♂, 1 ♀, Hunter Valley AM KS7322); 1 ♀, Lord Howe Island (AM KS68547); 3 ♂, 1 ♀, Merri Merri Creek, 2.5 km North of Quambone (AM KS76553, KS76559–60); 14 ♂, 3 ♀, Mullingar Station, Lower Murray-Darling region (AM KS67036–7); 1 ♂, 1 ♀, 5 juv., Narrabri (AM KS84102); 3 ♂, 3 ♀, Narran Lakes Reserve access track, 6.5 km from Narran Lakes Road (AM KS76550–2, KS76563); 3 ♀, 1 ♀ with eggsac, Norfolk Island (AM KS43951–2, KS43954, KS68883); 1 ♀, Norfolk Island, Burnt Pine (AM KS49891); 2 ♀, Norfolk Island, Captain Cook Memorial (ANIC); 1 ♀, Norfolk Island, Duncombe Bay (AM KS49895); 2 ♀, Norfolk Island, Mill Road (AM KS43953); 1 ♀, Nyngan-Canonba Road, 2.9 km South of Fairview Station junction (AM KS76555); 1 ♂, Road to Wanaaring, 12.7 km W of Mitchell Hwy junction (AM KS76284); 1 ♂, Spring Hill Station, Lower Murray-Darling region (AM KS66736); 1 ♂, Sturt National Park, 19.2 km S of Fort Gray Homestead on Cameron Corner Rd (AM KS84105); 1 ♂, Warren-Quambone Road, 0.7 km N of turnoff to Wyndabyne Station (AM KS76556); *Northern Territory*: 1 ♀, Cox River (SAM NN13129); 1 ♀, Curtin Springs (ANIC); 1 ♀, 2 juv., Tobermory Station, No. 8 Dam (QM S61119). *Queensland*: 1 ♀, Appel Channel, Mornington Island (SAM NN14015); 1 ♂, 2 juv., Barrow Creek (QM S21407); 6 ♀, Birdsville (QM W7186); 1 ♂, 1 ♀, Birdsville, near town (QM W6117); 2 ♂, 1 ♀ with eggsac, 2 ♀, 1 juv., Bowen (QM

←

from Tonga; SMF 2199); 30. ventral view of epigynum (holotype of *Lycosa watei* Rainbow from Coopers Creek, SA; SAM NN380); 31. ventral view of epigynum (holotype of *Lycosa strenua* Rainbow from Norfolk Island, NSW; SAM NN277). Scale bar: (19) 2.13 mm, (20–21) 0.48 mm, (22) 1.37 mm, (23) 2.55 mm, (24) 0.14 mm, (25–31) 0.65 mm.

S21412); 1 ♀, Bushy Island, Great Barrier Reef (QM S61116); 1 ♀, Cape Tribulation (QM S61108); 1 ♀, Claudie River mouth (QM S61131); 1 ♂, 2 ♀, Cluny Station Billabong (QM S61066); 1 ♀, Coopers Creek, between Cluny Station and Monkira (QM S61104); 3 ♂, 4 ♀, 7 juv., Curtis Island, S end of township (QM S61096S61103); 1 ♂, Eulo, 'Cookara' (QM S61098); 1 ♀ with eggsac, 2 ♀, Eurithethera Soak, Toomba Range (QM W7185); 2 ♀, 1 juv., Farmer Island, Great Barrier Reef (QM S61128); 1 ♀, 1 juv., Frederick Reef, North Reef Cay, Coral Sea (ANIC); 26 ♂, 7 ♀, 2 juv., Gatton, Queensland Agricultural College (QM S61069–71, S61074–9, S61081–5, S61087–90, S6112–4); 1 ♂, Grey Range, central tank, 'Orient' (QM S61099); 2 ♀, Halfway Islet, Great Barrier Reef (QM S61126); 1 ♂, 3 ♀, 1 juv., Hannah Point, North Molle Island (QM S61100); 6 ♂, 1 ♀, Jondaryan, 20 km S (QM W7189); 3 ♂, 5 ♀, 2 juv., Jumbo Bore, 'Norley', Thargomindah (QM S61101); 1 ♂, Lake Broadwater (QM S61095); 1 ♂, Lake Broadwater, near cottage (QM S61080); 1 ♀, Lake Hutter, N of Aramac (QM S61113); 1 ♂, 1 ♀, Lake Nuga Nuga (QM S61068); 1 ♂, Longreach (SAM NN14014); 1 ♀, Lucinda (QM S21414); 1 ♀, 1 juv., Lydeman Island, Great Barrier Reef (QM S61129); 1 ♀, MacArthur Cay, Great Barrier Reef (QM S61121); 2 ♀, Magra Islet, Great Barrier Reef (QM S61127); 1 ♀ with eggsac, 1 juv., Maydelaine Island (ANIC); 28 ♂, 31 ♀, 4 juv., Muncoonie Lakes (QM W6413–6, W7187); 1 ♂, Mundingburra (AM KS86384); 1 ♂, Murrumba Downs (QM S61093); 1 ♀, Pelican Island (QM S61125); 1 ♂, 1 ♀, 2 ♀ with eggsac, 3 juv., Raine Island (WAM T55434; QM S61073, S61145–7); 1 ♀, 1 juv., Saunders Islet, Great Barrier Reef (QM S61118); 1 ♀, Sherrard Island, Great Barrier Reef (QM S61120); 1 ♀, Stainer Islet (QM S61107); 1 ♀, Thargomindah (QM W7188); 1 ♀, 1 juv., Thursday Island, Nth side (QM S17225); 1 ♀, Tingalpa (QM S26112); 2 ♀, Townsville, common wetlands (QM S61094); 1 ♀, Townsville, Community Environmental Park (QM S61114); 1 ♀, 1 ♀ with eggsac, 1 ♀ with spiderlings, Townsville, near Fishermans Wharf (QM S61106, S61133); 1 ♂, Turtle Islet, Lihou Reef, Coral Sea (ANIC); 1 ♀, Vanrook Station, Gilbert River Crossing West side (AM KS44298); 1 ♀, Wenlock River (QM S21409). *Victoria*: 1 ♂, Avon River near Valencia Creek (WAM T47111); 2 ♂, 1 ♀, Barmah Forest (WAM T47112–3); 3 ♂, 2 juv., Booths Rd, 0.2 km S Murray Valley Hwy (MV K8771); 4 ♀, Murray Valley Hwy, 0.3 km NNW Walshs Bridge (MV K8691); 1 ♀, Murray Valley Hwy, Deep Ck Crossing (MV K8774); 1 ♀, Redcliffs (MV K8258). *Western Australia*: 1 ♂, 1 ♀, Amelia Heights (WAM 69/2072, 71/939); 1 ♀ with spiderlings, Argyle Downs Homestead, edge of Behn River (QM W5058); 2 ♀, Ashmore Reef, East Islet (AM KS68684); 1 ♂, 3 ♀, Attadale (WAM 71/900, 71/985–6, 71/1448); 1 ♀, Avon River, Northam (WAM 71/987); 1 ♂, Baskerville (WAM T47248); 6 ♂, 3 ♀, Beacon, ca. 15 km S, Askew Road (WAM T47147); 1 ♀ with spiderlings, Behn River, Argyle Downs, Ord River area (QM W5060); 1 ♂, Broome (WAM T47240); 2 ♀ with eggsac, Cannington (WAM 71/774, 71/838); 1 ♀, Carmel (AM KS86382); 1 ♂, Chillmoney Road, North, SW Binnu (WAM T47132); 5 ♂, Chillmoney Road, SW Binnu (WAM T47227); 1 ♀, 1 juv., Christmas Island, 1.5 miles N of South Point (ANIC); 1 ♀, Christmas Island (QM S61132); 1 ♂, 3 ♀, 2 juv., Cocos Keeling Island (QM S61134); 1 ♂, 6 ♀, Coolinup Nature Reserve (WAM T47130, T47141); 1 ♀, Cottesloe (WAM T53622); 4 ♂, Dumbleyung Lake North (WAM T47131, T47238); 1 ♀, Eneabba, AMC mine (WAM T553137); 1 ♀, Esperance (WAM 71/898); 1 ♀, Faure Island, Shark Bay (SAM NN14128); 12 ♂, 40 ♀, 5 juv., Goongarrie (WAM T48123, T48166); 1 ♀, Grass Patch, E of, 'Sieda' (WAM T53580); 1 ♀, Gunyidi, ca. 12 km W (WAM T47142); 1 ♀, Gutha, 37 miles North (WAM T51547); 2 ♀, Home Island, Cocos-Keeling Islands (ANIC); 1 ♂, 1 ♀, Jarrahdale (WAM T55768–9); 1 ♀, Kirwan (WAM 71/984); 4 ♂, Lake Bryde East Nature Reserve, Lake Bryde Rd (WAM T47146); 2 ♂, Lake Bryde West Nature Reserve, Lake Bryde Rd (WAM T47139); 1 ♀, 12 juv., Lake Cronin (WAM T48124); 1 ♀, Lake Gruszka (WAM T51548); 1 ♂, Lake Gulson, 65 km SE of Hyden (WAM T51474); 1 ♂, Lake Mollerin (WAM T47222); 6 ♂, 2 ♀, 1 juv., Lake Ninan Shire reserve (WAM T47143); 12 ♂, 2 ♀, 3 juv., Little Sandy Desert, 23.1 km ESE of Burranbar Pool (WAM T53420–2); 7 ♂, 24 ♀, 8 juv., Little Sandy Desert, 23.3 km ESE of Burranbar Pool (WAM T53417–9); 1 ♀, 2 juv., Lorna Glen

Station (WAM T55132); 1 ♂, Maitland River (WAM 71/1517); 1 ♀, Marangaroo (AM KS86383); 1 ♀, Mellish Reef (WAM T51413); 1 ♂, 1 ♀, Morawa-Perenjori Road (WAM T47144); 1 ♂, Mortlock Creek, Wongan Hills (WAM 99/1103); 1 ♀ with spiderlings, Murchison River (QM S61111); 1 ♀, Myaree (WAM T53532); 1 ♂, Nedlands (WAM T53461); 1 ♂, Noranda (WAM T53535); 1 ♂, Nugadong West Rd, SW Wubin (WAM T47136); 1 ♂, Nullagine (WAM T55307); 1 ♂, 1 ♀, Nullewa Lake (WAM T47140); 1 ♂, Oakajee Nature Reserve (WAM T47221); 1 ♀, Parry Creek Billabong (WAM T53691); 2 ♂, 2 ♀, 3 juv., R.G.C. Mine, 10 km S of Eneabba (WAM T51397–9); 5 ♂, 5 ♀, 3 ♀ with eggsac, Rossmoyne (WAM 71/561–2, 71/740, 71/835–7, 71/867–70, 71/940, 71/1446, T48122); 1 ♀, Separation Well (WAM T53510); 1 ♀, South Lake, near Perth (WAM T53508); 1 ♂, 2 juv., The Loop, Murchison River (WAM T53662); 1 ♀, 1 juv., Thirsty Point Waterhole, 1.5 miles E (WAM 71/1447); 1 ♀, Toolibin Lake (WAM T47133); 1 ♂, 3 ♀, Walkaway Nature Reserve (WAM T47135, T47235); 1 ♀, Wanneroo Lake (WAM 69/2071); 1 ♀ with eggsac, Warburton Ranges (WAM T53812); 1 ♂, 1 juv., Warr Well (WAM T51555); 1 ♀, Weelhamby Lake (WAM T47274); 1 ♀, Wittenoom Rd near Dempster Rd junction, E Gibson (WAM T47148); 1 ♀, Yannarie River at North West Coastal Hwy (WAM T53493). NEW CALEDONIA: 1 ♀, no exact location (SAM NN13935). VANUATU: 1 ♂, Espiritu Santo, Malac Village (SAM NN13936); 2 ♀, 2 juv., Malekula (AM KS84104). SOLOMON ISLANDS: 1 ♀, Vanikoro, Santa Cruz Group (AM KS84108).

Diagnosis.—The male and female genitalia of *H. crispipes* are very similar to those of *H. diyari* and *H. kuyani*. However, all three species can be easily distinguished by their color pattern (Figs. 19, 33, 41). Whereas the median band in *H. crispipes* is narrower than one-fourth the carapace width, it is one-third the width of the carapace in *H. diyari* and absent in *H. kuyani*.

Description.—*Male:* Carapace (Figs. 19, 23): Dorsal line straight in lateral view; dark brown, with light brown narrow median band; distinct light brown submarginal bands with three dark blotches; carapace covered with brown setae in dark areas and white setae in light brown parts and eye region; few black bristles in anterior half of median band; black bristles in head region between PE and posterior of PLE; 1 long bristle between AME. Sternum: Yellow-brown; covered with white setae, denser and longer towards margins; few brown bristles. Labium: Brown; front end truncate and white. Chelicerae: Light brown; covered with white setae and few brown bristles in basal half; three retromarginal teeth, with the median slightly larger; three promarginal teeth, with the median largest. Pedipalp (Figs. 20, 21, 24): Cymbium elongated, tip with 2–6 macrosetae; terminal apophysis sickle-shaped (Figs. 20, 24). Abdomen: Irregular dark grey; irregular yellow-brown median band; brown lanceolate heart mark with indistinct darker edges, that continues into a triangular, dark grey pattern in posterior half; covered with white setae and additional brown setae in darker area; venter uniformly yellow-brown and covered with white setae; spinnerets yellow-brown. Legs: Leg formula IV > I > II > III; all femora, patellae and tibiae brown, dorsally with indistinct grey annulations; metatarsi dark brown, metatarsus I with long dense hair-like setae; scopulous setae on all tarsi; spination of leg I (based on SAM NN13955): Femur: 6 dorsal, 2 apicoprolateral; patella: 1 prolateral, 1 retrolateral; tibia: 3 ventral pairs, 2 prolateral, 2 retrolateral, 1 dorsal; metatarsus: 2 ventral pairs, 1 apicoventral, 2 prolateral, 2 retrolateral, 1 apicoprolateral, 1 apicoretrolateral.

Female: Carapace: As male, submarginal blotches less distinct as the submarginal band is darker. Sternum: coloration light brown, covered with brown bristles of increasing length and density towards margins. Labium: Dark brown, front end truncate and white. Chelicerae: Dark brown, setae and bristles as male; three retromarginal teeth with the median largest, three promarginal teeth, with the median largest. Epigynum (Figs. 25–31): Ventral view: inverted T-shaped (Figs. 25, 27–31); dorsal view: round spermathecae, copulatory ducts short and twisted (Fig. 26). Abdomen: As male, pattern less distinct in particular in posterior half; venter yellowish-grey covered with brown setae; spinnerets as male. Legs: Leg formula and coloration as male; spination of leg I (based on SAM NN13970): Femur: 6 dorsal, 2 apicoprolateral; tibia: 3 ventral pairs, 1 (small) prolateral; metatarsus: 2 ventral

pairs, 1 apicoventral, 1 apicoprolateral, 1 apicoretrolateral.

Measurements: Male SAM NN13955 (female SAM NN13970): TL 10.1 (12.6), CL 5.1 (6.0), CW 4.1 (4.5). Eyes: AME 0.23 (0.26), ALE 0.17 (0.17), PME 0.46 (0.43), PLE 0.37 (0.34). Row of eyes: AE 0.92 (1.12), PME 1.09 (1.26), PLE 1.37 (1.60). Sternum (length/width) 2.4/1.95 (2.55/1.95). Labium (length/width) 0.63/0.57 (0.80/0.83). AL 5.25 (6.60), AW 2.55 (3.75). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 1.64 + 1.95 + — + 1.5 = 5.1, I 5.50 + 5.70 + 4.05 + 2.25 = 16.80, II 4.35 + 5.25 + 3.90 + 2.4 = 15.90, III 3.75 + 4.50 + 4.05 + 2.40 = 14.70, IV 5.10 + 6.15 + 6.00 + 3.00 = 20.25 (Pedipalp 1.95 + 2.25 + — + 1.50 = 5.70, I 4.05 + 5.25 + 3.00 + 2.10 = 14.40, II 3.90 + 4.95 + 3.00 + 1.95 = 13.80, III 3.60 + 4.20 + 3.15 + 1.95 = 12.90, IV 4.95 + 6.45 + 5.40 + 2.55 = 19.35).

Variation: Males (females) (range, mean ± s.d.): TL 6.0–17.1, 9.5 ± 1.7; n = 55; CL 3.5–8.7, 4.9 ± 0.8; n = 56; CW 2.6–6.3, 3.7 ± 0.6; n = 56 (TL 8.0–21.0, 13.6 ± 2.7, n = 86; CL 4.1–10.4, 6.0 ± 1.1, n = 86; CW 2.9–7.4, 4.4 ± 0.9; n = 86).

The size variation within *H. crispipes* is considerable and populations from offshore islands and reefs appear to be on average larger than the mainland specimens, a pattern also observed in vertebrates (e.g. Lomolino 1985, Boback 2003). The three dark blotches on the lateral margins of the carapace may not be as distinct as in the specimen illustrated (Fig. 19), and may be absent in some cases.

Distribution and habitat preferences.—*Hogna crispipes* is found on mainland Australia and offshore islands and reefs in the East and West of Australia (Fig. 32), as well as in New Zealand (Vink 2002) and on several Pacific islands (e.g. Tonga, New Caledonia, Vanuatu, and the Solomon Islands). While uncommon in artesian springs, this species is widely distributed across all of the major spring groups within South Australia (Table 1). It is usually found on the edges of the springs and in the ephemeral wet zone that exists beyond the permanent vegetated wetland.

Remarks.—The original description of *H. crispipes* was based upon male and female syntypes from Bowen and Rockhampton deposited at the Museum Godeffroy (L. Koch 1877); the precise number of specimens was not stated. While two female syntypes lodged in the BMNH and ZMH were examined during this study, we could not find any male syntypes in either of these museums or in the ZMB, where the majority of the material from the Museum Godeffroy is currently lodged. These must be considered lost. In addition, L. Koch's (1877) original description and illustrations suggest that the male syntype(s) is (are) not conspecific with the females. An inverted color pattern (light instead of dark median abdominal heart mark) and the structure of the pedipalp suggest that the male specimen illustrated is *Venatrix goyderi* and not *Hogna crispipes*. To provide nomenclatural stability for the name *H. crispipes*, one of the female syntypes is here designated as the lectotype.

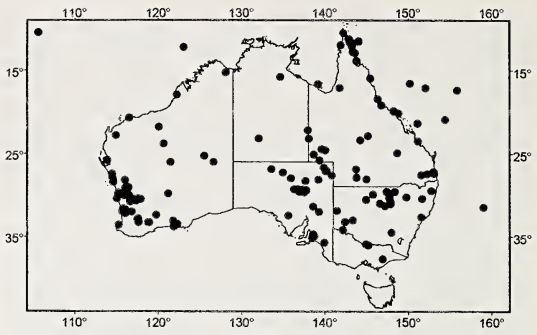
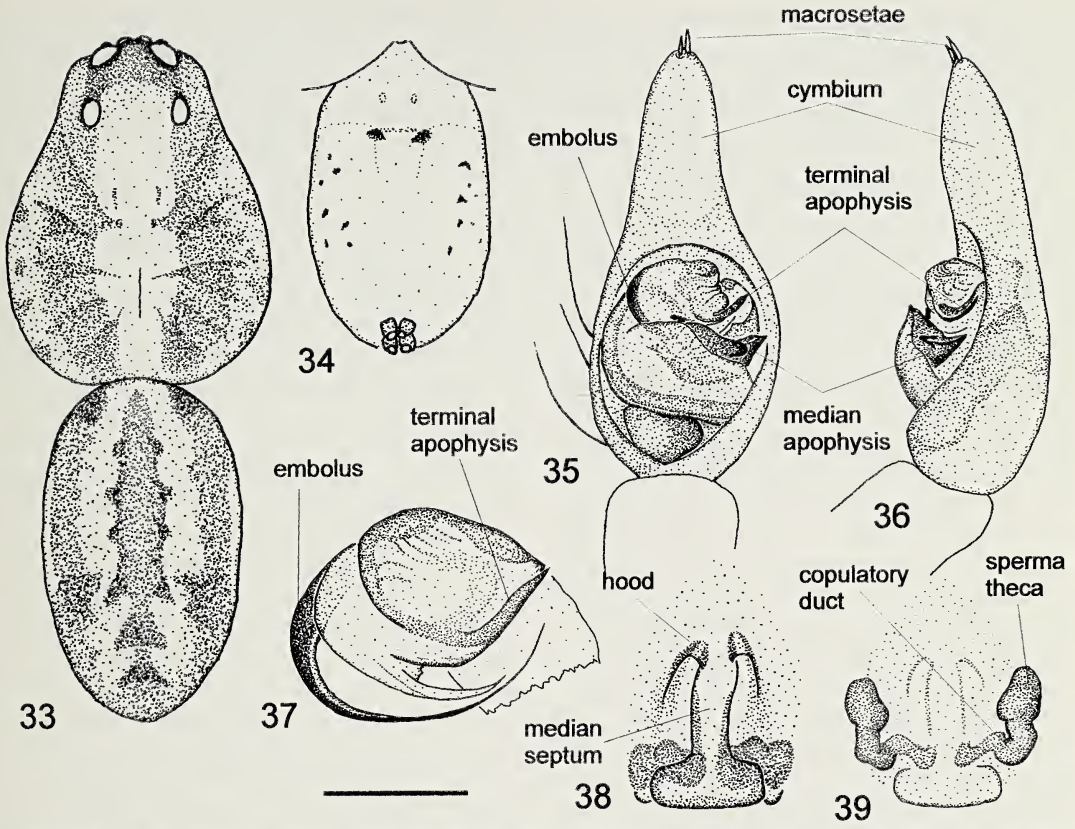


Figure 32.—Records of *Hogna crispipes* (L. Koch 1877) in Australia.

Hogna crispipes was redescribed and illustrated by McKay (1979a). A re-examination of the specimens included in McKay's revision revealed that the majority of the material is not conspecific with the type material of *H. crispipes*. Only two females from Behn River, Argyle Downs (WA) (QM W5058, W5060; McKay 1979a, fig. m) are conspecific with the female type material of *H. crispipes*. All other specimens described and illustrated belong to two undescribed *Hogna*. Although the genital morphology of both males and females of these undescribed species is very similar to *H. crispipes*, the carapace does not display the typical narrow median and blotched marginal bands, but is very similar to *Venatrix arenaris* (see Fig. 3).

The type material of *Lycosa crispipes*, *Lycosa pulveresparsa* L. Koch 1877, *Tarentula tongatabuensis* Strand 1911 (= senior syno-



Figures 33–39.—*Hogna diyari* new species: Male: 33. habitus and 34. ventral view of abdomen (holotype from Coongie Lake, SA; SAM NN14115); left pedipalp: 35. ventral and 36. retrolateral view, and 37. apical part of bulb (paratype from Coongie Lake, SA; SAM NN14116). Female (WAM T48035): 38. ventral and 39. dorsal view of epigynum. Scale bar: (33–34) 2.68 mm, (35–36) 0.73 mm, (37) 0.24 mm, (38–39) 0.70 mm.

nym of *Tarentula tanna* Strand 1913 (Ledoux & Hallé 1995)), *Lycosa waitei* Rainbow 1917 and *Lycosa rainbowi* Roewer 1951 (replacement name for *Lycosa strenua* Rainbow 1920), does not show any differences in somatic and genitalic characters that warrant status as different species. Therefore, *T. tongatabuensis*, *L. pulvere-sparsa*, *L. waitei* and *L. rainbowi* are considered junior synonyms of *H. crispipes*.

Recently, Vink (2002) placed *H. crispipes* (sub *G. tongatabuensis*) in the genus *Geolycosa*. However, this species does not conform very well to the generic description of *Geolycosa* (e.g. Dondale & Redner 1990). Vink (2002) argued that the genitalia of *H. tongatabuensis* conform more to *Geolycosa* than *Hogna*. However, comparison of the genitalic structure of *H. crispipes* with that of *H. radiata* as illustrated in Fuhn & Niculescu-Burlacu (1971) and Miller (1971) showed very good agreement. In addition, *Geolycosa* is characterized by a sloping dorsal line of the carapace, the absence of light median and submarginal bands on the carapace, and the absence of macrosetae at the tip of the male cymbium (Dondale & Redner 1990). None of these characters fit *H. crispipes*, which has a horizontal dorsal carapace profile, distinct light median and submarginal bands on the carapace, and 2–6 macrosetae on the tip of the cymbium. Therefore, *H. crispipes*, as well as the closely related *H. diyari* and *H. kuyani* are placed in *Hogna*.

Hogna diyari new species
Figs. 32–40

Types examined.—Holotype male, Australia, South Australia, Coongie Lake, 27°12′S, 140°10′E, 26–28 October 1995, on shoreline,

D. Hirst (SAM NN14115). Paratypes: 5 males, 2 females, data as holotype (SAM NN14111–14, NN14116–8).

Other material examined.—AUSTRALIA: *South Australia*: 1 ♂, Blanche Cup Mound Spring (SAM NN14083); 3 ♂, 1 ♀, 14 juv. Clayton Bore, 33 miles N of Marree (WAM 71/573–590); 1 ♂, Clifton Hills Station (SAM NN14103); 3 ♂, 1 juv., Coongie Lake (SAM NN14105–7); 1 ♂, Coongie, 6.2 km NW (SAM NN14104); 4 ♂, 6 ♀, 2 juv., Coward Springs Railway Bore (SAM NN14085–94); 1 ♀, Francis Swamp Mound Spring tail (SAM NN14084); 3 ♂, 2 ♀, Fred Springs (SAM NN14080–1; WAM T48034–6); 1 ♀, Jersey Spring (SAM NN14082); 1 ♂, Lake Cadibarrawirracanna (SAM NN14102); 2 ♀, 4 juv., Lake Hart (SAM NN14119–20); 3 ♂, 2 ♀, 2 ♀ with eggsac, Lake Hope channel, 3.9 km S Lake Appadare (SAM NN14095–101); 1 ♀, Seven Mile Creek, Clifton Hills (SAM NN141); 1 ♀, Stirtons Old Campsite, E edge of Cannuwalkaninna Dune (WAM 73/232). *New South Wales*: 1 ♂, 2 ♀, Broken Hill (SAM NN14079, NN14121–2); 2 ♂, 1 ♀, Kinchega National Park (AM KS69252, KS8410). *Queensland*: 1 ♂, Cluny Station Billabong (QM S61148); 1 ♂, Dynevor Lakes, E of Thargomindah (QM S61115). *Victoria*: 1 ♀, labeled 'Mcmillan Park, Sale. V' [possibly Sale, East Gippsland] (MV K8156).

Etymology.—The specific name is a noun in apposition honoring the Diyari people, an Aboriginal tribe representing the traditional custodians of parts of the land on which the South Australian artesian springs are found.

Diagnosis.—In contrast to the other two darker colored *Hogna* species of artesian springs, *H. crispipes* and *H. kuyani*, the carapace coloration of *H. diyari* is light brown with a wide yellow median band that constricts anteriorly of the fovea and narrows slightly posteriorly (Fig. 33). Most distinguishable is a pair of small black spots behind the epigastric furrow and up to eight spots along the lateral border of the yellow venter (Fig. 34).

Description.—*Male:* Carapace (Fig. 33): Brown, with wide yellow-brown median band that constricts anteriorly of fovea and narrows slightly in posterior half; irregular light marginal bands; head region dark brown; carapace covered with white setae, particularly in head region; additional brown setae in dark areas; six brown bristles in median band anteriorly of fovea with the posterior ones in a pair; black bristles in head region between PME and PLE, between PME and below AE. Sternum: Yellow-brown; densely covered with white setae, denser and longer towards margins. Labium: Light brown, basal half darker; front end truncate and white. Chelicerae: Basal half light brown with a dense cover of white setae and fewer brown bristles, apical half dark brown with few brown bristles; three retromarginal teeth, with the basal largest; three promarginal teeth, with the median largest. Pedipalp (Figs. 35–37): Cymbium elongated, tip with two macrosetae; median apophysis with ventral process; terminal apophysis sickle-shaped, embolus long and slender (Figs. 35, 37). Abdomen: Irregular grey brown; yellow-brown median band; brown lanceolate heart mark with dark grey patchy borders in anterior half, continuing into a triangular, dark grey pattern in posterior half; covered with white setae and additional brown setae in darker areas; few longer, brown bristles; venter yellow-brown with a pair of black spots behind epigastric furrow and irregular black spots laterally (Fig. 34); covered with white setae, black setae on black spots; spinnerets yellow-brown, with grey setae towards tips. Legs: Leg formula IV > I > II > III; tarsi and metatarsi dark brown, tibiae basally brown and apically dark brown, femora brown, femora III and IV with faint grey annulation dorsally; dense scopulous setae on all tarsi and metatarsi I and II; dense and hair-like setae dorsally on tarsi and metatarsi I and II. spination of leg I (based on holotype SAM NN14115): Femur: 6 dorsal, 2 apicoprolateral; patella: 1 prolateral, 1 retrolateral; tibia: 3 ventral pairs, 2 prolateral, 2 retrolateral; metatarsus: 2 ventral pairs, 1 apicoventral, 2 prolateral, 2 retrolateral, 1 apicoventral, 1 apicoretrolateral.

Female: Carapace: As male. Sternum: coloration as male, but fewer and shorter white setae. Labium, chelicerae and their dentition: as male. Epigynum (Figs. 38, 39): Ventral view: inverted T-shaped (Fig. 38); dorsal view: ovoid spermathecae, copulatory ducts connected posteriorly (Fig. 39). Abdomen: As male, pattern less distinct in particular in posterior half; venter and spinnerets as male. Legs: Leg formula IV > I > II > III; coloration as male; spination of leg I (based on

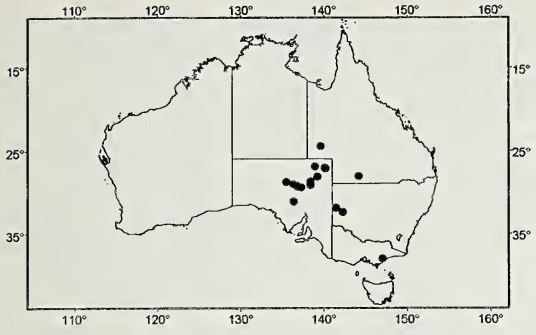


Figure 40.—Records of *Hogna diyari* new species in Australia.

paratype SAM NN14118): Femur: 6 dorsal, 2 apicoprolateral; tibia: 3 ventral pairs, 2 prolateral, 2 retrolateral; metatarsus: 2 ventral pairs, 1 apicoventral, 1 apicoprolateral, 1 apicoretrolateral.

Measurements: Male holotype SAM NN14115 (female paratype SAM NN14118): TL 13.5 (15.5), CL 6.6 (7.1), CW 5.1 (5.1). Eyes: AME 0.34 (0.29), ALE 0.26 (0.23), PME 0.71 (0.69), PLE 0.57 (0.60). Row of eyes: AE 1.34 (1.40), PME 1.66 (1.74), PLE 2.03 (2.4). Sternum (length/width) 2.8/2.6 (3.0/2.6). Labium (length/width) 0.83/0.83 (1.06/1.06). AL 7.1 (8.7), AW 4.1 (5.6). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 2.55 + 2.1 + — + 2.1 = 6.75, I 5.85 + 7.50 + 5.40 + 2.85 = 21.60, II 5.4 + 6.75 + 5.1 + 2.7 = 19.95, III 5.10 + 6.00 + 5.40 + 2.55 = 19.05, IV 6.30 + 7.65 + 7.50 + 3.15 = 24.60 (pedipalp 1.80 + 2.55 + — + 1.80 = 5.15, I 5.25 + 6.75 + 6.90 + 2.25 = 21.15, II 5.10 + 6.15 + 5.10 + 2.10 = 18.45, III 4.50 + 5.40 + 3.90 + 2.10 = 15.09, IV 5.85 + 7.35 + 6.15 + 2.85 = 22.20).

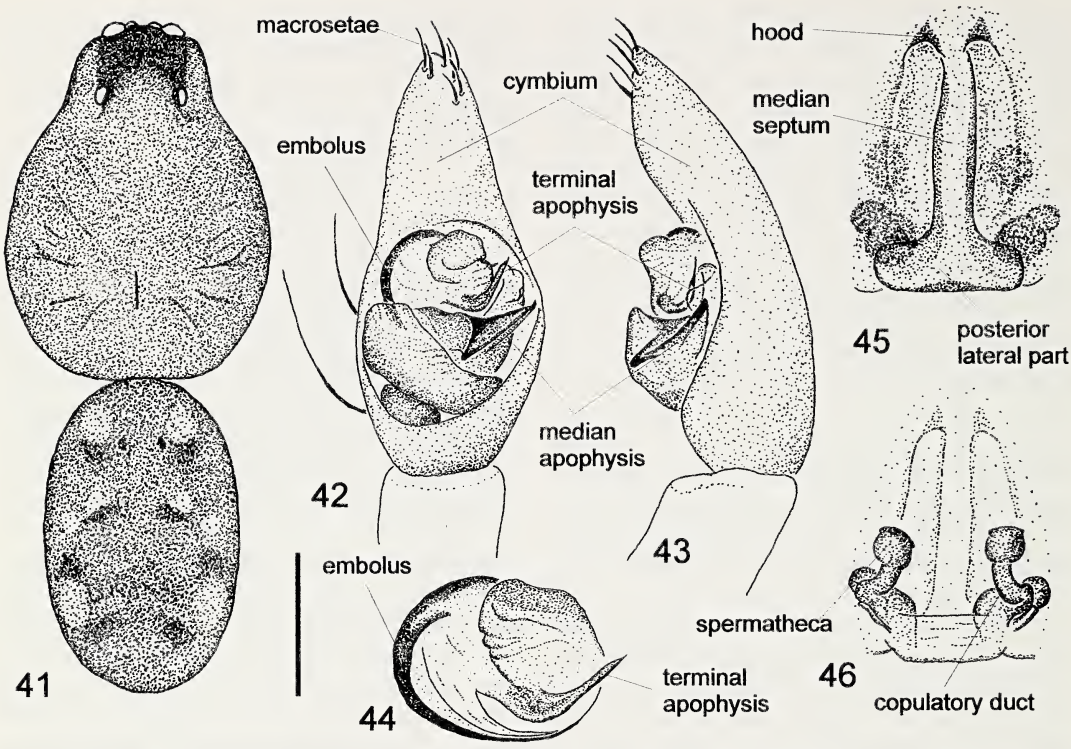
Variation: Males (females) (range, mean ± s.d.): TL 9.8–15.1, 12.1 ± 1.4; n = 23; CL 4.1–7.2, 6.0 ± 0.7; n = 25; CW 3.0–5.3, 4.3 ± 0.5; n = 25 (TL 12.7–17.6, 14.9 ± 1.4, n = 20; CL 5.9–8.1, 6.8 ± 0.7, n = 20; CW 4.2–6.5, 5.0 ± 0.6; n = 20).

Distribution and habitat preferences.—Most specimens of *H. diyari* have been found near water bodies in the dry interior of South Australia, Queensland and New South Wales. The single female from temperate Victoria may be erroneous, as the label is not entirely conclusive (Fig. 40). While uncommon in artesian springs this species is widely distributed across most of the major spring groups within South Australia (Table 1). It is rarely found around spring vents, preferring the ephemeral wet zone that exists beyond the permanent vegetated wetland.

Hogna kuyani new species
Figs. 41–47

Types examined.—Holotype male, Australia, South Australia, Coongie Lake, 27°12′S, 140°10′E, 26.-28.x.1995, on shore, D. Hirst (SAM NN14044). Paratypes: 1 male, Coongie Lake, 27°12′S, 140°10′E, iii.1987, pitfall trap, J Reid/Coongie Lake Study (SAM NN14029); 2 females, Coongie, 4.7 km SE, 27°12′10″S, 140°11′00″E, 14 March 1987, pitfall trap, J Reid/Coongie Lake Study 11E (SAM NN14032–3).

Other material examined.—AUSTRALIA: *South Australia*: 1 ♂, Appamurna Waterhole (SAM NN14027); 1 ♂, Clayton Bore, 33 miles N of Maree (WAM T51437); 1 ♂, Clifton Hill Outstation, 1.1 km E (SAM NN14069); 3 ♂, 1 ♀, 1 juv., Clifton Hills Outstation, 4.8 km NE (SAM NN14062–5); 3 ♂, Clifton Hills Outstation, 5.4 km E (SAM NN14066–8); 1 ♂, Clifton Hills Outstation, 8 km ENE (SAM NN14070); 3 ♂, Coongie, 1.77 km W (SAM NN14041–3); 1 ♀, Coongie, 11.4 km SE (SAM NN14034); 1 ♀, Coongie, 5.3 km SE (SAM NN14030); 1 ♂, Coongie, 7.89 km N (SAM NN14037); 2 ♂, Coongie, 9.95 km NNE (SAM NN14035–6); 1 ♂, Dickinna Hill, 15.5 km SSE (SAM NN14046); 1 ♂, Dudley Park Cemetery, Adelaide (SAM NN14049); 1 ♀, Emu Bay, 4 km SE, Kangaroo Island (SAM NN14050); 1 ♂, Greenfields Wetlands, Dry Creeklisbury (SAM NN14048); 1 ♀, Lake Palankarinna (SAM NN14026); 1 ♀, Moomba, 50 km N (SAM NN14025); 2 ♂, 2 juv., Morris Creek Bore (SAM NN14021); 1 ♂, near Roxby Downs adj. Borefield Rd (SAM NN14022); 6 ♂, 1 ♀, 1 juv., New Altona Downs, 32.5 km SW (SAM NN14052–8); 1 ♂, New Altona Downs, 13 km SE (SAM NN14028); 3 ♂, 1 juv., New Altona Downs, 36 km SW (SAM NN14059–61); 1 ♀, Whyalla (MV K8248). *New South Wales*: 1 ♂, Arcoola Creek Crossing on George Loop Road, Sturt National Park (AM KS84100); 2 ♂, 5 ♀, Broken Hill (SAM NN14072–8); 1 ♂, Connia Creek, 14.8 km S of Olive Downs Homestead, via Jump-Up Loop Road, Sturt NP (AM KS71564); 4 ♂,



Figures 41–46.—*Hogna kuyani* new species: Male: 41. habitus (holotype from Coongie Lake, SA; SAM NN14044); left pedipalp: 42. ventral and 43. retrolateral view, and 44. apical part of bulb (paratype from 1.77 km W of Coongie, SA; SAM NN14041). Female from 4.8 km SE Coongie (SAM NN14031): 45. ventral and 46. dorsal view of epigynum. Scale bar: (41) 2.84 mm, (42, 43) 0.60 mm, (44) 0.32 mm, (45, 46) 0.43 mm.

Mullingar Station, Lower Murray-Darling region (AM KS67040, KS84099); 3 ♂, 1 ♀, Sturt National Park (AM KS71040); 6 ♂, 1 ♀, 1 juv., Sturt National Park, 19.2 km S of Fort Grey Homestead, on Camerons Corner Road (AM KS51348); 1 ♂, Trilby, track to New Chum, 6.4 km from highway junction. *Queensland*: 1 ♂, Baryulahl gas well, 38 km S Ballera (SAM NN14360); 1 ♂, Cluny Station Billabong (QM S61149); 1 ♂, Muncoonie Lakes (QM S61150). *Western Australia*: 3 ♂, Camel Lake Nature Reserve (WAM T47229); 2 ♂, Coolinup Nature Reserve (WAM T47232); 1 ♂, 2 ♀, Coyrecup Lake Nature Reserve (WAM T47145); 36 ♂, 7 ♀, Dumbleyung Lake North (WAM T47226, T47237); 1 ♂, Grass Patch, E of, 'Sieda', '10 bagger dam' (WAM T53586); 1 ♂, 1 ♀, Gulson Lake Nature Reserve (WAM T47218, T48084); 1 ♂, 3 ♀, Lake Bryde West Nature Reserve, Lake Bryde Rd (WAM T47138, T47225); 1 ♂, Lake Daringdella (SAM NN14051); 1 ♀, Lake Moore (WAM T47217); 2 ♀, Midland (WAM 72/248); 2 ♂, 4 ♀, 5 juv., Molpar (WAM 71/1449–54); 44 ♂, 14 ♀, 7 juv., Nugadong West Rd, SW Wubin (WAM T47137, T47228); 1 ♀, Pallarup Nature Reserve, Lake Pallarup (WAM T47231); 1 ♂, 1 ♀, Reservoir Rd, W Kodinin (WAM T47233–4); 1 ♀, 1 juv., R.G.C. Mine, 10 km S of Eneabba (WAM T51396); 13 ♂, 6 ♀, 34 juv., Taarblin Lake, 10 km SW of Toolibin Lake (WAM T51450); 21 ♂, 10 ♀, 22 juv., Taarblin Lake, south-west shore (WAM T48055–7, T48060); 1 ♂ 1 ♀, Walkaway Nature Reserve (WAM T47134, T47236); 5 ♂, Wittenoom Hill Nature Reserve, Wittenoom Rd (WAM T47230); 1 ♀, 3 juv., Yuinmery (WAM T48125).

Etymology.—The specific name is a noun in apposition honoring the Kuyani people, an Aboriginal tribe representing the traditional custodians of parts of the land on which the South Australian artesian springs are found.

Diagnosis.—*Hogna kuyani* can be distinguished from *H. crispipes* and *H. diyari* by its

uniform, dark reddish-brown carapace coloration with a dense cover of silver-grey setae and the absence of median or submarginal bands. The median septum of the female epigynum is comparatively longer than that of the other two *Hogna* species (Fig. 45). The genitalic structure of *H. kuyani* is very similar to that of *H. pexa* Hickman 1944, which differs in its considerably lighter body coloration, in particular of the abdomen. This does not seem to be an artifact of its preservation as Hickman's (1944) original description confirms a "yellow [abdomen] with a median longitudinal brown patch in anterior half" in contrast to the dark grey abdomen of *H. kuyani*.

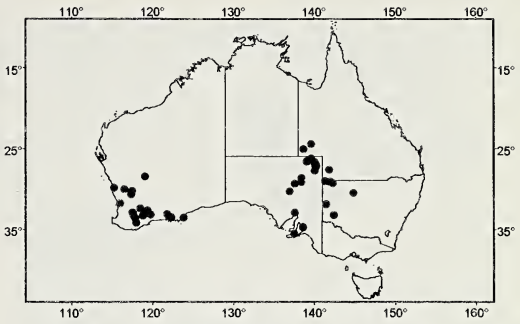


Figure 47.—Records of *Hogna kuyani* new species in Australia.

Description.—*Male:* Carapace (Fig. 41): Dark reddish-brown, with indistinct darker radial pattern; head region black; carapace covered with a thick layer of silver-grey setae (that rub off easily and may not be present in older specimens), brown bristles in head region; one long bristle between AME, four long bristles below AE. Sternum: Light brown with irregular grey pigmentation; densely covered with white setae, denser and longer towards margins. Labium: Dark brown, darkest in basal half; front end truncate and white. Chelicerae: Dark reddish-brown with a dense cover of white setae mainly in basal half; three retromarginal teeth, with the median largest; three promarginal teeth, with the median largest. Pedipalp (Figs. 42–44): Cymbium tip with ca. 6–8 macrosetae; median apophysis with ventral process that points basally; terminal apophysis sickle-shaped, embolus with a very thin tip (Figs. 42, 44). Abdomen: Dark grey-brown with an irregular pattern of dark and light spots; densely covered with silver-grey setae and fewer brown bristles in particular in anterior half; venter uniformly light brown and covered with white setae; spinnerets light brown. Legs: Leg formula IV > I > II > III; tarsi and metatarsi brown, tibiae and femora dark brown, femora with indistinct grey annulations; dense scopulous setae on all tarsi and metatarsi I and II; metatarsi I with long hair-like setae; femora, and less dense on tibiae and patellae, dorsally with dense, silver-grey setae. spination of leg I (based on holotype SAM NN14044): Femur: 6 dorsal, 2 apicoprolateral; patella: 1 prolateral, 1 retrolateral; tibia: 3 ventral pairs, 2 dorsal, 2 prolateral, 2 retrolateral; metatarsus: 2 ventral pairs, 1 apicoventral, 2 prolateral, 2 retrolateral, 1 apicoventral, 1 apicoretrolateral.

Female: Carapace, sternum, labium, and chelicerae: Coloration, setae and cheliceral dentition as male (carapace medially slightly lighter). Epigynum (Figs. 45, 46): Ventral view: Inverted T-shaped with long median septum (Fig. 45); ventral view: circular spermathecae, copulatory ducts connected posteriorly (Fig. 46). Abdomen: Coloration and setae as male. Legs: Leg formula IV > I > II > III; coloration as male; all tarsi and metatarsi I and II (only in apical half) with dense scopulae; spination of leg I (based on paratype SAM NN14032): Femur: 6 dorsal, 2 apicoprolateral; tibia: 3 ventral pairs, 1 (small) prolateral; metatarsus: 2 ventral pairs, 1 apicoventral, 1 apicoprolateral, 1 apicoretrolateral, 1 (small) prolateral.

Measurements: Male holotype SAM NN14044 (female paratype SAM NN14032): TL 11.3 (18.0), CL 6.2 (7.2), CW 4.7 (5.4). Eyes: AME 0.26 (0.29), ALE 0.17 (0.23), PME 0.63 (0.77), PLE 0.49 (0.60). Row of eyes: AE 1.17 (1.32), PME 1.63 (1.95), PLE 1.95 (2.35). Sternum (length/width) 2.9/2.0 (3.2/2.7). Labium (length/width) 0.74/0.74 (0.97/0.97). AL 5.3 (9.8), AW 3.3 (6.8). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 2.25 + 2.25 + — + 1.95 = 6.45, I 5.25 + 7.35 + 5.25 + 2.70 = 20.55, II 4.95 + 6.30 + 4.50 + 2.55 = 18.30, III 4.50 + 5.55 + 4.80 + 2.40 = 17.25, IV 5.85 + 7.35 + 7.50 + 2.85 = 23.55 (Pedipalp 2.85 + 2.85 + — + 1.80 = 7.50, I 5.10 + 7.20 + 3.90 + 1.95 = 18.15, II 5.10 + 6.30 + 4.05 + 1.95 = 17.40, III 4.50 + 5.55 + 4.35 + 1.95 = 16.35, IV 5.70 + 7.95 + 7.50 + 2.55 = 23.70).

Variation: Males (females) (range, mean ± s.d.): TL 8.5–22.3, 15.5 ± 3.3; n = 28; CL 5.1–10.5, 8.5 ± 1.6; n = 28; CW 3.6–8.3, 6.4 ± 1.3; n = 28 (TL 12.0–19.7, 16.2 ± 2.2, n = 14; CL 5.9–9.9, 7.8 ± 1.3, n = 14; CW 4.4–7.2, 5.8 ± 0.9; n = 14).

As in *H. crispipes*, the size variation in *H. kuyani* is remarkable. For example, males range from 8.5–22.3 mm body length, meaning that the largest specimens are nearly three times the size of their smallest conspecifics.

Distribution and habitat preferences.—This species is found widely across New South Wales, South Australia, Western Australia, and Queensland (Fig. 47). It is present in low numbers across a wide range of artesian springs in South Australia, but is most common in the springs around Hermit Hill (Table 1). *Hogna kuyani* can be found in unsaturated areas of wetland vegetation, where it makes shallow, wide burrows that are concealed by sheets of web covered in mud and litter.

Unknown subfamily
Genus *Tetralycosa* Roewer 1960

Tetralycosa Roewer 1960: 949 (name first listed as *nomen nudum* in Roewer 1955: 296).

Type species.—*Lycosa meracula* Simon 1909, by monotypy (Roewer 1960).

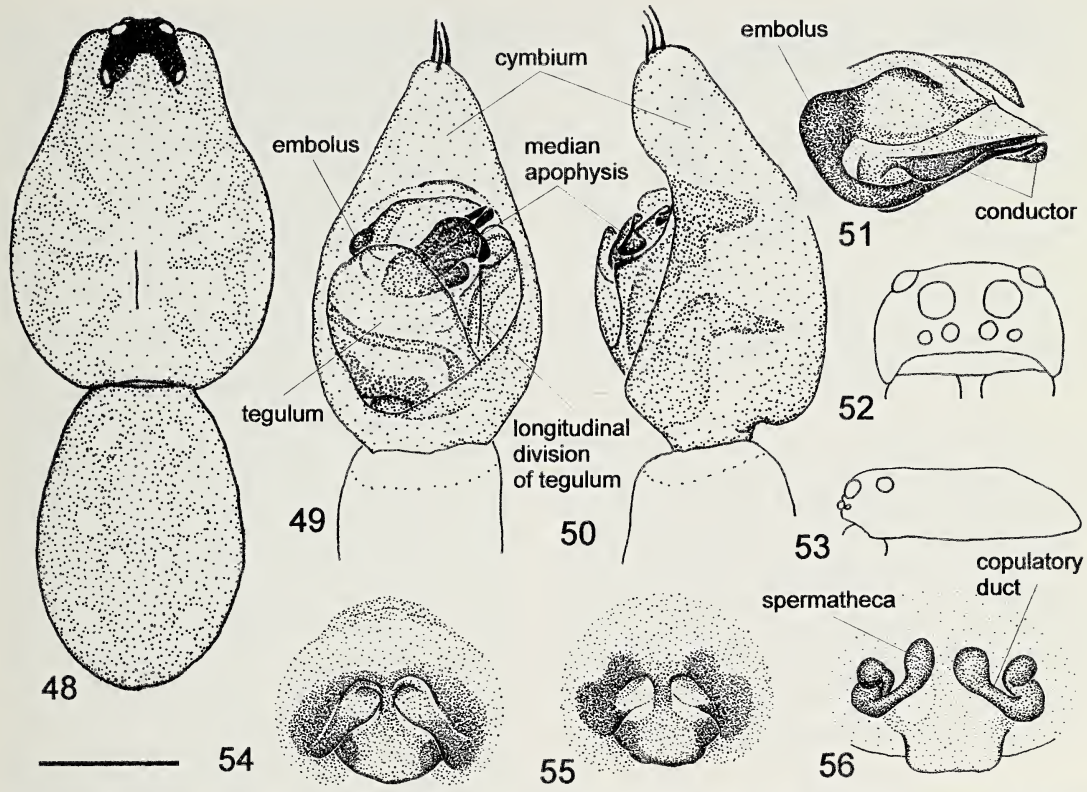
Diagnosis.—Males of *Tetralycosa* differ from all other lycosid genera by the combination of the following characters: reduced palea with well developed, thin embolus; conductor forms a shaft for the resting embolus; terminal apophysis absent; tegulum deeply divided; medium apophysis originating apically on tegulum and hook-shaped, opposing an apicomedially directed pointy protrusion on the retrolateral section of the tegulum. Females: epigynum with a wide median septum, sometimes partially hidden behind circular or oval sclerotized atrium.

Generic description.—Small to large wolf spiders (TL 4.5–22.0 mm). Males smaller than females. Carapace longer than wide, dorsal profile more or less straight in lateral view in smaller species (*T. arabanae*, *T. oraria*) (Fig. 53), but with an elevated head region and downward slope towards posterior end in larger species (*T. alteripa*, *T. eyrei*). Carapace coloration variable from a light yellowish brown (*T. arabanae*) to very dark brown (*T. eyrei*), without or with only an indistinct light median band. Abdomen coloration variable, generally with dark heart mark. AME larger than ALE, row of AE straight or slightly procurved (Figs. 52). Chelicerae generally with three promarginal and three retromarginal teeth, but 2–4 teeth on individual chelicerae possible on both margins. Leg formula IV > I > II > III or IV > II > I > III (*T. alteripa*, *T. eyrei*).

Tegulum deeply divided longitudinally in retrolateral half. Median apophysis located apically at tegulum and forming a ventrally directed hook that opposes an apicomedially directed pointy protrusion on the retrolateral section of the tegulum. Median apophysis with a basal lobe. Palea reduced. Embolus originating prolaterally on and curving ventrally around palea, long and slim. Ventrally directed lobe at the base of the embolus. Terminal apophysis well developed and forming a sclerotized shaft in which the embolus rests. Cymbium dorsally with dense, scopulous setae in apical half and without or only a few macrosetae on tip. Epigynum variable with a wide median septum sometimes only partially visible behind the sclerotized margins of the epigynum which only leave a round or oval atrium. Small round or oval spermathecae. Copulatory ducts short and twisted.

Remarks.—The monotypic genus *Tetralycosa*, with the type species *Lycosa meracula* Simon 1909, was initially listed by Roewer (1955). Subsequently, Roewer (1960) provided a diagnosis for this genus, characterized by the number of retromarginal cheliceral teeth and the arrangement of the eyes. McKay (1973) listed the species in *Lycorma* Simon 1885, following Guy (1966) who considered *Tetralycosa* a subgenus of *Lycorma*. Subsequently, McKay (1979c) synonymized *Tetralycosa* with *Lycosa*. This decision was based on the examination of two juvenile syntypes of *L. meracula*. The syntype series, however, also contains a mature male and a recent investigation of this specimen lodged at the MHNP revealed *Lycosa meracula* to be a junior synonym of *Trochosa oraria* (L. Koch 1876). Due to the unique pedipalp morphology of *T. oraria*, *Tetralycosa* is here reinstated as the valid genus and monophyletic group of Australian wolf spiders, most of which appear to favor saline conditions near salt lakes, mound springs or sea shores.

Roewer (1960) based the generic description of *Tetralycosa* mainly on somatic char-



Figures 48–56.—*Tetralycosa arabanae* new species: Holotype male from Jersey Spring, SA (SAM NN13871): 48. habitus; 49. left pedipalp, ventral; 50. left pedipalp, retrolateral; 51. male, apical part of bulb (WAM T47295, from Morris Creek Bore, SA); 52. eye arrangement; 53. lateral profile of crapace. Females: ventral view of epigynum: 54. WAM T47299; 55. WAM T47297 (from Gosse Springs, SA); 56. dorsal view of epigynum (WAM T47296, from Morris Creek Bore, SA). Scale bar: (48) 1.42 mm, (49–50) 0.35 mm (51) 0.13 mm, (52) 1.09 mm, (53) 1.49 mm, (54–56) 0.40 m.

acters, in particular the number of retromarginal teeth on the chelicerae and the arrangement of the eyes. Here, we revalidate this genus based on the unique morphology of the male pedipalp.

The subfamilial placement of *Tetralycosa* is unclear. The genus appears to have some affinities with the subfamily Pardosinae, as the conductor is "shaftlike, lying transversely along basal magin of palea" (Dondale 1986) and a "thick well-sclerotized basal part of palea concealed by tegulum" (Zyuzin 1993). However, a preliminary molecular analysis of a dataset from the 12S rRNA gene subunit, that included *T. oraria*, was not conclusive in regard to the subfamilial placement of this genus (Vink et al. 2002). Parsimony analysis resulted in the placement of *T. oraria*, together with the presumably lycosine species *Arctosa leopardus* (Sundevall 1833), as a sister-group to traditional lycosine (*Alopecosa*, *Lycosa*, *Trochosa*, *Varacosa*, *Venatrix*) and pardosine (*Pardosa*) genera combined. In contrast, a strict consensus tree of six maximum likelihood trees places *T. oraria* basally, as sister-taxon to all other lycosid species (Vink *et al.* 2002). *Tetralycosa* also shows some affinity with *Artoria*. The laminar lobe at the base of the embolus in *Tetralycosa* (Figs. 51, 58) may be homologous to the basoembolic apophysis in *Artoria*. In addition, the shaft-like conductor of *Tetralycosa* is situated similarly as the terminal apophysis (*sensu* Framenau 2002) in *Artoria*.

Four species are here included in *Tetralycosa*: *T. alteripa* (McKay 1976) new combination; *T. arabanae* new species; *T. eyrei* (Hickman 1944) new combination, and *T. oraria* (L. Koch 1876) new combination. All four species appear to be halophilic species.

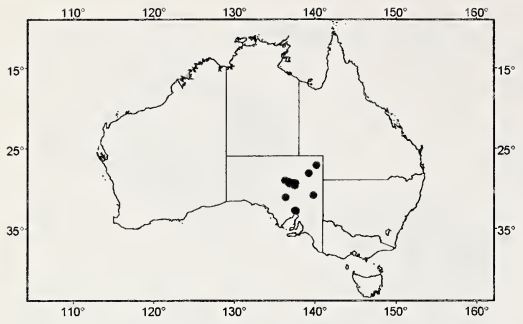


Figure 57.—Records of *Tetralycosa arabanae* new species in Australia.

Two representatives, *T. alteripa* and *T. eyrei*, are exclusively found on the surface of salt lakes in the dry interior of Australia (McKay 1976; Hudson 1996, 1997; Hudson & Adams 1996) and *T. oraria* is typically found on the foreshore and in sand dunes of ocean beaches in southern Australia and Tasmania (McKay 1979c). A full revision of this genus will be the subject of a forthcoming publication.

Tetralycosa arabanae new species
Figs. 48–57

Types examined.—Holotype male, Australia, South Australia: Jersey Spring, 29°20′S 136°45′E, 18.vii.1996, D. Niejalke (SAM NN13871). Paratypes: 1 male, 2 juveniles, same location as holotype, 18.vii.1996, D. Niejalke (SAM NN13872); 7 males, 2 females 1 female with 41 spiderlings, same location, 12.xi.1997, K-J Lamb (SAM NN13887–96).

Other material examined.—AUSTRALIA: *South Australia*: 1 ♂, Blanche Cup Mound Springs (SAM NN13884); 1 ♂, Buttercup Mound Spring (SAM NN13885); 1 ♀, Coongie Lake (SAM NN13869); 4 ♂, 1 ♀, Elizabeth Springs (North A) (SAM NN13878–82); 1 ♀, Elizabeth Springs (North B) (SAM NN13883); 1 ♀, 1 juv., Elizabeth Springs Bore (SAM NN13870); 2 ♂, 4 juv., Francis Swamp mound spring (SAM NN13876–7); 1 ♀ with 67 spiderlings, Gosse East Spring (SAM NN13886); 2 ♀, Gosse Springs (WAM T47297); 1 ♀, 1 juv., Hermit Hill Springs (SAM NN13873); 20 ♂, 10 ♀, 1 juv., Horse East Spring (SAM NN13897–916); 2 ♀, Horse Springs (WAM T47299); 1 ♀, Lake Frome (SAM NN13867); 1 ♀, Lake Hart (SAM NN13933); 1 ♀, 1 juv., Lake Hope Channel, 3.9 km S Lake Appadare (SAM NN13868); 2 ♂, 1 ♀, 1 juv., McLachlan Springs (WAM T47298); 1 ♂, 1 ♀, Morris Creek Bore (WAM T47295–6); 1 ♂, 4 juv., Old Finnis Spring (SAM NN13874); 1 ♂, Smith Spring (SAM NN13875, NN13929–32); 5 ♂, 2 ♀, 5 juv., Tregolana Salt Lake (SAM NN13862–4).

Etymology.—The specific name is a noun in apposition honoring the Arabana people, an Aboriginal tribe representing the traditional custodians of parts of the land where the South Australian artesian springs are found.

Diagnosis.—*Tetralycosa arabanae* is very similar to *T. oraria* in particular in regard to male pedipalp morphology. However, the lower tip of the conductor of the male pedipalp of *T. arabanae* has a triangular process pointing apically (Fig. 51). This process is absent in *T. oraria* (Fig. 58). Female genitalia of both species are easily distinguished as the triangular epigynum of *T. arabanae* is approximately as wide as long (Figs. 54, 55), whereas the ovoid epigynum of *T. oraria* is much wider than long (McKay, 1979c, figs. 1b, d, f).

Description.—*Male:* Carapace (Figs. 48, 53): Dorsal line straight in lateral view; light yellow-brown, sometimes with indistinct light brown radial pattern; eye field very dark brown; carapace covered with mainly white setae, few black setae posterior of fovea; few black bristles in eye field; four long brown bristles below AE, one long bristle between AME. Sternum: Yellow; white setae and fewer brown bristles both denser and longer towards margins. Labium: Brown; front end truncate and white. Chelicerae: Light brown; white setae basally and laterally, black setae apically near fangs; two retromarginal teeth of similar size; three promarginal teeth, with the median largest. Pedipalp (Figs. 49–51): Median apophysis a broad, ventrally directed hook and with basal lobe; embolus with a basal bulge and resting in a shaft formed by the conductor; lower tip of conductor triangular (Fig. 51); cymbium dorsally with scopulous setae in apical half, and few apical macrosetae. Abdomen: Olive-yellow; faint brownish heart mark in anterior half; three to four pairs of yellow spots, of which the anterior and posterior pair are largest; covered with white setae and few longer, brown bristles; venter yellow; setae as dorsally, but brown bristles lighter and shorter; spinnerets yellow. Legs: Leg formula IV > I > II > III; light yellow-brown, with faint annulations centrally and in

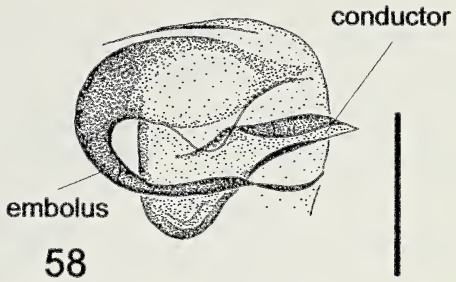
apical half of femora, in basal half of patella, and basally and centrally on tibia; tarsus and metatarsus of legs I and II darker (brown); spination of leg I (based on holotype SAM NN13871): Femur: 4 dorsal, 1 apicoprolateral, 1 apicoretrolateral; patella: 1 prolateral, 1 retrolateral; tibia: 3 ventral pairs, 2 dorsal, 2 prolateral, 2 retrolateral; metatarsus: 3 ventral pairs, 3 prolateral, 3 retrolateral; 1 apicoventral.

Female: Carapace, sternum and labium: as male. Chelicerae: Dark brown, generally much darker than in males; setae and bristles as male; cheliceral dentition as male. Epigynum (Figs. 54–56): Ventral view: triangular with convex posterior margin (Figs. 54, 55); dorsal view: small oval spermathecae, copulatory ducts directed anteromedially, small spermathecal organs (Fig. 56). Abdomen: As male. Legs: Leg formula IV > I > II > III; coloration as male, however tarsus and metatarsus of leg I and II not darker; spination of leg I (based on female SAM NN1389, reduced in comparison to males): Femur: 4 dorsal, 1 apicoprolateral; tibia: 1 apicoventral pair, 1 prolateral; metatarsus: 2 ventral pairs, 1 apicoventral.

Measurements: male holotype SAM NN13871 (female SAM NN13894): TL 7.3 (7.6), CL 4.0 (3.7), CW 2.8 (2.7). Eyes: AME 0.2 (0.2), ALE 0.14 (0.16), PME 0.28 (0.32), PLE 0.26 (0.16). Row of eyes: AE 0.82 (0.88), PME 0.76 (0.80), PLE 1.10 (1.20). Sternum (length/width) 2.0/1.5 (1.6/1.4). Labium (length/width) 0.51/0.52 (0.54/0.66). AL 3.1 (3.4), AW 2.3 (2.6). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 1.50 + 1.25 + — + 1.20 = 3.95, I 3.05 + 3.90 + 2.90 + 1.55 = 11.40, II 3.0 + 3.65 + 3.0 + 1.5 = 11.15, III 2.85 + 3.25 + 3.05 + 1.4 = 10.55, IV 3.55 + 4.20 + 4.0 + 1.8 = 13.55 (Pedipalp 1.25 + 1.25 + — + 1.0 = 3.5, I 2.35 + 3.15 + 1.95 + 1.1 = 8.65, II 2.30 + 2.90 + 1.9 + 1.05 = 8.15, III 2.25 + 2.25 + 2.05 + 1.05 = 7.9, IV 2.9 + 3.4 + 3.1 + 1.30 = 10.7).

Variation: males (females) (range, mean ± s.d.): TL 4.8–7.7, 6.3 ± 0.8; n = 23; CL 2.5–4.2, 3.3 ± 0.5; n = 24; CW 2.0–3.2, 2.5 ± 0.3; n = 24 (TL 6.6–11.1, 7.9 ± 1.2, n = 17; CL 3.1–5.8, 3.8 ± 0.6, n = 19; CW 2.2–3.6, 2.7 ± 0.4; n = 19).

Distribution and habitat preferences.—This species is restricted to arid South Australia (Fig. 57). It is found in the southern and eastern springs from Jersey Springs in the west to Mulligan Springs in the east (Table 1). *Tetralycosa arabanae* is largely restricted to the lower parts of the spring tail and the ephemeral wet regions beyond the permanent vegetated wetland. It has also been found near semi-permanent saline waterholes near Hermit Hill Springs.



Figures 58.—*Tetralycosa oraria* (L. Koch 1876): Male from Australind, WA (WAM 71/360), apical part of bulb. Scale bar: 0.21 mm.

NON-ARTESIAN SPRING LYCOSIDAE OF THE GENUS *TETRALYCOSA*

The following species are not part of the artesian spring fauna of South Australia, but are transferred to the *Tetralycosa* as they show the unique pedipalp morphology characteristic for this genus.

Tetralycosa alteripa (McKay 1976) new combination

Lycosa alteripa McKay 1976: 418–420, figs. 2, 2a–e; Brignoli 1983: 450; McKay 1985: 74.

Remarks.—*Tetralycosa alteripa* shows the typical pedipalp and epigynum structure of *Tetralycosa* (McKay 1976, 418–420, figs. 2, 2a–e; holotype male (WAM 70/41) and paratype males and females (WAM 70/42–46, 74/501) examined by VWF) and is therefore transferred from the northern hemisphere genus *Lycosa* to *Tetralycosa*. This species is typically found on the surface of salt lakes in South Australia and Western Australia (McKay 1976; Hudson 1997). An allozyme study suggests the existence of an undescribed, cryptic sister-species of *T. alteripa* in Western Australia (Hudson & Adams 1996).

Tetralycosa eyrei (Hickman 1944) new combination

Pardosa eyrei Hickman 1944: 24,25, plate 1, figs. 11–13; Roewer 1955: 185; McKay 1973: 378.
Lycosa eyrei (Hickman 1944): McKay 1985: 76; Platnick 1989: 370.

Remarks.—The pedipalp and epigynum structure of *T. eyri* is similar to that of *T. alteripa* (Hickman 1944: 24, 25, plate 1, figs. 11–13; holotype male (AM KS5738) and conspecific males and females (SAM NN13809–15, NN17384–5; MV K8126, K 8183, examined by VWF). As in *T. alteripa*, this species is typically found on the surface of salt lakes in South Australia and Victoria (Hudson 1996; Hudson & Adams 1996), although, allozyme data suggest the co-occurance of two cryptic species within *T. eyrei* (Hudson & Adams 1996). *Tetralycosa eyrei* has a sympatric distribution with the salt-lake dwelling scorpion *Australobuthus xerolimniorum* Locket 1990 (Hudson 1997).

Tetralycosa oraria (L. Koch 1876) new combination
Fig. 58

Lycosa oraria L. Koch 1876: 883–886, plate 76, figs. 2, 2a, 3, 3a; Simon 1909: 188; Rainbow 1911: 270; Bonnet 1957: 2656.
Lycosa candicans L. Koch 1877: 888–890, plate 76, figs. 5, 5a, 6, 6a, b; Rainbow 1911: 266; Hickman 1950: 5; Bonnet 1957: 2637. NEW SYNONYMY.
Lycosa sibyllina Simon 1909: 188, 189, fig. 7; Rainbow 1911: 272; Bonnet 1957: 2664; McKay 1973: 379; Moritz 1992: 325. Synonymized by McKay 1979c: 279.
Lycosa meracula Simon 1909: 190, 191; Rainbow 1911: 270; McKay 1985: 80; Platnick 1989: 372; Moritz 1992: 320. NEW SYNONYMY.
not *Lycosa meracula* Simon, *sensu* McKay 1979c: 264, figs. 9a–k (misidentification; not *L. meracula* but an undescribed species).
Crocodilosa oraria (L. Koch 1877): Roewer 1955: 238.
Tetralycosa meracula (Simon 1909): Roewer 1955: 296; Roewer 1960: 949; Rack 1961: 38.
Hogna sibyllina (Simon 1909): Roewer 1955: 253.
Trochosula candicans (L. Koch 1877): Roewer 1955: 304.
Trochosomma oraria (L. Koch 1877): Roewer 1960: 847; Roewer 1961: 14.
Ocyale oraria (L. Koch 1877): McKay 1973: 380.
Lycorma meracula (Simon 1877): McKay 1973: 380.
Trochosa candicans (L. Koch 1877): McKay 1973: 381; McKay 1979c: 293–294, fig. 4e; McKay 1985: 85; Platnick 1989: 390.
Trochosa oraria (L. Koch 1877): McKay 1979c: 279–282, figs. 1a–h; McKay 1985: 86; Platnick 1989: 391; Platnick 1993: 510.

Remarks.—The male pedipalp of *T. oraria* is very similar to that of *T. arabanae*. It can mainly be distinguished by the lower tip of the conductor, which has a triangular protrusion in *T. arabanae* (Figs. 51), but not so in *T. oraria* (Figs. 58). The wide, oval median septum of the epigynum of *T. oraria* (McKay 1979c: 279–282, figs. 1b, d, f) conforms to the general pattern of *Tetralycosa*.

Simon (1909) described *Lycosa meracula* based on one male and some immature spiders from (p. 191) "Stat. 5, Denham, *ad litus in detritus*; Stat. 65, Albany" collected during the 'Hamburger Südwest-Australische Expedition 1905' (Michaelsen & Hartmeyer 1907; Simon 1909). Three immatures from Denham are deposited in Hamburg (ZMH, Rack (1961)-catalogue 466), Berlin (ZMB 11085) and Perth (WAM 11/4303) (VWF, all examined). Therefore, the adult male lodged in Paris (MHNP 24964, labeled "*Lycosa meracula* E.S., Austr. occid. (Michaelsen)", VWF, examined) without accurate locality data must be regarded as the syntype from Albany. This adult male is conspecific with *T. oraria* L. Koch 1876, as there is no difference in somatic and genitalic characters between these species. Consequently, *L. meracula*, the type species of *Tetralycosa*, is considered a junior synonym of *T. oraria*. This also agrees with the type localities of both species, as *T. oraria* was described from King George Sound, the harbor bay of Albany (L. Koch 1876).

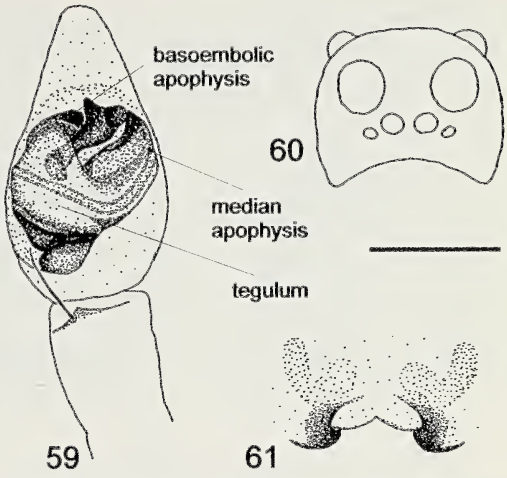
Not being aware of the existence of the mature male syntype at the MHNP, McKay (1979a) redescribed *T. meracula* based on adult material collected near the type locality, Denham, of the immature specimens which are lodged in Berlin and Perth. However, the species he illustrated is not conspecific with the adult male syntype of *T. meracula* from Albany, and therefore his treatment of this species must be regarded as erroneous. He also stated that (p. 267) "The record of this species from Albany [. . .] is erroneous, as the southern limit of this species appears to be just north of the Murchison River. [. . .] Station 65 'Albany' refers to station 65 Denham

[. . .] and not station 165 Albany." Although Simon (1909) was incorrect citing "Stat. 5" for Denham (actually Stat. 65; Stat. 5 refers to a marine surface collection near Denham) and "Stat. 65" for Albany (actually Stat. 165), McKay's (1979a) redesignation of the type locality for the male syntype from Albany to Denham appears to be incorrect. Simon's (1909) "Stat. 65, Albany" is most likely a transcription error of "Stat. 165, Albany".

It is likely that the immature syntypes of *L. meracula* are not, as McKay (1979a) suspected, conspecific with the adult male from Albany, as *T. oraria* has not been reported from as far north as Denham. However, the adult male remains the name-bearing specimen as it was described earlier (Simon 1909, pp. 190, 191) than the juveniles (p. 191) (recommendation 69A.10, ICZN 1999). More importantly, only the male syntype of *L. meracula* allows for an accurate identification of this species.

The original illustrations of *T. candicans* (L. Koch 1877) with the hook-shaped median apophysis of the male pedipalp and the oval epigynum strongly suggest a synonymy with *T. oraria*. McKay (1979c) also stressed the similarity of *T. oraria* and *T. candicans* but did not synonymize both species, as he was not able to investigate more than one female specimen (listed as *T. candicans* in Hickman (1950)) of this presumably eastern Australian species. *Tetralycosa oraria* was then only known from Western Australia. A comparison of type material of both species is not possible as no syntypes of *L. candicans* could be located in the Naturhistorisches Museum, Vienna (J. Gruber, personal communication) or 'Bradleys Collection' (whereabouts of this collection unknown) where, according to L. Koch (1877), they should be housed. Our recent investigations uncovered a large number of recently collected *T. oraria* in the AM, MV, SAM, TMAG, and QVMAG from eastern Australian states including Tasmania which leave no doubt that *T. candicans* and *T. oraria* are conspecific. Therefore, *T. candicans* is considered a junior synonym of *T. oraria*.

Tetralycosa oraria is mainly found on beaches and sand dunes along the southern coast of mainland Australia (Vic, SA, NSW, WA) and Tasmania.



Figures 59–61.—*Artoria howquaensis* Framenau 2002: Male from Howqua River, Vic (MV K7467): 59. left pedipalp, ventral; 60. eye arrangement. Female from from Howqua River, Vic (MV K7468): 61. dorsal view of epigynum Scale bar: (59) 0.30 mm, (60) 0.82 mm, (61) 0.30 mm.

Genus *Artoria* Thorell 1877

Artoria Thorell 1877: 531.
Artoriella Roewer 1960: 563 (name listed as *nomen nudum* in Roewer 1955: 233).
Trabaeola Roewer 1960: 582.

Remarks.—The genus *Artoria* Thorell was established with the description of the male of *A. parvula* Thorell 1877 from Sulawesi. Framenau (2002) reviewed the genus including the description of seven new species from floodplain habitats in Victoria. An alpine *Artoria* was recently recorded from Mt. Kosciusko (NSW) (Framenau 2004). The genus appears to be widespread in southeast Asia and the Australasian region with probably more than 50 undescribed species in Australia alone (Framenau 2002). Vink (2002) recently recorded three new species from New Zealand. The palpal morphology of *Artoria* is unique within the Lycosidae, and a preliminary molecular analysis suggests that this genus forms a monophyletic clade with *Anoteropsis* Koch, 1877 and *Notocosa* Vink 2002 (Vink et al. 2002). *Artoria* does not fit any of the current subfamilies defined by Dondale (1986), Alderweireldt and Jocqué (1993) or Zyuzin (1985, 1993).

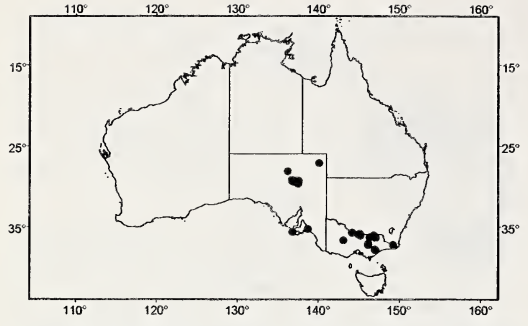


Figure 62.—Records of *Artoria howquaensis* Framenau 2002 in Australia.

Artoria howquaensis Framenau 2002
Figs. 59–61

Artoria howquaensis Framenau 2002: 217, 218, figs 9a–g, 10.

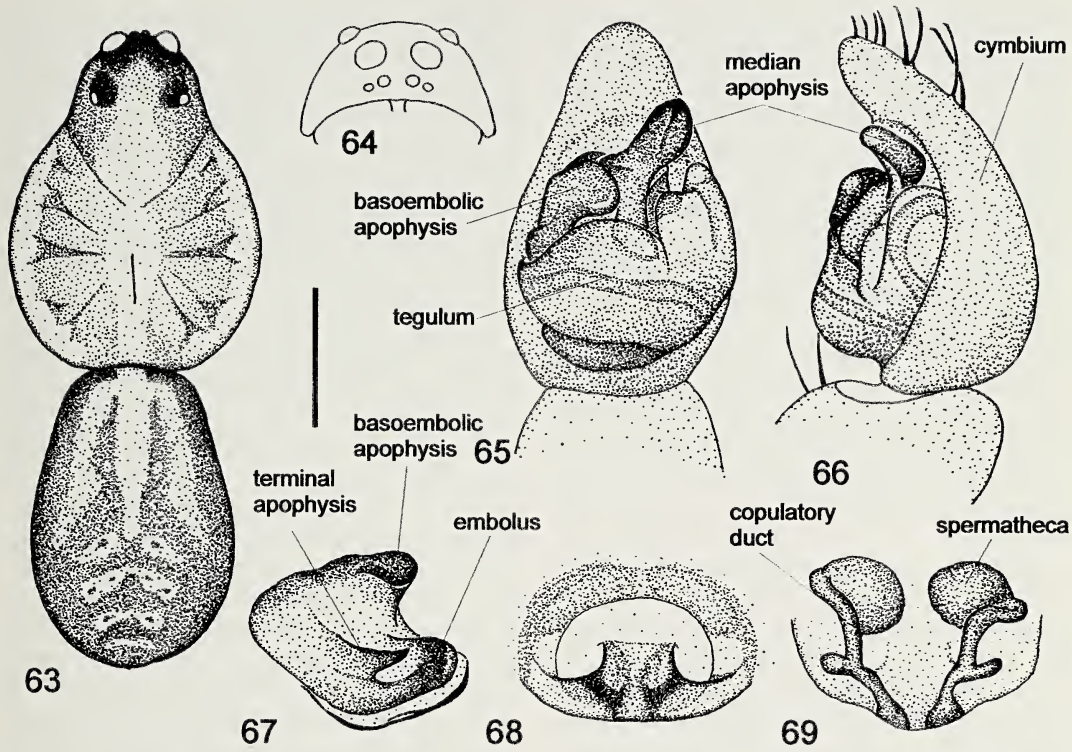
Diagnosis.—This is the smallest (TL 3.5–6 mm) and one of the most common wolf spiders at the South Australian artesian springs. It can easily be distinguished by its body coloration. The carapace is black, with distinct white marginal bands caused by a dense layer of white setae. The abdomen is dark grey to black, an indistinct lighter heart mark may be visible. The patella and tibia of the first leg of males are bright yellow. The tibia and basal half of the cymbium of the male pedipalp bear a dense cover of white setae. The median apophysis of the male pedipalp bears an apical triangular lobe (Fig. 59). The female epigynum is a simple, laterally sclerotized posterior atrium (Fig. 61).

Distribution and habitat preferences.—In addition to being widespread and common within the South Australian artesian springs (Table 1), this species has been found in lowland floodplains of rivers and other moist habitats in Victoria and South Australia, including Kangaroo Island (Framenau 2002; D. Hirst, pers. comm.) (Fig. 62). Within the artesian springs, *Artoria howquaensis* prefers *C. laevigatus* wetlands and can be found foraging on top of dense mats of vegetation. It is active mainly during the day and retreats to a silk shelter at the base of *C. laevigatus* during the night.

Artoria victoriensis new species
Figs. 63–70

Types examined.—Holotype male Australia, Victoria: Melbourne, 37°49′S, 144°58′E, 8 October 1956, A Neboiss (MV K7742). Paratype female, Kilsyth, 37°48′S 145°19′E, 11 October 1981, on fence, ME Roberts (MV K7741).

Other material examined.—AUSTRALIA: *South Australia*: 1 ♂, 1 ♀, 1 ♀ with eggsac, 4 juv., Adelaide foothills nr. Waite Campus (SAM NN13113–15); 1 ♀, 1 juv., Adelaide Parklands between Adelaide Zoo and Hackney Bridge (SAM NN13132); 4 ♂, 4 ♀, Belair (SAM NN13094–101); 1 ♀, Bolivar (SAM NN13139); 1 ♂, 3 ♀, Bridgewater, Mt Lofty Ranges (SAM NN13086–9); 1 ♀, Calpatanna Waterhole Conservation Park, Wedina Well (SAM NN13163); 2 ♂, 1 ♀, Cape St Albans Lighthouse, 5.25 km WNW, Kangaroo Island (SAM NN13068–70); 1 ♀, Carrieton Township, E side (SAM NN13161); 8 ♂, 4 ♀, 1 juv., Francis Swamp, mound spring near Leonard Bore (SAM NN1236–47); 1 ♀, Ceres, Furner (SAM NN13042); 1 ♂, Charleston Conservation Park (SAM NN13112); 2 ♂, 4 ♀, 2 juv., Chowilla, Nil Nil Bend (SAM NN617–9, NN13157–9); 2 ♂, 7 ♀, Cleland Conservation Park, cnr Wine Shanty & Pit Box tracks (SAM NN13102–11); 3 ♀, Conmurra, 4.4 km N telephone exchange (SAM NN13036–8); 1 ♂, Coorong area, 5 km ENE Tilley Swamp telephone exchange (SAM NN13047); 3 ♂, Coorong area, 1.5 km ENE Tilley Swamp telephone exchange (SAM NN13048–50); 3 ♂, Coromandel Valley (SAM NN1309–2); 1 ♂, Cox Scrub Conservation Park, 2 km S South tip (SAM NN13083); 1 ♀, Custon, 1.2 km S (SAM NN13056); 1 ♀, Flinders Ranges National Park, 1.7 km SW Wilpena Chalet (SAM NN13160); 2 ♀, Frances, 1.1 km NNE (SAM NN13054–5); 1 ♀ with eggsac, Greenfield Wetlands, Salisbury (SAM NN13140); 1 ♂, Inglewood Homestead, 1.3 km SSE (SAM NN13065); 1 ♀, King Fisher Spring, Dalhousie Springs (SAM); 1 ♀ with eggsac, Klemzig (SAM NN13131); 1 ♀, Kongorong Forest Reserve, 16.4 km WNN Headquarter (SAM NN13026); 1 ♀, Kongorong Forest Reserve, 17.3 km WNN Headquarter (SAM NN13025); 14 ♀, 1 juv., Kongorong, 14.5 km W telephone exchange (SAM NN13011–24); 1 ♀, Lake Malata South (SAM NN13162); 2 ♂, 4 ♀, Largs North (SAM NN13133–8); 1 ♂, Lucindale (SAM NN13043); 1 ♂, 1 ♀, 1 juv., Magill CAE, Adelaide (SAM NN13126–7); 1 ♂, 1 ♀, Magrath Flat, 9 km NW (SAM



Figures 63–69.—*Artoria victoriensis* new species: Male holotype from Melbourne, Vic (MV K7742): 63. habitus; 64. eye arrangement; 65. left pedipalp, ventral; 66. left pedipalp, retrolateral; 67. apical part of bulb (MV K7774, from near Baxter, Vic). Female: 68. ventral view of epigynum (MV 7741, from Kilsyth, Vic); 69. dorsal view of epigynum (MV 7740, from Yarra Valley Park, Vic). Scale bar: (63) 1.18 mm, (64) 1.01 mm, (65, 66) 0.38 mm, (67) 0.27 mm, (68, 69) 0.33 mm.

NN13148–9); 1 ♂, Melville Gully, Belair National Park (SAM NN13093); 1 ♀, Millewa Road, NE Hahndorf (SAM NN13085); 2 ♀, 1 juv., Millicent Airport, 11 km SW (SAM NN13027–8); 1 ♀, Millicent Airport, 14 km SW (SAM NN13029); 3 ♀, Minecrow trip point, NNE (SAM NN13044–6); 4 ♀, 2 ♀ with spiderlings, Mitcham (SAM NN13116–21); 12 ♀, Monarto Zoo (SAM NN14200–11); 1 ♀, Mt Benson telephone exchange, 8.7 km ENE (SAM NN13039); 1 ♂, 2 juv., Mt Compass, 21 km ESE (SAM NN13080); 1 ♀, Mt Compass, 22 km ESE (SAM NN13082); 1 ♂, Mt Compass, 9 km E (SAM NN13081); 3 ♂, Mt Rough, 12.1 km NNE (SAM NN13051–3); 1 ♂, Muston, Kangaroo Island (SAM NN13067); 1 ♂, 1 juv., Muston, Kangaroo Island, in midchannel of Pelican Lagoon (SAM NN13066); 2 ♀, Myponga, Mt Lofty Ranges (SAM NN13154–5); 1 ♀, Nappyalla (SAM NN13146); 1 ♂, 1 juv., nr. Pyap (SAM NN13151); 1 ♀, 1 juv., Old Kings Station, 2 km W (SAM NN13147); 1 ♂, Parawa, 2 km WNW (SAM NN13078–9); 5 ♂, 1 ♀, Parawa, 5 km ENE (SAM NN13072–77); 1 ♀, Penola Forest Reserve, 19.7 km NW Headquarter (SAM NN13030); 5 ♀, 1 juv., Penola Forest Reserve, 5 km NNE Headquarters (SAM NN13031–5); 1 ♀, Point Sturt, Lake Alexandrina (SAM NN13150); 1 ♂, Pooginagorie, 3.7 km NE (SAM NN13057); 2 ♀, 1 juv., Pyap, 2 km S (SAM NN13152–3); 2 ♀, Robe substation, 5.3 km S (SAM NN13040–1); 1 ♂, Scott Creek Conservation Park, MacKreath Creek (SAM NN13084); 5 ♂, Scott Creek, S of Morgan, near River Murray (SAM NN13141–5); 1 ♀, Tarkeerip, 6.1 km NE (SAM NN13064); 3 ♂, 3 ♀, Teatrick, 0.4 km WSW (SAM NN13058–63); 1 ♂, Tindale East Cave (AM KS52385); 1 ♀ with eggsac, Torrens Park, Magill CAE (SAM NN13122); 1 ♀, Torrens Park (SAM NN13123); 1 ♀, 1 ♀ with eggsac, Tusmore (SAM NN13124–5); 1 ♂, Victor Harbor (SAM NN13071); 3 ♂, Windsor Gardens (SAM NN13128–30). *New South Wales*: 30 ♂, 28 ♀, 1 juv., Coleambally

irrigation area (AM KS58090, KS58127, KS58164, KS58183, KS58235, KS58311, KS67076, KS67152, KS67342, KS67348, KS67354, KS67412, KS67506, KS67674, KS67678, KS67684, KS68649, KS68654, KS68662, KS67764, KS71271); 2 ♂, Crown residency, corner of New England Highway and Old Tamworth Road (AM KS82846, KS82854); 1 ♂, 2 ♀, Gilgandra, 39 km NNW, turnoff to Warrumbungles National Park (AM KS76597–8, KS76600); 1 ♀, Gin Gin, 2.5 km NW, on road to Riverview Station (AM KS76601); 1 ♂, Kwiambal National Park, East side, 150m South of Road (AM KS82858); 1 ♂, 1 ♀, McIntyre River, 2.8 km S of Boggabilla on Bruxner Highway (AM KS76603, KS76605); 1 ♀, Moree (AM KS32588); 1 ♂, 6 ♀, Wambianna Station, 7.5 km NW Gin Gin (AM KS76599, KS76602, KS76604, KS76606, KS76704); 1 ♀, Weemelah, S of, 150m North of bridge over Gingham Watercourse (AM KS76706). TASMANIA: 1 ♀, Bird Island, George Rocks (QVMAG 13:44297); 1 ♀, 1 ♀ with eggsac, Launceston (QVMAG 13:42995–6); 2 ♀ with eggsac, Launceston, 43 High St (QVMAG 13:44298); 1 ♀ with spiderlings, Launceston, Kings Meadows (QVMAG 13:42070); 1 ♂, Mt Chapell Island, Bass Strait (QVMAG 13:44299); 1 ♂, Waterhouse, South Croppies Point (QVMAG 13:43254). *Victoria*: 1 ♀, no exact location, 1923 (MV K7654); 1 ♀, no exact location ('Teacher's Training College') (MV K7649); 4 ♂, 3 ♀, Barmah Forest (WAM T53795, T55467); 1 ♂, near Baxter (MV K7774); 4 ♂, 4 ♀, Bendigo, LaTrobe University (CVIC); 1 ♀, 1 juv., Bendigo (MV K7658); 1 ♂, 2 ♀, 1 juv., Camberwell (MV K7653); 16 ♂, 4 ♀, Cohuna, Kervins Rd, Barr Ck (MV K8116); 2 ♀, 2 juv., Dalyenong Flora Reserve, Plantation Tk, 900 m S Gum Flat Tk (MV K9247, K9249); 2 ♀, 6 juv., Deep Ck, 7 km SSE Barmah (MV K8724); 1 ♂, 1 ♀, 2 juv., Deep Lead Flora Reserve, Deep Lead Rd, 800 m NE of Western Hwy (MV K9226); 1 ♂, 1 ♀, 3 juv., Deep Lead Flora Reserve, 800 m SW Garnard Park/Deep Lead Rd along Deep Lead Rd (MV K9045, K9232); 1 ♂, 1 ♀, 1 ♀ with spiderlings, 11 juv., Deep Ck, 7 km SSE Barmah (MV K8719, K9057); 2 ♂, East St Kilda (MV K7650); 3 ♀, Eynesbury Estate, Werribee (MV K9111, K9116, K9143); 1 ♀, Glen Waverley (MV K7651); 2 ♂, 1 juv., Glen Waverley, Watsons Rd (MV K7735); 4 ♀, Goulburn River, 12 km SSE Nathalia (MV K9029, K9041); 3 ♂, 1 ♀, Graytown, 200 m N of Heathcote/Nagambie Rd, 80 m W on drive to abandoned house (MV K9238, K9262); 1 ♀, Hamilton (MV K7657); 2 ♀, Kilsyth, 38 Mountfield Rd (MV K7644–5); 1 ♀ with spiderlings, 1 ♀ with 16 spiderlings, 2 juveniles, Kotupna Barmah Rd at Ellingtons Bridge (MV K8748, K9053); 1 ♀, 1 juv., Lerderderg Gorge, 9 km NNW of Bacchus Marsh (MV K7655); 6 ♂, 1 ♀, 2 juv., Maldon State Forest, 1.7 km along Red White and Blue Tk from Pullens Rd (MV K9246, K9250, K9253); 1 ♀ with spiderlings, Melbourne, in museum (MV K7656); 1 ♀, Merbein (AM KS32465); 1 ♂, Mitchell Link Tk, 200 m W Mitchell Tk (MV K9219); 1 ♀, Morrisons (MV K7648); 1 ♀, Murray Valley Hwy, Deep Ck Crossing (MV8775); 9 ♂, 6 ♀, 5 juv., Mt Bolangum Forest Reserve, 5.7 km N Andersons Rd, then 200 m on minor Tk (MV K9209, K9229, K9233); 1 ♂, Mt Ida Flora Reserve, 2.3 km NW along Rodney Tk from Dargie Tk (MV K9244); 1 ♀, Nangiloc (AM KS86408); 1 ♀, Natimuk (MV K7646); 1 ♀ with spiderlings, North Melbourne (MV K7647); 2 ♂, 2 ♀, Point Cook (MV K9113–4, K9135); 1 ♂, 1 ♀, Point Cook, opposite carpark 1 (MV K9106, K9108); 1 ♀, Point Cook, 100 m E of Recreation Beach area (MV K9109); 1 ♀, Point Cook, lower sanddune (MV K9112); 2 ♀, Point Cook, lower edge (MV K9115); 6 ♂, 6 ♀, 10 juv., Pomfrets Rd, 0.6 km S Picola-Katunga Rd (MV K8767, K9034, K9050); 7 ♂, 4 ♀, Potter Creek, 1.7 km S of Western Highway (MV K7652); 3 ♀, Rathbones Rd, 3.0 km E Booths Rd (MV K8727, K8746); 3 ♂, 5 juv., Reedy Lake Wildlife Reserve, 600 m W Goreys Rd along Reedy Lake Rd (MV K9259); 1 ♂, 1 juv., Reedy Lake Wildlife Reserve, 2.1 km S along Reedy Lake Rd from Davies Rd (MV K9297); 1 ♀, 1 ♀ with eggsac, Spring Gully (CVIC); 2 ♀, State Forest, 3.5 km NE Yambuna (MV K8708, 8759); 1 ♂, Upper Lurg (CVIC JSt104); 1 ♀, Werribee morticain Saltmarsh (MV K9110); 2 ♀, Werribee Treatment farm (MV K9117); 1 ♀ with eggsac, West Brunswick (MV K8119); 1 ♂, Western Railway Rd (MV K9133); 2 ♀, Williamstown (MV K9107); 2 ♀, Yarra Valley Park (MV K7740).

Etymology.—The species name is an adjective in apposition and refers to the Australian state Victoria, which represents the center

of the distribution and the state where the holotype was found.

Diagnosis.—Males of *A. victoriensis* can be distinguished from all other Australian *Artoria* by the unique shape of the median apophysis that resembles an upside-down sock in ventral view. The female epigynum is uniquely oval-shaped, with a white center and a sclerotized posterior rim reaching medially into this center.

Description.—*Male:* Carapace (Fig. 63): Brown, with distinct light brown median and submarginal bands; head region black; dark grey radial pattern; carapace covered with white setae, particularly dense in median and submarginal bands and between PE; four brown bristles in median band anteriorly of fovea; two rows of black bristles between PME; few black bristles posterolateral of PME. Sternum: Light brown with dense, dark grey pigmentation; sparsely covered with brown bristles mainly towards margins and frontal border. Labium: Brown; front end truncate and white. Chelicerae: Uniformly brown; covered with long white setae and few brown bristles; three retromarginal teeth, with the median largest; three promarginal teeth, with the basal smallest. Pedipalp (Figs. 65–67): Cymbium tip with approx. eight macrosetae; median apophysis shaped like an upside-down sock in ventral view; embolus stout and blunt, terminal apophysis a pointy hook (Fig. 67). Abdomen: Dark grey; yellowish-brown lanceolate heart mark in anterior half; irregular yellow patches lateral of heart mark; three yellow chevrons in posterior half; covered with white setae and few longer, brown bristles; venter yellow-brown with irregular dark grey patches; covered with white and fewer brown setae; anterior spinnerets black, posterior spinnerets yellow-brown. Legs: Leg formula IV > I > III > II; light brown, with distinct dark grey annulation which is in particular distinct on lighter ventral side of legs; spination of leg I (based on holotype MV K7742): Femur: 3 dorsal, 1 apicoprolateral; tibia: 3 ventral pairs, 2 prolateral; metatarsus: 3 ventral pairs, 2 prolateral, 1 apicoventral, 1 apicoretrolateral.

Female: Carapace: As male, more brown bristles in median band anteriorly of fovea. Sternum: Yellowish-brown with dense, dark grey pigmentation; sparsely covered with long brown bristles and few brown setae. Labium: as male. Chelicerae: Uniformly dark brown; covered with long white setae and few brown bristles; dentition as male. Epigynum (Figs. 68–69): Ventral view: oval shaped, wide sclerotization reaching from posterior margin into center (Fig. 68); dorsal view: large oval spermathecae, copulatory ducts connected laterally; small spermathecal organs (Fig. 69). Abdomen: As male, light pattern less distinct; venter yellow-brown few dark grey patches in particular posterior of epigastric furrow; covered with white and fewer brown setae; all spinnerets light brown. Legs: Leg formula IV > I > III > II; coloration as male, annulations less distinct; spination of leg I (based on paratype MV K7741): Femur: 3 dorsal, 1 apicoprolateral; tibia: 3 ventral pairs, 1 prolateral; metatarsus: 3 ventral pairs, 3 prolateral, 1 apicoventral.

Measurements: Male holotype MV K7742 (female paratype MV K7741): TL 5.55 (6.5), CL 3.0 (3.0), CW 2.2 (2.2). Eyes: AME 0.08 (0.10), ALE 0.08 (0.09), PME 0.30 (0.30), PLE 0.20 (0.22). Row of eyes: AE 0.50 (0.54), PME 0.76 (0.80), PLE 0.98 (1.00). Sternum (length/width) 1.40/1.20 (1.45/1.2). Labium (length/width) 0.42/0.4 (0.44/0.42). AL 2.4 (3.1), AW 1.9 (2.1). Legs: Lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 1.05 + 1.05 + — + 1.05 = 3.15, I 1.75 + 2.45 + 1.55 + 0.85 = 6.60, II 1.7 + 2.15 + 1.30 + 0.7 =.5.85, III 1.6 + 2.0 + 1.6 + 0.7 =.5.9, IV 2.1 + 2.75 + 2.4 + 1.0 = 8.25 (Pedipalp 1.05 + 1.0 + — + 0.75 = 2.8, I 1.8 + 2.35 + 1.3 + 0.75 = 6.2, II 1.7 + 2.15 + 1.2 + 0.75 = 5.8, III 1.65 + 1.85 + 1.5 + 0.7 = 5.9, IV 2.2 + 2.75 + 2.45 + 0.95 = 8.35).

Variation: Males (females) (range, mean ± s.d.): TL 3.5–6.3, 4.6 ± 1.0; n =10; CL 1.9–3.3, 2.6 ± 0.5; n =11; CW 1.4–2.3, 1.9 ± 0.3; n =11 (TL 5.2–8.4, 6.4 ± 0.7, n = 19; CL 2.2–3.6, 3.0 ± 0.4, n =20; CW 1.6–2.8, 2.2 ± 0.3; n =20).

Distribution and habitat preferences.—This species is most common in temperate Victoria, South Australia and New South Wales (Fig. 70), where it can typically be found in open, moderately moist habitats. It is also common in suburban Adelaide and Melbourne. Within the South Australian artesian springs, *A. victoriensis* has been found at Kingfisher Springs in the Dalhousie Springs complex and at Big Depot Springs in the Francis Swamp complex (Table 1), where it

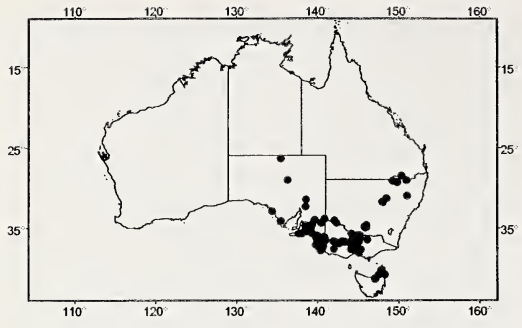


Figure 70.—Records of *Artoria victoriensis* new species in Australia.

inhabits low open vegetation on saturated substrates.

Remarks.—It is possible that the artesian springs populations were established by human introduction as this species is most common in highly populated suburban regions in South East Australia and has been found at artesian springs that are frequented by tourists. Females with eggsac or spiderlings have been found mainly in November and December, but also in September, February, and March.

DISCUSSION

The wolf spider fauna at South Australian artesian springs comprises a number of wetland dependent species that have broad distributions, as well as others that appear to be more closely associated with the springs. Of the nine lycosids recorded during this study, seven occur in other Australian and overseas wetland habitats, such as river floodplains and lake shores (*A. howquaensis*, *A. victoriensis*, *H. crispipes*, *H. diyari*, *H. kuyani*, *V. arenaris*, and *V. goyderi*). In contrast, *V. fontis* and *T. arabanae* appear to be largely restricted to artesian springs and have only rarely been found in other wetland habitats.

The biology and habitat preferences of the artesian spring species are poorly understood. *Venatrix goyderi* and *H. crispipes* are mostly found at bore drains and it is possible that these species are recent arrivals to the region as they are rarely found at undisturbed artesian springs. The high dispersal capability of both species is also supported by their wide distribution, that includes offshore islands and island states including New Zealand. *Venatrix arenaris* and *V. fontis* are both nocturnal species and are found mainly in the permanent wetland areas of the spring vent and tail, while the remaining species appear to be diurnal with some inhabitating the margins of the springs.

Artesian spring wolf spiders in South Australia, like many lycosids, are dependent on a constant supply of water. For example, some lycosids are exclusively found near rivers (e.g. Manderbach & Framenau 2001, Framenau et al. 2002), lakes (Greenstone 1983), or coastal shore lines (e.g. McKay 1974; Döbel et al. 1990; Morse 1997, 2002). Certain behavioral adaptations may facilitate colonization of habitats near water bodies, such as mobile brood care, the capability to walk on the surface of the water (e.g. Ehlers 1939), and the ability to use polarized light for orientation (Papi 1955; Papi & Tongiorgi 1963; Ortega-Escobar & Muñoz-Cuevas 1999). Most riparian species have been recorded to use water bodies as retreats when predators are present and they can stay under water for a considerable period of time by trapping air in the dense cover of setae surrounding their body (V.W. Framenau & T.B. Gotch pers. obs.). However, an intriguing aspect of the lycosids associated with artesian springs is how they colonize these tiny, isolated habitats in an otherwise inhospitable environment, given that several species are known to be extremely susceptible to even short periods of hot, dry conditions.

Short distance dispersal by ballooning within spring groups (i.e., where springs are separated by 50–1000 m) has been observed after monsoonal storms (T.B. Gotch pers. obs.), and dispersal may also occur during infrequent localized floods when spiders could float between springs. However, it is unknown how spiders move between more distant spring complexes (i.e., over 10's to of 100's km), as these species are unable to survive for more than a few hours away from free water during summer (T.B. Gotch pers. obs.). It is possible that long distance ballooning may occur after summer rainfall when climatic conditions are optimal for ballooning, and/or that waterborne spider movement occurs as a result of extensive regional flood events. However, these events occur very rarely in the case of regional floods, while the chance of successful long distance ballooning must be considered very small, given that springs represent tiny targets, and the prevailing wind directions are largely west to east. Current research assessing the genetic differences among artesian

spring lycosid populations along flood channels in comparison to more remote populations is aimed at testing indirectly whether one of these dispersal methods is more likely than the other.

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THE PREY OF A LITHOPHILOUS CRAB SPIDER *XYSTICUS LOEFFLERI* (ARANEAE, THOMISIDAE)

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ABSTRACT. The natural prey of the crab spider *Xysticus loeffleri* Roewer 1955, living under stones, was studied. The percentage of feeding specimens in the population studied was low (1.4–4.6%), and it declined with the beginning of the breeding period. Investigation has shown that *X. loeffleri* is a polyphagous predator. Representatives of twelve arthropod orders were found in its diet. Arachnids (opilionids and spiders) formed the major food component constituting ca. 70% of prey captured. No insect order was present in any considerable percentage. Several worker ants were observed as prey suggesting that *X. loeffleri* is a myrmecophagic spider. Seven incidences of cannibalism were recorded, which all involved predation on adult conspecifics (two males and five females). The length of prey killed by *X. loeffleri* ranged between 1.25 and 15.00 mm (mean 4.68 mm) and constituted from 14.3–187.5% (mean 64.2%) of length of their captors. The most frequently captured prey were small arthropods not exceeding half the size of the spiders.

Keywords: Crab spiders, lithophilic, prey, opilionids, cannibalism

Thomisidae Sundevall 1833 (the true crab spiders) is one of the largest families of spiders including about 2000 species (Coddington & Levi 1991). Most crab spiders are typical cursorial hunters which do not use silk for prey capture; instead, they lie in ambush and wait until prey comes within reach of their long forelimbs and seize it. In many terrestrial communities thomisids are among the dominant invertebrate predators, exerting significant pressure on prey populations (Young & Edwards 1990; Bogya & Mols 1996; Jennings & Cutler 1996; Nyffeler 1999). Despite the common occurrence and predatory significance of crab spiders, few studies have addressed their natural diet. A survey of the spider literature revealed only eleven works that included quantitative data on the prey of Thomisidae (Broekhuysen 1948; Nyffeler & Benz 1979; Morse 1979, 1981, 1983; Ricek 1982; Lubin 1983; Dean et al. 1987; Agnew & Smith 1989; Castanho & Oliveira 1997; Romero & Vasconcellos-Neto 2003). All crab spiders studied in these works inhabit vegetation or ground litter strata. However, many thomisids are known to live under stones. Unlike most cursorial spiders, which use spaces under rocks only as temporary shelters, a variety of thomisid species spend their entire life span here. Physical and microclimatic conditions of this microhabitat differ strongly from those of the surrounding environment (Cloudsley-Thompson 1955). These conditions influence the composition of local invertebrate fauna and thereby the prey available to crab spiders. What is the prey spectrum of the Thomisidae living underneath rocks? How much does it differ from the diets of spiders occurring in other microhabitats?

To answer these questions, I conducted an investigation of the natural prey of the crab spider *Xysticus loeffleri* Roewer 1955, which is among the commonest spiders found under stones in Azerbaijan. The range of this species also includes Turkey, Iran, Middle Asian republics of the former Soviet Union, and Afghanistan (Marusik & Logunov 1994). This is a pronounced lithophilous spider. Over the last several years I observed thousands of individuals of *X. loeffleri* under rocks, while none was seen on the open surface. Like most thomisids, *X. loeffleri* are typical ambushers which spend most of their time sitting immobile on the underside of rocks awaiting prey. These spiders have an annual life cycle (Guseinov, unpubl. data). Adult females are present from September through May, while males are found only in autumn, which ap-

pears to be the mating season (one mating pair was observed). Oviposition usually begins in early spring and continues to the end of May. Females spin hemispherical egg sacs on the underside of rocks which they guard until the young emerge (Guseinov, unpubl. data). Some females were observed guarding a second egg sac near the first empty cocoon. So, *X. loeffleri* seems to be an iteroparous spider.

METHODS

Investigation was carried out at "Bailov Park" in Baku City, Azerbaijan (40°38′N; 49°83′E). This habitat was characterized by pines *Pinus eldaricus* Medw., with an undergrowth of short ephemeral grasses, predominantly of *Calendula persica* C.A.M., *Senecio vernalis* W. & K., *Medicago denticulata* W., *Carduus arabicus* Jaqu., *Hirschfeldia incana* (L.), *Erodium cicutarium* (L.), *Hedypnois cretica* W., *Pterotheca marschalliana* (Rchb.), *Torularia contortuplicata* (Stapf.), *Ornithogalum gossonei* Ten., *Gagea tenuifolia* (Boiss.), *Poa bulbosa* L., *Anisanthea rubens* (L.), *Aegilops biuncialis* Vis., *Hordeum leporinum* Link., *Koeleria phleoides* (Vill.), *Bromopsis* sp. Stones were prevalent on the ground in the study area, with *X. loeffleri* being among the commonest spider species under these stones.

Two consecutive generations of *X. loeffleri* were observed throughout the study period. Spiders of the first generation were studied from 14 February–2 April 1997. Seven surveys were conducted during this time (approximately once a week), which took about 13 hours. Spiders of the second generation were investigated from 9 September 1997–21 May 1998. Thirty-eight surveys were made during this period (on average one per week, but numbers of surveys varied greatly between different months: from one in September and October, when spiders were rare under stones, to six-seven in winter months, which were the peak of spider abundance). Over 56 hours were spent on these surveys.

All surveys were done in daylight hours between 11:00 and 17:00. During surveys, rocks in the study area were overturned and the mouthparts of each individual *X. loeffleri* found were inspected with a 4 power lupe to prevent small prey being overlooked. Stones were chosen randomly, but because the study area was not large (ca. 2500 m^2) about 60–70% of all appropriate sized stones (15–80 cm in diameter) in the study area were examined during each survey. Considering the low mobility of *X. loeffleri* it is highly likely that most spiders were observed repeatedly throughout the study period. Specimens with prey in their chelicerae were placed in separate vials containing 75% ethyl alcohol and brought back to the laboratory for measurement and prey identification. Spiders without prey were left in the field. At the same time, all spiders observed were classified into the following groups: (1) males; (2) solitary females; and (3) females guarding their egg sacs. During every survey, the numbers of spiders with and without prey were counted separately for each of these groups. A few additional prey items were collected during occasional observations in the spring and autumn of 1999 and the spring of 2000. Voucher specimens of *X. loeffleri* and their prey items were deposited at the Institute of Zoology of the Academy of Sciences of Azerbaijan.

A chi square test was used for statistical treatment of the data. Only raw numbers (count data), not proportions, were used for analysis throughout the paper.

RESULTS

Feeding percent.—Only 16 *X. loeffleri*-males were seen throughout the study period (none with prey). Thus, they are omitted in the following consideration and all subsequent references are to females.

Of 2023 female observations made during the study period, only 80 (4.0%) included spiders with prey in their chelicerae. Females of first generation were observed feeding significantly less frequently (6 prey records of 423 observations [1.4%]) than females of second generation (74 prey records of 1600 observations [4.6%]) ($\chi^2 = 8.232$; $df = 1$; $P < 0.001$). Among females of the second generation, spiders observed in winter months (December–February) had the lowest feeding percentages compared to spiders observed in autumn (September–November) and spring (March–May) (Table 1); the difference is significant ($\chi^2 = 4.168$; $df = 1$; $P < 0.05$). Although these winter-feeding females exhibited higher percent of prey capture compared to solitary females of the first generation, the difference is not significant ($\chi^2 = 1.857$; $df = 1$; $P > 0.1$). The percentage of feeding speci-

Table 1.—Monthly variation in the number of spiders observed feeding in second generation female *Xysticus loeffleri*. Females found attending egg sacs are referred to as guarding. Females found without egg sacs are referred to as solitary.

Month	Number of surveys	Number of spiders observed			Number of spiders feeding			Percentage of spiders feeding		
		Solitary ♀♀	Guarding ♀♀	Σ	Solitary ♀♀	Guarding ♀♀	Σ	Solitary ♀♀	Guarding ♀♀	Σ
Sep./Oct.	2	25	—	25	2	—	2	8.0	—	8.0
Nov.	3	118	—	118	10	—	10	8.5	—	8.5
Dec.	7	357	—	357	18	—	18	5.0	—	5.0
Jan.	6	324	—	324	10	—	10	3.1	—	3.1
Feb.	7	284	—	284	19	—	19	6.7	—	6.7
Mar.	4	117	—	117	10	—	10	8.5	—	8.5
Apr.	5	27	213	240	2	2	4	7.4	0.9	1.7
May	4	4	131	135	—	1	1	—	0.8	0.7

mens among guarding females of second generation (3 prey records of 344 observations [0.9%]) was significantly lower than among their solitary counterparts (71 prey records of 1256 observations [5.7%]) ($\chi^2 = 12.929$; $df = 1$; $P < 0.001$). Guarding females of first generation were also observed feeding less frequently (none found with prey in 89 observations) than solitary females (6 prey records of 334 observations [1.8%]). However, these data are not sufficient for statistical analysis.

Prey composition.—Altogether 88 prey items were taken from *X. loeffleri*. These were distributed among twelve arthropod orders (Table 2). Arachnids formed the major component in the food of *X. loeffleri* (ca. 70%). Opiliones (Phalangiidae, *Opilio* spp.) was the dominant prey order constituting 40.9% of the total prey. Spiders represented by 10 species from 5 families accounted for 28.4% of all prey caught (Table 3). Thomisidae were most abundant (52% of all spiders killed), followed by Theridiidae Sundevall 1833 (28%), Gnaphosidae Pocock 1898 (12%), and Oecobiidae Blackwall 1862 (8%). Seven conspecifics were captured by *X. loeffleri*, including five females and two males.

Insects comprised 29.5% of all prey records. However, no insect order was present in any considerable percentage (more than 10%). Most abundant were Coleoptera and Hymenoptera, 9% and 8% respectively. Coleoptera consisted of four adult beetles (Carabidae, Curculionidae, Histeridae) and four larvae (Carabidae). Hymenoptera included two parasitic wasps (Ichneumonidae) and five worker ants (Formicidae) represented by four *Messor denticulatus* Lepeletier and one *Leptothorax* sp. The remaining insects comprised three Hemiptera (Lygaeidae, Nabidae, Pyrrhocoridae), two Thysanura (Machilidae, Lepismatidae), two Collembola (Sminthuridae), one Psocoptera (unidentified), one Homoptera (Aphididae), one Embiomorpha (Oligotomidae: *Haploembia solieri* Ramb.) and one Lepidoptera larvae (Noctuidae). The only centipede captured by *X. loeffleri* was a lithobiid.

Feeding phenology.—The study period covered the entire life span of adult females of the second generation and allowed me to consider seasonal changes in their diet. As seen from Table 4, there are differences in monthly distribution of some prey taxa captured. While most arthropods were primarily caught in winter (December–February), adult beetles and ants were captured only in autumn (September–November) and spring (March–May). This difference becomes more striking if we examine the distribution of prey taxa captured between periods reflecting changes in the temperature regime. Harvestmen and most other arthropods were caught only during the cool season (late autumn–early spring). In contrast, Formicidae and adult Coleoptera were captured only during the warm periods (early autumn and late spring). Spiders were caught throughout the course of the study.

Length of prey.—Eighty-two prey items were measured. Their lengths varied from 1.25–15.00 mm (mean ± SD: 4.68 ± 3.10 mm) and constituted from 14.3–187.5% (64.2

Table 2.—Prey taken by *Xysticus loeffleri* under stones. The larvae of holometabolous insects are marked with an asterisk. Otherwise, holometabolous insects are adults.

Prey taxa	N	%
Insecta		
Collembola		
Sminthuridae	2	2.3
Thysanura		
Machilidae	1	1.1
Lepismatidae	1	1.1
Embiomorpha		
Oligotomidae	1	1.1
Psocoptera		
Unidentified	1	1.1
Homoptera		
Aphididae	1	1.1
Hemiptera		
Lygaeidae	1	1.1
Nabidae	1	1.1
Pyrrhocoridae	1	1.1
Coleoptera		
Carabidae	1	1.1
Carabidae*	4	4.5
Curculionidae	2	2.3
Histeridae	1	1.1
Hymenoptera		
Ichneumonidae	2	2.3
Formicidae	5	5.7
Lepidoptera		
Noctuidae*	1	1.1
Arachnida		
Opiliones		
Phalangiidae	36	40.9
Araneae		
Oecobiidae	2	2.3
Theridiidae	7	8.0
Gnaphosidae	3	3.4
Thomisidae	13	14.8
Chilopoda		
Lithobiomorpha		
Lithobiidae	1	1.1
Total	88	100.0

± 42.2%) of the size of their captors which ranged from 4.75–9.00 mm (7.37 ± 0.95 mm). Size distribution of prey is shown in Fig. 1. The most abundant were small arthropods not exceeding half the size of the spiders, which accounted for 53.7% of the total prey measured. To this group belonged collembolans, an aphid, opilionids, a *Leptothorax* ant, oecobiids, theridiid spiders, and conspecific males. Medium-sized prey (from 50–100% of spider body length) constituted 25.6% and included a psocopteran, curculionid beetles, a lygaeid bug, *Ozyptila*, *Xysticus* sp., gnaphosid spiders, some *Messor* ants and some conspecific females. One fifth of the prey of *X. loeffleri* (20.7%) consisted of large arthropods exceeding the length of their captors. These were thysanurans, an embiomorpha, nabid and pyrrhocorid bugs, carabid beetles, lepidopteran larvae, ichneumonid wasps, a lithobiid centipede, some *Messor* ants and some conspecific females.

DISCUSSION

As is typical of cursorial spiders (Nentwig 1986; Nyffeler et al. 1994), the percentage of feeding specimens in the population of *X. loeffleri* was low. The difference in percentage of feeding specimens between two generations is probably due to the fact that most of the observations of first generation females were made in February and early March, characterized by low temperatures, which probably resulted in inhibited prey activity and, as a consequence, low prey capture by spiders. This assumption is confirmed by the data on seasonal changes in the feeding percent of solitary females of the second generation. Spiders observed in winter months were found feeding significantly less frequently than spiders observed in autumn and spring. In contrast, the difference between these winter-feeding females and solitary females of first generation was not significant. Despite the fact that egg-guarding females occurred only in warm period (late spring), in both years the percentage of feeding specimens among them was lower than among solitary females. Unlike females of an anthophilous thomisid, *Misumena vatia* (Clerck 1757), which build their reproductive nests on leaves, far away from their typical hunting site, flowers (Morse 1985), *X. loeffleri* females construct their egg sacs on the underside of rocks i.e. at the same site where they usually forage. This enables the spiders to catch prey during egg guarding period. However, most thomisids are pronounced ambushers, and the choice of prey-rich foraging sites is an important trait of their

Table 3.—Spiders captured by *Xysticus loeffleri*.

Spider species	N	Sex-age stage
Oecobiidae		
Oecobius maculatus Simon	2	1 submale, 1 female
Theridiidae		
Enoploghatha gemina Bosmans et Van Keer	5	1 male, 3 females, 1 subfemale
Enoplognatha quadripunctata Simon	1	1 female
Theridion melanurum Hahn	1	1 female
Gnaphosidae		
Drassodes lapidosus (Walckenaer)	1	1 juvenile
Haplodrassus dalmatensis (L. Koch)	2	2 juveniles
Thomisidae		
Ozyptila tricoloripes Strand	3	1 submale, 2 females
Xysticus loeffleri Roewer	7	2 males, 5 females
Xysticus sp.	3	3 females

feeding strategy (Morse & Fritz 1982; Beck & Connor 1992). While guarding their eggs, female *X. loeffleri* have no opportunity to change their locations apparently resulting in the declined percent of prey capture compared to solitary females.

Investigation has shown that *X. loeffleri* is a polyphagous predator feeding on a wide range of prey. The predominance of opilionids in its diet is unusual. To my knowledge no spiders are known to feed on harvestmen in any considerable percentage. Thus it might be suspected that *X. loeffleri* specializes on opilionids as an unusual less available prey to spiders. However, this fact is more likely due to the abundance of harvestmen in the environment of *X. loeffleri*. The density of potential prey has not been quantified, but, subjectively, opilionids appeared to be one of the most numerous arthropods inhabiting spaces under stones. Furthermore, some other hunting spiders, such as *Philaeus chrysops* (Poda 1761), *Ozyptila tricoloripes* Strand 1913, *Thanatus kitabensis* Charitonov 1946 and *Drassodes lapidosus* (Walckenaer 1802), were repeatedly seen feeding on harvestmen in this microhabitat. In contrast, only two opilionids were found among about 1500 prey organisms

Table 4.—Monthly distribution of prey taxa captured by second generation female *Xysticus loeffleri*. In round brackets are the mean monthly temperatures (°C). In square brackets are the numbers of spider observations made during a given month.

Prey taxa	Sep. (18.8) [8]	Oct. (17.5) [17]	Nov. (10.8) [118]	Dec. (6.2) [357]	Jan. (3.9) [324]	Feb. (3.0) [284]	Mar. (6.6) [117]	Apr. (12.9) [240]	May (14.2) [135]
Opiliones			3	6	6	13	3		
Araneae	1		3	6	2	2	5	1	
Formicidae			1					2	1
Coleoptera (adult)		1	1					1	
Coleoptera (larvae)				3		1			
Ichneumonidae							2		
Hemiptera				1	1				
Homoptera			1						
Thysanura			1			1			
Collembola				2					
Psocoptera						1			
Lepidoptera					1				
Lithobiomorpha						1			

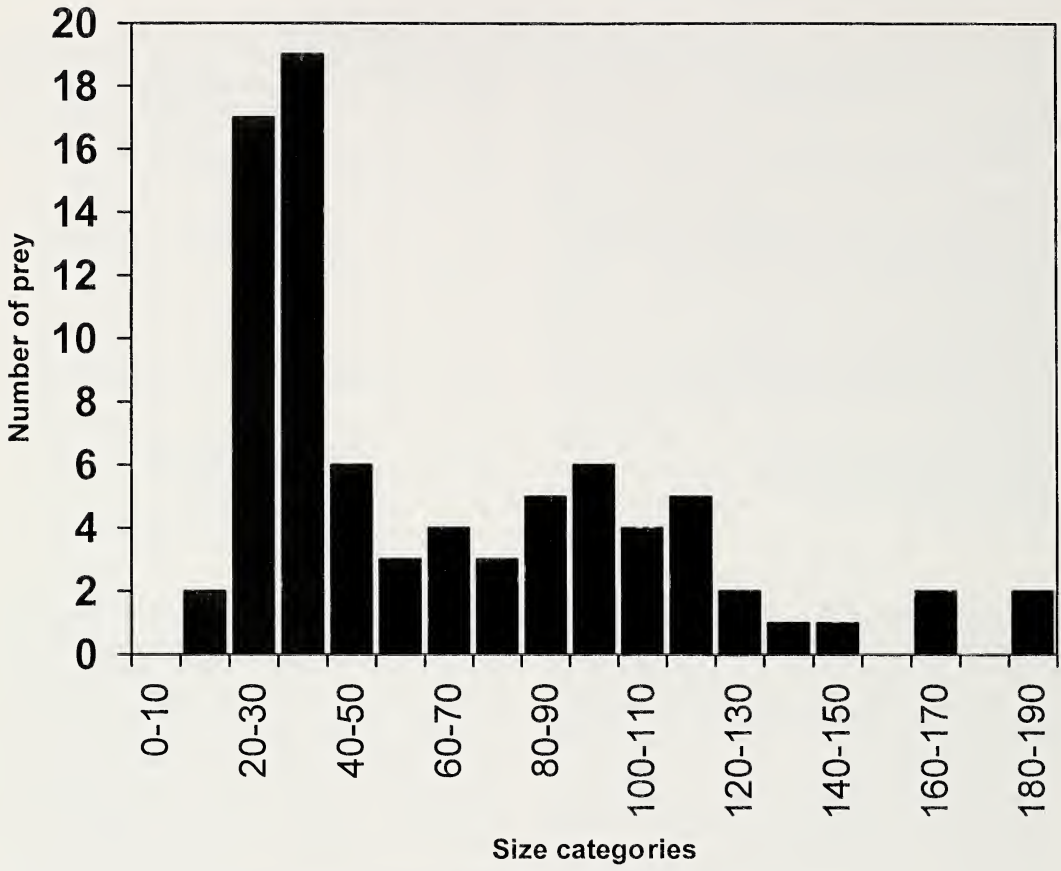

Figure 1.—Distribution of prey in different size categories.

taken from various species of cursorial spiders frequenting other microhabitats (bare ground, herbaceous vegetation, ground litter, bark of trees, stone walls etc.) in the vicinity of Baku City in years 1997–1999 (Guseinov 1999). Thus, opilionids do not seem to be invulnerable prey to cursorial spiders, which probably take them in proportion to their abundance. Which, in turn, apparently depends on the type of microhabitat occupied by the spiders. It is remarkable that some insects (Thysanura, Embiomorpha, Coleoptera larvae) as well as a lithobiid centipede captured by *X. loeffleri* are also characteristic inhabitants of spaces under rocks, but usually lacking among the prey of spiders from other microhabitats (Bristowe 1941; Nentwig 1987; Nyffeler 1999). On the other hand, winged insects (especially Diptera), constituting a substantial part of the food of most cursorial spiders (Nentwig 1986; Guseinov 1997), are almost entirely missing in the diet of *X. loeffleri*. The tight, constricted spaces under rocks are not favorable environment for winged insects and, as a consequence, crawling arthropods prevail among the prey of *X. loeffleri*.

The high proportion of spiders in the diet of *X. loeffleri* is also probably due to their abundance in its habitat. Many spiders are known to occur under stones and during the cool season their number may even increase in this microhabitat. Although *X. loeffleri* captured mainly cursorial spiders, several individuals of the family Theridiidae most of which are typical web builders were also eaten. The webs of spiders serve not only for prey capture, but are also as efficient defensive devices. Thus only a small minority of spiders are able to invade alien webs and prey upon their residents (Jackson 1992). Most theridiids spin large three-dimensional space-webs. However, the habits of theridiids captured by *X. loeffleri* are apparently different from this common pattern of life style. These spiders were fre-

quently found on the underside of rocks without any silk or with several short threads laid down over the substrate. Therefore, they do not appear to be a more "difficult" prey for predators than typical cursorial spiders.

Xysticus loeffleri is a cannibalistic spider with conspecifics constituting 8% of its prey. Such a high rate of cannibalism is unusual for crab spiders which generally do not hunt conspecifics (Bristowe 1941; Broekhuysen 1948; Morse 1981, 1983; Ricek 1982), but similar to rates of cannibalism of other cursorial spiders from families Salticidae Blackwall 1841 (Jackson 1977), Lycosidae Sundevall 1833 (Schaefer 1974; Framenau et al. 1996), Oxyopidae Thorell 1870 (Turner 1979; Nyffeler et al. 1987a, 1987b, 1992) and Sparassidae Bertkau 1872 (Henschel 1994). Moreover, it should be emphasized that most conspecifics killed by *X. loeffleri* were mature females (71.4%), with size comparable to that of their captors, whereas in cannibalistic lycosid spiders larger individuals usually catch smaller ones (Edgar 1969; Hallander 1970; Yeargan 1975). But such a situation is excluded in the case of *X. loeffleri* because the population consisted of individuals of the same age (Guseinov, unpubl. data).

Despite the fact that worker ants are not acceptable prey to most cursorial spiders (Nentwig 1986), they were found in the diet of *X. loeffleri*, though in low proportion (5%). At the same time, it is known that worker ants compose a considerable portion (30–35%) of the food of some species of the genus *Xysticus* (Nyffeler & Benz 1979; Guseinov 1997). It should be clarified, therefore, whether *X. loeffleri* is a poor predator of ants or if ants are simply underrepresented in the species' habitat. Some data correspond to the second assumption. All ants were caught in early autumn and late spring. Yet, the number of prey records at that time was significantly lower than that in the cool season because the frequency of surveys conducted was low in early autumn and most females had oviposited in late spring resulting in a low prey capture among those females. Thus one can suppose that if the number of prey records in warm periods was greater, then the proportion of observations of ants in the diet of *X. loeffleri* might be larger.

Although small arthropods predominated in the diet of *X. loeffleri*, it does not signify that spiders prefer prey of this size category. This fact is more likely due to the abundance of small prey in the spiders' habitat, since the dominant prey type, opilionids, consisted primarily of small specimens. Probably the appropriate prey size range for *X. loeffleri* is within 20–120% of spiders' body size, since larger or smaller organisms were rare in its diet (see Fig. 1).

Earlier students of crab spiders have pointed out that thomisids often catch very large prey (Lovell 1915; Hobby 1931, 1940; Turner 1946). In feeding expiriments, most cursorial spiders preferred prey not exceeding their own size, whereas the crab spiders, *Xysticus cristatus* (Clerck 1757), readily accepted insects two times larger than themselves (Nentwig & Wissel 1986). Although *X. loeffleri* sometimes captured very large arthropods, most of its prey (ca. 80%) were not exceeding spider length. This is similar to prey size spectra of "typical" cursorial hunters (Salticidae, Lycosidae, Oxyopidae, Sparassidae) (Nentwig & Wissel 1986; Hayes & Lockley 1990; Nyffeler et al. 1992; Henschel 1994), but in striking contrast to flower-dwelling Thomisidae, which commonly feed on prey significantly larger than themselves (Nentwig & Wissel 1986; Guseinov 1999). Experimental investigation is required to clarify whether this difference is due to the difference in size of prey available on flowers and under stones or anthophilous crab spiders are superior toward *X. loeffleri* in catching large prey.

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FIRST SPECIES OF *HESPEROPILIO* (OPILIONES, CADDOIDEA, CADDIDAE) FROM SOUTH AMERICA

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ABSTRACT. This paper describes the first South American species of *Hesperopilio* Shear 1996, a genus previously known from a single species, *H. mainae* Shear 1996, from Western Australia. The new species is known from a single adult female and is one of the largest and most colorful species of the superfamily Caddoidea. The generic diagnosis of *Hesperopilio* is emended to accommodate information from the new species.

RESUMEN. En el presente artículo se describe la primera especie sudamericana de *Hesperopilio* Shear 1996, un género previamente representado por una sóla especie, *H. mainae* Shear 1996, de Western Australia. La nueva especie se conoce de una sóla hembra adulta y es de las más grandes y más coloridas de la superfamilia Caddoidea. La diagnosis genérica de *Hesperopilio* se enmienda para acomodar la información de esta nueva especie.

Keywords: *Hesperopilio*, Opiliones, harvestman, Chile, systematics, South America, new species

Until recently, the acropsopilionine faunas of the Australian Region (*Acropsopilio* Silvestri 1904, *Austropsopilio* Forster 1955, *Hesperopilio* Shear 1996, *Tasmanopilio* Hickman 1957), South Africa (*Caddella* Hirst 1925) and the New World (*Acropsopilio*) displayed little generic overlap, with the principal exception being the presence of *Acropsopilio* in the Australian Region, the Americas and Japan. However, a new species from the "Australian" genus *Austropsopilio* was recently discovered in southern South America (Cokendolpher & Maury 1990; Shultz & Cekalovic 2003), thus further increasing the similarity of acropsopilionine faunas of the two continents. This paper continues this trend by describing a new South American species of *Hesperopilio*, a genus formerly known from one species from Western Australia, *H. mainae* Shear 1996. The new species is substantially larger and more colorful than the Australian species, and its discovery further highlights the close biogeographic connection between the Australian and South American opilion faunas.

The material examined for this study is lodged in the American Museum of Natural History, New York (AMNH).

SYSTEMATICS

Hesperopilio Shear 1996

Hesperopilio Shear, 1996: 456.

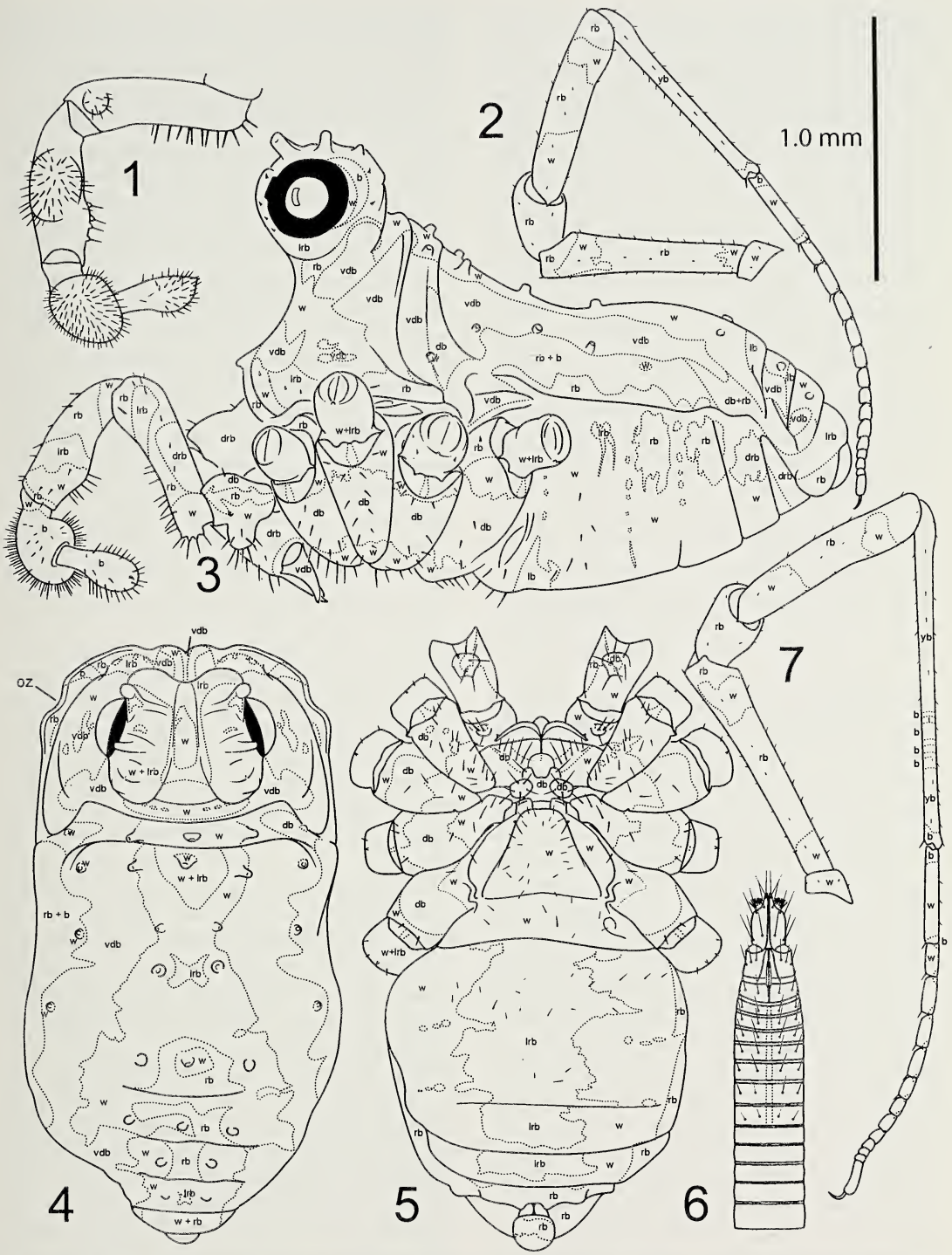
Type species.—*Hesperopilio mainae* Shear 1996, by original designation.

Emended generic diagnosis.—Caddidae with ocularium large, broad, not projecting beyond anterior margin of carapace; ocularium with broad median furrow, each carina with longitudinal row of five variably developed protuberances. Female palpal femora without ventral apophyses but with midventral row of stout spines; patella with prolateral field of glandular spines, tibia inflated and prolaterally spinose. Ovipositor with terminal apparatus composed of three bilaterally paired apical segments and shaft composed of 10 or 12 unpaired segments.

Hesperopilio magnificus new species
Figs. 1–7

Type data.—Holotype female: CHILE: Provincia Chiloé: Isla Grande de Chiloé, Chepu (42°00′S, 73°58′W), 14 January 2002, Tomás Cekalovic (AMNH).

Etymology.—The species is named for its magnificent coloration and comparatively large size.



Figures 1–7.—*Hesperopilio magnificus*, adult female, holotype: 1. Right pedipalp, prolateral aspect; 2. Right leg I, retrolateral aspect; 3. Body, left lateral aspect; 4. Body, dorsal aspect; 5. Body, ventral aspect; 6. Ovipositor, ventral aspect; 7. Right leg III, retrolateral aspect. Abbreviations: OZ = ozopore; b = brown; db = dark brown; lb = light brown; lrb = light reddish brown; rb = reddish brown; vdb = very dark brown; w = white, yb = yellowish brown. Scale bar applies to all figures.

Diagnosis.—*Hesperopilio magnificus* is the first species of its genus known from South America. At. 2.3 mm long, the holotype is substantially larger than female *H. mainae* (1.6 mm) (Shear 1996) and has a much more complex coloration (Figs. 2–5, 7), including an asymmetrical white "hour glass" dorsal figure bordered by dark brown bands; dorsal transverse rows of white tubercles; and white and reddish-brown striped legs. The prolateral spine field of the palpal patella is inflated in *H. magnificus* (Fig. 1); the patella-tibia joint operates so as to bring the prolateral surfaces of the patella and tibia in apposition rather than the ventral surfaces (Fig. 1); the tibia is greatly inflated (Figs. 1, 3); the tarsus is proportionally larger in *H. magnificus* (subequal to tibia) (Figs. 1, 3); the palpal claw is greatly reduced (Fig. 3). The carinal tubercles of the ocularium vary greatly in size, the second being the largest, followed by the third; the remainder are reduced to low bumps. The ovipositor shaft has more unpaired segments (12 instead of 10 in *H. mainae*) and there are more setae (12 or 8) per seta-bearing segment than in *H. mainae* (6).

Description of female holotype.—Dorsal surface: Anterior margin with shallow median emargination (Fig. 4). Ozopores located at level of coxa I, open laterally, indicated dorsally by wide, shallow emargination. Surfaces of carapace slope upward steeply to form dorsal "peak" on which ocularium is mounted (Fig. 3). Ocularium large; width, including lenses, over one-half width of carapace; wide, shallow median furrow; carinae with two pairs of large transverse ridges terminating laterally with dorsolaterally projecting, blunt-ended processes; smaller ridges between and posterior to large ridges (Figs. 3, 4). Metapeltidium with one transverse row of tubercles and dorsal surface of opisthosoma with seven segmentally arranged, transverse rows of tubercles (Fig. 4). First (metapeltidial) and second (first opisthosomal) rows with five tubercles (one median, two medial, two lateral), rows 3 and 4 with four tubercles (two medial, two lateral), row 5 with three tubercles (one median, two medial) and two lateral white spots may correspond to lateral tubercles, row 6 with three (one median, two medial), and rows 7 and 8 with two tubercles (medial only). First four tergal somites of the opisthosoma not demarcated externally except by patterns of tubercles and coloration, tergite 5 distinguished anteriorly by incomplete transverse groove, tergites 6, 7, 8 + 9 and anal operculum demarcated by transverse grooves.

Ventral surface: Epistomal lobe ("labrum") short, blunt (Fig. 5). Coxapophysis I with white, transverse lateral portion and brown medial portion with row of six long setae. Labium with thin, transparent distal portion and sclerotized brown basal portion terminating in pair of setae. Coxapophysis II with white, transversely oriented basal portion terminating in brown lobe with 'crown' of six setae. Coxa III without coxapophysis, extending medially to base of distal lobe of coxopophysis II. Coxa IV without coxapophysis, extending anteromedially to level of coxa III; margin adjacent to operculum with one large seta; coxa terminating anteriorly under the genital operculum with small, medially projecting lobe. There is a pair of ventrally projecting rectangular processes between the labium and anterior margin of genital operculum that appears to represent a portion of the *arculi genitales*. Coxa I with about 20 setae, coxae II-IV with eight or fewer setae. Genital operculum narrowing gradually toward slightly rounded anterior margin; surface with about 15 scattered setae. Ventral surface of opisthosoma with a few scattered setae, otherwise smooth; segmentation indicated by rows of sigilla. Preanal sternite with posterior median notch.

Chelicera: Proximal segment mottled brown, red-brown and white, with a few scattered setae. Second segment mottled brown and white with about 20 setae, most arranged in an imperfect longitudinal row on the anterior surface. Cheliceral fingers dark brown, inner margins toothed.

Palp: The palp is illustrated in Figs. 1–2, 5. Trochanter with large, blunt process projecting from distal ventral surface, terminating in crown of about seven macrosetae. Femur: cylindrical, expanded slightly at distal end; proximal ventral end with rounded prominence; proximal two-thirds of ventral surface with imperfect longitudinal row of about 12 stout macrosetae; distal prolateral surface with blunt-ended process terminating in crown of about nine macrosetae; otherwise surface with a few scattered setae. Patella: subequal to femur; middle third of prolateral surface greatly expanded to form sub-hemispherical promi-

nence with numerous, evenly spaced, glandular macrosetae; distal half of ventral surface with imperfect line of four stout, tubercle-based macrosetae; otherwise with a few scattered setae, especially on dorsal and distal retrolateral surfaces. Tibia: proximally narrower than adjacent patella, makes sharp dorsal bend at one-quarter of length and expands in diameter distally; distal three-quarters of prolateral surface expanded to form large hemispherical prominence covered with numerous, evenly spaced glandular macrosetae; otherwise surface with a few scattered setae. Tarsus: narrow proximally but expanded distally; distal half of prolateral surface expanded into a rounded prominence with about 40 glandular macrosetae; distal half of retrolateral surface with numerous, distally projecting microsetae and a few scattered larger setae.

Legs: Only leg I and leg III from the right side were attached to the holotype specimen (Figs. 2, 7); all other legs missing.

Coloration: Dorsal surface with prominent flat-white central figure beginning anteriorly as median stripe on ocularium and continuing posteriorly to anal operculum (Fig. 4). Central figure broad (about one-third width of body) posterior to ocularium, gradually narrows posteriorly reaching narrowest point (about one-fifth width of body) at third row of tubercles; figure broadens posteriorly to almost full width of body at posterior margin of tergite 5; figure substantially narrower on tergite 6 and gradually narrows to the anal operculum. Central figure with asymmetrically shaped, median islands of light reddish brown, associated with median and medial white tubercles. Central figure bordered laterally by dark brown longitudinal bands with irregular margins. Dark bands begin anteriorly along an irregular line that begins medially at the base of the ocularium and extends posterolaterally to a level near the anterior margin of coxa III; dark bands narrow posteriorly as their lateral borders move progressively away from the lateral margins of the body. Dark bands bordered laterally by an ill-defined band of mixed light brown and reddish brown, with reddish brown dominating at the lateral periphery. White lateral tubercles form a curved longitudinal row along the border of the dark and mixed brown-reddish brown bands. A narrow strip of reddish brown continues anteriorly around the margin of the carapace. An irregular transverse, opalescent-white band crosses the carapace anterior to the ocularium, two thin fingers of which project anteriorly to either side of the anterior emargination separated by a dark brown median line and bordered laterally by two dark brown islands. The opalescent-white band contains dark brown islands which appear to indicate sites of muscle attachment. A large black band encircles each lens; the band projects slightly anteriorly. A white area borders the black band posteriorly, remaining lateral portions of ocularium light reddish brown; mid-dorsal portion of ocularium is white with irregular, light-reddish-brown island.

Ventral surface of opisthosoma, including genital operculum, mostly flat white, interrupted laterally by islands of reddish brown and medially by a very irregular light reddish-brown central figure and transverse rows of sigilla. Preanal sternite uniformly reddish brown. Coxae with broad dark brown bands separating proximal and distal white regions. Medial surfaces of stomotheca white, except for basal plate of labium, terminus of coxapophysis of leg II and region of coxapophysis of leg 1 bearing row of long setae. "Lips" of coxapophysis of palp and leg I and distal portion of labium translucent.

Ovipositor: Long, dorsoventrally flattened (Fig. 6), dorsal and ventral surfaces similar, terminal apparatus with three bilaterally paired segments, shaft with 12 unpaired segments. Ultimate paired segment elongate, heavily pigmented (brown), with well-developed sensory organ inserted on distolateral concavity; each segment with one basal ring of six socketed setae, one distal ring of six socketed setae and three medial apical socketed setae. Each sensory organ domelike with about 20 seta-like projections. Penultimate paired segment heavily pigmented, each with ring of five socketed setae; segment divided medially by "lips" of ovipore. Antepenultimate paired segment similar to shaft segments but divided medially. Shaft segments decreasing in pigmentation proximally, thin longitudinal membranes along each lateral surface divides each segment into dorsal and ventral plates; dorsal and ventral plates of distal eight shaft segments and antepenultimate paired segment with two pairs of socketed setae. Shaft segments with setae also with reduced pigmentation along midline of dorsal and ven-

tral surfaces giving the superficial impression that the plates are divided. Apparent seminal receptacles present at level of proximal margin of terminal shaft segment; obscured by dark cuticle of segment but appearing as transverse dark band, associated with a pair of thin-walled sacs that project proximally to the level of shaft segment 3.

Adult male and immatures: Unknown.

Distribution.—Known only from the type locality.

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ROLE OF THE ANTERIOR LATERAL EYES OF THE WOLF SPIDER *LYCOSA TARENTULA* (ARANEAE, LYCOSIDAE) DURING PATH INTEGRATION

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ABSTRACT. Spiders of the species *Lycosa tarentula* (Linnaeus 1758) (Araneae, Lycosidae) use a vector navigation system while homing under natural conditions. Under laboratory conditions, in the absence of information relative to the sun's position or any pattern of polarized light, *L. tarentula* uses a path integration system which consists of turning at a fixed angle similar to one that could carry it to its burrow. In the absence of light, the angle is random. In this study we ask whether the spiders acquire the information about the angle turned during the outward journey through the anterior lateral eyes (ALEs), whose visual fields are directed towards the ground. To answer this question, two groups of animals were studied: one group with only the ALEs covered and another group with all eyes except ALEs covered. Our results show that ALE information alone is adequate to obtain the angle at which the animal should turn when homing.

Keywords: Direction estimation, spiders, optical flow

Animals that are central foragers move from a central point (nest, burrow) to find food or mates. After this displacement, these animals must be able to reach that central point. Path integration (PI) is one of the most frequently used mechanisms to get it (Papi 1992). While moving, the animal measures and integrates the angles (rotations) as well as distances travelled to obtain a vector whose orientation indicates home direction and whose length indicates the distance, so that it can always take a direct path back to its starting point. That means that the animal does not retrace its outward journey.

Information about changes of direction can be obtained in arthropods through exoskeletal sense organs (Seyfarth et al. 1982; Mittelstaedt 1983; Görner & Claas 1985; Durier & Rivault 1999) or by the use of biological compasses based on the sun or the pattern of celestial polarized light (Wehner 1997; Homberg 2004; Mappes & Homberg 2004). In several insects, it has been shown that they use translational image motion (optic flow) to estimate flight- or running distances (review: Srinivasan & Zhang 2004) In particular, several studies made with honeybees (Srinivasan et al. 1997) demonstrated that honeybees integrate over time the image velocity that is experienced during the flight and that this measurement is independent of image structure (Si et al. 2003). In another experiment, Ugolini (1987) displaced wasps from their nests to various sites, released them, and observed their homing trajectories. He found that they headed accurately towards their nests if they had been displaced in a transparent container but not when they had been displaced in an opaque container.

In spiders, homing has been thoroughly studied in the funnel web spider *Agelena labyrinthica* (Clerck 1757), which can use visual cues together with tactile and proprioceptive ones (Görner & Claas 1985). Homing has also been studied in the nocturnal ctenid spider *Cupiennius salei* (Keyserling 1877) (Seyfarth & Barth 1972; Seyfarth et al. 1982; Barth 2002). It was demonstrated that *C. salei* needs proprioceptive information for homing because animals that have been surgically altered (e.g., spiders with the lyriform slit sense organs of the femur and tibia destroyed mechanically) returned with less success to the site from which they had been chased. In *C. salei*, Schmid (1997) noted differences in the kind of locomotion depending upon whether they were in bright light (normal walking movements with eight legs) or complete darkness (first pair of legs used as antennae).

In Lycosidae, the first studies about homing were realized in the European species *Arctosa perita* (Latreille 1799) (Papi 1955; Papi & Tongiorgi 1963). This species displays so-called "zonal orientation" or "orientation to Y axis," which means that after an active or passive displacement away from the shore, they orient and move perpendicular to the shore until they reach it. Papi (1955) demonstrated that *A. perita* could find the shore from which it had been displaced only if the sky was not heavily overcast. Later, the contributions of innate and learned components to astronomical orientation were analyzed by Papi & Tongiorgi (1963). Magni et al. (1964) showed that the anterior median eyes (AMEs) were primarily responsible for homing behavior by using celestial polarized light in *A. variana* Koch 1847. However, the structural basis for polarization sensitivity in AMEs was not found (Bacetti & Bedini 1964). The first study that discovered the structural basis for polarization sensitivity in Lycosidae was by Melamed & Trujillo-Cenoz (1966) in *Lycosa erythrognatha* Lucas 1836 (= *L. raptoria* Walckenaer 1837) followed by the research on *L. tarentula* (Linnaeus 1758) (Kovoor et al. 1993). Recently, Dacke et al. (2001) have found the same structural basis in *Lycosa godeffroyi* L. Koch 1865 and other lycosids.

Lycosa tarentula is a circum-Mediterranean wolf spider that typically lives in a burrow in which the superior part is delimited by little twigs held together by silk (Ortega-Escobar 1986). The depth and diameter of the burrow is correlated with the spider's size (Ortega-Escobar 1986). The prosoma of *L. tarentula* females is variable in size: it can measure from 6.0–9.5 mm in width (unpub. data).

The visual system of the lycosid spider *Lycosa tarentula* has been studied both from the behavioral (orientation to nest: Ortega-Escobar & Muñoz-Cuevas 1999; Ortega-Escobar 2002a; locomotor activity rhythms: Ortega-Escobar 2002b; Ortega-Escobar et al. 1992) and structural aspects (Kovoor et al. 1992, 1993, 1999, 2005a, b). In the study by Ortega-Escobar & Muñoz-Cuevas (1999), when spiders were under an overcast sky, they did not orient homewards; instead, they turned an almost constant angle for PI or path integration. In an indoor study (Ortega-Escobar 2002a), individuals of *L. tarentula* were displaced by moving them along a two-leg trajectory with a 90° angle between legs; at the end of the outbound path, the spider was lifted and placed in an arena with its body axis oriented at random. When this procedure was carried out under illumination, the spiders showed PI by turning a constant angle and walking in search of the burrow, while in darkness (really under red light to which they are insensitive) they also showed PI but in this case they turned a random angle. Thus, it is possible that *L. tarantula* needs visual information about their movement (optic flow) and given the visual fields of their eyes (Land 1985), the eyes that could give more precise information about optic flow would be the anterior lateral eyes (ALEs) which look towards the ground. The aim of the present study was to check what eyes provide to *L. tarentula* the most reliable information about directional changes in PI in the laboratory in the absence of celestial cues. In a first approach, I have analyzed the contributions of anterior lateral eyes (ALEs) versus the rest of the eyes.

METHODS

Experimental animals.—Twelve lab-reared adult females of *L. tarentula* were used. They were maintained in individual containers measuring 17 × 13 × 8 cm, big enough for them to move around to dig burrows. They were fed blow flies (*Calliphora vomitoria*) and given water twice a week. These animals had been captured from a wild population in Madrid (central Spain; N 40° 32′ W 3° 42′) and went through the final 2–3 molts in the laboratory; all were close to the same age and all trials were conducted after maturation.

Experimental procedure.—To begin the study of homing orientation, animals were placed in a terrarium measuring 60 × 30 × 35 cm. This terrarium had a 15 cm deep substratum of soil similar to the natural substrate (Fig. 1 right); in the middle of one long side of the terrarium, an artificial burrow was built, similar to that which the spider digs in the field. After 5 days of habituation to the terrarium, the experiment began. During these 5 days, spiders were mostly in the burrow during the daytime and moved about during some hours at night. To displace the spiders, they were gently removed from the burrow and pushed along the edge of the terrarium on a path traversing half the length and the full width of the terrarium. When the spider ar-

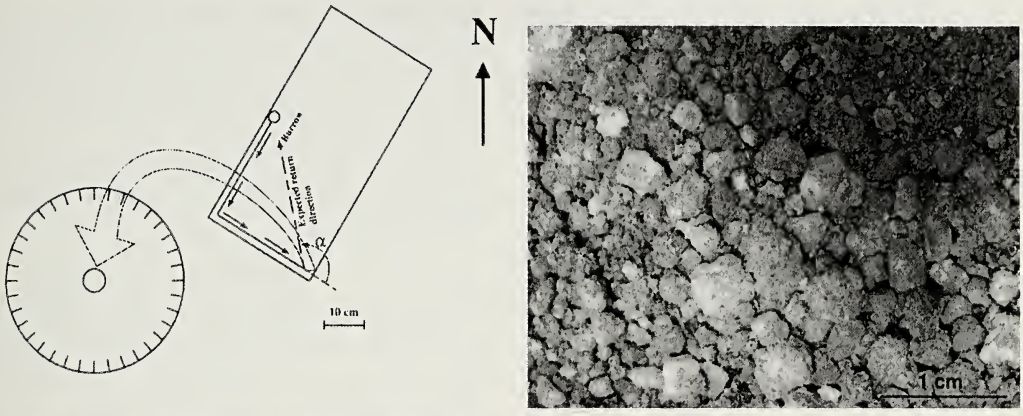


Figure 1.—*Left:* Setup used to study homing in *L. tarentula*. Right, top view of terrarium in which the animal lived during the study; arrows indicate the outward path. Left, dorsal view of the arena in which the animal was left after being taken from the right corner opposite to the burrow. Burrow direction was at 350°. The big arrow indicates the transfer of the animal to the center of the arena (shown at half of its actual size in relation to the terrarium). To go to the burrow, the spider must turn an angle of 135° in its terrarium. *Right:* Aspect of the substratum of the terrarium.

rived at the end of the path, it was placed into a transparent open glass container and transferred to the center of an arena 90 cm in diameter (wall height, 48 cm; visual angle, 47°) (Fig. 1 left). There, if the animal turned at an angle of 135° towards the left, it would be oriented to its burrow. Both the terrarium and the arena were in a room without natural lighting. The room was lit in the daytime (0800–2000 h) with white light by two SYLVANIA™ Standard F36W fluorescent tubes producing 200 lux at the floor level of the arena. Each animal was used in 8 trials (eight control trials and eight experimental trials; see below) and placed in one of the following compass directions at random: 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°. The spider's orientation was recorded when it was at a distance of 20 cm from the center of the arena. If the spider had not moved during 20 minutes it was returned to the terrarium. The floor of the arena was thoroughly cleaned with ethanol before each test. All the trials were run between 11 and 18 h with lights on.

All spiders (n = 12) were observed first with all eyes uncovered (control test; eight trials for each animal). Afterwards, spiders were assigned at random to one of two groups. One set of spiders (n = 6) had all eyes but the ALEs covered (uncovered ALEs group, experimental test), while the other set (n = 6) had only the ALEs covered (covered ALEs group, experimental test). Therefore, we had two groups: "uncovered ALEs group" and "covered ALEs group" that were observed without eye covering (control test) and with eye covering (experimental test). To cover the eyes, the animals were anesthetized with ether, their legs restrained with adhesive plaster and their eyes covered by first applying a layer of collodion over the anterior region of the prosoma; then by applying two layers of water-soluble black paint (Van Gogh); and, finally, by applying another layer of collodion. Eye occlusion was checked in each case after the completion of runs using a stereo microscope.

Automated video tracking.—The image of the arena was captured by an Ikegami ICD-42B B/W CCD video camera and displayed on a Sony™ Trinitron color video monitor. Simultaneously, the video signal was digitized by a Targa 1 frame grabber that was interfaced with a personal computer supporting an object video-tracking system (Etho-Vision, Noldus Information Technology, Wageningen, The Netherlands). The paths supplied by Etho-Vision were later digitized. The best-fitting line to a trajectory was computed by the method of principal axes (Sokal & Rolf 1995).

The following parameters were determined in both conditions (covered or experimental and uncovered or control eyes) in both groups: (1) topographic bearing of the digitized homeward path when the spider crossed a virtual circle 20 cm in diameter from the starting point of the return; (2) angle (α angle) of the

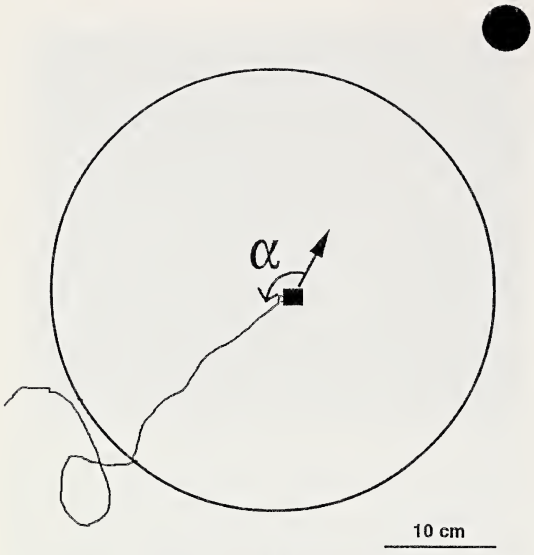


Figure 2.—Example of a homeward path in the arena. The black square in the center represents the point where the spider is placed, and its orientation is indicated by the arrow; the black circle represents the burrow compass direction; α is the angle between the initial orientation and final bearing (where homing path crosses the circle).

body axis when the spider crossed the virtual circle with respect to the starting position of the body axis; as the animal could turn either clockwise or counterclockwise, the α angle was always taken counterclockwise, which was the expected direction for the animal to turn in the terrarium (Fig. 2); (3) turning direction (clockwise or counterclockwise).

Statistical analyses.—The directions followed by the animals were analyzed as circular variables according to Batschelet (1981). For first-order statistics, the Rayleigh test was used to determine whether the observed homing directions from particular individuals were significantly oriented. To see if the deviation between individual significant vectors and the angle of home direction (Fig. 2) was significant we used the confidence interval for the mean angle ($P < 0.05$; Batschelet 1981). On the second-order level, Moore's and Mardia-Watson-Wheeler's tests (Batschelet 1981) were used to test directionality significance and differences in the orientation of the subjects between control and experimental tests respectively.

The percentage of turning in the correct direction (counterclockwise) was analyzed by a two X two repeated measure analysis of variance with the type of eyes (PMEs/PLEs/AMEs, and ALEs) and covering (control -without eye covering-, and experimental -with eye covering-) as factors.

Voucher specimens have been deposited in the Museo Nacional de Ciencias Naturales (Madrid, Spain).

RESULTS

Homing in uncovered ALEs group (control test).—Homing paths followed by the spiders in the arena were either roughly straight, finishing with a sudden turn either to the right or to the left, followed by a turn in the opposite direction, as described previously (Ortega-Escobar 2002a) or they walked until they touched the arena wall. This series of turns has also been observed when the animal is taken from the burrow without having been displaced and transferred to the center of the arena. This type of behavior, called "systematic search" (Wehner & Wehner 1986), was not analyzed in this study.

Topographic bearings: None of the six spiders oriented themselves towards the burrow position or towards another point of the room in a constant way in the eight trials (Fig. 3 top, left).

α *angle:* α was non-randomly oriented in all six animals (Table 1 and Fig. 4 top, left). The mean vectors of the six animals were not randomly distributed (Moore's test: $D = 1.277$, $P < 0.05$). Table 1 shows the mean angle and length of the vector for each animal. In two animals the turn that the spider should have made to go to the burrow in the terrarium (135°) was included in the confidence interval of the mean, but their mean vectors were statistically significant (Fig. 4 top, left).

Homing in uncovered ALEs group (experimental test).—The homing paths in the experimental test were similar to those shown by animals when all eyes were uncovered.

Topographic bearings: Only one of the six spiders oriented itself towards one point of the room in a consistent way in the eight trials. (Fig. 3 bottom, left). The other five animals oriented themselves at random.

α *angle:* α was non-randomly oriented in all six animals (Table 1 and Fig. 4 bottom, left). The mean vectors of the six animals were not randomly distributed (Moore's test: $D = 1.353$, $P < 0.05$). Table 1 shows the

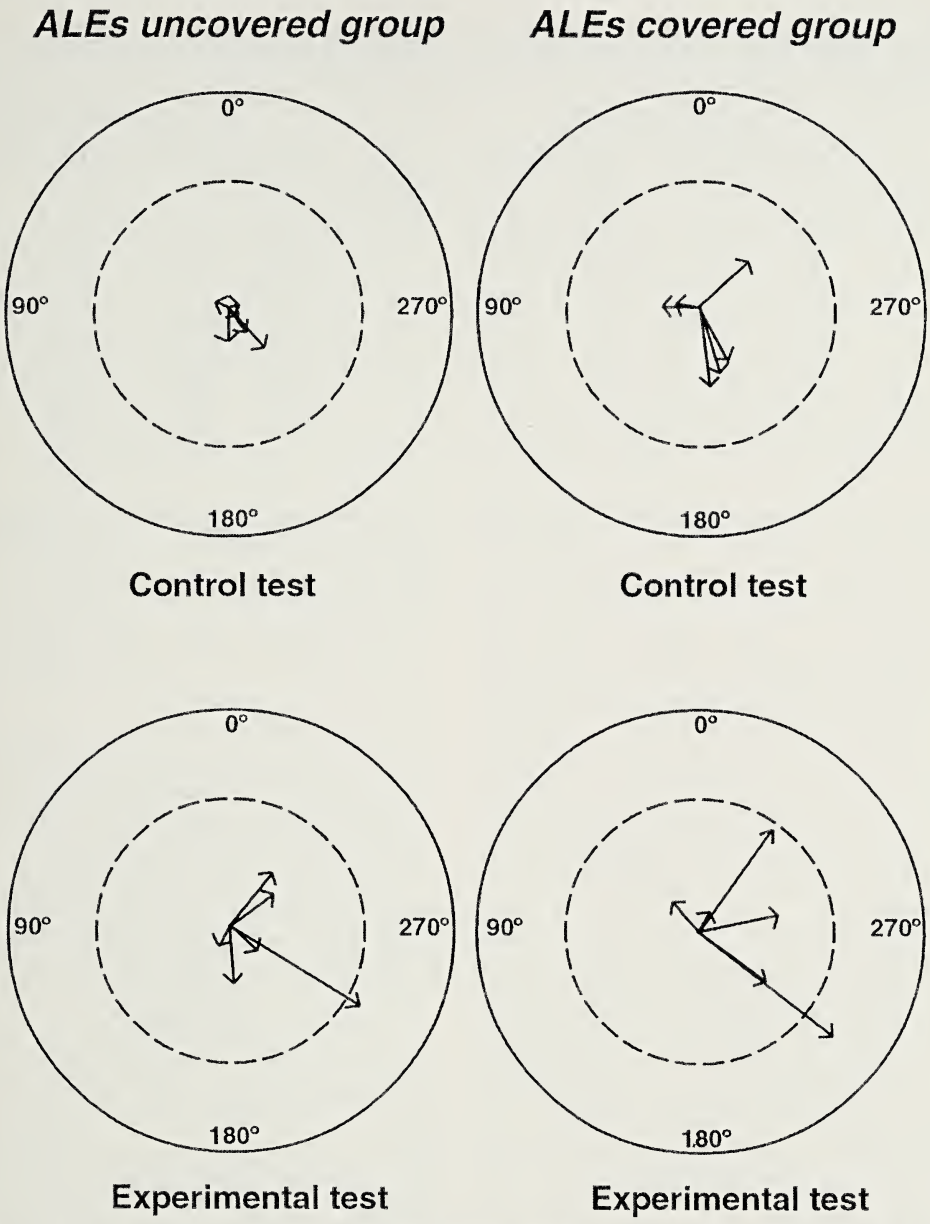


Figure 3.—*Top left:* Mean vectors (control test) of topographical bearings of the uncovered ALEs group. The dashed circle indicates the critical r-value of $P = 0.05$. 0° indicates the magnetic North. *Top right*: Mean vectors (control test) of topographical bearings of the covered ALEs group. *Bottom left:* Mean vectors (experimental test) of topographical bearings of the uncovered ALEs group. *Bottom right:* Mean vectors (experimental test) of topographic bearings of the covered ALEs group.

mean angle and length of the vector for each animal. In four animals, the turn that the spider had to make to go to the burrow in the terrarium (135°) was included in the confidence interval of the mean.

Homing in covered ALEs group (control test).—As expected, the homeward paths of these animals were very similar to those observed for the other group (ALEs uncovered group).

Topographic bearings: None of the six spiders oriented itself towards the burrow position or towards another point of the room in a consistent way in the eight trials (Fig. 3 top, right).

Table 1.—α angle (mean α angle (θ) and vector length (r)) in the controls and tests of both groups. Asterisks indicate the degree of significance of the first and second order data; *, $P < 0.05$.

	Covered ALEs group					Uncovered ALEs group			
	All eyes uncovered		ALEs covered			All eyes uncovered		ALEs uncovered	
Individual	θ	r	θ	r	Individual	θ	r	θ	r
1	159°	0.87*	61°	0.39	1	154°	0.81*	146°	0.80*
2	38	0.71*	42	0.56	2	164	0.83*	172	0.80*
3	134	0.65*	318	0.14	3	169	0.74*	158	0.91*
4	165	0.66*	51	0.27	4	165	0.95*	154	0.93*
5	161	0.87*	204	0.69*	5	195	0.91*	187	0.75*
6	60	0.68*	55	0.55	6	122	0.94*	137	0.96*
Group means	126	0.64	42	0.51		162	0.93*	159	0.96*
Mardia test	$R_1^2 = 14.91$, $P < 0.05$					$R_1^2 = 0.27$, NS			

α *angle:* The α angle (Fig. 4 top, right) was non-randomly oriented in all the animals of this group. The mean vectors of the six animals were randomly distributed (Moore's test: $D = 0.923$, $P > 0.05$). Table 1 shows the mean angle and length of the vector for each animal. In four animals the turn that the spider had to make to go to the burrow in the terrarium (135°) was included in the confidence interval of the mean. In the other two animals, the 135° value was not included in the confidence interval of the mean, but their mean vectors were statistically significant (Fig. 4 top, right).

Homing in covered ALEs group (experimental test).—The homeward paths of the animals with covered ALEs were very similar to those observed when no eye was covered. However, in several animals, circular pathways were observed (Fig. 5). These circular pathways were not used for the analysis.

Topographic bearings: Only one of the six spiders oriented itself towards a point of the room in a consistent way in the eight trials (Fig. 3 bottom, right).

α *angle:* The α angle (Fig. 4 bottom, right) was randomly oriented in all but one of the animals of this group. In this animal, this angle (Table 1) has a value of 204°, very different from 135°; this value was not included in its confidence interval.

Comparison of α angle in control tests between both groups.—To test if both groups have the same mean orientation in control tests we have used the Mardia-Watson-Wheeler test. In this case, $R_1^2 = 1$, NS, therefore there is no difference in the α angle between both groups.

Percentage of turning in the expected direction (see Methods).—Turning in the expected direction by the six animals of the uncovered ALEs group (control test) was 70.8 ± 6.5 % (mean ± SD), while among the six in the covered ALEs group (control test) it was 87.5 ± 19.4 % (Fig. 6).

In experimental tests, 75 ± 22.4% of the animals with only the ALEs uncovered turned in the expected direction while 50 ± 22.4% of those animals with only ALEs covered turned in the expected direction.

The ANOVA of the percentage of turning in the expected direction showed no effects for the two factors and significant effects for the interaction ($F_{1,10} = 15.625$, $P = 0.003$).

DISCUSSION

As in a previous study (Ortega-Escobar 2002a), the present results show that during the day *L. tarentula* does not orient itself towards the topographic burrow position in the absence of tacto-chemical information and the presence of distant visual landmarks of the laboratory. The results agree with what has been observed when the animals could use neither the sun nor the polarized light pattern for homing (Ortega-Escobar & Muñoz-Cuevas 1999).

With all the eyes uncovered, this study shows that *L. tarentula* tries to return home by turning a fixed angle, α, near to 135°. The turn near to 135° would let the animal walk to a point near the burrow if its orientation had not been changed in the arena.

If *L. tarentula* used only proprioceptive information for homing, it should be able to turn an α angle near to 135° when it was displaced

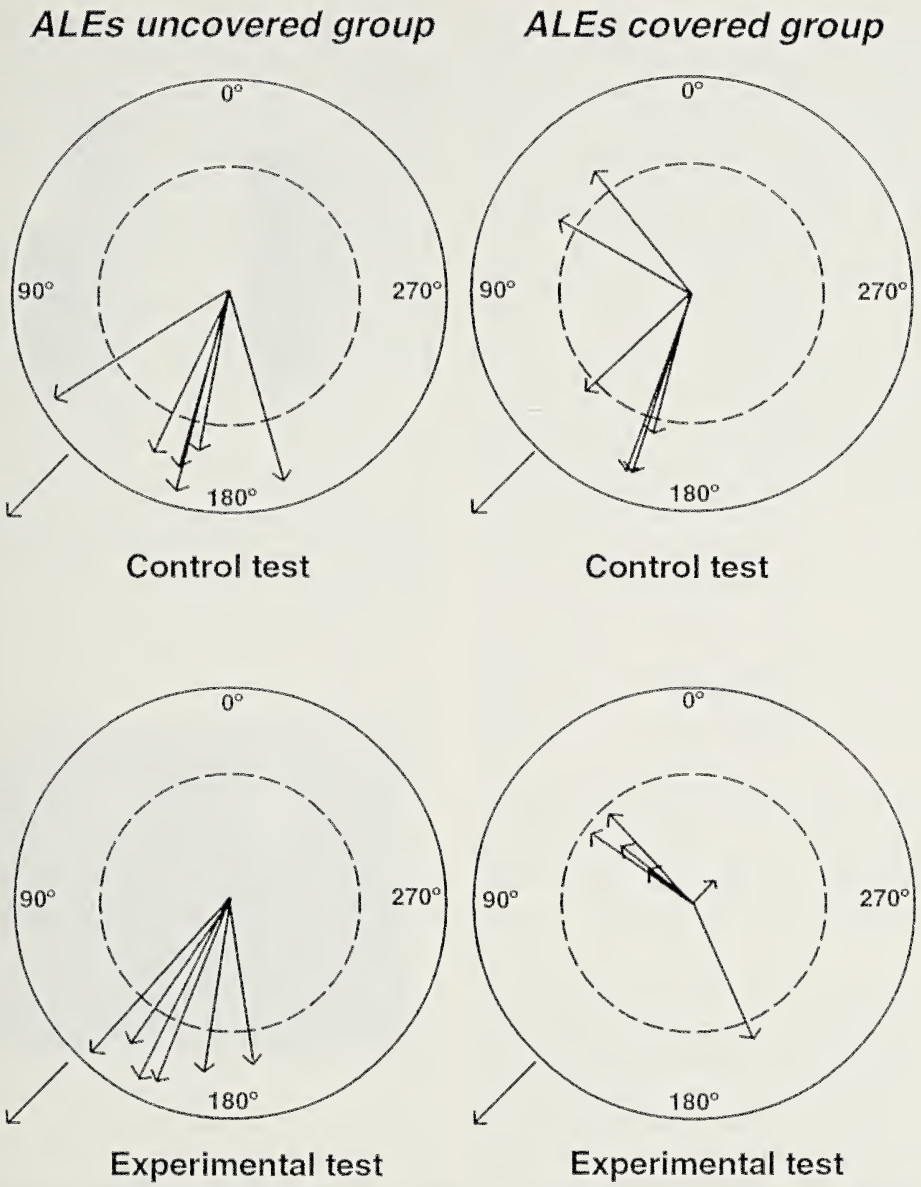


Figure 4.—*Top left:* Mean vectors (control test) of α of the uncovered ALEs group. The dashed circle indicates the critical r-value of $P = 0.05$. 0° indicates that the animal walks in the same direction that it has been placed in the arena. The external arrow represents the angle the spider has to turn in the terrarium to go back to the burrow (α= 135°). *Top right:* Mean vectors (control test) of α of the covered ALEs group. *Bottom left:* Mean vectors (experimental test) of α of the uncovered ALEs group. *Bottom right:* Mean vectors (experimental test) of α of the covered ALEs group.

in the darkness. The previous study (Ortega-Escobar 2002a) had shown that this is not the case. Therefore, there must be some kind of visual information that the spider must use for homing. The present results exclude the possibility of using distant visual landmarks given that topographic bearings are not constant. There is another possibility to estimate the angle α: the use of the self-induced optic flow through some eyes. The visual field of ALEs is disposed in such a way that optic flow through them is more constant than optic flow through the other eyes (Fig. 7). As the animal walks, the distance to the ground is rather con-

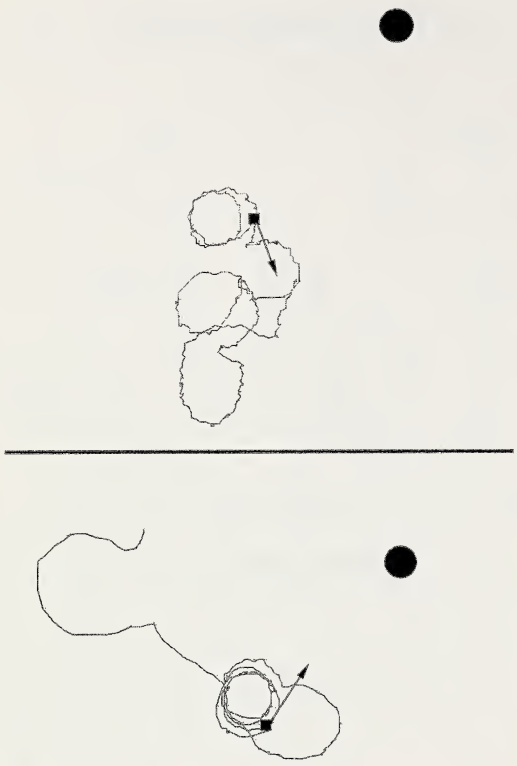


Figure 5.—Two examples of homeward paths of two different spiders with only ALEs covered. Black square represents the initial position of the spider; arrow represents the initial body direction; black circle represents burrow direction.

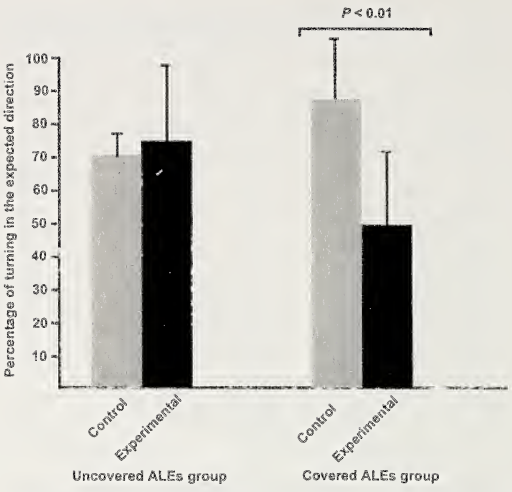
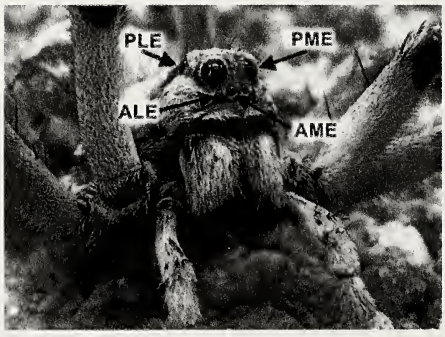


Figure 6.—Percentage of turning in the expected direction (mean ± SD) in the control and experimental tests of both groups.



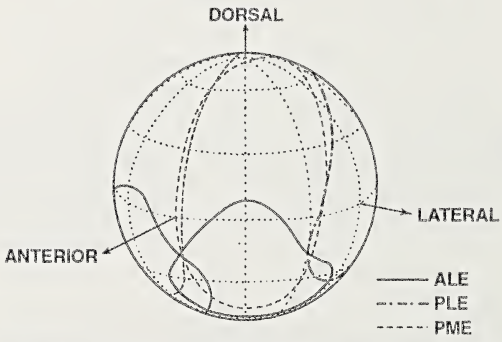


Figure 7.—*Top:* Frontolateral picture of *L. tarentula* showing the positions of the eyes. ALE: Anterior lateral eye; AME: Anterior median eye; PLE: Posterior lateral eye; PME: Posterior median eye. *Bottom:* Schema showing the visual fields of the different eyes of *Lycosa tarentula* (taken from Land 1985).

stant and they mainly image the ground on which the animal walks. On the other hand, the other eyes image different objects and the optic flow is more complex in relation to the distance to the eyes. It is proposed that *L. tarentula* is able to perceive the optic flow of the natural soil of the terrarium where it is displaced, and afterwards it uses this information to turn in the correct direction and angle even if it is placed over an unstructured substrate such as the white substratum of the arena. Are the ALEs able to discriminate the small pebbles of the terrarium soil? One measure of the resolution capacity of a simple eye is the sampling frequency, υ_s (Land & Nilsson 2002) such that $\upsilon_s = 1/(2\Delta\Phi)$ where $\Delta\Phi$ is the interreceptor angle. Using the values obtained by Kovoor & Muñoz-Cuevas (1996/1997) for *L. tarentula* female, for the ALEs $\upsilon_s = 0.30$ cycles/degree which means that a grating consisting of two stripes, one black and one white, will occupy 3.33° of the visual field.

Supposing that the distance between the ALEs and the soil is 1 cm, the sampling frequency of these eyes is high enough to distinguish between the small pebbles that the spider finds while she walks about in the terrarium. Additional experiments will be needed in which the animal is trained to walk in an artificial structured environment (e.g., a grating of black and white stripes with a certain frequency) and then tested in an unstructured environment (white substratum) or a differently structured one (e.g., a grating perpendicular to the training one).

The main results presented in this study (Figs. 4 & 6) clearly demonstrate that visual input gathered through ALEs influences the spider's estimate of the turning angle to reach home. The mean vectors of animals with only ALEs uncovered do not differ statistically from the mean vectors of these animals when they could use visual information gathered through all eyes.

However, the results obtained when all the other eyes (PMEs, PLEs, and AMEs) were uncovered and only ALEs covered show that the visual information gathered through the former eyes is not usable for homing. In fact, results under this condition are not different from those obtained when animals walked in darkness during the outward and homeward paths (Ortega-Escobar 2002a). Anterior lateral eyes seem to transfer information about the direction of turning and the angle turned because when they are not functional, the animal turns clockwise or counterclockwise at random and at a random angle.

In the wild in the daytime, female *L. tarentula* walk out of their burrows only when there is prey or another member of the species present, while at night they walk out spontaneously. This behavior must also be based on some differences between the states of the eyes in the day and at night and between the visual fields of the different eyes. *Lycosa tarentula* would achieve PI by using proprioceptive and visual information gathered through the anterior lateral eyes (ALEs), which have ventral visual fields whose images change very little when the animal walks in comparison with the images through the anterior median (AMEs), posterior median (PMEs) or posterior lateral eyes (PLEs), which move quickly, given their visual fields. This is the easiest way to associate the proprioceptive with the visual information generated by the ALEs. Besides, the rhabdoms of the ALEs have been shown (Kovoor et al. 1995) to be capable of functioning well between 12 and 19 h, the time when these experiments were carried out. In the PMEs and PLEs, membrane synthesis takes place at this time, and they are not in a good functional state. However, they probably could function well under a light intensity higher than that used in this experiment.

It seems that there is a specialization in the functioning of *L. tarentula* eyes as it has been proposed for another lycosid, *Rabidosa rabida* (Walckenaer 1837) (Rovner 1993) and for the ctenid *Cupiennius salei* (Schmid 1998). ALEs are specialized for navigation when sun/polarized-light pattern compasses are not available and to set the locomotor activity rhythm to LD cycles (Ortega-Escobar 2002a, b). AMEs are specialized for navigation with the sun or the pattern of polarized light (Ortega-Escobar & Muñoz-Cuevas 1999). PMEs do not seem to function in homing (this study; Ortega-Escobar & Muñoz-Cuevas 1999) but other studies (Rovner 1993) suggest that they are involved in recognizing form.

In the other two well-studied spiders, *Cupiennius salei* and *Agelena labyrinthica*, the possible differential role of the eyes in path integration has not been studied in the former, but it has been well documented in the latter (Görner & Claas 1985). *Cupiennius* (Seyfarth et al. 1982) was studied in a situation in which it could be shown that the spider did not need to retrace its outward journey; but animals with specific eye coverings were not studied. In *A. labyrinthica*, "the experiments to date have not revealed whether the different types of eye have separate functions with respect to optical navigation by a light source" (Görner & Claas 1985: p. 281). Consequently, the kind of visual navigation studied in *A. labyrinthica* was quite different from the present study of *L. tarantula*, and no comparison is possible.

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AN EXAMINATION OF AGONISTIC INTERACTIONS IN THE WHIP SPIDER *PHRYNUS MARGINEMACULATUS* (ARACHNIDA, AMBLYPYGI)

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ABSTRACT. Intraspecific interactions in adult whip spiders (*Phrynus marginemaculatus*) were investigated in a laboratory setting to quantify agonistic interactions and to determine predictors of contest outcome. Males were initially paired with size-symmetric or size-asymmetric opponents to assess the effect of size symmetry on contests. Three weeks later, the same males were paired with either the same opponent, or a different opponent to determine whether or not individuals remember earlier encounters. Finally, we quantified aspects of female-female contests. Agonistic encounters between males are characterized by varying degrees of pedipalpal opening, elevation displays, and rapid flicking (~ 29 Hz) of the antenniform leg. Duration of elevation displays was a predictor of contest outcome, with individuals being more likely to win if they held an elevated posture for longer than their opponent during the contest. Relative size influenced both contest duration and weight loss, with contests between size-symmetric males lasting longer and resulting in greater weight loss than size-asymmetric contests. In second contests, familiar encounters were both shorter in duration and involved fewer aggressive displays than unfamiliar second contests, suggesting that males were able to remember previous opponents. Females were less likely to exhibit aggressive displays than males, and female contests were shorter in duration than male contests. Overall, the results of our study suggest that agonistic interactions in *P. marginemaculatus* are extremely complex, varying with the sex and size-symmetry of individuals and involving elaborate signaling, and that there may be a large role for learning and memory.

Keywords: Agonistic interactions, amblypygid, intrasexual selection, intrasexual competition, learning and memory

Intrasexual competition is prevalent throughout the animal kingdom and is often manifest in agonistic encounters between males with examples ranging from frogs (Bee et al. 1999; Gerhardt 1994; Davies & Halliday 1978), to horned beetles (Emlen 1997; Rasmussen 1994), to jumping spiders (Faber & Baylis 1993; Taylor et al. 2001). Typically, agonistic interactions between males are driven by competition for access to mates, shelter and other limited resources (Andersson 1994; Huntingford & Turner 1987), with the winner of the contest often gaining first access to these resources (Huntingford & Turner 1987; horned beetles, Emlen 1997; and the copperhead snake *Agkistrodon contortrix*, Schuett 1997).

In order to avoid costly escalation and injury that could potentially lead to decreased fitness or death, males of many species may assess traits that are correlated with their opponent's quality through ritualized displays (Bee et al. 1999; Bradbury & Vehrencamp 1998). Male-male contests often select for this ritualized aggressive behavior in order to decrease risk during opponent assessment. These ritualized contests can involve displays of weaponry, postures that accentuate body size, and minor physical contact (such as pushing, touching or wrestling) (Huntingford & Turner 1987; cichlid fish, Neat et al. 1998). Ritualization of male-male contests often leads to exaggeration of male characters that correlate with size, strength or motivational state (e.g., hunger or ready access to a mate) (Andersson 1994), and as a result to sexual dimorphisms in body size and weaponry (Huntingford & Turner 1987; Andersson 1994).

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Most studies of agonistic behavior have focused on aggressive interactions between males; however, female-female contests are also observed in some taxa, for example in cichlids (Draud et al. 2004), whip spiders (Weygoldt 1969, 2000) and pied flycatchers (Dale & Slagsvold 1995). Because males and females employ different strategies to maximize reproductive success, it is not surprising that selection has acted differentially on the sexes to result in different agonistic behaviors between males and females (Draud et al. 2004).

Most studies of intrasexual contests have also focused on animals that rely predominantly on vision (e.g., cichlid fish (Neat et al. 1998; Barlow et al. 1986; Draud et al. 2004) jumping spiders (Faber & Baylis 1993; Taylor et al. 2001)) or their acoustic sense (e.g., territory defense in orthopterans (Greenfield & Minckley 1992), frogs (Bee et al. 1999; Davies & Halliday 1978)) in the early stages of a contest. In these systems, individuals begin displaying visually or acoustically from a distance and only progress to tactile displays and physical contact in prolonged or escalated contests (Faber & Baylis 1993; Neat et al. 1998; Davies & Halliday 1978). There are few studies of intraspecific contests in nonvisual specialists that do not rely on acoustic cues, stemming perhaps from difficulties associated with studies in other sensory modalities or observer biases toward the importance of vision and acoustics. Whip spiders (Arachnida, Amblypygi) represent such a group; in these animals, agonistic displays between males are prevalent (Weygoldt 2000), yet they do not use visual or long-range acoustic signals for communication, but instead rely on other sensory channels such as chemical, tactile, seismic or near field vibrations.

Whip spiders are strictly nocturnal and comprise one of the smaller arachnid orders about which surprisingly little is known (Harvey 2003). They walk on three pairs of legs, and are unique among arachnids in that their front pair of legs is extremely elongate and modified into sensory structures. These antenniform legs, or whips, function similarly to insect antennae and are able to detect airborne odors, contact chemicals and mechanical stimuli (Hebets & Chapman 2000; reviewed in Foelix & Hebets 2001). Due to the prevalence of sensory structures located on their antenniform legs, it is not surprising that whip spiders appear to use these structures to obtain sensory information about their surroundings in addition to using them for communication with other individuals (Weygoldt 2000; Foelix & Hebets 2001).

Despite the apparent ubiquity of male contests in whip spiders, quantitative behavioral studies are currently lacking. Here, we take a quantitative approach to exploring the agonistic encounters between male *Phrynus marginemaculatus* Koch 1841, and compare these male-male interactions to agonistic encounters between females. We provide a complete description of agonistic interactions in this species, evaluate determinants of contest outcomes, identify the influence of prior agonistic experience on fighting behavior and explore potential differences between the sexes.

METHODS

Specimens.—Adult male and female whip spiders (*Phrynus marginemaculatus*) were collected from Big Pine Key, Florida on November 6–9, 2002 and were housed individually in the laboratory in 10.5 × 8.5 × 8.5 cm clear plastic cages in a controlled reversed 12L:12D light cycle. We reversed their light cycle so activity coincided with normal daylight hours. In order to provide a constant source of water, holes were drilled in the bottom of each cage and cotton wicks were placed in the holes. Cages were arranged in water filled tubs (35 × 55 cm), and the cotton wicks were placed in the water, providing the animals with water ad libitum. Animals were fed 1–2 small crickets once a week. Each cage was provided with two pieces of wire screen taped to adjoining walls to serve as a surface upon which the animals could climb. All individuals were housed in the laboratory for at least 2 months prior to experiments.

Individual observations.—To measure, mark and sex the animals, individuals were anesthetized with carbon dioxide. Animals were placed on top of a porous polyurethane sheet mounted on a plastic pipette box. Carbon dioxide was delivered into this apparatus from a tank, after being passed through a flask containing water to add moisture to the gas. Each animal was individually marked with two small colored dots of non-toxic paint using Deco Color paint pens. Ten colors of paint were assigned a number from 0–9 (for ex-

ample, red = 0, orange = 1) and were used to mark each individual with a two-digit ID number. Measurements of individuals were taken, including cephalothorax width (CW) and cephalothorax length (CL), total antenniform leg length (leg I), pedipalp femur length, pedipalp tibia length, and leg II femur length using a standard metric ruler under a compound dissecting scope (Leica WILD M3Z). As autotomization and the loss of appendages due to injury are common in nature, all quantitative comparisons using antenniform leg length measurements were made using the length of the longer appendage. The sex of every individual was confirmed. While anesthetized, whip spiders lift their genital operculum and evert their genitalia; females can be distinguished from males and juveniles by the presence of a pair of sclerotized claspers (orange in color) in their epigynum (Weygoldt 2000). Voucher specimens are deposited in a private collection (Hebets).

Experimental arena.—All contests were run in the dark and were viewed through the LCD screen of a Sony Nightshot camcorder. Contests were run in a circular (24.5 cm diameter) arena constructed of clear plastic mounted on poster board (0.16 cm thickness) with a glue gun. The arena floor consisted of removable paper inserts. The walls were cleaned with 70% ethanol and the floor was replaced between staged contests to remove any possible chemical residues from previous trials. All contests were videotaped (Sony Nightshot DCR-TRV25 Digital Handycams, 30 frames/s) simultaneously in two planes (top and side) with identical cameras, both using an infrared light source. The top view camera was positioned approximately 52 cm directly above the arena while the side view camera was positioned approximately 30 cm from the arena.

Behavioral observations.—Three sets of behavioral contests were run: size matched versus mismatched male-male contests, experienced male-male contests (males with laboratory fighting experience) and female-female contests (with no previous laboratory fighting experience).

For naïve male-male contests, we had 11 pairs of males separated into two treatments: size-symmetric contests (n = 5) and size-asymmetric contests (n = 6). Size-asymmetric individuals were animals with more than 10% difference in cephalothorax width while size-symmetric males had less than 10% difference in cephalothorax width. Naïve contests were staged between 1–8 March 2003. Experienced male-male contests consisted of eleven contests involving all of the males from the naïve male-male contests (10 size-symmetric, 1 size-asymmetric). For experienced males, we were interested in the effect of prior experience on male performance and thus, our two treatment categories were: re-matches involving identical pairings as in the naïve male-male contests (n = 5, size-symmetric), and novel pairings in which males were paired with opponents with whom they had no previous experience (n =6, 1 size-asymmetric, 5 size-symmetric). Experienced contests were staged between 27 March–17 April 2003. In the female-female contests, females were randomly assigned opponents resulting in 9 pairs (7 size-symmetric, 2 size-asymmetric. These contests were staged between 11 August–4 September 2003. Contests for all three groups were initiated at least 60 min after the beginning of the 12 hr dark cycle.

For all trials, opponents were introduced to opposite sides of the arena, each in a 2 cm diameter clear vial, within 5 sec of each other. The vials were flipped over onto the arena floor so that they entrapped the newly introduced animals. Since all trials were run in the dark and the introduction vials likely blocked any chemical stimuli, immediately upon introduction, the animals were likely unaware of each other's presence. Animals were allowed to acclimate for 2 min before the vials were simultaneously lifted to release the enclosed individuals and begin the trial. Individuals were allowed to freely interact and contests began when the individuals made first contact, and ended when one individual was deemed the loser. "Loser" was assigned to the individual in a contest that retreated to a distance of three body lengths or greater with continued progression away from the opponent. Immediately before and immediately after each contest, individuals were weighed (AE Mettler 100 Analytical scale) and weight loss was used as a proxy for energy expended by an individual for a given contest.

Analysis of behavior.—Video recording of contests was conducted using a Sony DVCAM digital video recorder. Videotapes were played back at 30 frames/second and

Table 1.—Behavioral ethogram for whip spider agonistic encounters.

Behavior	Description of behavior
Orient	Turning to face the opponent.
Approach	Moving toward the opponent to a distance of three body lengths or shorter.
1st contact	Initial contact by an individual's antenniform leg on the body and/or appendages of the opponent.
Inadvertent contact	Initial contact by both opponents without first orienting.
Contact	Both individuals touching each other with the antenniform legs (no antenniform leg flicking by either opponent).
Explore while other flicks	One individual touching the opponent with the antenniform legs while the opponent antenniform leg flicks.
Pedipalpal opening display	"Open palp," opening one or both pedipalps partially or fully: (asymmetric) partial pedipalp opening, (asymmetric) full pedipalp opening.
Partial pedipalp open	Both pedipalps open with the tips not touching and with the angle between the femur and tibia less than 90°.
Asymmetric partial pedipalp open	One pedipalp open the same angle as in 'partial pedipalp open.'
Full pedipalp open	Both pedipalps open with the angle between the femur and tibia greater than or equal to 90°.
Asymmetric full pedipalp open	One pedipalp open with the angle between the femur and tibia greater than or equal to 90°.
Pedipalpal contact	Opponents fully open their pedipalps, elevate themselves, lock pedipalps and attempt to push their opponent over or away.
Antenniform leg flick	"Flick," rapid back and forth movement of the antenniform leg directed at various parts of an opponent's body and/or appendages.
Retreat	Moving away from the opponent to a distance of three body lengths or greater with continued progression away from the opponent.

frame-by-frame for detailed analysis. For the video analysis, we noted when each individual started and ended various behaviors (see Table 1 for behaviors and descriptions of behaviors analyzed). Total duration of each behavior performed by an individual in a given contest was calculated, as was the proportion of total contest time an individual performed each behavior. Contests and video analysis started as soon as initial contact between two individuals occurred. Analysis ended as soon as a retreat by an individual was observed.

An ethogram of male contest behaviors was constructed by defining repeated behaviors that appeared to play major roles in the contests (Table 1). Next, a descriptive behavioral transition diagram was constructed from analyzing the 11 naïve male contests (Experiment 1; Fig. 1). Behavioral transitions between defined behaviors occurring after the first initial contact of two individuals were noted for winning and losing individuals in all contests. Transitions for winners and losers were calculated separately. We were interested in the order of behavioral transitions, e.g., how likely is it that a double pedipalp open display will follow a flick display as compared to an asymmetric pedipalp open display. To address this, we calculated the proportion of time a given behavior followed a focal behavior by taking the total number of behavioral transitions involving the focal behavior, and dividing it by the number of times it was followed by a given behavior. We then used these proportions to construct a transition diagram with the focal behavior expressed as the first behavior at the foot of the arrow and the given behavior at the arrowhead (Fig. 1). The widths of the arrows represent the proportion of times these behaviors occurred in the given order.

High-speed video analysis.—We captured high-speed video of antenniform leg flicking

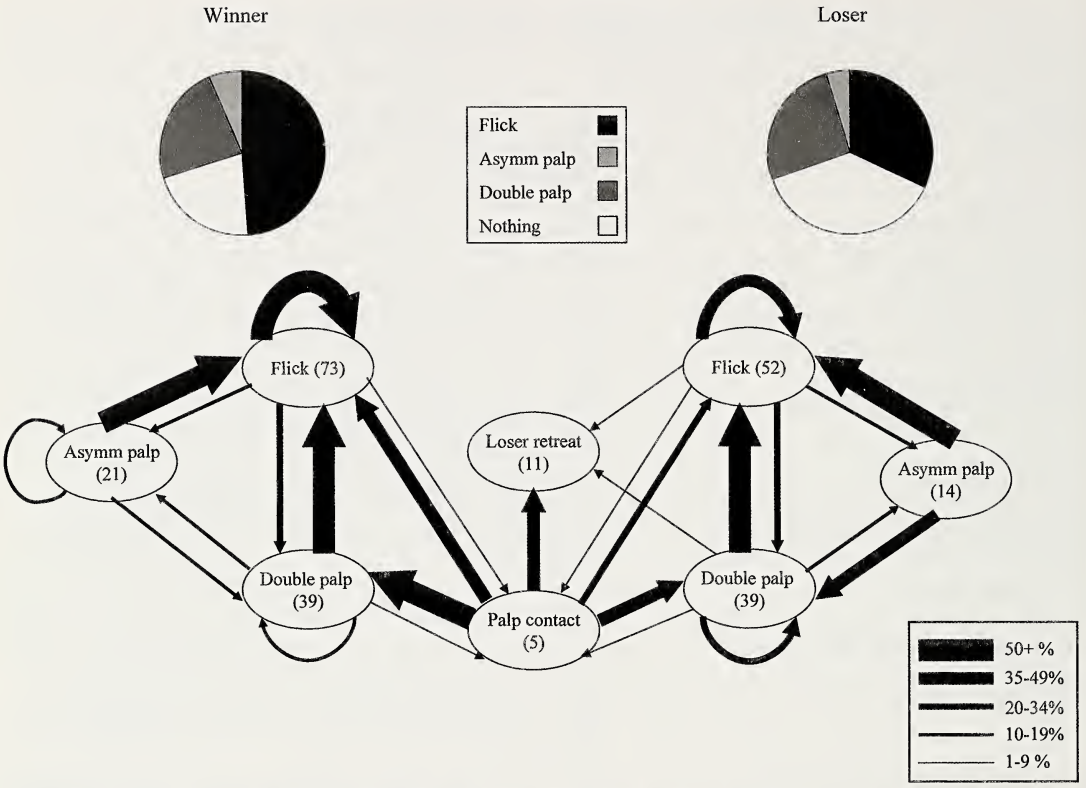

Figure 1.—A behavioral transition diagram that shows the flow of behaviors for male-male agonistic behavior in *P. marginemaculatus* (n = 11). The widths of the arrows represent the proportion of times the behavior at the arrowhead followed the behavior at the foot of the arrow. The pie charts above show the fractions of contest duration that winners versus losers flick and perform displays of asymmetric and double pedipalp opening.

to calculate flicking rate and to more closely examine the biomechanics of antenniform leg flicking. Because the light level necessary to capture high-speed video can disturb the animals and possibly influence contest outcome, three contests independent of the those used for previous analyses were staged between randomly chosen males after the completion of the other contests. High-speed video was captured using a motion scope high-speed video camera at 1000 frames/s and then transferred over to digital video (SONY DVCAM digital videocassette recorder). Video clips were analyzed by measuring the flicking frequency of antenniform legs and by characterizing the rapid flicking motion of the antenniform legs.

Statistical analyses.—Contest durations and body size measurements are reported as the mean ± standard deviation. Comparisons of contest duration and contest characteristics were made using a one-way ANOVA. Comparisons of contest durations of size-asymmetric versus size-symmetric male contests and of first and second trials between familiar males were made using a one-tailed t-test. Likelihood measures for behaviors associated with either male or female contests were done using Fisher's exact probability test. Logistic regression is an appropriate model to use in identifying predictors of outcomes of animal contests (Hardy & Field 1998), and predictors of contest outcome were evaluated using binomial logistic regression analysis. Correlation analyses, t-test analysis, and ANOVA were run using JMP IN 4.0.4 software. Differences in means for variables entered in the logistic regression analysis were calculated using a one-tailed, one-way ANOVA using STATA. Logistic regression, and prediction calculations were made using STATA.

RESULTS

Contest description.—Male contests of *P. marginemaculatus* are characterized by an exploratory period when the opponents first approach one another and make contact. This involves contact of the antenniform legs by one contestant onto various parts of the opponent's body (e.g., contact on the cephalothorax, the pedipalps, the legs or the opisthosoma). This exploratory period can be followed by the retreat of one individual, but more commonly progresses to aggressive displays (naïve males, 100%, $n = 11$; experienced males, 82%, $n = 11$). Aggressive displays are characterized by rapid antenniform leg flicking and pedipalpal opening displays (see Table 1) and in a given contest are often performed by both opponents (in naïve male contests, 91%, $n = 11$; in experienced male contests, 64%, $n = 11$). In a typical contest, animals vary their body position relative to the ground and relative to each other. Starting with the initial contact, individuals elevate themselves above their normal resting posture in an elevation display and they continue to vary their height off the ground throughout the contest. In escalated contests, during a bout of antenniform leg flicking, opponents often push forward then retreat back slightly, giving the general impression of a fencing tournament. Individuals frequently take an asymmetric stance in which they flick one antenniform leg at their opponent, and position that side of their body closer to their opponent while maintaining a distance of about 2–3 body lengths (Fig. 2). The pedipalp that is furthest away from the opponent is often open fully while the pedipalp closest to the opponent is often mostly closed. During these asymmetric stances, the opisthosoma is also directed away from the opponent in a posture previously described by Weygoldt (1969) and characteristic of whip spider agonistic encounters (Weygoldt 2000; also described in Alexander 1962).

Aggressive displays escalated to pedipalpal contact in 27% ($n = 11$) of contests between naïve males and 9% of contests between experienced males ($n = 11$). Pedipalpal contact is characterized by the appearance from above that the open pedipalps of opponents are pressed together. From the side view, it appears as though the more important contact is cheliceral contact between opponents, but with our recording devices we were unable to confirm this. During pedipalpal contact both individuals approach slowly, elevate themselves off the ground and fully open their pedipalps. Contact between individuals is brief and the front pair of walking legs sometimes loses contact with the ground as the animals quickly attempt to push their opponent away or over. This was always followed by the retreat of one individual in this study. No cases were observed in which injury or death were inflicted. In all cases involving pedipalpal contact, opponents were of similar size, and in the case involving experienced males, the males had not been previously paired with one another. On average, males lost 1.06 ± 1.43 mg ($n = 34$) of body weight through the duration of a contest.

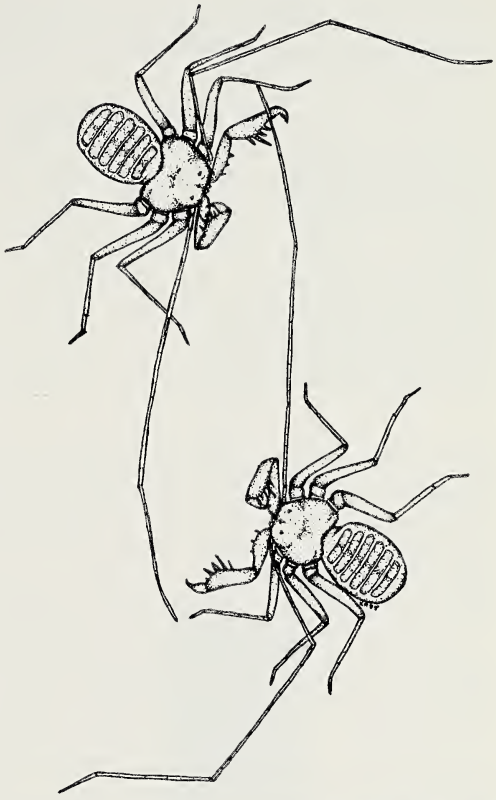

Figure 2.—Typical asymmetric stance in a contest of *P. marginemaculatus*. Individuals are approximately 1.5 cm in length from the front of the carapace to the tip of the abdomen.

Size-symmetric vs size-asymmetric contests.—Since there were no detectable differences between first and second contests as

Table 2.—Laboratory contests of *P. marginemaculatus*. * $P < 0.05$.

	Total # of individuals	Individuals flicking	Individuals opening the pedipalps	Contests escalated to pedipalpal contact
Size-symmetric males	20	90%	95%	30%
Size-asymmetric males	14	93%	79%	14%
Males	34	91%*	88%*	24%
Females	18	50%*	50%*	33%
Familiar males 1st contest	10	100%*	100%*	20%
Familiar males 2nd contest	10	60%*	60%*	0%
Unfamiliar males 1st contest	12	92%	83%	17%
Unfamiliar males 2nd contest	12	83%	83%	33%

long as both contests involved unfamiliar individuals (see effects of experience below), we included in these analyses all size-symmetric and size-asymmetric trials from an individual's second contest as long as it was with an unfamiliar individual (size-symmetric $n = 10$, size-asymmetric, $n = 7$). Aggressive displays of antenniform leg flicking and pedipalpal opening were no more/less likely to be observed in size-symmetric male contests versus in size-asymmetric male contests (antenniform leg flicking, Fisher's exact $P = 1.00$, two-tailed; pedipalpal opening, Fisher's exact $P = 0.28$, two-tailed; Table 2). Size-symmetric male contests were longer in duration than size-asymmetric contests (size-symmetric male contest duration = 745.1 ± 378.7 s, $n = 10$; size-asymmetric male contest duration = 447.0 ± 255.0 s, $n = 7$; $t_{15} = 2.06$, $P = 0.05$; Fig. 3). Also, males paired with males of similar size lost more weight during the contest than males paired with males of a different size (Welch's ANOVA: size-symmetric weight loss = 1.46 ± 1.75 mg, $n =$

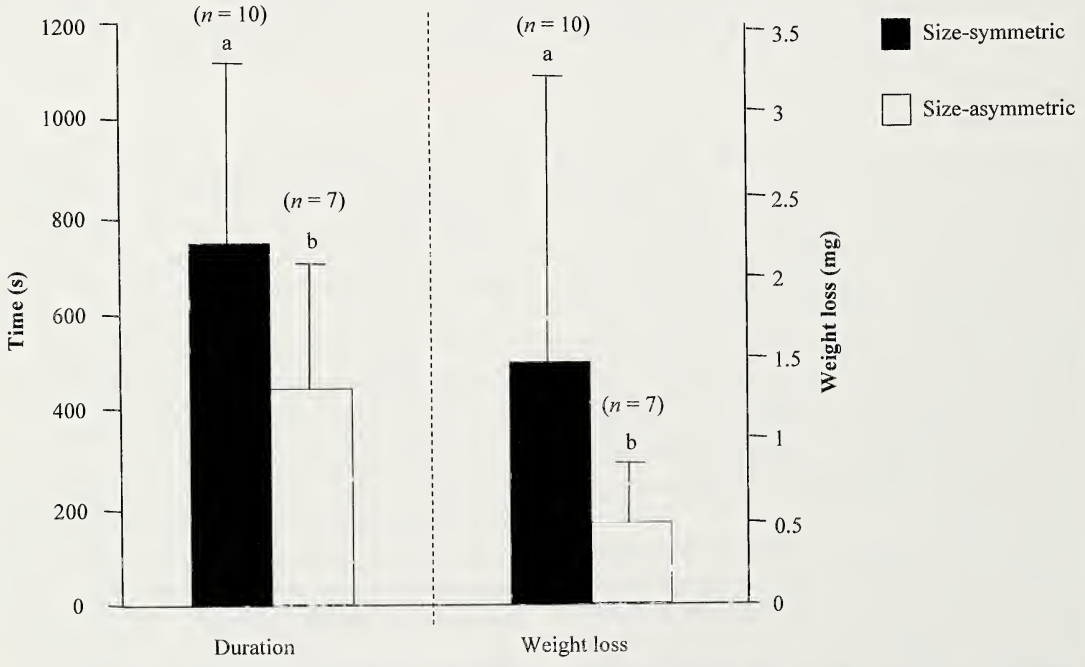

Figure 3.—Size-symmetric versus size-asymmetric contest duration and weight loss. Size-symmetric contests were significantly longer in duration than size-asymmetric contests and the mean weight loss in size-symmetric contests was greater than in size-asymmetric contests. Different letters indicate significant differences at $P < 0.05$.

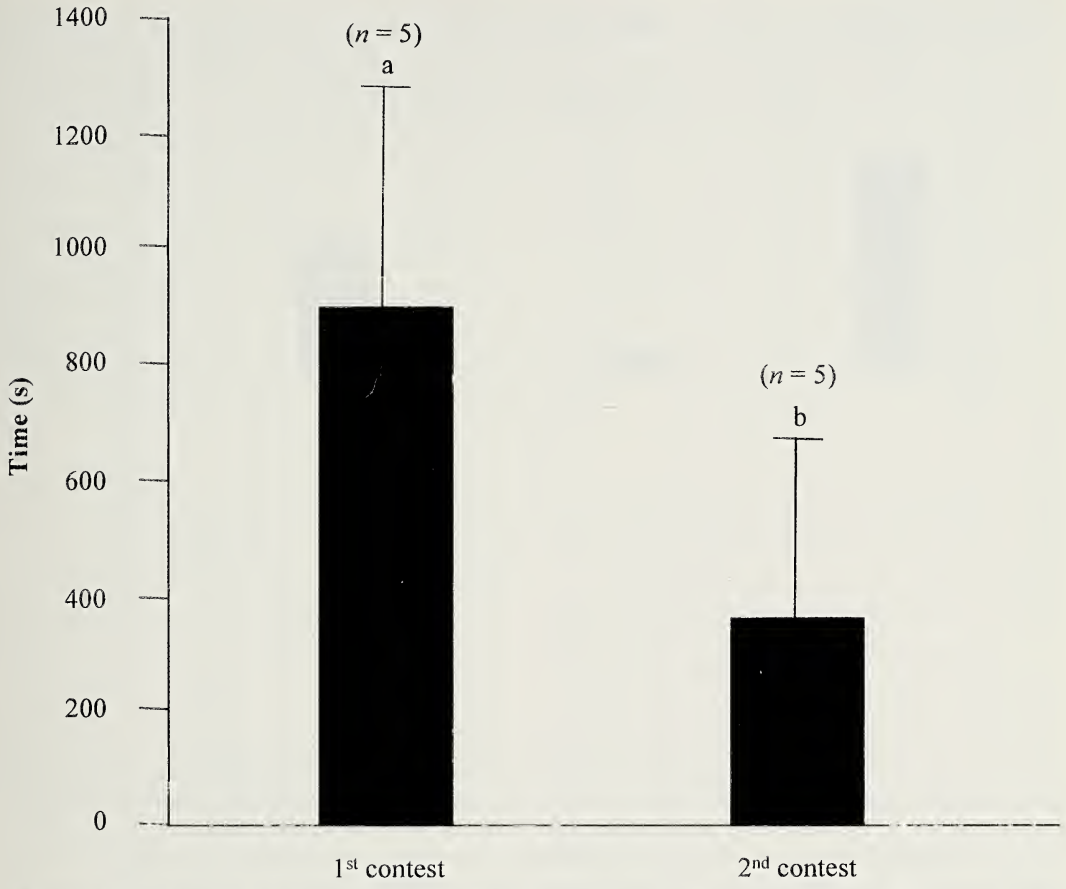

Figure 4.—The effect of experience on subsequent encounters. The contest duration for males in their first contest was longer than the contest duration for the same (familiar) pairs in their second contest. Different letters indicate a significant difference at $P < 0.05$.

20; size-asymmetric weight loss = 0.49 ± 0.36 mg, $n = 14$; df = 21, F = 5.8, $P = 0.03$; Fig. 3).

Experienced male-male contests.—We looked at the effects of experience on contest duration, likelihood of pedipalpal opening displays, and likelihood of antenniform leg-flicking displays in two groups of male-male contests: those between males paired with a familiar opponent and those between males paired with an unfamiliar opponent.

Contests between familiar males were significantly shorter in their second contest encounter as compared to their first contest encounter (familiar male second contest duration = 374.0 ± 320.5 s; first male contest duration = 902.0 ± 356.0 s; $t_8 = 2.05$, $P = 0.02$; Fig. 4). Males re-paired with a familiar opponent were also less likely to perform aggressive displays of pedipalpal opening and antenniform leg flicking in the second contest against a given opponent (pedipalpal opening: Fisher's exact, $P = 0.04$, one-tailed; antenniform leg-flicking: Fisher's exact, $P = 0.04$, one-tailed; Table 2), and there were no cases of pedipalpal contact in the second contest.

In comparing contests between the first laboratory encounters for males and contests between males re-paired with an unfamiliar opponent, we found no statistical difference between contest durations (naïve male contest duration = 650.2 ± 384.2 s, $n = 11$; experienced unfamiliar male contest duration = 571.2 ± 330.6 s, $n = 6$, $F_{1,15} = 0.18$, $P = 0.68$). Furthermore, males were no less likely to perform aggressive displays of pedipalpal opening and antenniform leg-flicking in their second contest paired with a different opponent than in their first contest (pedipalpal opening: Fisher's exact, $P = 0.705$, one-tailed;

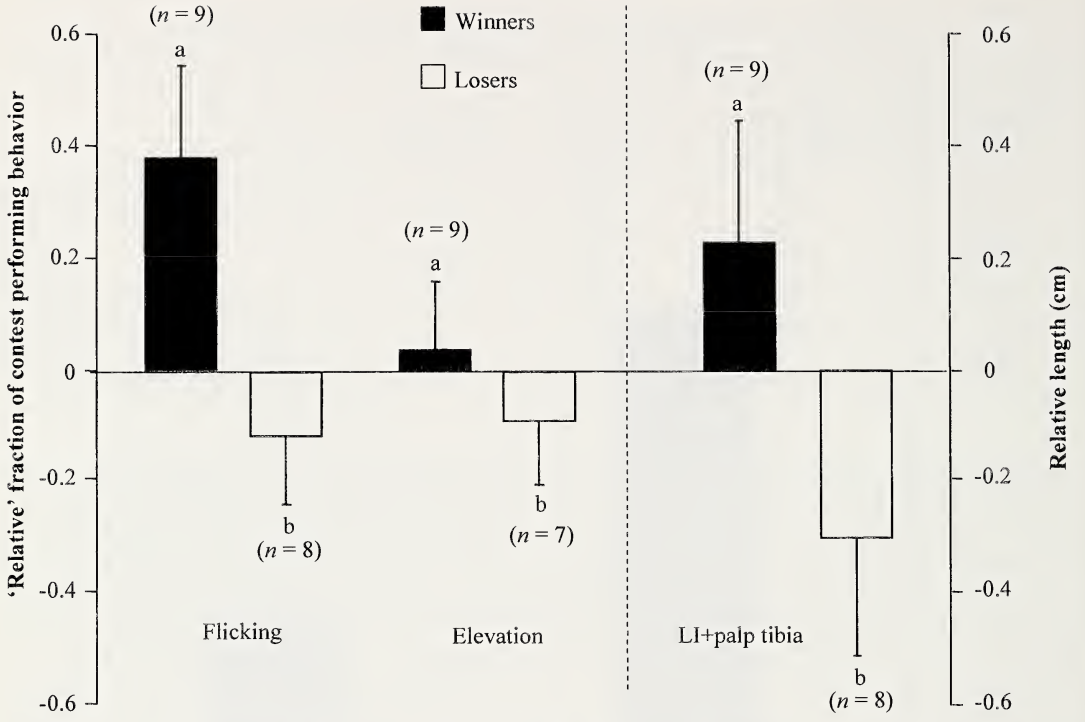

Figure 5.—A comparison of winners versus losers for 'relative' proportion of contest duration spent antenniform flicking and spent elevated higher than the opponent as well as a comparison of winner's and loser's weaponry size (tibia of pedipalp plus antenniform leg). There were significant differences between winners and losers in 'relative' flicking and elevation as well as weapon size using one-tailed ANOVA, but these characters were not statistically significantly correlated with contest outcome in our logistic regression models (see Table 3). Different letters indicate a significant difference at $P < 0.05$.

antenniform leg-flicking: Fisher's exact, $P = 0.50$).

Predictors of contest outcome.—In testing for predictors of contest outcome, we chose to examine four characters: fraction of contest duration in which an individual flicked his antenniform leg(s) as a measure of display intensity, the length of the tibia of the pedipalp plus the length of the antenniform leg as a measure of weapon size (these are the two appendages most heavily used during agonistic displays), cephalothorax width as a measure of body size, and the fraction of contest duration during which one individual held his elevation display higher than his opponent as a potential measure of both body size and motivation. Instead of using the raw values for each of the characters described above, we used the values relative to an individual's opponent. Thus, for each character, we calculated the 'relative' value by subtracting the value for one individual minus that of his opponent. We calculated a relative value for only one individual from each pair so as to not replicate the data ('winners' values are 'losers' values multiplied by negative one). For these analyses, we included all naïve male trials as well as all experienced male trials involving unfamiliar opponents.

Using a one-tailed ANOVA to compare the group means, we found that winners averaged statistically significantly greater 'relative' values for the elevation display, antenniform leg flicking, and weapon length (reported as mean ± S.E; flicking: winners = 0.370 ± 0.169, $n = 9$; losers = −0.122 ± 0.115, $n = 8$, difference = −0.492 ± 0.205, approx df = 13.8, $P = 0.02$; weapon size: winners = 0.219 ± 0.223, $n = 9$, losers = −0.305 ± 0.210, $n = 8$, difference = −0.524 ± 0.306, df = 15, $P = 0.05$; elevation: winners = 0.0288 ± 0.125, $n = 9$, losers = −0.094 ± 0.112, $n = 7$, difference = −0.382 ± 0.168, df = 14, $P = 0.02$; Fig. 5) and there was a trend for greater 'relative' cephalothorax width in winners (reported with mean ± S.E; CW: winners =

Table 3.—Logistic models predicting contest outcome. Relative elevation above the opponent is the best predictor of outcome.

Model variables	Logistic coef	Estimated s.e.	z-test	p-value
1. Relative elevation	3.5	1.9	1.83	0.067
2. Relative flick	4.6	2.8	1.63	0.104
3. Relative CW	1.0	0.7	1.44	0.150
4. Relative LI + palp	1.4	0.9	1.52	0.128
5. Relative flick	4.2	3.4	1.26	0.207
Relative elevation	2.3	2.0	1.11	0.267
6. Relative flick	4.2	3.4	1.21	0.226
Relative LI + palp	2.2	2.8	0.77	0.444
Relative CW	−0.8	1.9	−0.44	0.660
Relative elevation	1.2	2.6	0.47	0.641

0.394 ± 0.271, n = 9, losers =−0.225 ± 0.284, n = 8, difference =−0.619 ± 0.393, df = 15, P = 0.07). Even with differences between winners and losers, we lack enough information to have discriminatory power for predicting outcome using logistic regression. Furthermore, because the 'relative' variables entered into the logistic models are strongly correlated ('relative' elevation and 'relative' flicking, Coef = 0.593, P = 0.02; 'relative' elevation and 'relative' CW, Coef = 0.521, P = 0.04), we ran into problems building a statistically significant model with multiple variables. We ran logistic regression analyses using the following combinations: all four 'relative' variables together, each 'relative' variable separately, and both 'relative' antenniform leg flicking and 'relative' elevation together (see Table 3). Our best model uses the 'relative' elevation as a predictor of outcome (Coef = 3.50, SE Coef = 1.91, P = 0.07), followed by 'relative' antenniform leg flicking (Coef = 4.63, SE Coef = 2.85, P = 0.10). Predictive ability for the elevation model and flicking model are summarized in Table 4.

Examining all individuals in all 17 contests, we found that all characters analyzed were strongly correlated with the fraction of total contest time one individual was higher than his opponent (flick fraction versus fraction higher elevation: Coef = 0.4836, P = 0.005; CW versus fraction higher elevation: Coef = 0.4218, P = 0.02; LI + palp tibia length: Coef = 0.3487, P = 0.05), and also LI + palp tibia length was highly correlated with CW (Coef = 0.9443, $P \leq 0.0001$).

Table 4.—Using the relative elevation and flicking logistic models for predicting contest outcome, predictions for winners can be made.

Model and cutoff probability	Actual won/lost	Prediction	
		Won	Lost
Elevation, 50%	won = 9	7	2
	lost = 7	2	5
Flicking, 50%	won = 9	6	3
	lost = 8	4	4

Initial contact was made by four males that subsequently lost the contest, four males that subsequently won the contest, and two initial contacts appeared inadvertent. The behavioral transition diagram (Fig. 1) shows the progression of behaviors by winning and losing males during a male-male contest. A total of 138 behavioral transitions were observed in winning males and 113 behavioral transitions in losing males.

Female-female contests.—Contests between *P. marginemaculatus* females appeared qualitatively similar to those between males, however, there were significant differences in some aspects of the contests. Again, because no differences were found between males repaired with an unfamiliar male in their second contest and males in their first contest, we compiled data from naïve male contests and experienced male contests between males repaired with unfamiliar opponents. Females were less likely to exhibit antenniform leg flicking than were males (females, 50%, n = 18; male, 91%, n = 34; Fisher's exact, P = 0.001, one-tailed; Table 2). Females were less likely to exhibit aggressive displays of pedipalpal opening than were males (females, 50%, n = 18; males, 88%, n = 34; Fisher's

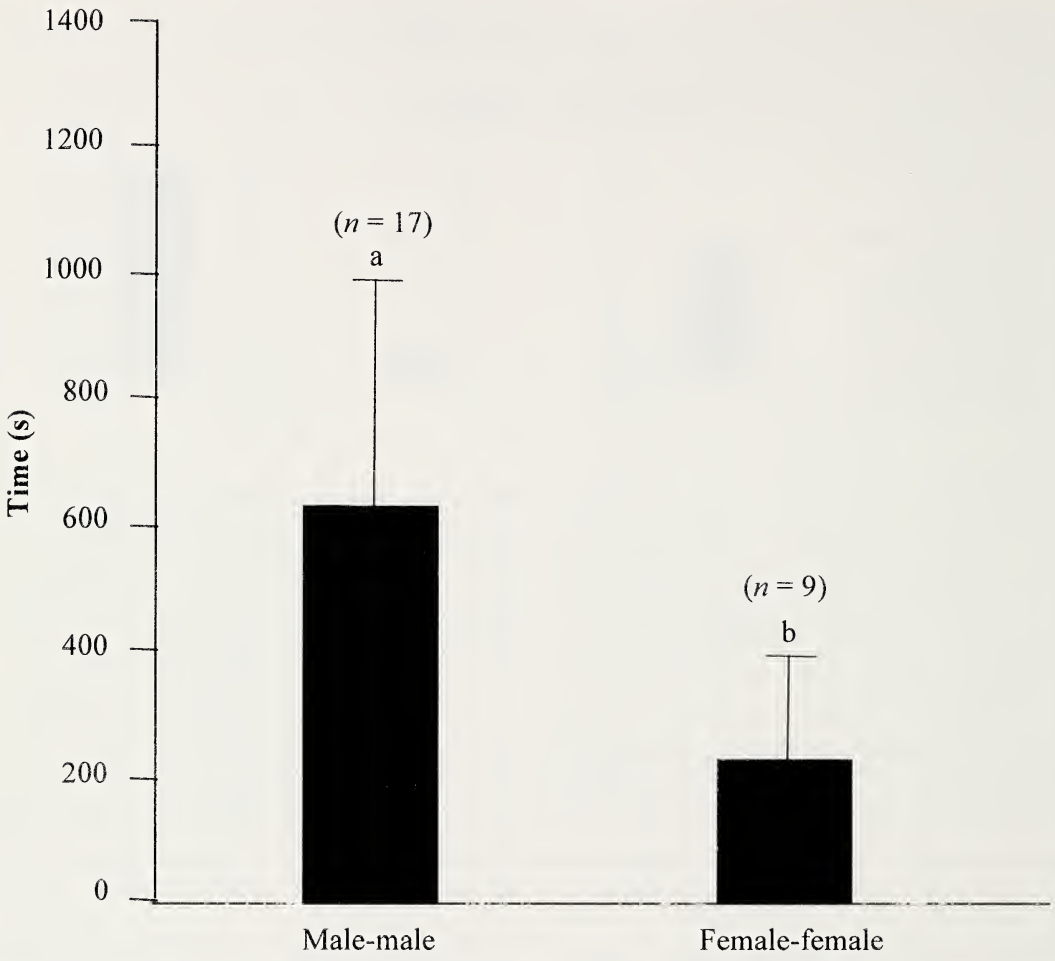

Figure 6.—Female-female versus male-male contest duration. Female contest duration was significantly shorter that male contest duration. Different letters indicate a significant difference for $P < 0.05$.

exact, $P = 0.004$, one-tailed; Table 2). Female contests were significantly shorter in duration than male contests (female contest duration = 225.6 ± 160.7 s, $n = 9$; male contest duration = 622.3 ± 357.7 s, $n = 17$; $F_{1,24} = 9.9$, $P = 0.004$; Fig. 6). In three of the nine female-female contests, individuals escalated to pedipalpal contact (one size-symmetric contest, two size-asymmetric contests). While not statistically significant, females lost almost half the weight that males lost during a contest (male weight loss = 1.46 ± 1.75 mg, $n = 20$; female weight loss = 0.54 ± 0.58 mg, $n = 12$; $F_{1,30} = 3.0695$, $P = 0.09$).

High-speed video.—Of the three male-male contests we recorded under high speed video, we observed antenniform leg flicking in only two of the pairs. In one contest, one individual flicked at a rate of 29.5 Hz and his opponent did not flick. In another contest, one individual flicked at a maximum of 27 Hz and his opponent flicked at a maximum of 28 Hz.

An animal normally flicks the antenniform leg across the body of his opponent, directing contact back and forth between the walking legs and the pedipalps. However, sometimes antenniform leg flicking does not result in contact with the opponent, but rather occurs next to the opponent. When antenniform leg flicking is viewed at a slower speed (1000 frames/sec), it is much easier to discern the particular pattern of antenniform leg movement. The following description of this movement is qualitative, as quantitative characterization of the motion was not performed. A back-and-forth movement originates from the base of the femur and the two-thirds of the antenniform leg closest to the body of an an-

imal stay relatively stiff. The outer third of the antenniform leg is held out straight along the axis of the leg, but appears slightly limp and its movement is slightly out of phase with the inner part of the leg.

DISCUSSION

Male-male contests.—This study demonstrates that intraspecific contests in *Phrynus marginemaculatus* are ritualized and have a natural progression from an exploratory period of light contact to more aggressive displays of antenniform leg flicking and pedipalpal opening. No contests resulted in injury or death, and escalation to pedipalpal contact was observed in only four of twenty-two male-male contests and three of nine female-female contests. Theory predicts that when opponents in an agonistic interaction are similar in size, escalation is more likely to occur (Parker 1974). This is consistent with our results in that all four cases where pedipalpal contact occurred were between males of similar size. However, only one of the three cases where pedipalpal contact occurred between females was between females of similar size.

The results of this study are similar to Weygoldt's (1969) study of *P. marginemaculatus*, but differ in some basic descriptive aspects as well as in the comparison of male and female contests. Weygoldt (1969) recounts that opposing animals try to flick the antenniform leg underneath the opponent. While we found that this behavior varied greatly between contests, we saw no evidence that animals were attempting to flick under the opponent as opposed to on top of them. Weygoldt (1969) also describes the female contests as being much more "spectacular." Data analysis revealed that female contests are shorter in duration with less displaying of aggression (potentially due to their shortened duration), but have a higher likelihood to escalate. Weygoldt (1969) further reports that females flick their antenniform legs extremely rapidly and that males flick their legs much more slowly and in a biomechanically different manner. In this study, in both initial observations and examination of videotapes, no apparent differences were discovered between male and female antenniform leg flicking, and males as well as females flicked their antenniform legs at a rate too fast to be determined using regular speed video recordings. However, we did not observe any female-female contest with high-speed video and therefore, we cannot adequately address the relative rates of antenniform leg flicking between males and females.

The results in the behavioral transition diagram show that antenniform leg flicking composed a large proportion of the originating behaviors for both winning males and losing males. Winning males tended to flick their antenniform legs more often than losing males. Antenniform leg flicking is clearly important in determining contest outcomes. Unfortunately, this study only addresses durations and numbers of behaviors, and does not quantify the speed with which the antenniform leg is moved. Antenniform leg flicking could demonstrate an individual's motivation level, or if it is energetically expensive, it could demonstrate the current fitness of a male. Future studies are needed to explore these possibilities.

Predictors of contest outcome.—Animals in conflict have been shown to assess asymmetries between themselves and their opponent which can be used in resolving agonistic encounters. These characters can include body size (Taylor & Jackson 2003) and call frequency (Bee et al. 1999; Davies & Halliday 1978) or weapon size (Weygoldt 2000; Sneddon et al. 1997), and can influence contest outcome (Maynard Smith & Parker 1976). In this study, the best logistic regression model shows that a longer relative amount of time spent at a height higher than an opponent best predicts outcomes of male-male contests. Using this model at a cutoff of 50% probability of winning, we can predict contest outcome fairly well. Whip spiders normally spend their time flat against the substrate but perform an elevation display during agonistic encounters. Elevation displays may signal motivation or likelihood of escalation. If there is a discrepancy in motivation between two opponents, the less motivated opponent may give up more easily. Elevation displays could also provide information on body size or weapon size since both these characters are highly correlated with time elevated higher than an opponent. Larger individuals will have longer legs and subsequently be able to push up higher than a smaller opponent. Body size is likely to influence contest outcome as it is a good indicator

of age and fighting ability in other animals (Olsson & Shine 2000).

Theory predicts that when opponents in an agonistic interaction are similar in size, escalation is more likely to occur (Parker 1974). Aggressive displays of antenniform leg flicking and pedipalpal opening did not occur more often in contests between males of similar size than in males of different size. Fight duration is also predicted to be longest between individuals of similar size, and shortest with a large body-size asymmetry (Parker 1974). This prediction has been supported in studies of bowl and doily spiders (Leimar et al. 1991) and jumping spiders (Faber & Baylis 1993), and our study further supports the prediction with longer contests between size-symmetric males versus size-asymmetric males. Furthermore, males lost more weight in contests against opponents of similar size. This increased weight loss is potentially related to contest duration.

Effects of experience.—We observed effects of prior contest experience on later contests. In contests where males were subsequently re-paired with the same opponent, in the second contest, males were less likely to exhibit aggressive displays and contest durations were significantly shorter. However, when males were re-paired with a different opponent, the likelihood of exhibiting aggressive displays was no different, and the contest duration was no different. This finding suggests that the males were able to remember previous opponents over the three-week time period that elapsed in between trials and retained effects of earlier contest experience.

Female-female contests.—Female-female contests were similar to male-male contests, suggesting that ritualized agonistic encounters in *P. marginemaculatus* have experienced similar selection pressures in males and females. Weygoldt (1969) suggests that the contests lower the density of individuals in an area. While the contests were similar in general progression, there were subtle behavioral differences between female and male contests. Females were less likely to display the aggressive behaviors of antenniform leg flicking and pedipalpal opening than males, and female-female contests were shorter in duration than male-male contests. These behavioral differences may be due to sexual selection pressure also acting on the male contests, especially if fighting behavior plays a role in a male's ability to find mates successfully. In crab spiders (Hoefler 2002) and jumping spiders (Faber & Baylis 1993), contest duration and escalation increase when contestants were in the presence of a female. In the field, male-male contests may predominantly occur when there is ready access to a female. Thus, the longer and more aggressive contests by male *P. marginemaculatus* seen in the laboratory may reflect typical battles in the field. Males may have more at stake than females: a potential mating in addition to territory defense, as territory defense is a likely context for agonistic behavior in whip spiders (Weygoldt 2000).

Potential role of agonistic interactions.—In spiders, male-male agonistic behaviors have been described in the context of competition for mate access (Schmitt et al. 1990). Winning males often mate with females (Huntingford & Turner 1987). A study examining the ecology and behavior of a whip spider closely related to *Phrynus marginemaculatus*, *P. parvulus* (Hebets 2002), suggests that males wander in search of mates while females remain in a home crevice over extended periods of time (Hebets 2002). When males encounter other males while wandering, they engage in agonistic behavior (Hebets pers. obs.). In *P. marginemaculatus*, males may be more mobile than females, and therefore may encounter each other more in the field. If this is the case, then there would be stronger selection on ritualization of male contests versus female contests, and this could explain the tendency for females to escalate to pedipalpal contact faster and for female contest duration to be shorter. The agonistic behaviors observed in *P. parvulus* likely reflect competition for mates in addition to territory defense (Weygoldt 2000). Whether or not male fighting behavior in *P. marginemaculatus* is associated with mate access has not yet been studied. Although sexual selection may be a selective force behind the fighting behavior of *P. marginemaculatus*, it cannot be the exclusive selective force shaping agonistic behavior since females demonstrate fighting behaviors similar to male fighting behaviors. Individuals of *P. marginemaculatus* are typically found individually under limestone rocks on the Florida Keys and part of their agonistic interactions may reflect territoriality, with in-

dividuals defending their home rock. Extensive field studies exploring their natural history and behavior are necessary to draw a more conclusive picture of the selective forces acting on contests in *P. marginemaculatus*.

Most studies of intraspecific competition have focused on visual or auditory animals (Barlow et al. 1986; Faber & Baylis 1993; Taylor & Jackson 2003). However, whip spiders are unique in that they most likely do not rely on sight or sound for communication. They provide a novel system for studying communication in a non-visual animal. In order to better determine what cues individuals use to assess their opponent, further studies with larger sample sizes need to be conducted. Also, further investigation of the natural history of *P. marginemaculatus* would provide a good framework within which their complex ritualized fighting behavior can be studied. As this study has shown, the antenniform leg is heavily utilized in intraspecific contests and tactile cues likely play a large role in intraspecific contests in *P. marginemaculatus*.

Conclusions.—This study characterizes male-male contests in the whip spider *P. marginemaculatus*, investigates effects of experience on male fighting behavior, and compares male contests with female contests. Elevation displays potentially play an important role in intraspecific contests, and can be used to predict contest outcome with some accuracy. Our results indicate that males retain effects of previous contest experience and remember previous opponents for at least three weeks. We found that female contests were shorter in duration and more intense than male contests, suggesting stronger selection pressure on male-male fighting behavior. This study suggests that whip spiders have complex behaviors in which learning and memory may play a large role.

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FOUR NEW CRAB SPIDERS FROM TAIWAN (ARANEAE, THOMISIDAE)

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ABSTRACT. Examination of some thomisid specimens collected from Taiwan, three species are newly recorded from this fauna: *Misumenops pseudovatius* (Schenkel 1936), *Phrynarachne ceylonica* (O.P.-Cambridge 1884), *Xysticus croceus* (Fox 1937). In addition, four new species are described: *Lysiteles digitatus*, *L. torsivus*, *Takachihoa onoi*, and *Tmarus lanyu*.

Keywords: Thomisidae, *Lysiteles*, *Takachihoa*, *Tmarus*, Taiwan

The Thomisidae is a large family comprising 164 genera and 2,042 species (Platnick 2005) and is distributed worldwide. This family is commonly called the crab spiders for the body is generally strong, slightly flattened and the legs are laterigrade. Members of this family are small to large (3–23 mm) species, which build no webs and capture small insects by lying in wait. They are usually found on trees, shrubs and grasses, especially on flowering plants, as well as in leaf litter and under stones on the ground (Foelix 1996).

Although some thomisid species have been previously recorded from Taiwan (Ono 1977, 1980, 1992; Chen 1996; Song & Zhu 1997), the fauna has not been fully studied. Only 12 Taiwanese species belonging to 10 genera have been previously recorded: *Alcimochthes limbatus* Simon 1885, *Diaea subdola* O.P.-Cambridge 1885, *Lysiteles amoenus* Ono 1980, *L. silvanus* Ono 1980, *Misumenops tricuspidatus* (Fabricius 1775), *Oxytate striatipes* L. Koch 1878, *Runcinia albostriata* Bösenberg & Strand 1906, *Takachihoa truciformis* (Bösenberg & Strand 1906), *Thomisus labefactus* Karsch 1881, *T. okinawensis* Strand 1907, *Tmarus taiwanus* Ono 1977 and *Xysticus chui* Ono 1992 (Ono 1977, 1980, 1992; Chen 1996; Song & Zhu 1997; Platnick 2005). Recently, we examined some thomisid specimens collected from Taiwan, and found that three species are new to this fauna: *Misumenops pseudovatius* (Schenkel 1936), *Phrynarachne ceylonica* (O.P.-Cambridge 1884) and *Xysticus croceus* Fox 1937. Another four species are new to science and described here under the names of *Lysiteles digitatus*, *L. torsivus*, *Takachihoa onoi* and *Tmarus lanyu*.

METHODS

Type specimens are deposited in the National Museum of Natural Science, Taichung, Taiwan (NMNS). All measurements given are in mm. Palp measurements are shown as: total length (femur, patella, tibia, tarsus). Leg measurements are shown as: total length (femur, patella and tibia, metatarsus, tarsus). Abbreviations used in this study are: AME = anterior median eye; ALE = anterior lateral eye; PME = posterior median eye; PLE = posterior lateral eye; MOA = median ocular area.

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SYSTEMATICS

Family Thomisidae Sundevall 1833

Key to genera from Taiwan

1. Chelicerae with strong teeth on both margins of fang furrow; body with granulations and tubercles on dorsum ..... *Phrynarachne*
   Chelicerae lacking teeth; body otherwise 2
2. Tarsi with claw tufts formed by tenent hairs 3
   Tarsi lacking claw tufts or with undeveloped tufts formed by simple hairs 4
3. Eye area wide, almost as wide as cephalothorax; retrolateral tibial apophysis of male palp not much developed; female epigynum with only one guide pocket ..... *Alcimochthes*
   Eye area narrow, only half as wide as cephalothorax; retrolateral tibial apophysis of male palp much developed; female epigynum with a pair of guide pocket ..... *Oxytate*
4. Clypeus wide; tubercles of PLE larger than those of ALE ..... *Tmarus*
   Clypeus narrow; tubercles of PLE smaller than those of ALE 5
5. Body and legs somber-colored, yellowish to blackish brown; leg I only a little longer than leg IV; inhabiting ground and low herbs ..... *Xysticus*
   Body and legs bright-colored, white, yellow, green or light brown; leg I much longer than leg IV; inhabiting plants 6
6. Cephalothorax with long thoracic setae; retrolateral tibial apophysis of male palp simple and sclerotized; body and legs relatively somber 7
   Thoracic setae usually short or lacking; retrolateral tibial apophysis of male palp much developed and basally not sclerotized; body and legs usually green-colored 8
7. Female abdomen longer than wide; embolus of male palp short and thick; spermathecae of female epigynum large ..... *Lysiteles*
   Female abdomen as wide as or wider than long; embolus of male palp long and filiform; spermathecae of female epigynum small ..... *Takachihoa*
8. Conical protuberance present between ALE and PLE; male much smaller than female .. 9
   Conical protuberance absent between ALE and PLE; male not much smaller than female 10
9. Abdomen as wide as or wider than long; protuberance between ALE and PLE well-developed ..... *Thomisus*
   Abdomen much longer than wide; protuberance between ALE and PLE small .... *Runcinia*
10. MOA longer than wide; embolic division of male palp winding around tegulum; epigynum with soft protuberance ..... *Diaea*
    MOA wider than long; embolic division of male palp winding around tegulum or very short with basal structure; epigynum rarely with undeveloped protuberance .... *Misumenops*

Genus *Lysiteles* Simon 1895

Lysiteles Simon 1895:998; Ono 1988:132; Song & Zhu 1997:119.

Type species.—*Lysiteles catulus* Simon 1895, by original designation.

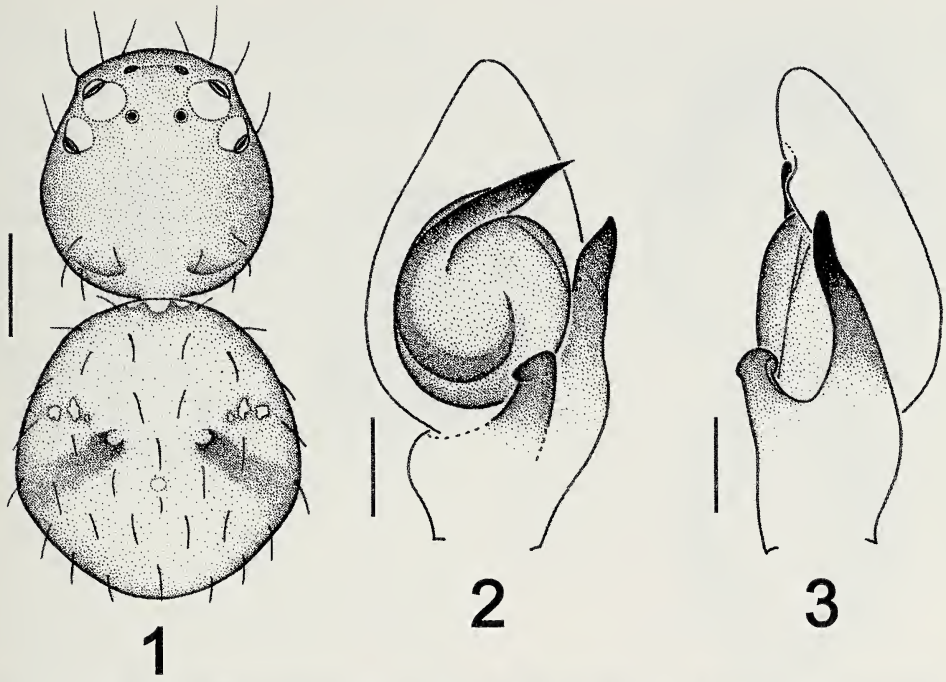
Diagnosis.—Small thomisids with well developed eyes. Male palp with ventral and retrolateral tibial apophyses; retrolateral tibial apophysis strongly sclerotized; palpal bulb without apophyses; embolus short, thick and twisted. Female epigynum with a sclerotized fold, with intromittent orifice situated in the fold; spermathecae globular (Ono 1988).

Remarks.—This genus is represented by 38 species distributed in Bhutan, China, Nepal, Philippines, India, Russia, Korea and Japan (Platnick 2005). Among them, two species, *Lysiteles amoenus* Ono 1980 and *L. silvanus* Ono 1980, are currently reported from Taiwan.

Lysiteles digitatus new species

Figs. 1–3

Type material.—Male holotype, Lanyu (22°02′N, 121°33′E), Taitung County, Taiwan, February 2001, K.C. Chen (NMNS-THU-Ar-02-0302); 1 male paratype, Taitung County,



Figures 1–3.—*Lysiteles digitatus* new species: 1. Male, dorsal view; 2. Left palp, ventral view; 3. Left palp, retrolateral view. Scale lines: 0.5 mm (Fig. 1); 0.1 mm (Figs. 2, 3).

Taiwan, August 2000, K.C. Chen (NMNS-THU-Ar-02-0301).

Etymology.—The specific name is from the Latin "digitatus", and refers to the finger-like distal part of the retrolateral tibial apophysis of the male palp.

Diagnosis.—This species resembles *L. maius* Ono 1979 (Ono 1979, 1980), but differs from the latter in that the abdomen lacks large dark patches, the embolus is long, with its tip dagger-like, and the retrolateral tibial apophysis of male palp is almost three times as long as the ventral tibial apophysis (Figs. 2, 3); whereas in *L. maius*, the dorsum of male abdomen has large dark patches, a short embolus, and the retrolateral tibial apophysis is only slightly longer than the ventral tibial apophysis.

Male.—Total length 1.70–2.65. Holotype total length 2.65; cephalothorax 1.33 long, 1.09 wide; abdomen 1.36 long, 1.21 wide. Carapace orange, with some long setae (Fig. 1). Chelicerae, endites, labium, sternum and legs orange. Legs with a few long spines and fine hairs. Abdomen earthy yellow, with a few small white spots and 2 brown patches, scattered with some long setae. Both eye rows recurved. AME-AME: AME-ALE (0.14: 0.09), PME-PME: PME-PLE (0.17: 0.27); AME: ALE: PME: PLE (0.08: 0.14: 0.05: 0.12). MOA 0.29 long, front width 0.31, back width 0.29. Clypeus width 0.21. Labium longer than wide (0.22: 0.16). Sternum longer than wide (0.65: 0.60). Measurements of palp and legs: palp 0.97 (0.22, 0.16, 0.13, 0.46); leg I 3.88 (1.31, 1.50, 0.65, 0.42), II 4.41 (1.36, 1.58, 0.87, 0.60), III 2.59 (0.78, 0.94, 0.46, 0.41), IV 2.72 (0.88, 0.99, 0.44, 0.41). Leg formula: 2, 1, 4, 3. Palpal bulb simple; embolus short, tip pointed in ventral view; ventral tibial apophysis short, apically with a blunt hook; retrolateral tibial apophysis long, with its distal part finger-like (Figs. 2, 3).

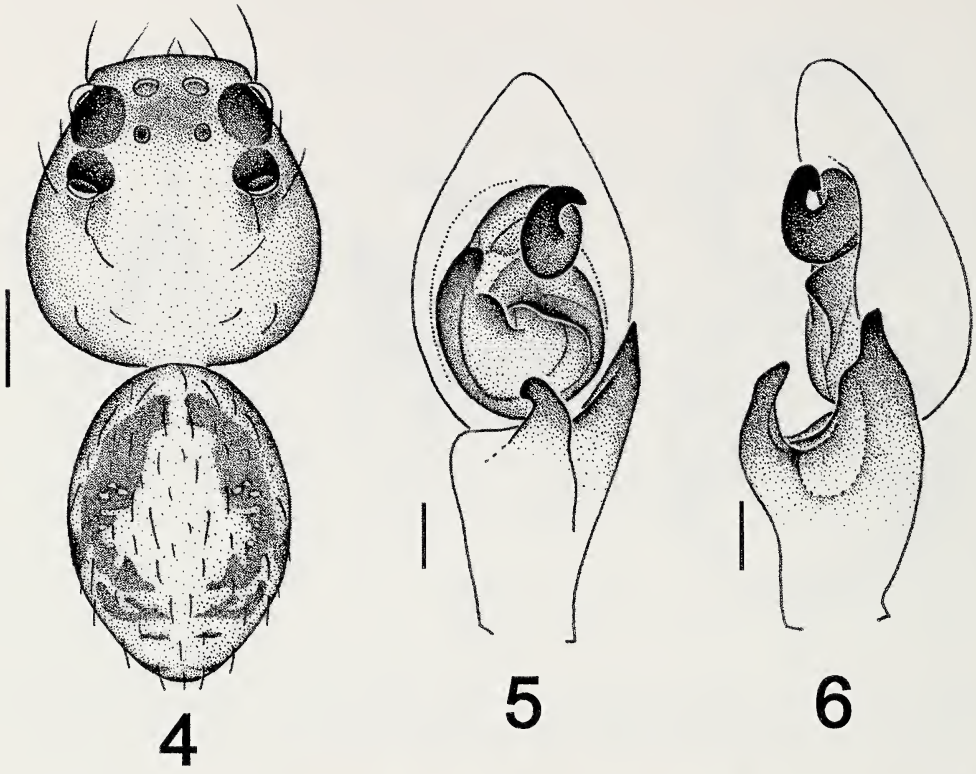
Female.—Unknown.

Distribution.—This species is only known from Taitung County, Taiwan.

Lysiteles torsivus new species
Figs. 4–6

Type material.—Male holotype, Lanyu (22°02′N, 121°33′E), Taitung County, Taiwan, February 2001, K.C. Chen (NMNS-THU-Ar-02-0316).

Etymology.—The specific name is from the Latin "torsivus", and refers to the curved embolus of the male palp.



Figures 4–6.—*Lysiteles torsivus* new species: 4. Male, dorsal view; 5. Left palp, ventral view; 6. Left palp, retrolateral view. Scale lines: 0.5 mm (Fig. 4); 0.1 mm (Figs. 5, 6).

Diagnosis.—This species is identified as new rather than the male of *Lysiteles amoenus* (Ono 1980) from Taiwan, because the carapace is trapeziform, and the posterior eye row is longer than the anterior row (Fig. 4); whereas in *L. amoenus*, the carapace is almost quadrate, and the posterior eye row is narrower than the anterior row. The new species is also similar to *L. silvanus* Ono 1980, but can be easily distinguished from the latter by the short and thick embolus of the male palp, which is curved in the opposite direction, and the retrolateral apophysis is dagger-shaped in ventral view (Figs. 5, 6).

Male.—Holotype total length 3.15; cephalothorax 1.53 long, 1.41 wide; abdomen 1.76 long, 1.19 wide. Carapace orange, with some long setae, eye region deep brown (Fig. 4). Chelicerae orange, outer lateral margin of front surface deep brown. Endites, labium and sternum yellow. Sternum with many long setae. Legs yellow, distal end of tibiae and tarsi orange. Legs with many spines and setae, tibiae I and II with 2 pairs of ventral spines, metatarsi I and II with 3 pairs of ventral spines. Abdomen yellow, with some long and short setae; dorsum with gray brown patches and a few small yellowish spots; venter with lateral longitudinal gray brown markings in posterior half. Both eye rows recurved. AME-AME: AME-ALE (0.12: 0.13), PME-PME: PME-PLE (0.16: 0.31); AME: ALE: PME: PLE (0.14: 0.21: 0.12: 0.117. MOA 0.29 long, front width 0.38, back width 0.35. Clypeus width 0.26. Labium longer than wide (0.39: 0.26). Sternum wider than long (0.85: 0.82). Measurements of palp and legs: palp 1.71 (0.66, 0.30, 0.23, 0.52); leg I 5.90 (1.80, 2.07, 1.35, 0.68), II 6.26 (1.89, 2.30, 1.35, 0.72), III 3.78 (1.26, 1.35, 0.72, 0.45), IV 3.83 (1.17, 1.35, 0.81, 0.50). Leg formula: 2, 1, 4, 3. Palpal bulb simple; embolus thick and curved; ventral tibial apophysis short and apically hooked; retrolateral tibial apophysis long, dagger-shaped as seen in ventral view (Figs. 5, 6).

Female.—Unknown.

Distribution.—This species is only known from Taitung County, Taiwan.

Genus *Misumenops* F.O.P.-Cambridge 1900

Misumenops F.O.P.-Cambridge 1900:134; Ono 1988:156; Song & Zhu 1997:136.

Type species.—*Misumena maculis-parsa* Keyserling 1891, by original designation.

Diagnosis.—Small to medium-sized thomisids. Tubercles of lateral eyes connate, lateral eyes much larger than median eyes. Male palp with retrolateral, ventral and intermediate tibial apophyses, ventral tibial apophysis digitiform and retrolateral tibial apophysis frequently with dorsal tooth. Female epigynum with central hood, intromittent orifices situated at both sides of hood, spermathecae usually small and tubular (Ono 1988).

Remarks.—Some 123 species and three subspecies of *Misumenops* have been reported worldwide, which are distributed in America and Asia (Platnick 2005). Only one species, *Misumenops tricuspidatus* (Fabricius 1775), was previously recorded from Taiwan.

Misumenops pseudovatius (Schenkel 1936)

Misumena pseudovatia Schenkel 1936:132, fig. 48.
Misumenops pseudovatius (Schenkel): Song & Zhu 1997:141, fig. 101, figs. 101A-D; Song, Zhu & Chen 1999:483, figs. 279C, K.

Material examined.—TAIWAN: *Taitung County*: 1 ♂, Lanyu (22°02′N, 121°33′E), August 2000, K.C. Chen (NMNS-THU-Ar-02-0303); 1 ♂, Lanyu (22°02′N, 121°33′E), August 2000, K.C. Chen (NMNS-THU-Ar-02-0304); 1 ♂, Taichung City (24°11′N, 120°35′E), 1 May 2000, J.N. Hwang.

Diagnosis.—This species resembles *Misumenops tricuspidatus* (Fabricius 1775) (Song & Zhu 1997) in the coloration and body shape, but can be easily distinguished from the latter by the central hood of the female epigynum, the large and almost rectangular spermathecae; the very small ventral tibial apophysis of male palp, and the presence of a dorsal tooth on the retrolateral tibial apophysis.

Female.—See descriptions and illustrations of Song & Zhu (1997).

Male.—See descriptions and illustrations of Song & Zhu (1997).

Distribution.—China and neighboring islands; Bhutan.

Genus *Phrynarachne* Thorell 1869

Phrynarachne Thorell 1869:37; Ono 1988:23; Song & Zhu 1997:25.

Type species.—*Thomisus rugosus* Walckenaer 1805, by original designation.

Diagnosis.—Medium to large-sized thomisids. Eyes small, subequal in size. Cephalothorax with granulations, abdomen with many tubercles. Retrolateral tibial apophysis of male palp spiniform and long, palpal bulb simple, embolus filiform and winding around tegulum. Female epigynum with a sclerotized plate; spermathecae reniform (Ono 1988).

Remarks.—Members of the genus *Phrynarachne* have been mainly reported from Asia and Africa, and 28 species and two subspecies have been reported (Platnick 2005). This genus is new to Taiwan.

Phrynarachne ceylonica (O.P.-Cambridge 1884)

Ornithoscatoides ceylonica O.P.-Cambridge 1884: 201, plate 15, fig. 3.
Phrynarachne ceylonica (O.P.-Cambridge): Thorell 1891:97; Ono 1988:25, figs. 11–17

Material examined.—TAIWAN: *Taitung County*: 1 ♀, Lanyu (22°02′N, 121°33′E), August 2000, S.Y. Du (NMNS-THU-Ar-01-0031); *Pingtung County*: 1 ♀, Nan-Jen Shan (22°05′N, 120°50′E), March 1999, Y. Y. Chen (NMNS-THU-Ar-01-0032).

Diagnosis.—This species is similar to *Phrynarachne katoi* Tikuni 1955 (see Ono 1988) in body shape and coloration, but can be easily distinguished from the latter in that the epigynum has no central hood under the epigynal plate, the spermathecae have anteriorly situated glands, the ventral tibial apophysis of male palp is curved distally and the cymbium is expanded retrolaterally.

Female.—See descriptions and illustrations of Ono (1988).

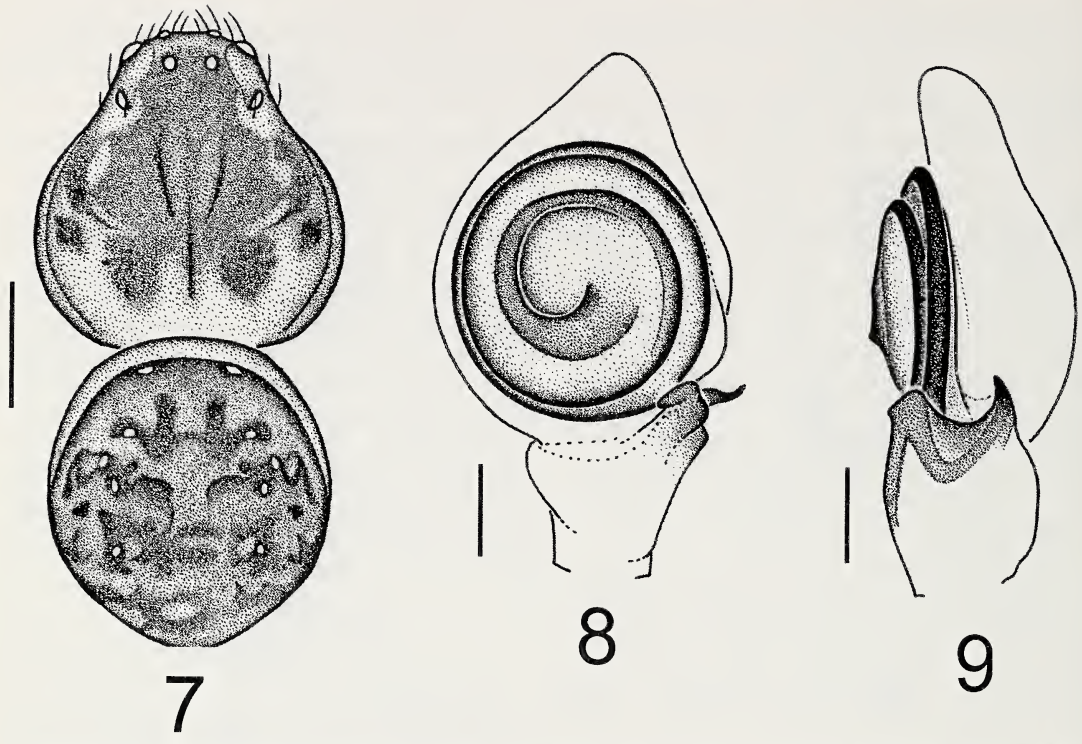
Male.—See descriptions and illustrations of Ono (1988).

Distribution.—China and neighboring islands; Japan; Sumatra; Nicobar Islands; India; Sri Lanka.

Genus *Takachihoa* Ono 1985

Takachihoa Ono 1985:28; Ono 1988:152; Song & Zhu 1997:135.

Type species.—*Oxyptila truciformis* Bösenberg & Strand 1906, by monotypy.



Figures 7–9.—*Takachihoa onoi* new species: 7. Male, dorsal view; 8. Left palp, ventral view; 9. Left palp, retrolateral view. Scale lines: 0.5 mm (Fig. 7); 0.1 mm (Figs 8, 9).

Diagnosis.—Small thomisids. Cephalothorax with clavate setae in females. Male palp with ventral and retrolateral tibial apophyses, palpal bulb without apophyses, embolus long and filiform, winding twice around the tegulum. Female epigynum is weakly sclerotized, with a median hood, and small, globular spermathecae. *Takachihoa* is similar to *Synaema* Simon 1864, but differs from the latter in that the female epigynum is weakly sclerotized and bears no chitinized plates, and the ventral tibial apophysis of male palp is large and securiform (Ono 1988).

Remarks.—Two species of *Takachihoa* have been previously named from China, Japan and Indonesia (Platnick 2005), and we here add a third species from Taiwan.

Takachihoa onoi new species
Figs. 7–9

Type material.—Male holotype, Lanyu (22°02′N, 121°33′E), Taitung County, Taiwan, August 2000, K.C. Chen (NMNS-THU-Ar-02-0308); 1 male paratype, Lanyu (22°02′N, 121°33′E), Taitung County, Taiwan, February 2001, K.C. Chen (NMNS-THU-Ar-02-0309).

Etymology.—The specific name is a patronym in honor of the well-known Japanese araneologist, Dr H. Ono.

Diagnosis.—The new species resembles *Takachihoa truciformis* (Bösenberg & Strand 1906) (see Ono 1988) in the shape of the male palp, but differs from the latter in that the ventral tibial apophysis is axe-shaped in ventral view and the retrolateral tibial apophysis is not bifurcated in lateral view (Figs. 8, 9).

Male.—Total length 2.43–2.45. Holotype total length 2.45; cephalothorax 1.24 long, 1.34 wide; abdomen 1.29 long, 1.19 wide. Carapace red brown, with black brown patches and several setae. Chelicerae yellow brown, with gray brown pigment on front surface. Endites yellow brown, lateral margins gray brown. Labium reddish brown, distal part pale. Sternum yellow brown. Legs I and II red brown, with gray brown spots on femora; basal parts of coxae, trochanters and femora of legs III and IV yellowish brown, rest red brown. Tibiae I and II with 4 pairs of ventral spines, metatarsi I and II with 3 pairs of ventral spines. Dorsum of abdomen yellow brown, scattered with irregular black brown

patches, anterior margin yellowish brown; venter earthy yellow, with 2 grayish brown patches in front of spinnerets. Both eye rows recurved. AME-AME: AME-ALE (0.12: 0.08), PME-PME: PME-PLE (0.10: 0.22); AME: ALE: PME: PLE (0.05: 0.12: 0.04: 0.07). MOA 0.18 long, front width 0.23, back width 0.22. Clypeus width 0.08. Labium slightly wider than long (0.20: 0.19). Sternum longer than wide (0.68: 0.65). Measurements of palp and legs: palp 1.08 (0.38, 0.21, 0.13, 0.36); leg I 4.00 (1.16, 1.38, 0.88, 0.58), II 5.30 (1.48, 1.87, 1.39, 0.56), III 2.75 (0.90, 1.02, 0.46, 0.37), IV 2.69 (0.85, 0.99, 0.48, 0.37). Leg formula: 2, 1, 3, 4. Palpal bulb simple, without apophyses; embolus long and filiform, winding around tegulum in two circles; ventral tibial apophysis large and axe-shaped in ventral view; retrolateral tibial apophysis not well developed with its distal end single, not bifurcated (Figs. 8, 9).

Female.—Unknown.

Distribution.—This species is only known from Taitung County, Taiwan.

Genus *Tmarus* Simon 1875

Tmarus Simon 1875:259; Ono 1988:53; Song & Zhu 1997:44.

Type species.—*Aranea pigra* Walckenaer 1802, by original designation.

Diagnosis.—Medium-sized thomisids. MOA nearly as long as wide. Male palp with ventral and retrolateral tibial apophyses, frequently with intermediate and distal tibial apophyses, palpal bulb is simple, lacking apophyses, embolus usually short and thick. Female epigynum usually with a median hood, spermathecae small, globular, oval or reniform (Ono 1988).

Remarks.—Although some 210 species are currently included in the genus *Tmarus* (Platnick 2005), only *T. taiwanus* Ono 1977 was previously recorded from Taiwan. We here report on a new Taiwanese species.

Tmarus lanyu new species
Figs. 10–14

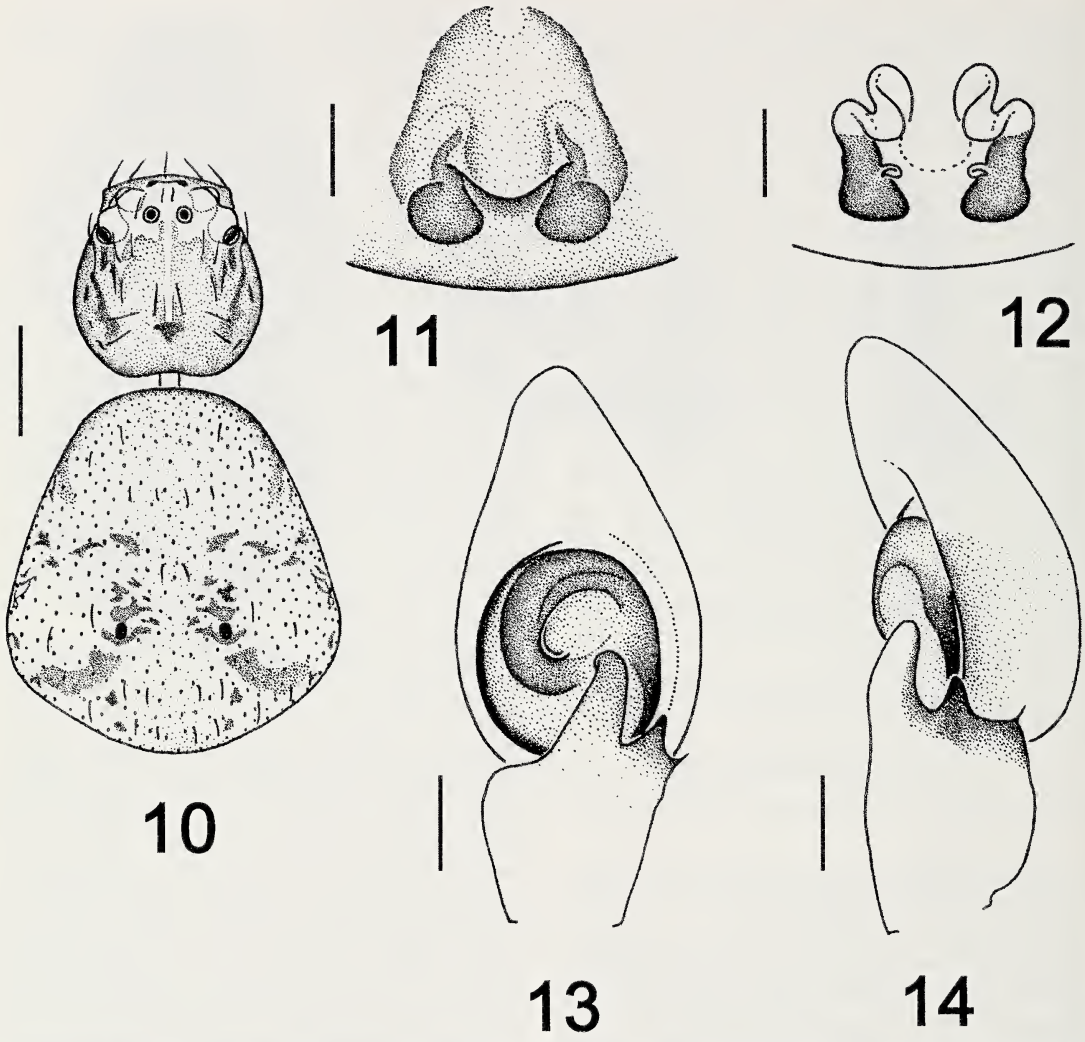
Type material.—Female holotype, Lanyu (22°02′N, 121°33′E), Taitung County, Taiwan, 19 February 1997 (NMNS-THU-Ar-01-0035). Paratypes, all from Lanyu (22°02′N, 121°33′E), Taitung County, Taiwan: 1 female, 18 February 1997 (NMNS-THU-Ar-01-0044); 1 male, 17 February 1997, I-Min Tso (NMNS-THU-Ar-01-0042); 2 females and 2 males, February 2001, K.C. Chen (NMNS-THU-Ar-02-0296~0297, 0299~0300); 1 female, August 2001, K.C. Chen (NMNS-THU-Ar-02-0295); 1 male, August 2000, K.C. Chen (NMNS-THU-Ar-02-0298).

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

Diagnosis.—The new species resembles *Tmarus komi* Ono 1996 in the shape of the male palp but differs from the latter in having a palpal bulb longer than wide, a small and distal retrolateral tibial apophysis, and a spinous tibial apophysis (Figs. 13, 14); whereas in *T. komi*, the palpal bulb is wider than long, the retrolateral tibial apophysis is wide and with a dorsal tooth. The new species is also similar to *T. taiwanus* Ono 1977 but can be distinguished from the latter by the epigynum with a median hood and the connecting duct long and curved (Figs. 11, 12).

Female.—Total length 5.13–5.18. Holotype total length 5.13; cephalothorax 1.71 long, 1.62 wide; abdomen 3.33 long, 2.88 wide. Carapace orange, with some black brown patches and a few long setae; eye region white, with some fine setae. Chelicerae orange, blackish brown on anterior lateral surface, with white spots on front surface; both promargin and retromargin lacking teeth. Labium blackish brown with basal part paler. Palps, endites, sternum and legs yellow. Legs with some spines and setae. Abdomen white, with numerous brown speckles; dorsum scattered with a few brown patches and a pair of red brown spots; venter with a wide longitudinal yellow brown band behind the genital groove. Both eye rows recurved. AME-AME: AME-ALE (0.14: 0.13), PME-PME: PME-PLE (0.16: 0.35); AME: ALE: PME: PLE (0.10: 0.22: 0.10: 0.21). MOA 0.47 long, front width 0.33, back width 0.42. Clypeus width 0.20. Labium longer than wide (0.44: 0.23). Sternum longer than wide (0.91: 0.75). Measurements of legs: I 5.59 (1.76, 2.07, 1.11, 0.65), II 5.89 (1.89, 2.16, 1.19, 0.65), III 4.38 (1.43, 1.56, 0.85, 0.54, IV 4.64 (1.53, 1.58, 0.99, 0.54). Leg formula: 2, 1, 4, 3. Epigynum with a median hood, connecting ducts long and membranous, spermathecae almost reniform (Figs. 11–12).

Male.—Total length 2.97–3.33. Male total length 3.24; cephalothorax 1.43 long, 1.36 wide; abdomen 2.03 long, 1.24 wide. Abdo-



Figures 10–14.—*Tmarus lanyu* new species: 10. Female, dorsal view; 11. Epigynum; 12. Vulva; 13. Left palp of the male, ventral view; 14. Left palp of the male, retrolateral view. Scale lines: 1.0 mm (Fig. 10); 0.1 mm (Figs. 11–14).

men relatively longer and narrower. Other characters as in female holotype. Measurements of palp and legs: palp 1.43 (0.52, 0.29, 0.20, 0.42); leg I 6.26 (2.07, 2.16, 1.26, 0.77), II 6.26 (1.98, 2.25, 1.31, 0.72), III 4.46 (1.35, 1.62, 0.90, 0.59), IV 4.55 (1.53, 1.53, 0.90, 0.59). Leg formula: 1, 2, 4, 3. Palp with ventral, retrolateral and distal tibial apophyses; ventral apophysis digitiform, retrolateral apophysis small, and distal apophysis spinous; bulb longer than wide, embolus long and filiform (Figs. 13, 14).

Remarks.—The new species is closely related to *Tmarus komi* Ono 1996 from Japan. But as Ono mentioned in his paper, *T. komi* is a peculiar member of *Tmarus* in having the legs without well-developed spines and the male palp with a simple bulb and long, filiform embolus (Ono 1996). Rather than creating a new genus for them, we have followed Ono (1996) and placed the new species temporarily in the genus *Tmarus* because many species of this genus from Southeast Asia still need to be studied.

Distribution.—This species is presently only known from Taitung County, Taiwan.

Genus *Xysticus* C.L. Koch 1835

Xysticus C.L. Koch 1835:16, 17; Ono 1988:77; Song & Zhu 1997:64.

Type species.—*Aranea audax* Schrank 1803, by original designation.

Diagnosis.—Medium-sized thomisids. Cephalothorax domed, not flattened; head wide with strong setae. Tubercles of ALE and PLE connate. Legs with developed spines. Male palp generally with ventral and retrolateral tibial apophyses, as well as intermediate tibial apophysis in some species-groups; palpal bulb tegulum sometimes has two or three apophyses. Female epigynum heavily sclerotized lacking guide pocket and frequently with median septum; spermathecae large, globular or reniform (Ono 1988).

Remarks.—Although 354 species and 12 subspecies are recorded in this genus (Platnick 2005), only *X. chui* Ono 1992 has been reported from Taiwan. We here report the first record of *X. croceus* Fox 1937 from Taiwan.

Xysticus croceus Fox 1937

Xysticus croceus Fox 1937:19, fig. 11; Ono 1988: 89, figs. 79–82; Song & Zhu 1997:77, figs. 47A–D; Song, Zhu & Chen 1999:501, figs. 285C, M.

Material examined.—TAIWAN: *Nantou County*: 1 ♂, Hui-Sun Forest Station (24°06′N, 121°03′E), 24 April 1999, I. C. Chou (NMNS-THU-Ar-01-0031).

Diagnosis.—This species resembles *Xysticus ephippiatus* Simon 1880 (Song & Zhu 1997) in body shape and coloration, but differs from the latter in that the anterior depression of the female epigynum is flat and its posterior margin strongly recurved, the smaller spermathecae, and the wider and longer retrolateral tibial apophysis of male palp.

Female.—See descriptions and illustrations of Song & Zhu (1997) and Ono (1988).

Male.—See descriptions and illustrations of Song & Zhu (1997) and Ono (1988).

Distribution.—*Xysticus croceus* occurs in China and its neighboring islands, as well as India, Nepal, Bhutan, Korea and Japan.

ACKNOWLEDGMENTS

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A REVIEW OF THE LINYPHIID SPIDER GENUS *SOLENYSA* (ARANEAE, LINYPHIIDAE)

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ABSTRACT. The present paper gives a review of the *Solenysa* spiders. Five of the six known *Solenysa* species were examined, including the types of *S. longqiensis*, *S. wulingensis* and *S. circularis*. Illustrations of these five species as well as diagnoses and distributional data of all species are provided.

Keywords: Taxonomy, Asia, China, Korea, Japan, spiders, ant mimicry

The linyphiid spider genus *Solenysa* was established by Simon (1894) for the sole species *Solenysa melloteei* Simon 1894 from Japan. *Solenysa* remained as a monotypic genus until five additional species were described from China and Korea during the 1990s, including *S. longqiensis* Li & Song 1992, *S. wulingensis* Li & Song 1992, *S. circularis* Gao et al. 1993, *S. protrudens* Gao et al. 1993 and *S. geumoensis* Seo 1996.

Members of the genus appear to be ant mimics and have the posterior part of the carapace drawn into a tubular extension reminiscent of the constricted waist of ants. Further, the epigynum of the females is connected to the abdomen by a long, transparent tube or solenoid. A similar structure is found in some other linyphiids such as *Wubanoides* Eskov 1986 from the Palaearctic region (Tanasevitch 1996: figs. 7–9) and *Metalepthyphantes* Locket 1968 from Africa (Locket 1968: figs. 27, 33).

This paper reviews the genus *Solenysa*. Type specimens of *S. longqiensis*, *S. wulingensis*, *S. circularis* and fresh specimens of *S. protrudens* and *S. melloteei* have been examined and illustrated. Further diagnoses and distributional data of all six known species are provided.

METHODS

Specimens were examined and measured using an SZ11-Olympus stereomicroscope. Further details were studied under an Olympus BX40 compound microscope. All illustrations were made using a drawing tube and inked on ink jet plotter paper. Male palps and female epigyna were examined and illustrated after they were dissected from the spider's bodies. Vulvae of female epigyna were cleared in boiling KOH solution to dissolve non-chitinous tissue, and the embolic divisions of male palps were excised by breaking the column (the membranous connection between the suprategulum and the radix). For examination of the genital structures under transmitted light microscopy, male palps and epigyna were immersed in 75% alcohol solution, while embolic divisions and vulvae were mounted in Hoyer's Solution.

For each species, the synonyms are taken verbatim from Platnick's spider catalogue (Platnick 2003). Updated information about the distribution of each species in China is provided at the provincial level. The names of localities and distribution data are given according to current Chinese standard (see Peng et al. 2003).

All measurements are in millimeters. Terminology for the somatic morphology and genital structures follow Hormiga (2002). The abbreviations used as follows:

Somatic morphology: AER = anterior eye row; ALE = anterior lateral eye; AME = anterior median eye; AME-ALE = distance between AME and ALE; AME-AME = distance between AMEs; AMEd = diameter of AME; PER = posterior eye row; PLE = posterior lateral eye; PME = posterior median eye; PMEd = diameter of PME; PME-PLE = distance between PME and PLE; PME-PME = distance between PMEs.

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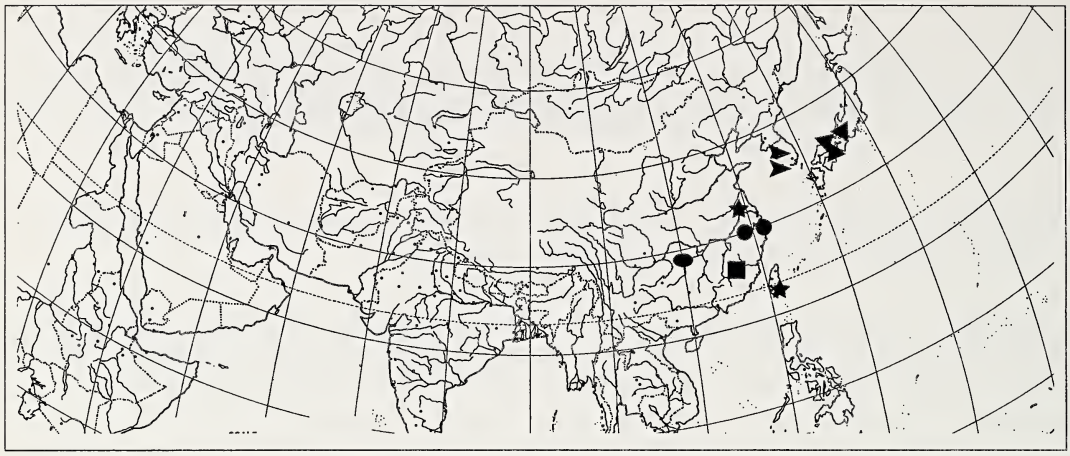


Map 1.—Distribution of *Solenysa* spiders. Circles = *S. circularis* Gao et al.; arrowhead = *S. geumoensis* Seo; square = *S. longqiensis* Li & Song; triangles = *S. melloteei* Simon; star = *S. protrudens* Gao et al.; and ellipse = *S. wulingensis* Li & Song.

Male palp: DSA = distal suprategular apophysis; E = embolus; EM = embolic membrane; LC = lamella characteristica; P = paracybium; PCA = proximal cymbial apophysis; R = radix; SPT = suprategulum; T = tegulum; TA = terminal apophysis; TS = terminal sclerite.

Epigynum: CD = copulatory duct; CO = copulatory opening; FD = fertilization duct; S = spermatheca; SL = solenoid.

The specimens studied here are deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (IZCAS), and in Jilin University, Changchun, China (JLU, formerly called Norman Bethune University of Medical Science).

TAXONOMY

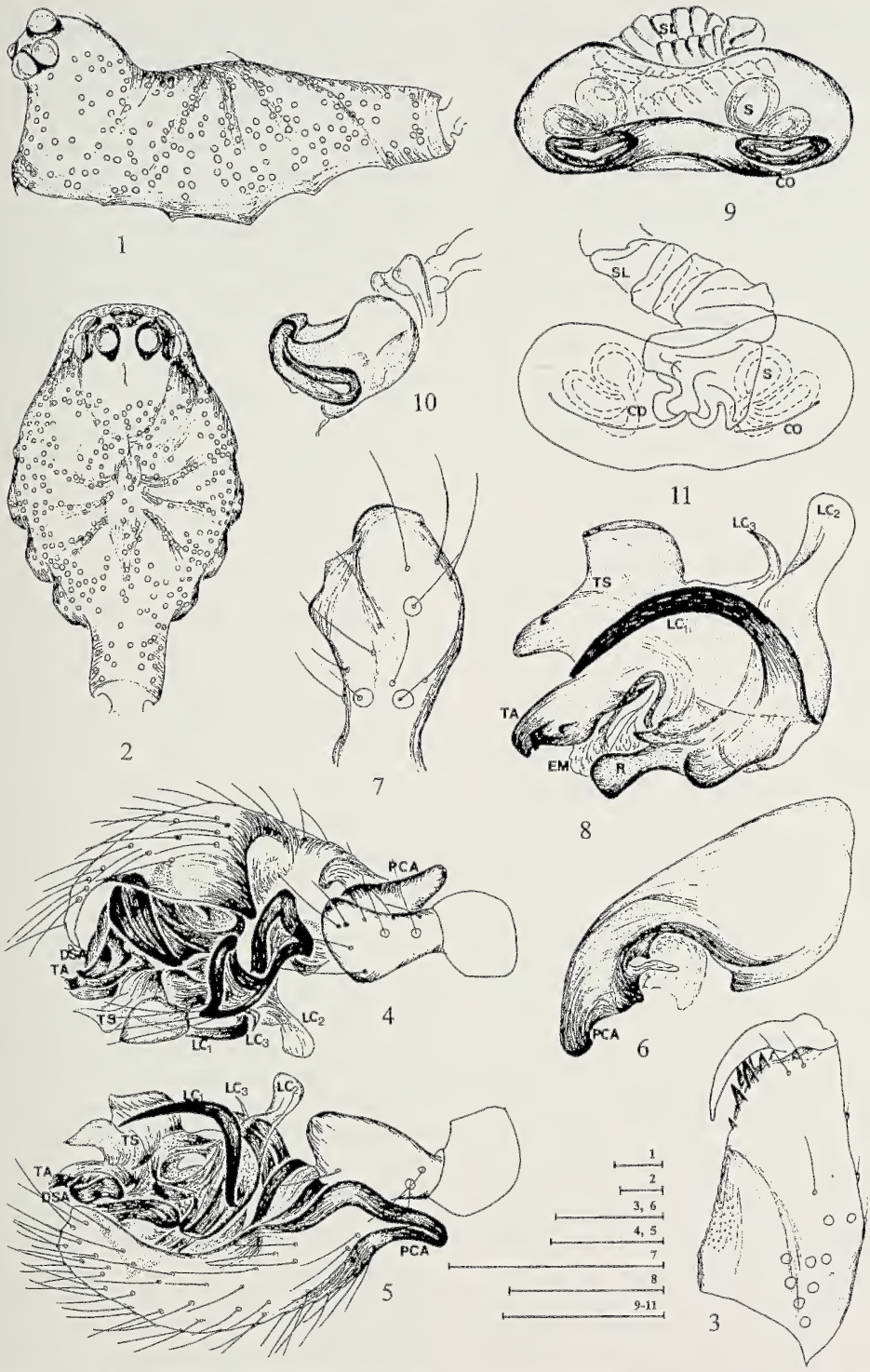
Family Linyphiidae Blackwall 1859
Solenysa Simon 1894

Solenysa Simon 1894: 677.

Type species.—*Solenysa melloteei* Simon 1894, by monotypy.

Diagnosis.—*Solenysa* species can be distinguished from other linyphiids by their very small body size (total length 1.11–1.70) and their unique body appearance; especially by the tubular extension of the posterior end of the carapace and by the many impressed, round pits scattered all over the carapace (Figs. 1, 2). Cymbium usually with one or two large proximal apophyses (Fig. 4). Paracymbium L-shaped. Lamella characteristica well developed, divided in two or three branches. Epigyne protruding well sclerotized connected to the abdomen by a long, transversally wrinkled, membranous solenoid base, which is packed between the epigynum and abdomen in the nonfunctional stage (Fig. 9).

Description.—Small spiders, total length of males 1.11–1.61, females 1.27–1.70. Both sexes similar in general appearance with little interspecific variation. Caparace chestnut-brown, with numerous impressed, round pits; fine radial striae little darker in color. Carapace in dorsal view elongated oval, slightly constricted at level of cervical groove; sides behind cervical groove distinctly crenate, with four lobes beside coxae; posterior part of carapace drawn into tubular extension (Fig. 22); cephalic region turret-like bearing AMEs in front, PMEs at top, ALEs and PLEs on its lateral sides (Fig. 1). AMEs black and very small, their diameter about half of others', rest of eyes subequal; AER recurved, AME-AME almost equal to AMEd and AME-ALE longer, PER almost straight, PME-PME equal to PMEd and PME-PLE shorter, ALE and PLE juxtaposed. Clypeus broad, concave immediately bellow ocular area, sloping in convex line towards frontal margin. Chelicerae slightly lighter in color than carapace, with some round pits frontally and some granules anterolaterally; promargin with 4 and retromargin with 2–4 teeth; lateral sides with distinct stridulating ridges. Sternum darker in color than carapace, roundish heart-shaped, with many



Figures 1–11.—*Solenysa circularis* Gao et al. 1. carapace, lateral view; 2. carapace, dorsal view; 3. right chelicera, anterior view; 4. left male palp, retrolateral view; 5. left male palp, prolateral view; 6. left male palpal cymbium, dorsal view; 7. right palpal tibia, dorsal view; 8. left male palpal embolus division, dorsal view; 9. epigynum, ventral view; 10. epigynum, lateral view; 11. vulva, dorsal view. Scale bars = 0.1 mm.

granules, each carrying long hair. Legs long and slender; tibia I–IV and patella I–IV with a dorsal spine shorter than diameter of tibia. Tm I 0.17–0.26. Tm IV absent.

Male pedipalp: Tibia with one prolateral and two retrolateral trichobothria (Fig. 17). Cymbium normally with one or two large, proximal apophyses, outstanding in retrolateral view (Fig. 4), except in *S. wulingensis* and *S. geumoensis* (Fig. 43). Paracymbium small, L-shaped, furnished with several long apical hairs, deeply curved and with torsion at its middle. Tegulum triangular in retrolateral view (Fig. 4). Distal suprategular apophysis large and well sclerotized. Shape of embolic membrane variable. Lamella characteristica conspicuously large, normally with two or three branches, at least two of them well developed (Fig. 8): the first sword-shaped or spike-like, strongly sclerotized, the second ribbon-like and the third variable in shape or even missing (Fig. 18). Terminal apophysis strongly sclerotized, usually with 1–3 teeth. 'Terminal sclerite' located in menbranous region between radix and lamella, continuous with base of lamella, varying in shape and appearance.

Epigynum: Protruding and well sclerotized, variable in shape, connected with abdomen by long, transversally amply wrinkled, membranous solenoid base, which in nonfunctional stage is folded between epigynum and abdomen.

Remarks.—The members of the genus *Solenysa* seem to be ant mimics and have the posterior part of their carapace drawn into a tubular extension resembling the waist of ants. Further, the epigynum of the females is connected to the abdomen by a long solenoid base. Similar structures are found e.g. in *Wubanoides* Eskov 1986 (Tanasevitch 1996: figs. 7–9) and *Metalepthyphantes* Locket 1968 (Locket 1968: figs. 27 & 33). However, *Solenysa* can be easily distinguished from all other linyphiid genera by its unique appearance as described above.

Distribution.—China, Korea and Japan (Map 1). Specimens can be found amongst grass, leaf-litter and other detritus, but are very rare in museum collections.

Solenysa circularis Gao et al. 1993
Figs. 1–11

Solenysa circularis Gao et al. 1993: 66, figs. 7–10; Song et al. 1999: 204, figs. 116H–I, N–O.

Material examined.—CHINA: *Zhejiang*: Mt. Tianmushan (30.4°N, 119.5°E), female holotype and 1 male paratype (JLU); Mt. Putuoshan (30.0°N, 122.4°E), 1 female paratype (JLU).

Diagnosis.—The male of *S. circularis* is easily recognized by the cone-shaped, posteriorly directed cymbial apophysis (Fig. 4) and by the conspicuous, curved spike-like branch of lamella characteristica in prolateral view (Figs. 5, 8). The epigynum of the female (Fig. 9) is similar to that of *S. protrudens* (Fig. 38), but is more rounded and distinctly bulging laterally.

Description.—Total length 1.27. Carapace 0.73 long, 0.44 wide. Abdomen 0.57 long, 0.43 wide. Tm I 0.26. Tm IV absent. Chelicerae with 4 promarginal and 2 retromarginal teeth (Fig. 3). For further measurements and a detailed description of somatic morphology see Gao, Zhu & Sha (1993).

Male palp (Figs. 4–8): Lamella characteristica tripartite (Fig. 8); the first branch biggest, curved spike-like, well sclerotized, second one short and blunt, and third one smallest, falciform. Terminal apophysis with two small apical processes at its dorsal side: one truncate, one coniform. Terminal sclerite large, foliaceous, bipartite. Embolus and embolic membrane shortest among the five species described in this paper, even shorter than terminal apophysis. Anterior part of radix drawn into handle-like extension.

Epigynum (Figs. 9–11): Wider than long, sides rounded, posterodorsal part in lateral view turned anteriorly; solenoid base partly visible (Fig. 9), 3 times as long as the length of epigynum, twisting anteriorly and connected with its dorsally side.

Distribution.—Known only from the original localities in Zhejiang Province, China (Map 1).

Solenysa geumoensis Seo 1996

Solenysa melloteei Namkung 1986: 13, figs. 6–10 (misidentification).

Solenysa geumoensis Seo, 1996: 157; Namkung 2002: 182, figs. 17.35a–b.

Material examined.—None.

Diagnosis.—Judging from the illustrations by Namkung (1986, 2002), the male of *S. geumoensis* is close to that of *S. wulingensis* as both have cymbium without outstanding proximal apophysis (Namkung 1986, fig. 9) and in

prolateral view basically similar lamella characteristica (Namkung 1986, fig. 8). They differ in that one branch (exactly which one is not clear) of the lamella characteristica of *S. geumoensis* has a forked tip (Namkung 1986, fig. 7) while *S. wulingensis* has all branches entire (Fig. 46). Furthermore, the apical portion of the paracymbium of *S. geumoensis* is longer than that of *S. wulingensis* (Namkung 1986, fig. 7). Epigynum half round shape, posterior part wider than anterior part, the transparent vulval structures convergent anteriorly (Namkung 1986, fig. 10).

Description.—See Namkung (1986, 2002).

Distribution.—Korea (Map 1).

Remarks.—*Solenysa geumoensis* is thought to be written by Seo in 1996, but the original description on this species is not easy to obtain. A further study on this species will be necessary in future, in case that we can get the types or fresh material.

Solenysa longqiensis Li & Song 1992
Figs. 12–20

Solenysa longqiensis Li & Song, 1992: 6, figs. 1A–G; Song et al. 1993: 861, figs. 17A–G; Li et al. 1994: 80, figs. 18, 19; Song et al. 1999: 204, figs. 116J, K, Q, R.

Material examined.—CHINA: *Fujian:* Jiangle County (26.7°N, 117.4°E), Mt. Longqi, Yujiaping Town, 10 August 1991, male holotype, 1 male and 6 female paratypes (IZCAS).

Diagnosis.—The male of this species can be distinguished from all other *Solenysa* males by the bipartite lamella characteristica (Fig. 18) and the peculiarly twisted cymbial apophysis (Figs. 15–17). The female has a somewhat apple-shaped epigynum (Fig. 19), like that of *S. melloteei* (Fig. 29), but distinctly broader apically and the transparent vulval structures are different. Further the solenoid base of *S. longqiensis* is twisted under a triangular cover while that of *S. melloteei* is exposed.

Description.—Total length 1.47, Carapace 0.80 long, 0.50 wide. Abdomen 0.76 long, 0.45 wide. Tm I 0.22. Tm IV absent. Chelicerae with 4 promarginal and 3 retromarginal teeth (Fig. 14). For further measurements and a detailed description of somatic morphology see Li & Song (1992).

Male palp (Figs. 15–18): Tibia slightly longer than patella. Two proximal cymbial apophysis with twisted bases in dorsal view (Fig. 17). Embolic division (Fig. 18) conspicuously large. Lamella characteristica with two well-developed, ribbon-like branches, apex of first one with a strongly sclerotized claw, second one with truncate, somewhat serrate end. Embolus slightly longer than lamella characteristica. Embolic membrane petale-shaped. Terminal apophysis fist-like. Radix quadrangular.

Epigynum (Figs. 19–20): Apple-shaped, widest close to its anterior edge, about 1.5 times wider than long. Solenoid base about three times as long as the length of epigynum, covered with triangular extension of abdomen.

Distribution.—Known only from the type locality in Fujian Province, China (Map 1).

Solenysa melloteei Simon 1894
Figs. 21–30

Solenysa mellottei [sic] Simon 1894: 677; Oi, 1960: 153, figs. 52–54.

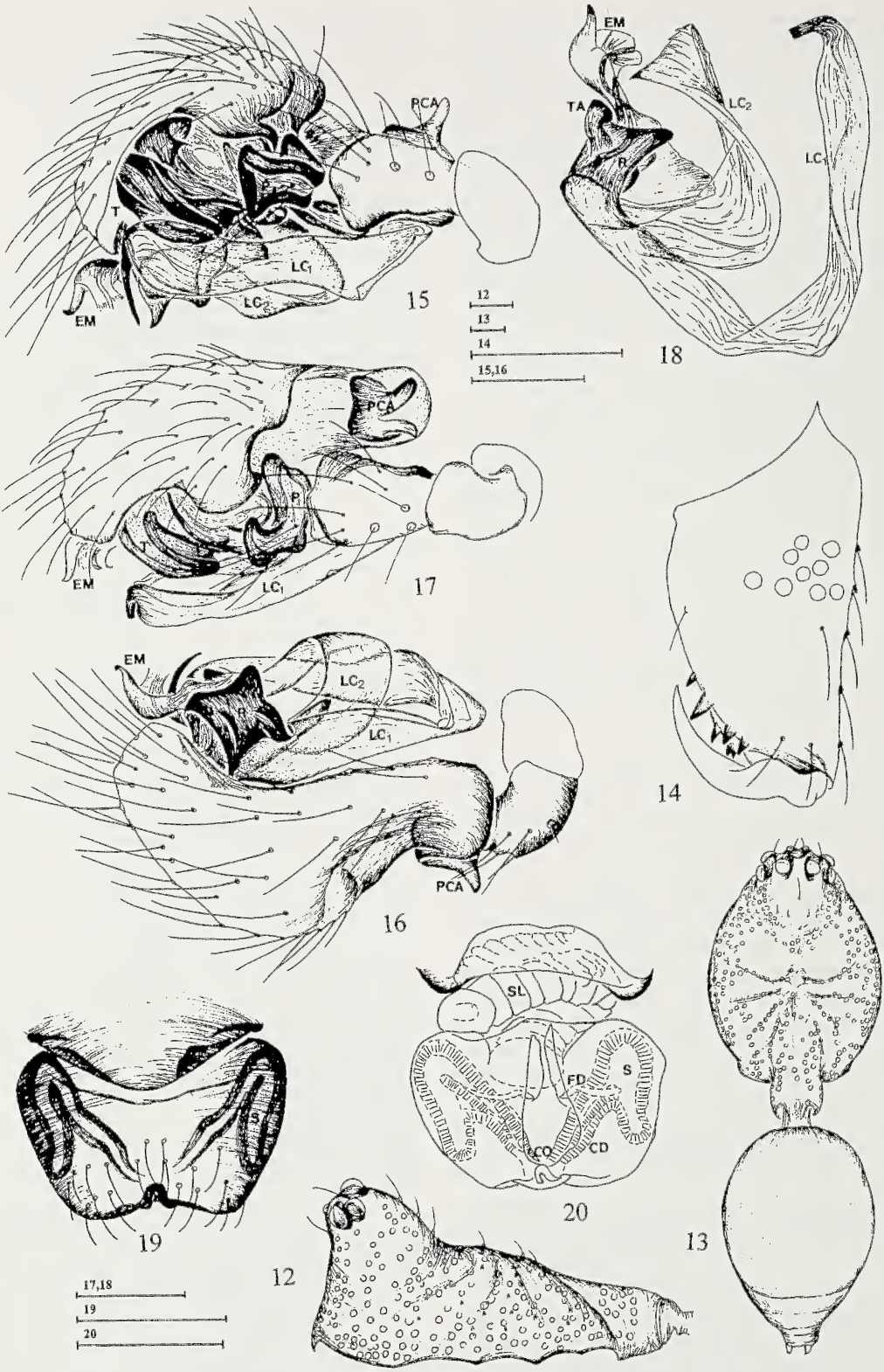
Solenysa mellotteei [sic] Simon: Yaginuma 1986: 78, fig. 42.2; Irie & Saito 1987: 23, fig. 21; Chikuni 1989: 56, fig. 48.

Material examined.—JAPAN: no detailed data, 1 male and 1 female (IZCAS).

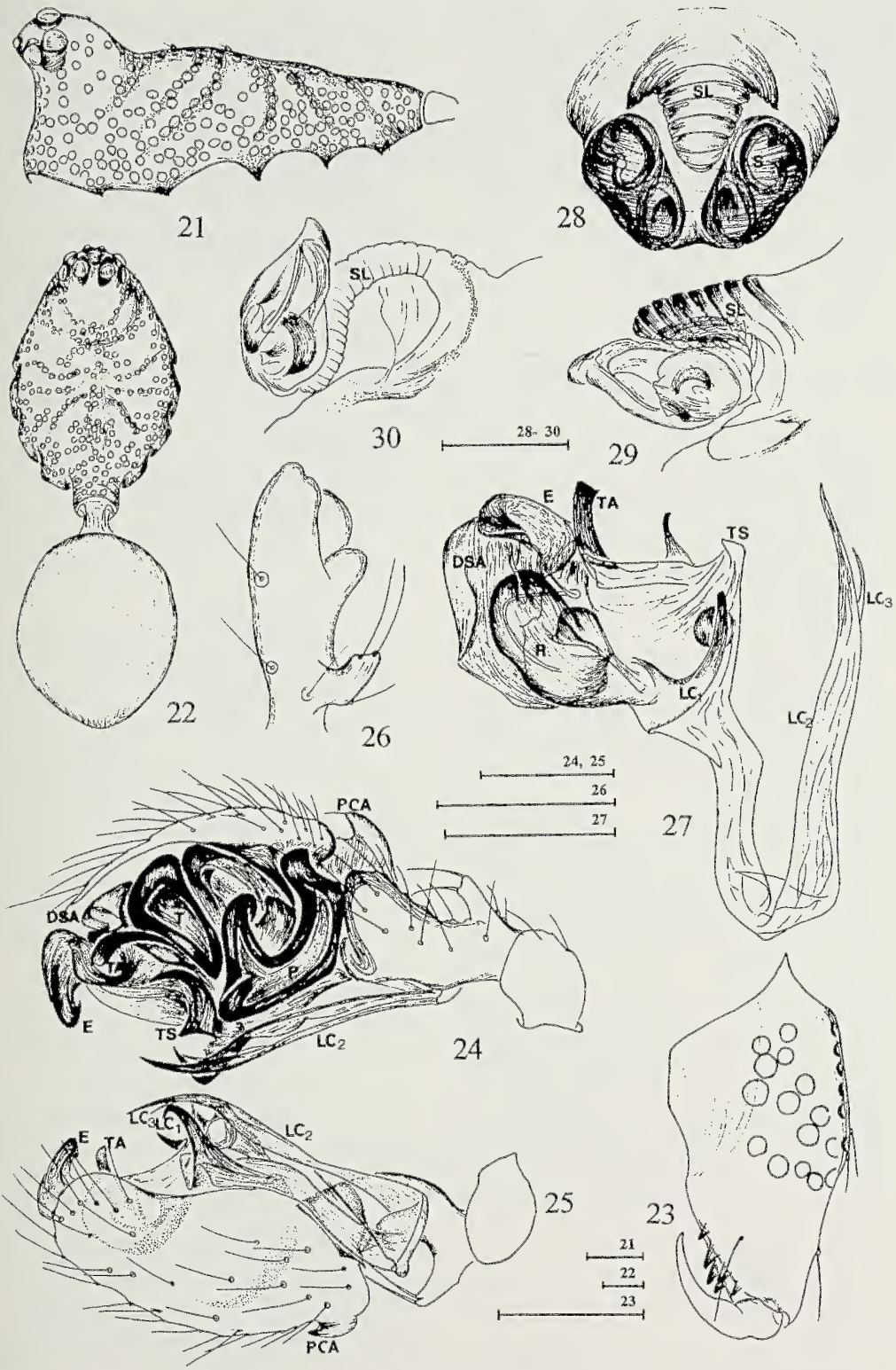
Diagnosis.—The male of this species can be distinguished from all other *Solenysa* males by the broad, coiled embolus and the hook-like cymbial apophysis (Fig. 24). Epigynum (Fig. 28) somewhat apple-shaped, like that of *S. longqiensis* (Fig. 19), but apically narrower and transparent vulval structures of different shape. Solenoid base without cover.

Description.—Total length 1.27. Carapace 0.77 long, 0.45 wide. Abdomen 0.50 long, 0.43 wide. Tm I 0.17. Tm IV absent. Chelicerae with 4 promarginal and 2 retromarginal teeth (Fig. 23). For further measurements and a detailed description of somatic morphology see Oi (1960).

Male palp (Figs. 24–27): Tibia twice as long as patella (Fig. 24), with a dorsal apophysis bearing two long bristles (Fig. 26). Cymbium with a forward pointing, hook-like proximal apophysis (Fig. 24). Lamella tripartite, the first branch short, spike-like and well sclerotized; second one ribbon-like, long and slender, tapering off distally; third one small and thin (Fig. 27). Embolus plate-like, half spiral with a hooked tip (Fig. 24). Embolic membrane indiscernible. Terminal apophysis truncate, with a sickle-shaped dorsal process



Figures 12–20.—*Solenysa longqiensis* Li & Song: 12. carapace, lateral view; 13. carapace, dorsal view; 14. left chelicera, anterior view; 15. left male palp, retrolateral view; 16. left male palp, prolateral view; 17. left male pedipalp, dorsal view; 18. left male pedipalp embolus division, dorsal view; 19. epigynum, ventral view; 20. vulva, dorsal view. Scale bars = 0.1 mm.



Figures 21–30.—*Solenysa melloteei* Simon: 21. carapace, lateral view; 22. carapace, dorsal view; 23. left chelicera, anterior view; 24. left male palp, retrolateral view; 25. left male palp, prolateral view; 26. left palpal tibia, dorsal view; 27. left male pedipalp embolus division, dorsal view; 28. epigynum, ventral view; 29. epigynum, lateral view, lifted; 30. epigynum, lateral view, expanded. Scale bars = 0.1 mm.

(Figs. 24, 27). Terminal sclerite triangular, blunt tipped. Radix short, wide and bipartite.

Epigynum (Figs. 28–30): Apple-shaped, widest at its middle, about 1.8 times wider than long. Solenoid base exposed, short, about twice as long as the length of epigynum, and can lift epigynum inversely in nonfunctional stage.

Distribution.—Apparently restricted to Japan (Map 1).

Solenysa protrudens Gao et al. 1993
Figs. 31–39

Solenysa protudens Gao et al. 1993: 65, figs. 1–6; Song et al. 1999: 204, figs. 116L, M, P, S.

Material examined.—CHINA: *Taiwan:* Taidong (22.7°N, 121.1°E), Lanyu, August 2000–February 2001, 3 males and 2 females (IZCAS). The type material was deposited in JLU but could not be found despite thorough checking of the collection by the authors.

Diagnosis.—The male of this species can be distinguished from all other *Solenysa* males by the stout, erect cymbial apophysis (Fig. 34), petal-shaped embolic membrane and well-developed branches of lamella characteristica (Figs. 34, 35). Epigynum similar to that of *S. circularis*, but more angular with nearly straight sides (Fig. 38).

Description.—Total length 1.67. Carapace 0.83 long, 0.50 wide. Abdomen 0.90 long, 0.50 wide. Tm I 0.22. Tm IV absent. Chelicerae with 4 promarginal and 4 retromarginal teeth (Fig. 33). For further measurements and a detailed description of somatic morphology see Gao et al. (1993).

Male palp (Figs. 34–37): Tibia nearly twice as long as patella, with small dorsal process bearing two long bristles (Fig. 34). Cymbium with a stout and erect proximal apophysis, pointing dorsally. Lamella characteristica tripartite (Fig. 37), the first and third branches sword-shaped, robust, well-sclerotized, the latter longer than the former; the second ribbon-like, with denticles on its distal end. Embolus slightly longer than lamella characteristica. Embolic membrane petale-shaped, with two processes. Terminal apophysis small, triangular (Fig. 37).

Epigynum (Figs. 38, 39): Rectangular, about three times as wide as long. Solenoid base about three times as long as the length of epigynum.

Distribution.—Known from China (Jiangsu, Taiwan) (Map 1).

Solenysa wulingensis Li & Song 1992
Figs. 40–46

Solenysa wulingensis Li & Song 1992: 7, figs. 2A–E; Song & Li 1997: 404, figs. 6A–E; Song et al. 1999: 204, figs. 117A, B.

Material examined.—CHINA: *Hunan:* Zhangjiajie National Nature Reserve (29.1°N, 110.4°E), Dayong City, 13 August 1990, male holotype and 2 male paratypes (IZCAS).

Diagnosis.—The male of this species can be easily distinguished from all other *Solenysa* males by the rudimentary cymbial apophysis (Fig. 45). The female is unknown.

Description.—Total length 1.40. Carapace 0.80 long, 0.50 wide. Abdomen 0.67 long, 0.45 wide. Tm I 0.19. Tm IV absent. Chelicerae with 4 promarginal and 3 retromarginal teeth (Fig. 42). For further measurements and a detailed description of somatic morphology see Li & Song (1992).

Male palp (Figs. 43–46): Tibia slightly longer than patella. Cymbial apophysis small, nearly inconspicuous (Figs. 43, 45). Paracymbium strongly curved at its middle, proximal end with small lateral curvature. Lamella characteristica tripartite (Fig. 46), first branch spike-like, well sclerotized, second one largest, ribbon-like, tapering off distally, third one small, thin. Embolus (Fig. 46) short, embolic membrane flower-shaped. Terminal apophysis with two apical and one median process. Terminal sclerite foliaceous. Radix elongated, blunt tipped.

Female: Unknown.

Distribution.—Known only from the type locality in Hunan Province, China (Map 1).

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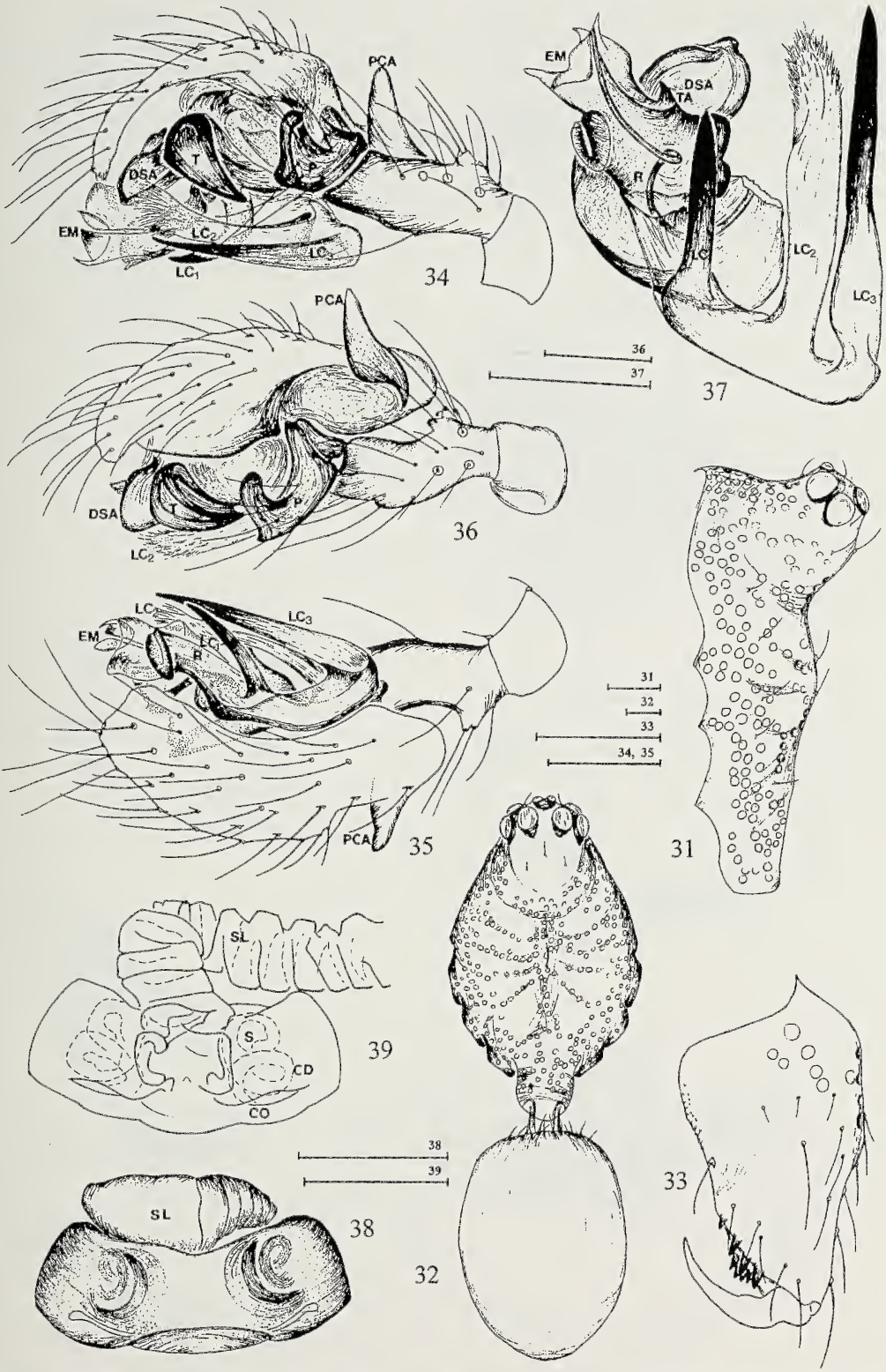
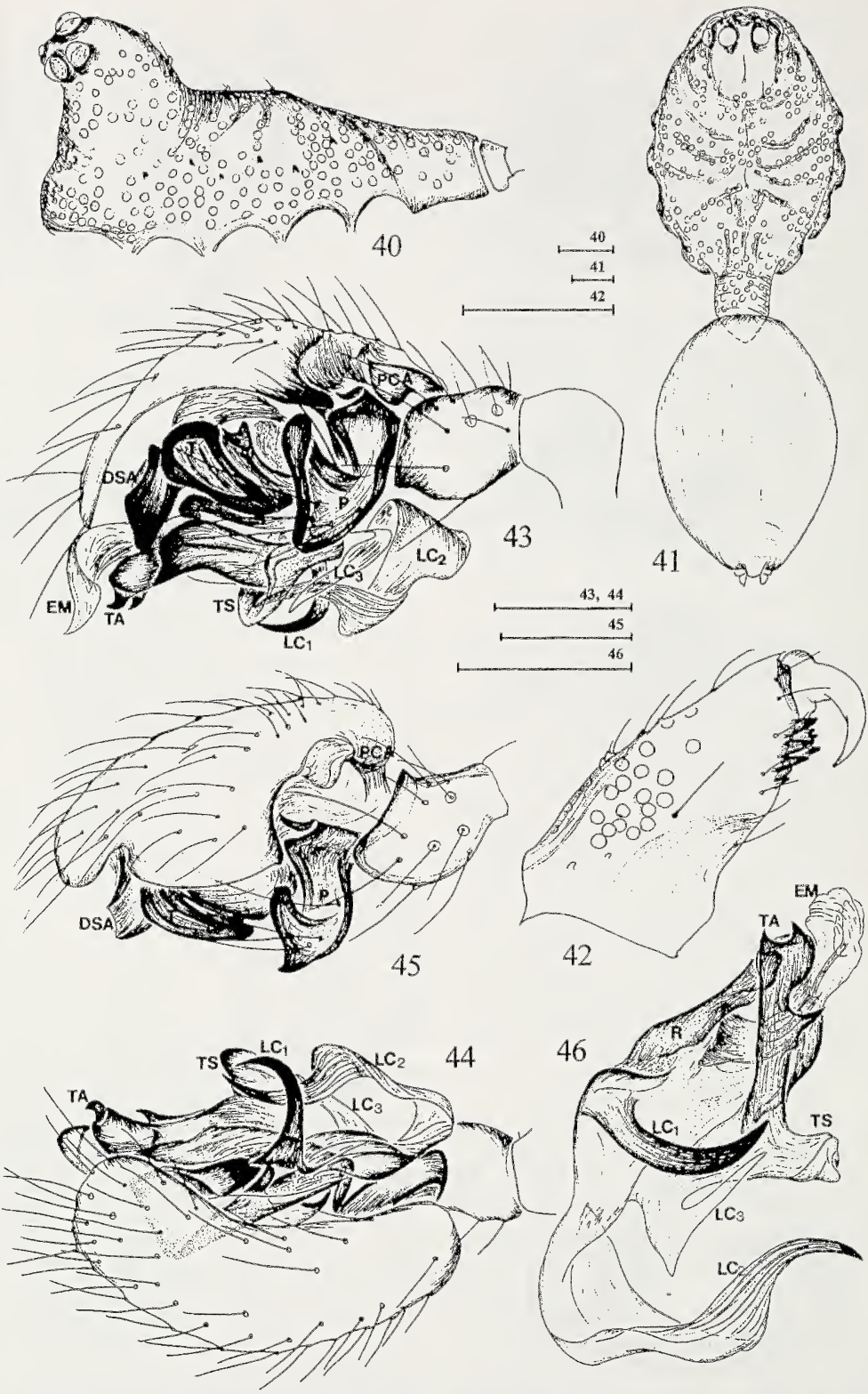


Figures 31–39.—*Solenysa protrudens*: 31. carapace, lateral view; 32. carapace, dorsal view; 33. left chelicera, frontal view; 34. left male palp, retrolateral view; 35. left male palp, prolateral view; 36. left male palp, dorsal view; 37. left male palp embolus division, dorsal view; 38. epigyne, ventral view; 39. vulva, dorsal view. Scale bars = 0.1 mm.



Figures 40–46.—*Solenysa wulingensis* Li & Song: 40. carapace, lateral view; 41. carapace, dorsal view; 42. left chelicera, anterior view; 43. left male palp, retrolateral view; 44. left male palp, prolateral view; 45. left male palp, dorsal view; 46. left male pedipalp embolus division, dorsal view. Scale bars = 0.1 mm.

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SPIDER SIZE AND GUARDING OF OFFSPRING AFFECT *PARAPHIDIPPUS AURANTIUS* (ARANEAE, SALTICIDAE) RESPONSE TO PREDATION THREAT

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ABSTRACT. We tested the hypothesis that the response of *Paraphidippus aurantius* (Lucas 1833) (Salticidae) to a simulated threat of predation would depend on a combination of spider size and reproductive status. In ponderosa pine forests of Colorado we located nests with spiders of varying sizes that were either adult female spiders guarding offspring or juvenile female and male spiders. To simulate a predator threat we applied a disturbance to the sides of spider nests using repeated puffs of air expressed from a rubber bulb or by blowing. We recorded the threat intensity (number of puffs) required to displace spiders from their nests, and then monitored the immediate responses of spiders to this threat. The threat intensity required to displace spiders guarding offspring was 2.3 times that of non-guarding spiders, and guarding spiders fled less than half as far as non-guarding spiders. Spider size had no effect on the threat intensity required for displacement, but larger spiders fled further than small ones. We then destroyed nests and monitored the long term responses of the spiders. Nests containing offspring were constructed with 4.6 times the mass of silk as those without offspring. When spiders rebuilt their nests, spider tenure in rebuilt nests did not differ between guarding spiders and non-guarding spiders. Spider size was negatively related to nest tenure for non-guarding spiders, but there was no such relationship for guarding spiders. These results suggest that both the short term and long term outcomes of interactions between *P. aurantius* and other predators may be influenced by a combination of spider size and offspring guarding behavior.

Keywords: Size-structured intraguild predation, parental care, anti-predator strategy

Predators prey not only upon herbivores, but also upon each other in what has been termed intraguild predation (Polis and McCormick 1987; Polis et al. 1989; Polis and Holt 1992; Rosenheim et al. 1995). The predators that have been shown to feed upon spiders include ants (Wise 1993; Halaj et al. 1997; Eubanks 2001; Mooney & Tillberg 2005), birds (Askenmo et al. 1977; Dickson et al. 1979; Gunnarsson 1983; Wise 1993), and other spiders (Pollard 1983; Fink 1987; Austin 1988; Wise 1993). Often intraguild predation is size-structured, whereby the role of predator and prey is determined by the relative mass of the two interacting predators (Werner & Gilliam 1984; Claessen et al. 2002; De Roos et al. 2003). For example, whether *Hogna helluo* (Walckenaer 1837) (Lycosidae) preys upon *Pardosa milvina* (Hentz 1844) (Lycosidae), or vice versa, changes based on which spider is larger at the time of the encounter (Persons & Rypstra 2001).

Models of optimal reproductive behavior predict that a predator's response to the threat of intraguild predation may also shift with changing reproductive status and investment in offspring (Curio et al. 1984; Coleman et al. 1985; Sargent & Gross 1985; Curio 1987; Coleman & Gross 1991). Juveniles may optimize fitness by avoiding potential predators, while adults guarding young or defending nests may optimize their fitness by confronting potential predators and protecting these maternal investments. Maternal protection of eggs and juveniles has been shown in many spiders (Kaston 1948; Eberhard 1974; Matlack & Jennings 1977; Patel & Bradoo 1981; Hoffmaster 1982; Pollard 1983; Fink 1987; Cushing 1989; Hie-

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ber & Uetz 1990; Horel & Gundermann 1992; Gundermann et al. 1997) against threats as diverse as parasitoids, heterospecific predators, conspecific predators, and even pathogenic molds (Pollard 1983; Fink 1986; Austin 1988; Horel & Gundermann 1992; Hieber et al. 2002). The response of spiders to the threat of intraguild predation has been shown to vary based on offspring-protection. Hoffmaster (1982) found that *Philoponella cuminamensis* (Simon 1891) (Uloboridae) without eggs was significantly more likely to drop from their webs when attacked by hummingbirds than those with eggs. Similarly, when *Uloborus glomosus* (Walckenaer 1842) (Uloboridae) was exposed to artificial stimuli by Cushing and Opel (1990), spiders with eggs remained in place longer than those without. Thus the outcomes of intraguild predation may also change based on the reproductive status of the interacting predators.

In the present study we investigated the hypothesis that a spider's response to the threat of a potential predator is likely to vary as a function of both spider size and whether or not the spider is engaged in offspring protection. Using *Paraphidippus aurantius* (Lucas 1833) (Salticidae) as a model organism, we subjected (1) juvenile spiders (small males and females, sex undetermined) and (2) larger, adult females spiders guarding eggs or spiderlings to a simulated threat of predation. We documented both the immediate (time scale of seconds to minutes) and long term (time scale of days to weeks) responses to this threat. Using these data, we identified the separate effects of spider size and reproductive status on behavior, and also whether there was interaction between these effects such that effect of spider size on behavior differed between spiders with and without offspring.

METHODS

This study was conducted at the Manitou Experimental Forest, an administrative unit of the U.S. Department of Agriculture Forest Service Rocky Mountain Experiment Forest in Woodland Park, Colorado USA (39°06′02″N, 105°05″32′W). We worked in mature stands of ponderosa pines (*Pinus ponderosa* Laws. var. *scopulorum*) at an elevation of approximately 2400 m with an understory of herbaceous vegetation and pine saplings.

Paraphidippus aurantius builds small, compact silk nests at the base of pine needle clusters. When these nests are destroyed, *P. aurantius* either rebuilds in the same location or disperses from the sapling (Mooney & Haloin in press). Adult females lay eggs in nests, and spiderlings can remain within or near nests for several days. By late July there are some juveniles, very few adult males, and of the adult females, most have eggs or offspring (Mooney unpubl. data). Thus, the spiders with which we worked were either (1) adult females guarding eggs and spiderlings ('guarding spiders') or (2) male and female juveniles ('non-guarding spiders'). Voucher specimens of *P. aurantius* are deposited at Denver Museum of Nature and Science.

We conducted our first replication of our experiment in 2000. On 22 July we located 22 spiders nesting in saplings and simulated a predator threat by applying force to the nest exterior walls with gentle mouth blowing. We then destroyed each nest, noting whether there were eggs or spiderlings, or whether the nest was empty. In 2001 we conducted a second, modified replication of the experiment. In mid July we located 30 occupied nests. On July 24 we simulated a predator threat by applying force to the nest walls with puffs of air expelled from a rubber bulb at one second intervals, counted the number of puffs required before each spider left its nest, and noted the distance the spider traveled. We visually estimated spider length to the nearest millimeter and collected the nest. Under a dissecting microscope we noted whether there were (1) eggs or spiderlings or (2) whether the nest was empty. We then removed any eggs and spiderlings and weighed the nest silk using a Mettler HK 60 precision balance. In the field we checked for spiders eight times over the next 21 days, specifically on days 1 (one day after nest destruction), 2, 8, 9, 10, 13, 14, and 21. On each visit we noted whether the spider was present and whether it had rebuilt a nest (see Mooney & Haloin in press for information on nest site fidelity).

All analyses were performed using PROC GLM of SAS 6.12 (SAS Institute 1996). Type III sums of squares were used when sample sizes were unbalanced (Zar 1999). Unless otherwise stated, assumptions of normality and heteroskedasticity were met and analyses were performed on untransformed variables.

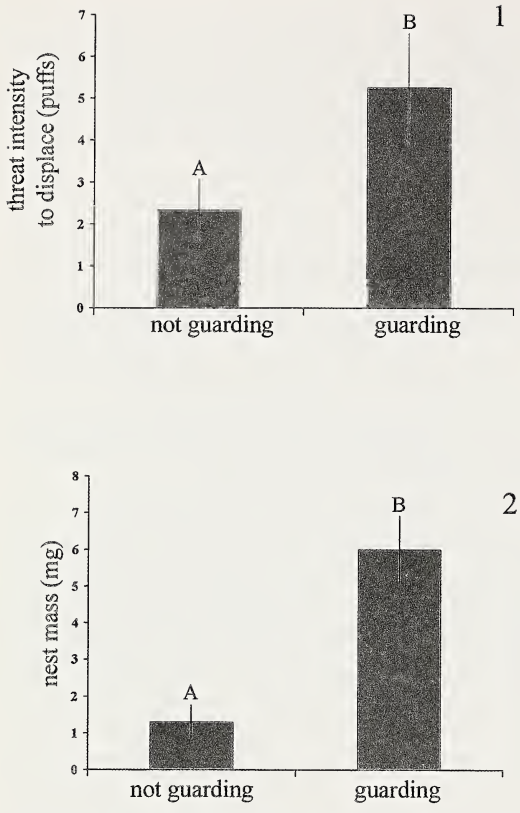


Figure 1.—Mean (± 1 standard error) threat intensity (number of puffs of air) required to displace guarding and non-guarding spiders for spiders tested in 2001. Means differed significantly ($P < 0.05$), as indicated by differing letters above means.

Figure 2.—Mean nest mass (± 1 standard error) for guarding and non-guarding spiders. Means differed significantly ($P < 0.05$), as indicated by differing letters above means.

RESULTS

Of the 30 spiders studied in 2001, 15 were guarding eggs ($n = 6$), spiderlings ($n = 6$), or both ($n = 3$) at the time the experiment was initiated. Brood sizes ranged from 6 to 36 ($n = 13$) with a mean of 18 ± 2.5 (mean ± 1 standard error). Guarding spiders ($n = 15$) were 6 + 2.2 mm in length, while non-guarding spiders ($n = 15$) were 5 ± 2.7 mm and this difference was significant ($F_{(1,28)} = 12.06$, $P = 0.002$).

We tested for effects of spider guarding (a discrete variable) and size (a continuous variable) on the threat intensity required to displace spiders (puffs of air). There was no effect of spider size on threat intensity ($F_{(1,26)} = 1.56$, $P = 0.22$), nor was there interaction between spider guarding and size ($F_{(1,26)} = 1.13$, $P = 0.29$). We dropped spider size from the analysis and a one-way ANOVA showed that threat intensity was significantly higher for guarding than non-guarding spiders. Non-guarding spiders ($n = 15$) required 2 ± 0.8 puffs to be displaced while guarding spiders ($n = 15$), required 5 ± 0.3 puffs ($F_{(1,28)} = 5.02$, $P = 0.033$) (Fig. 1).

The test for an effect of spider guarding and size on empty nest mass (mg silk) suggested no significant relationship between spider size and nest mass ($F_{(1,26)} = 1.60$ $P = 0.22$), nor was there interaction between spider guarding and size ($F_{(1,26)} = 0.14$ $P = 0.71$). We dropped spider size from the analysis and a one-way ANOVA showed that the nests of guarding spiders ($n = 15$) were constructed with 6.0 + 0.9 mg of silk while nests of non-guarding spiders ($n = 15$) weighed only 1.3 ± 0.5 mg and this difference was highly significant ($F_{(1,28)} = 21.53$, $P < 0.0001$) (Fig. 2)

The test for the effects of spider guarding and size on the distance spiders traveled immediately following displacement (linear cm) showed a significant, positive relationship between spider size and travel distance ($F_{(1,26)} = 4.92$ $P = 0.0355$), and there was no interaction between spider guarding and size ($F_{(1,26)} = 0.01$ $P = 0.95$) (Fig. 3). Controlling for spider size, the adjusted mean travel distance for guarding spiders ($n = 15$) was 2.4 cm, while the adjusted mean for non-guarding spiders ($n = 15$) was 5.3 cm, and this difference was significant ($F_{(1,26)} = 8.17$ $P = 0.0083$) (Fig. 3).

To assess whether guarding of offspring affected spider nest rebuilding decisions, we combined data from the 2000 and 2001 disturbance experiments. In total there were 21 guarding and 31 non-guarding spiders. Sixty-two percent (13 spiders) of guarding spiders dispersed from the experimental saplings following our simulated threat of predation, while 48% (15 spiders) of non-guarding spiders dispersed. The number of spiders dispersing did not differ based on offspring guarding ($X_{(3)} = 2.48$, $P = 0.48$). Spiders that rebuilt were 5 ± 0.3 mm in length (mean ± standard error), while spiders that dispersed were 5 ± 0.3 mm and this difference was not significant ($F_{(1,28)} = 0.21$, $P = 0.65$).

The test for the effects of spider guarding

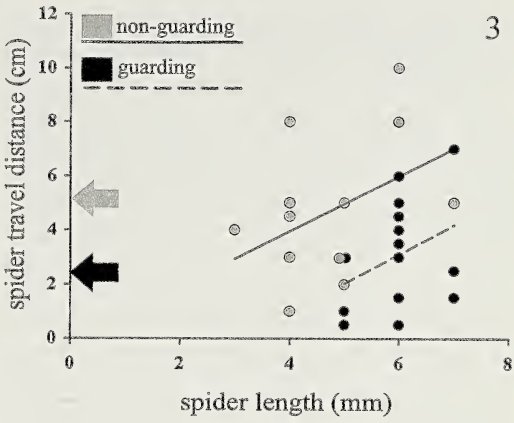
and size on tenure in rebuilt nests showed a trend towards an interaction between spider guarding and size ($F_{(1,26)} = 3.64$, $P = 0.0677$) (Fig. 4). Separate analyses of the relationship between spider size and post-disturbance tenure found no relationship for guarding spiders ($F_{(1,13)} = 0.74$, $P = 0.41$) but a significant, negative relationship for non-guarding spiders ($F_{(1,13)} = 4.67$, $P = 0.0498$). The mean tenure of guarding and non-guarding spiders was 8.8 ± 1.9 days and 7.5 ± 1.9 days respectively, and this difference was not significant ($F_{(1,28)} = 0.24$, $P = 0.63$).

DISCUSSION

There were significant differences between guarding and non-guarding spiders in their immediate responses to our simulated predation threat. Less than half the disturbance intensity was required to displace non-guarding spiders as compared to those guarding offspring. The hesitancy of guarding spiders to flee their nests may not necessarily place them at greater risk of predation because their nests are built with nearly five-times more silk, and this may afford them greater protection from potential predators. Controlling for size, we saw that when spiders did leave their nests, non-guarding spiders fled over twice as far as guarding spiders.

In these comparisons of guarding and non-guarding spiders we did not control for sex or life-stage differences; guarding spiders were adult females while non-guarding spiders were juvenile females and males. However, by controlling for spider size in our comparisons we eliminated at least one important characteristic that differs between adults and juveniles. These results suggest that the outcome of interactions between *P. aurantius* and other predators is likely shaped, in part, by whether or not the spider is a female engaged in offspring guarding behavior.

Spider size did not affect the intensity of disturbance required to displace spiders. When spiders did flee, larger spiders ran further than small ones, contrary to the expectation that larger spiders might remain to confront the challenge. It may be that magnitude of the perceived threat was sufficiently great that all spiders, large and small alike, made the decision to evade the risk, with larger spiders using their relative size advantage to flee further than their smaller conspecifics.



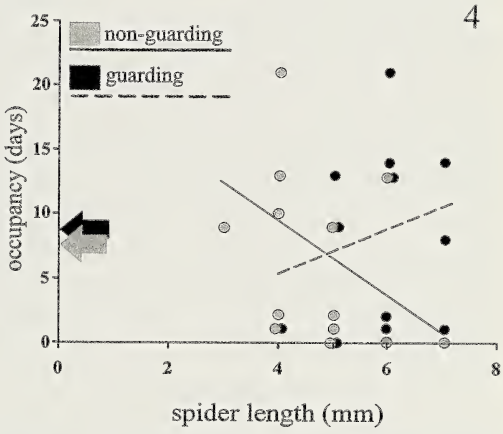


Figure 3.—Relationship between spider length and spider travel distance for guarding spiders (black circles and dashed line) and non-guarding spiders (shaded circles and solid line). The mean spider travel distance for both groups, adjusted for spider length, are shown with black and shaded arrows respectively, and differed significantly ($P < 0.05$).

Figure 4.—Relationship between spider length and occupancy tenure of rebuilt nests for guarding spiders (black circle and dashed line) and non-guarding spiders (shaded circles and solid line). Spider size was negatively related to nest occupancy for non-guarding spiders ($P = 0.0498$). There was no such relationship for guarding spiders ($P = 0.41$). The interaction between guarding and size was close to significant ($P = 0.0677$). The mean post-disturbance tenures of guarding and non-guarding spiders are shown with black and grey arrows respectively.

Neither spider guarding nor size affected the decision of whether to rebuild the nest or to disperse. For non-guarding spiders, small spiders occupied rebuilt nests longer than larger ones. There was no such relationship between spider size and guarding spiders. Dispersion likely carries greater risks for smaller spiders, and this risk seems to be reflected in the decisions of non-guarding spiders. Egg laying may change risk-avoidance decisions such that for guarding spiders, size is of less important than offspring guarding in the decision of when to disperse. Other work has shown that the reproductive status significantly alters spider behaviors (Horel & Gundermann 1992; Bessekon & Horel 1996).

Intraguild predation is interesting because often either of the two interacting predators can become predator or prey. Our work suggests that outcome of predator-predator interactions are likely to be structured by both the size and reproductive status of the predators. Furthermore, we have presented evidence that predator sizes and reproductive status may interact, such that the nature of size-structured interactions may depend on whether or not the predators are engaged in offspring guarding behaviors.

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SPIDER DIVERSITY IN COFFEE PLANTATIONS WITH DIFFERENT MANAGEMENT IN SOUTHEAST MEXICO

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ABSTRACT. We tested the hypothesis that coffee systems with organic management have higher spider diversity by comparing a control (rainforest area) and two coffee systems, one with organic and the other with conventional management. Spiders were sampled every two weeks over three months during the dry season and three months during the rainy season in 2000. Spider alpha diversity was analyzed using Shannon and Simpson indices. We also used the Cody index for beta diversity and cluster analysis for analyzing changes in species abundance hierarchies. 2261 individuals were collected (including juveniles and adults) representing 20 families, 56 genera and 97 species. In most cases the alpha diversity indices showed no relation between management gradient and spider diversity. When compared across seasons, spider diversity differed significantly only in organic management. Species turnover among the three sites (Cody index) was highest between the two coffee farms but not so clearly in the dry vs. rainy season; the conventional management shared the fewest species with the forest. Cluster analysis showed changes in abundance hierarchy related to management type. Our results did not support the proposed hypothesis of a direct positive correlation between management gradient and alpha spider diversity. In contrast, beta diversity showed that management and seasons influenced species composition.

Keywords: Araneae, agroecosystems, management gradient, species composition

Spiders are ubiquitous predators that are abundant and diverse in agricultural ecosystems. Spider assemblages have the ability to limit population growth of arthropod pests alone or in combination with other natural enemies (Mansour et al. 1980; Oraze & Grigarick 1989; Riechert & Bishop 1990; Carter & Rypstra 1995).

Different studies have shown that spiders' influence on prey populations depends on spider density or biomass. Therefore, relatively high spider abundance has been considered a requirement for pest control in agricultural systems (Greenstone 1999; Riechert 1999; Sunderland & Samu 2000), but the role of spider diversity in prey regulation is less understood.

A diverse assemblage of spiders may occupy a variety of biotopes in agroecosystems and, as a whole, are likely to be active throughout the day. Therefore, a diverse spider assemblage will leave fewer refuges for potential prey in time and space. Due to variation in spider size and/or prey capture strategies, spiders should be able to capture prey that vary in size and/or developmental stages (Sunderland 1999; Henaut et al. 2001). For example, Riechert et al. (1999) found that there seemed to be no single spider species that regulates pests or maintains temporal consistency, as well as a diverse assemblage of spider species.

The complexity of vegetation structure has been suggested to be an important habitat component that affects spider density and diversity in both natural ecosystems (Lowrie 1948; Barnes 1953; Barnes & Barnes 1955; Greenstone 1984) and agroecosystems (Hatley & MacMahon 1980; Alderweireldt 1994;

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Rypstra & Carter 1995; Downie et al. 1999). Vegetation structure could influence spiders through a variety of biotic and abiotic factors, namely structures for webs, temperature, humidity, level of shade cover, abundance and type of prey, refuges from natural enemies and intraguild predation (Wise 1993; Samu et al. 1999; Rypstra et al. 1999).

Coffee agroecosystems are particularly useful systems for exploring how vegetation structures affect spiders diversity and density. It has a diversified arthropod fauna (Ibarra 1990; Ibarra & García 1998) and a range of different management systems (Perfecto et al. 1996; Moguel & Toledo 1999). Coffee plantations commonly include shade trees normally used to regulate sun intensity on coffee shrubs, but the level of shade used is variable according to land management practices. Land management also affects arthropod density, since density and cover of shade trees, and agronomic inputs are important regulators of correlated microclimatic and structural variables, that in turn affect other biological factors (Perfecto et al. 1996). Shade tree density, height, and diversity vary along a management gradient from "rustic" (introduction of coffee shrubs in the undisturbed forest) to "unshaded monocultural" systems. Reduction or elimination of tree shade cover and/or introduction of agrochemicals could cause a variety of changes, e. g., increased soil and air temperatures, a lower soil water content, a decreasing abundance and diversity of soil microorganisms, and a decrease of soil fertility (Moguel & Toledo 1999). Furthermore, a greater diversity and abundance of shade trees and the lack of agrochemical inputs in coffee farms promotes the presence and preservation of a higher associated biodiversity than in conventional coffee systems (Perfecto & Snelling 1995; Perfecto et al. 1996; Greenberg et al. 1997).

On a conventional coffee farm in Mexico, Ibarra (1990) found that natural enemies (predators and parasites) accounted for 25% of total arthropod abundance and 41% of total arthropod species richness. This suggests that the abundance and diversity of natural enemy assemblages could make a significant contribution in regulating insect herbivores (spiders were found to be an important component of the natural enemy guild, comprising 25% of species richness and 56% of abundance for this guild excluding ants).

The aim of this study was to quantify the effects of coffee management upon spider diversity. We tested the hypothesis that coffee systems with organic management have higher spider diversity than coffee systems with conventional management by comparing systems along a management gradient from an uncultivated area (rainforest) to two coffee systems differing in management practices.

METHODS

Study areas.—We established three study sites as a shade gradient, from a small rainforest area to two coffee plantations with different types of vegetative structure and management. The two plantations, Irlanda (15° 10′ N, 92° 20′ W, elevation 830–900 m) and Hamburgo (15° 10′ N, 92° 19′ W, elevation 900–990 m) are located 65 km and 60 km, respectively, to the NNW of Tapachula, Chiapas, Mexico. The two coffee farms are contiguous and differ markedly in vegetative arrangement, shade intensity (diversity, height and density of shade trees) and agrochemical inputs. Hamburgo follows a modern conventional coffee system, with low shade tree density (15 shade trees per ha, interspersed with coffee shrubs) and a low diversity of shade trees (two *Inga* species and one *Miconia* species, with regulated height of 5–7 m). Coffee shrubs (about 3330 coffee shrubs per ha) are planted in straight lines (regardless of slope variations) and agrochemical inputs (synthetic insecticides, herbicides and fertilizers) are used twice at year (September and May). In contrast, Irlanda uses an organic technology with higher shade tree density (50 trees per ha, interspersed with coffee shrubs) and higher diversity of shade trees (four *Inga* species and several native trees, with height varying between 5 to 25 m), coffee shrubs (about 3060 coffee shrubs by ha) are planted along contours, and without use of agrochemical inputs (Ibarra et al. 1995). Several areas inside Irlanda have never been cultivated; one of these, "Reserva la Montañita," has rainforest vegetation and high tree density (about 55 trees per ha) and was used as control site.

Spider sampling.—We sampled every two weeks for three months in the dry season (February–April 2000) and again for three months in the rainy season (June–August

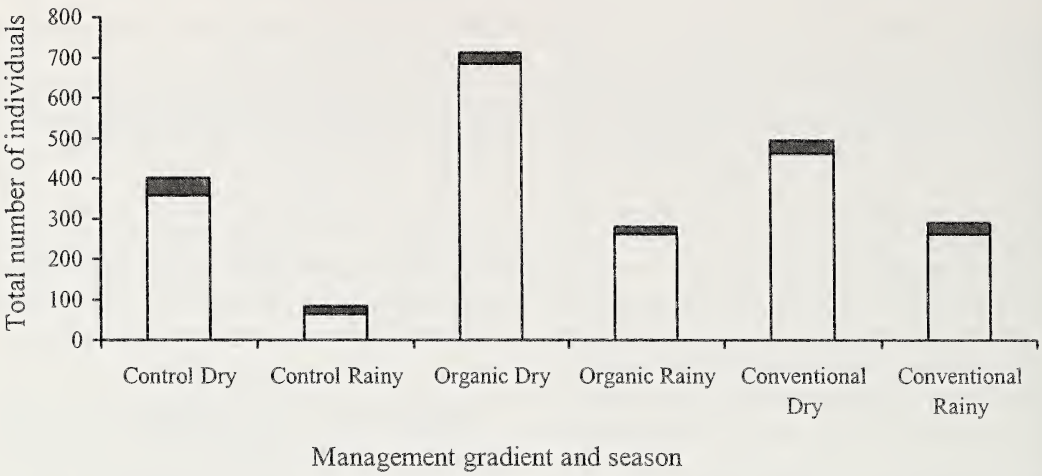

Figure 1.—Number of spider specimens collected from different management sites and seasons. White bars represent web-builder spider guild. Diagonal bars represent hunter spider guild.

2000) for a total of six samples in each site during each season. At each site, two collectors (MAPR and JAGB) searched for spiders visually through the entire shrub (leaves, branches and trunks) and removed them by hand (Churchill & Arthur 1999). During sampling, eight coffee plants were chosen at random on each study site, (each collector sampling four plants). The plants were not contiguous shrubs and were separated from each other by a minimum of two coffee plants, and were sampled only once throughout the study to avoid negative sampling effects. Due to periodical pruning practices, the coffee shrubs are all about the same height and volume in each site. As the control site lacked coffee bushes, spiders were sampled from one species of native bush (a woody species of the genus *Piper*) similar to the coffee plants with respect to height, architecture and foliage structure. Care was made to use always the same type and size of *Piper* plants. The specimens were preserved in 80% ethanol and determined to the taxonomic level of species or undetermined species (when a species level determination was not possible). The specimens were deposited in the Arachnological Collection of El Colegio de la Frontera Sur located in Tapachula, Chiapas, Mexico. Undetermined species were compared with similar determined species located in the Arachnological Collection to reduce determination fails.

Analyses.—We analyzed species' alpha diversity using Shannon (H′) and Simpson (D) indices. These two indices were chosen because they reflect two different aspects of diversity: Shannon's index is more sensitive to rare species, and Simpson's index is sensitive to changes in the abundance the most common species (Magurran 1988). Calculations of these indices were made with totals of species and undetermined species, and functional groups (web builders and cursorial hunters) for each site and season. We used the Hutchinson t tests to detect significant differences in H′ values between sites and seasons. The Cody index was used to evaluate beta diversity (rate of species change) between sites (Magurran 1988). Cluster analyses were used to detect differences according to their relative abundance in the species composition for sites and seasons (McCune & Mefford 1997).

RESULTS

We collected 2261 individuals, including juveniles and adults: 992 from the organic management site, 485 from the control site and 784 from the conventional management site. The collected specimens represented 20 families, 56 genera and 98 species, including 54 species determined only to genus and 14 species determined only to family, because they were juveniles and consequently could not be determined to genus or species level. Nevertheless, they were carefully compared with the determined species in the ECOSUR collection, and with the other collected species

Table 1.—Spider species diversity indices by management site and spider grouping. Values are noted for dry season and rainy season.

	Species richness		Shannon index		Simpson index	
	Dry	Rainy	Dry	Rainy	Dry	Rainy
Control all spiders	47	30	2.77	2.94	0.111	0.084
Organic all spiders	32	36	1.54	2.59	0.346	0.126
Conventional all spiders	51	45	2.87	2.75	0.103	0.152
Control web builders	37	24	2.54	2.78	0.134	0.101
Organic web builders	24	27	1.36	2.37	0.375	0.143
Conventional web builders	38	33	2.67	2.45	0.117	0.185
Control hunters	10	6	1.51	1.16	0.367	0.455
Organic hunters	8	9	1.75	2.04	0.208	0.149
Conventional hunters	13	12	2.19	2.18	0.153	0.156

in the corresponding family or genus, and could be recognized as distinct morphospecies. Abundance decreased in all sites from dry (1608) to rainy season (653) (Fig. 1)

Alpha diversity.—The conventional management site had the highest species richness in both seasons, for both web-building and hunting spider guilds. The sites with the lowest species richness (for all spiders and functional groups) were the organic management in the dry season and the control site for the rainy season (Table 1).

Dry season: Shannon Index: Overall, spider diversity was significantly higher in conventional management than in organic management ($t = 16.3$, df = 920, $P < 0.005$) and in the control ($t = 14$, df = 551, $P < 0.05$) (Table 1). For the functional groups, the web builders showed the same trend as the overall spider analysis, with significantly higher diversity in conventional management than in organic management (Table 1) ($t = 17$, df = 724, $P < 0.001$) and in the control ($t = 13.8$, df = 325 $P < 0.001$). For the hunting spiders, the highest diversity was recorded in conventional management and lowest in control, showing significant differences only between these two sites ($t = 2.63$, df = 103, $P < 0.025$). Simpson index: Total and web building spider dominance was highest in organic management and lowest in conventional management (Table 1). However, for hunting spiders, the control showed the highest dominance and conventional management the lowest.

Rainy season: Shannon Index: Spider diversity was significantly higher in control than in organic management for all spiders ($t = 2.38$ df = 53, $P < 0.05$) and web builders ($t = 2.62$, df = 20 $P < 0.01$) (Table 1). For the hunting spiders, diversity was higher in conventional management than in the control site ($t = 3.21$, df = 67.3 $P < 0.005$), and in the control site was lower than in the organic management site ($t = 2.71$, df = 18.5, $P < 0.025$). Simpson index: Total and web building spiders' dominance was highest in conventional management and lowest in control (Table 1), whereas the hunters showed the opposite trend, with control having the highest dominance and organic management the lowest.

Seasons contrast: Shannon Index: In comparing overall spider diversity for each site, only organic management differed significantly by season ($t = 10.9$, df = 1020, $P < 0.005$). Furthermore, only web building spiders in organic management differed significantly between seasons ($t = 11.3$, df = 967, $P < 0.005$).

Beta diversity.—Highest values for all spiders using the Cody diversity index were recorded in both seasons among conventional management and control. On the other hand, the lowest exchange of species was found in both seasons between organic management and conventional management, being the most similar in species composition (Table 2). Web builders shared the same pattern as all spiders in both seasons. In the dry season, hunting spiders were most similar between the control and organic management but in the rainy season were most similar between conventional management and organic management.

During the dry season, some species were found at only one site. *Spintharus flavidus*

Table 2.—Cody diversity indices for spider collected by management sites and spider grouping. Values are noted for dry season/rainy season.

	Total spiders	Web builders	Hunters
Control vs Organic	19.5/17.5	14.5/12.5	5/4.5
Control vs Conventional	22.5/19	15.5/13.5	7.5/5
Organic vs Conventional	18/12.5	11/9	7.5/3.5

Hentz 1850 (Theridiidae), *Exalbidion sexmaculatum* (Keyserling 1884) (Theridiidae) were exclusive to control plots; *Verrucosa arenata* (Walckener 1833) (Araneidae) and *Tama* sp. (Hersilidae) were found only in organic management; *Cheiracanthium* sp. (Miturgidae), *Dictyna* sp. (Dyctinidae) and *Verrucosa* sp. (Araneidae) were present only in conventional management during both seasons.

Cluster analysis.—Cluster analysis showed that during both seasons spiders four species group form: dominants, subdominants, commons and rare (less than two individuals). In the dry season *Leucauge* sp. was dominant in all sites, *L. argyra* (Walckenaer 1842) (Tetragnathidae) was subdominant in the control and dominant in the coffee plantations, and *Jalapyphantes* sp. (Linyphiidae) was dominant in the control, subdominant in organic management and common in conventional management (Fig. 2). In the rainy season, *Leucauge* sp. was common in the control site and dominant in the coffee plantations. *Leucage argyra* was dominant in the control site, subdominant in organic management and common in conventional management. *Wulfila* sp. (Anyphaenidae) was particularly dominant in the control site; *Jalapyphantes* sp. was common in the control plot, dominant in organic management and subdominant in conventional management. *Spermophora* sp. (Pholcidae) was subdominant in the control, dominant in organic management and rare in conventional management. *Theridion omiltemi* Levi 1959 (Theridiidae) was rare in the control site, dominant in organic management and subdominant in conventional management (Fig. 2).

DISCUSSION

Most studies regarding the role of shade tree density and diversity in coffee plantations have found a higher species diversity in more diverse coffee agroecosystems (Perfecto et al. 1996; Greenberg et al. 1997). Perfecto & Snelling (1995) found that species diversity of ground-foraging ants decreased with shade reduction whereas coffee-foliage-foraging ant diversity did not change along the same shade gradient.

In our study, there was no apparent trend between management and spider diversity. Most cases (11 out of 18), according to species richness, Shannon and Simpson indices, showed no relation between management and spider diversity. In only two cases did we find that spider diversity decreased with management intensification. Surprisingly, in five cases, we found an increase in spider diversity as land management increased. These results are contrary to what has previously been reported (Perfecto et al. 1996; Greenberg et al. 1997), and there are several possible explanations. An uncontrolled factor that could affect spider diversity was the presence and density of insectivorous birds, which are known to predate spiders intensely (Gunnarsson 1998). Some studies have found that shaded coffee plantations have higher bird species richness and abundance than poor shaded plantations (Perfecto et al. 1996; Moguel & Toledo 1999), this different predation level could affect spiders' abundance and composition, by selectively reducing numbers of those spiders species more exposed to bird predation. Another explanation is the possibility that relative diversity levels change between years, as we only made a one-year study, and therefore results should be interpreted with caution.

The organic management site had the lowest spider species richness and diversity, and the highest dominance in the dry season (according to all alpha indices used) with the exception of hunting spiders. In both seasons, web-building spiders were more abundant and had higher species richness than hunting spiders. Among the web-building spiders, *Leucauge argyra* and *Leucauge* sp. were found disproportionately abundant in all sites, but

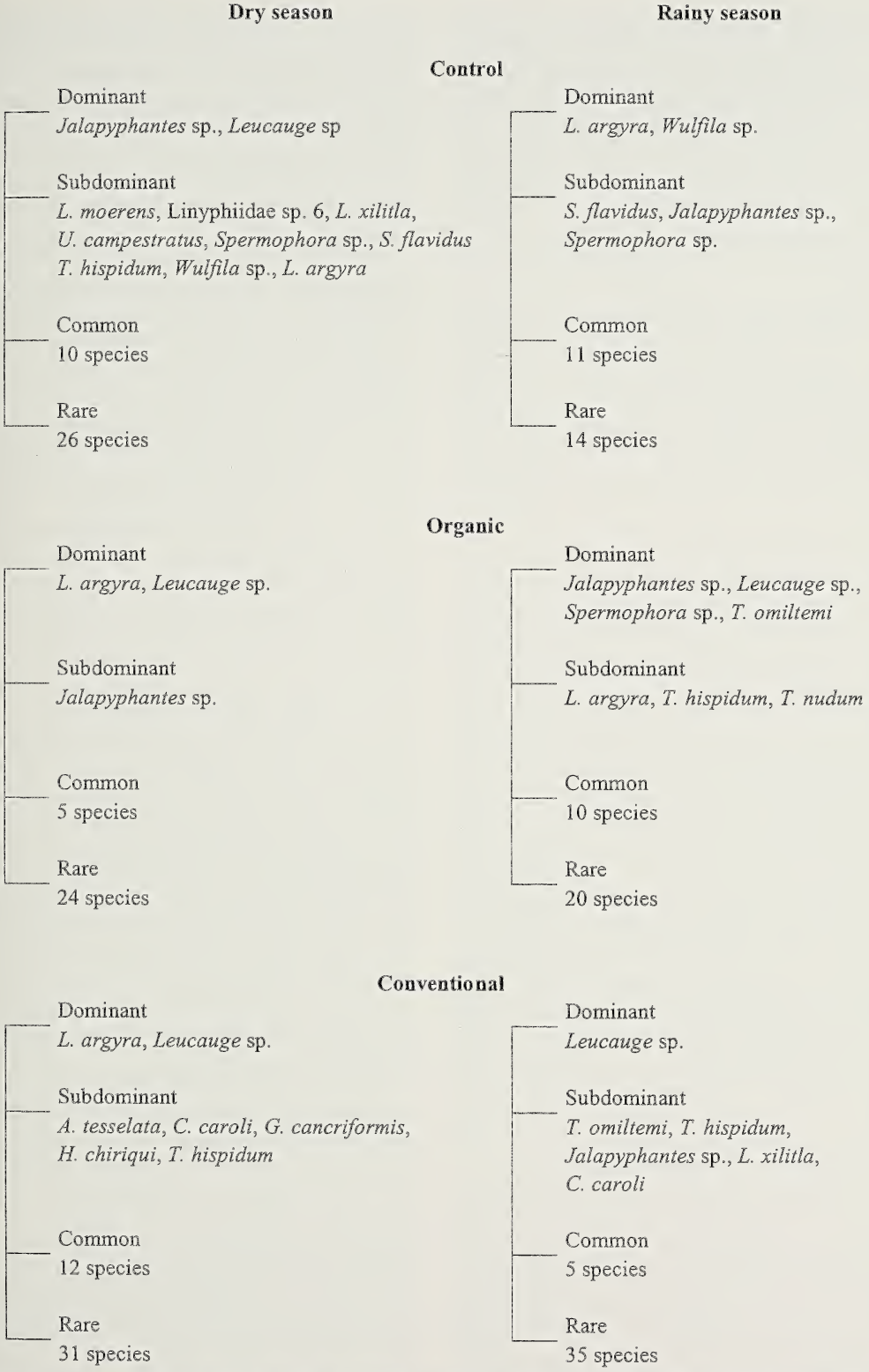

Figure 2.—Cluster analyses showing abundance species hierarchies for different management sites and seasons.

most notably in organic management. The extreme dominance of the *Leucauge* spp. in organic management was the cause for the high values estimated by Simpson index (which is more sensitive to dominant species). The Shannon index values are most affected by species richness and secondarily by evenness. The organic management with low species richness and extreme dominance (reduced evenness) therefore had low Shannon index values.

Several authors consider that dominant species tend to exploit resources more efficiently than non-dominant species (Agnew & Smith 1989; Mason et al. 1997). Extreme dominance of *Leucauge* spp. in organic management compared to control and conventional management in the dry season may be because the optimum, in shade and humidity conditions, for these species are those of the organic management (intermediate between the control and the conventional sites). *Leucauge mariana* has been reported as a very abundant species in disturbed habitats in Central America (Eberhard 1988; Eberhard & Huber 1998). For these reasons, these species could be more abundant in the coffee systems than in the control site, but the dominance of this species should be subject of a particular study.

Spider diversity under the organic management significantly increased in the rainy season due to an increase in species richness and a decrease in the dominant species abundance. In contrast, in conventional management and control, there were no significant differences between the seasons. Theoretically, when populations of competitive dominant species decrease or disappear, species diversity might increase (Putman 1994). In organic management, in the rainy season, *Leucauge* spp. were less common. This could explain why *Spermophora* sp. and *Theridion omiltemi* were more frequently encountered in the rainy season, and became dominant species.

As indicated by the beta diversity index, turnover of species between organic and conventional management in the dry season was similar to the corresponding value between organic and control site. However, in the rainy season, organic and conventional management shared more species than did organic management and control site. These results support the existence of a gradient in species composition, from control site to conventional management, with organic as intermediate, although in the rainy season the difference between organic and conventional management was reduced. This might be explained because in the rainy season the interference of clouds and rain with solar irradiation reduces the differences in temperature and humidity, making the coffee farms more similar in these variables.

Additionally, the exclusive presence of a spider species at one site may be related to the existence of a favorable microclimate and/or an adequate web support for these species. For example, *Spintharus flavidus* and *Epeirotypus brevipes* O. P.-Cambridge 1894 were found only in the control siteand not at other the sites. *Spintharus flavidus*, had been poorly studied taxonomically and is common under the leaves of bushes (Levi 1954), so it is possible that it could prefer the non disturbed control site, in opposition to the periodically perturbed coffee plantations. On the other hand, *E. brevipes* was found only on control habitat, and is known that the spiders of this family live almost exclusively in wet or humid, shaded forest habitats (Coddington 1986). Some species collected were singletons, as in the case of *Dolichognatha* sp. and *Tetragnatha* sp., and could reflect a demographic rarity (Halfter & Ezcurra 1992).

In the dry season, *Leucauge* sp. and *L. argyra* were among the dominant and subdominant species at all sites, showing that they were not affected by the management gradient. However, with a seasonal change from dry to rainy season, *L. argyra* became considerably less abundant in all sites and was dominant in control (17 individuals), subdominant in organic management (15) and common in conventional management (7).

Alpha diversity comparisons did not support our hypothesis that spider diversity decreases with decreasing shade. The extreme dominance of the *Leucauge* spp., and possibly the higher density of predatory birds, affected the results at this level. In contrast beta diversity results (analyzed by Cody index) and the cluster analyses, supported the existence of a gradient of species composition from control to conventional management, showing effects at structural community level, with changes of species hierarchy due to coffee management.

With the use of a *Piper* plant species as

control, which probably has chemical components distinct to those of the coffee plant, arises the possibility of having different effects on the insect fauna associated with this plant, and hence indirectly on the spider fauna. Some species in the *Piper* genus have been reported to have compounds with deterrent or insecticide properties (e.g. Dyer et al. 2003; Siddiqui et al. 2003; Lale & Alaga 2001). But Marquis (1991) found that the number of insect herbivore species on the *Piper* plants found in La Selva, Costa Rica, varied greatly with plant species, some species can support a high diversity of insects (e. g. *P. arieianum* with 95 herbivore species). As we could not determine the species of the control plant, the differences in diversity between the control and the two coffee systems found in this work should be taken with caution.

These results reflect only the differences in spider community at the understory level (coffee bushes) for the year of study; but it will be interesting to analyze the whole agroecosystem, including arboreal, herbaceous and soil strata.

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SYSTEMATICS OF THE AFRO-MACARONESIAN SPIDER GENUS *SANCUS* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. We review the systematics of the tetragnathid spider genus *Sancus* Tullgren, hitherto known from a single species from Kilimanjaro. The type species *Sancus bilineatus* Tullgren is redescribed and diagnosed from the only other known species, *S. acoreensis* (Wunderlich) new combination. *Leucognatha* Wunderlich is a junior synonym of *Sancus*, which thus eliminates two monotypic tetragnathid genera. A phylogenetic analysis of 15 tetragnathid and eight outgroup genera confirms the monophyly of *Sancus* and places it precisely in Tetragnathidae. We discuss the phylogenetic relationships among tetragnathid genera and the peculiar biogeography of *Sancus*, now known from east African mountains (Kilimanjaro and Mt. Kenya) and from the Azores in the northeastern Atlantic.

Keywords: Tetragnathidae, *Sancus*, *Leucognatha*, taxonomy, phylogenetics, biogeography

No taxonomic treatment of the tetragnathid genus *Sancus* exists in the literature since Tullgren's (1910) original description of a species from Kilimanjaro and the genus has remained monotypic until now (Platnick 2004). The original description of *Sancus bilineatus* Tullgren 1910 included illustrations of both the epigynum and palpus (Tullgren 1910: figs. 87–88). However, the illustrations are insufficient to reliably confirm the placement of *Sancus* in Tetragnathidae. *Sancus* has traditionally been placed among the "metines" ("metids," "Metinae"), a taxonomic concept often changing status and rank (see Taxonomic History). "Metines" have been shown to be a paraphyletic assemblage of tetragnathid genera nested between Nephilinae and Tetragnathinae (Hormiga et al. 1995). However, the placement of *Sancus* has never been tested phylogenetically. We are currently studying the higher level phylogenetics of Tetragnathidae, with emphasis on taxa formerly classified as "metines" (Alvarez-Padilla & Hormiga in prep.) and on nephilines (Kuntner 2005, 2006a & b). Although the 'metines' are being recovered as monophyletic in our preliminary phylogenies, this name cannot be used, as the crustacean family name Metidae Boeck 1872 (based on *Metis* Philippi 1843), has priority over the spider family group name Metinae Simon 1894 (based on *Meta* C.L. Koch 1836).

Here, we reassess the validity and monophyly of the genus *Sancus*, provide a new diagnosis and circumscription, test its phylogenetic placement within the Tetragnathidae, redescribe the types of *S. bilineatus*, and propose *Leucognatha* Wunderlich 1992 (described as endemic in the Azores) as a junior synonym of *Sancus*. The genus is now known from east African mountains (Kilimanjaro and Mt. Kenya) and from the archipelago of the Azores in the northeastern Atlantic.

Taxonomic history.—Tullgren (1910) established the genus *Sancus* to accommodate a new species from Kilimanjaro, *S. bilineatus*

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[2] Since the acceptance of this paper, Kuntner (2005, 2006a & b) has presented newer analyses, which dispute the tetragnathid placement of nephilines, and elevate the clade (*Clitaetra(Herennia(Nephila* + *Nephilengys*) to family rank, Nephilidae. However these new hypotheses do not affect *Sancus*.

Tullgren 1910. Following Simon's (1894) classification Tullgren listed *Sancus* within the family Argiopidae, which then included genera from the modern superfamily Araneoidea (see Griswold et al. 1998 for the current systematics). Further, Tullgren (1910) placed *Sancus* in Simon's group Meteae, close to the genera *Chrysometa* Simon and *Meta* Koch. Tullgren diagnosed *Sancus* from the other genera within the group by the straight posterior eye row. Petrunkevitch (1928) listed *Sancus* within the argiopid subfamily Metinae. While Bonnet (1958) retained *Sancus* within Argiopidae, Roewer (1942) listed Metinae (including *Sancus*) within the Araneidae. Brignoli (1983) treated the Metidae (with *Sancus*) as a family, but Dippenaar-Schoeman & Jocqué (1997) list *Sancus* in Metinae (Tetragnathidae). *Sancus*, along with most genera from the group Meteae (*sensu* Simon) are now in the family Tetragnathidae (Platnick 2004).

Leucognatha Wunderlich 1992 was described as a monotypic genus (containing *L. acoreensis* Wunderlich 1992) endemic to the Azores archipelago in the northeastern Atlantic. *Leucognatha* was diagnosed, among other features, to lack femoral trichobothria, chelicheral denticles (between ridges), and median and terminal apophyses, and to possess a basal-retrodorsal outgrowth on male palpal cymbium (= cymbial basal process, see below) and a shallow grove frontally (= epigynal ventral depression, see below) on the distinctly sclerotized epigynum. Wunderlich (1992) placed *Leucognatha* in the tetragnathid subfamily Leucauginae (see Discussion). His description and illustrations of *L. acoreensis* prompted us to examine the type series for possible congeneric status with *Sancus*.

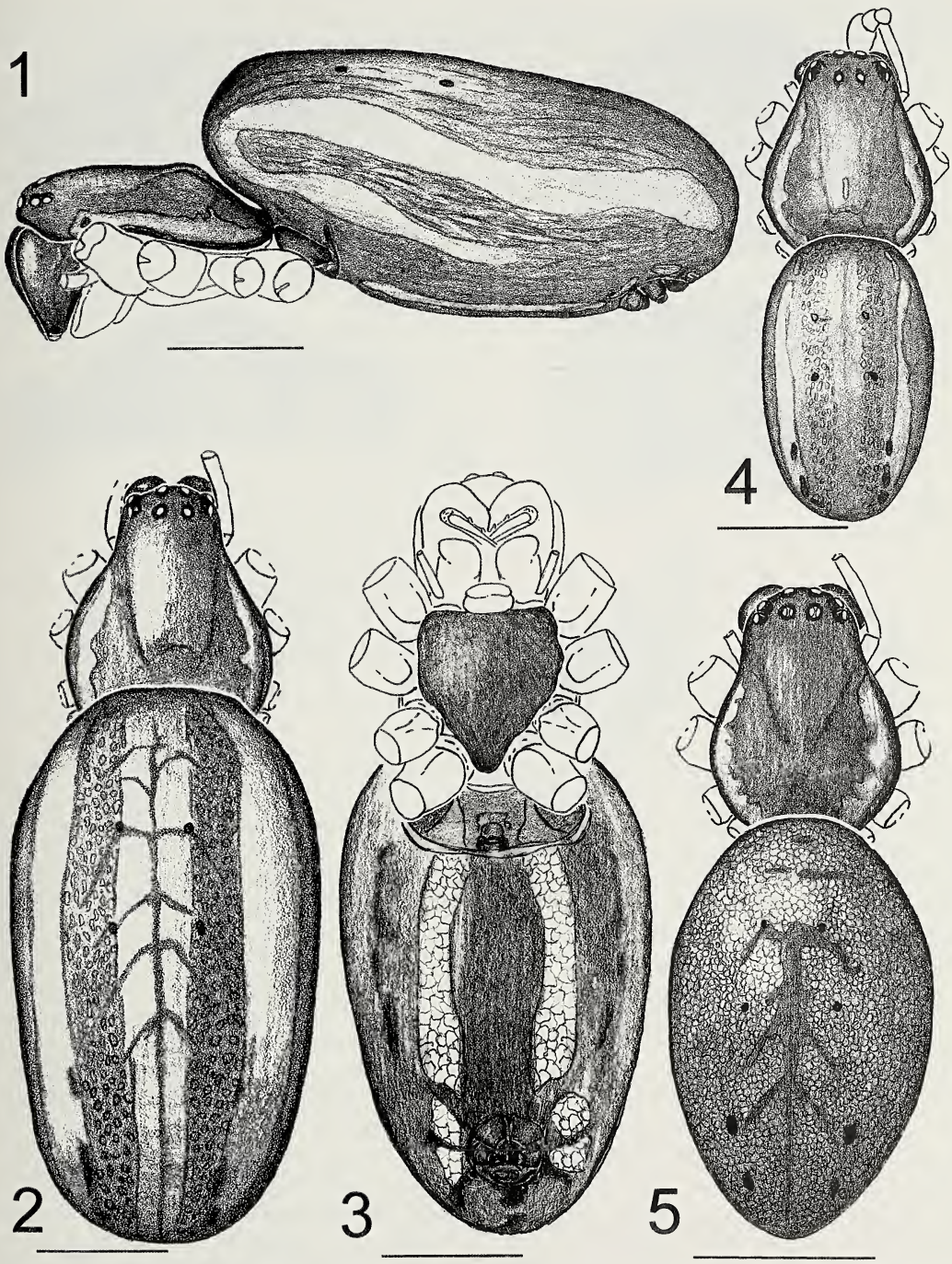
METHODS

Specimens.—The types were borrowed from the collections of the Swedish Museum of Natural History (SMNH) in Stockholm and donated from Jörg Wunderlich's private collection (Straubenhardt, Germany). The latter were deposited in the collections of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. We examined the available identified and unidentified tetragnathids in the collections of USNM, the American Museum of Natural History (AMNH) in New York, and the California Academy of Sciences (CAS) in San Francisco. We found a single female *S. bilineatus* in USNM. In all other collections we failed to find *Sancus*. Additionally, *Sancus* is apparently absent from the following European museums with rich African collections: Royal Museum for Central Africa (RMCA), Tervuren, Belgium (R. Jocqué in litt.), Muséum national d'histoire naturelle (MNHN), Paris (own data), Museum fuer Naturkunde der Humboldt-Universitaet, Berlin (ZMB, J. Dunlop in litt.) and the British Museum of Natural History (BMNH), London (J. Beccaloni in litt.).

Taxonomic methods.—General taxonomic methods follow Hormiga (2002). Morphological observations and illustrations of external structures were made using a Leica MZ APO dissecting microscope with a camera lucida. Internal genitalic structures were cleared in methyl salicylate (Holm 1979), mounted on a temporary slide (Coddington 1983) and examined and illustrated under compound microscope Leica DMRM with a camera lucida. Measurements were taken using a reticle calibrated in millimeters. Illustrations were rendered on coquille board and scanned for digital manipulation in Adobe Photoshop 7.0. The maps were redrawn in Adobe Illustrator 10 from the Microsoft Encarta Interactive World Atlas 2000 templates. All plates were assembled and labeled in Adobe Illustrator 10.

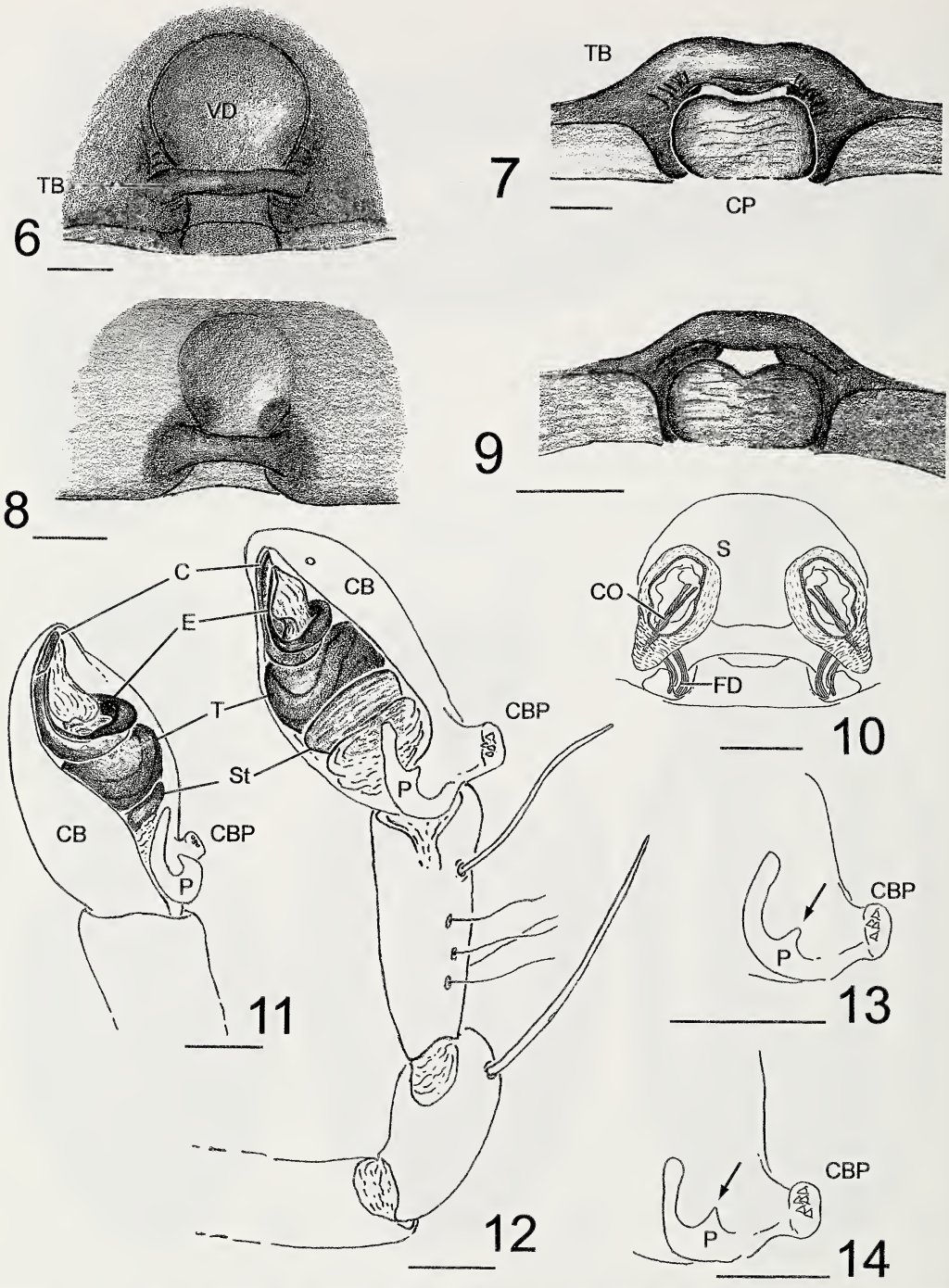
Anatomical abbreviations.—ALE = anterior lateral eyes; AME = anterior median eyes; C = conductor; CB = cymbium; CBP = cymbial basal process; CO = copulatory opening; CP = epigynal caudal plate; E = embolus; FD = fertilization duct; P = paracymbium; PLE = posterior lateral eyes; PME = posterior median eyes; S = spermatheca; St = subtegulum; T = tegulum; TB = epigynal posterior transverse bar; VD = epigynal ventral depression.

Character analysis.—The morphological examination of the two *Sancus* species implied the placement of the genus in the family Tetragnathidae. To test such phylogenetic placement and the monophyly of *Sancus*, we used the published data matrix of Hormiga et al. (1995) containing 14 tetragnathid genera plus eight genera from seven outgroup families (Table 1) scored for 60 morphological and behavioral characters. We coded both *Sancus* species for all 60 characters (Table 2) and add-



Figures 1–5.—*Sancus* somatic morphology. 1–4. *Sancus bilineatus*. 1–3. female syntype, lateral (1), dorsal (2), ventral (3); 4. male syntype, dorsal; 5. *Sancus acoreensis*, female paratype, dorsal. Scale = 1.0 mm.

ed three new characters. These new characters, described below, are numbered as characters 61–63. The entries for *Sancus* behavior (characters 42–53) and the spinneret morphology (characters 54–60) remain missing (marked as question marks) due to lack of data and specimens. Below, we explain selected character codings. While we point out some errors in Hormiga et al. (1995) we did not change the codings from that published



Figures 6–14.—*Sancus* genitalic morphology. 6, 7, 10. *S. bilineatus* female syntype epigynum, ventral (6), caudal (7), dorsal, cleared (10); 8, 9. *S. acoreensis*, female paratype epigynum, ventral (8), caudal (9); 11–13. *S. bilineatus* male syntype left palp, ventral (11), ectal (12), detail of paracymbium, paracymbial apophysis (arrow) and cymbial basal process, ectal (13); 14. *S. acoreensis*, male paratype, detail of paracymbium, paracymbial apophysis (arrow) and cymbial basal process, ectal. Scale = 0.1 mm. See Methods for anatomical abbreviations.

Table 1.—Terminal taxa from Hormiga et al. (1995) with the addition of *Sancus* species (this analysis).

Family	Taxon	Author and year
Uloboridae	*Uloborus*	Latreille 1806
Araneidae	*Araneus*	Clerck 1757
	Argiope	Audouin 1826
Linyphiidae	*Linyphia*	Latreille 1804
Pimoidae	*Pimoa*	Chamberlin & Ivie 1943
Theridiidae	*Steatoda*	Sundevall 1833
Nesticidae	*Nesticus*	Thorell 1869
Theridiosomatidae	*Epeirotypus*	O. P.-Cambridge 1894
Tetragnathidae	*Phonognatha*	Simon 1894
	Clitaetra	Simon 1889
	Nephila	Leach 1815
	Herennia	Thorell 1877
	Nephilengys	L. Koch 1872
	Azilia	Keyserling 1881
	Dolichognatha	O. P.-Cambridge 1869
	Meta	C. L. Koch 1836
	Chrysometa	Simon 1894
	Metellina	Chamberlin & Ivie 1941
	Leucauge	White 1841
	Tetragnatha	Latreille 1804
	Glenognatha	Simon 1887
	Pachygnatha	Sundevall 1823
	Sancus bilineatus	Tullgren 1910
	Sancus acoreensis	(Wunderlich 1992)

matrix as such revision was beyond the scope of this paper and will be done elsewhere.

Character 21: (erroneously labeled as Ch. 22 in Hormiga et al. 1995: 329). Cymbium orientation in *Sancus* is mesal (Fig. 4). At least nephilines and certain 'metines' were miscoded in Hormiga *et al.* (1995) as they also exhibit the "araneid" mesal orientation.

Character 25: Sancus has the paracymbial secondary process (Hormiga et al. 1995: fig. 6B) and it is procurved. We think the feature is better termed the cymbial basal process (CBP, Figs 11–14) because it arises from the cymbial base rather than from the paracymbium.

Character 31: The character state "a close association between the conductor and embolus, usually coiling together", a synapomorphy of Tetragnathidae (Hormiga et al. 1995), is difficult to interpret and needs redefinition. In most tetragnathines the embolus and the conductor indeed spiral (e.g. Levi 1980: figs. 174–176). In nephilines the conductor fully encloses the embolus (e.g. Levi 1980: figs. 25, 26; Hormiga et al. 1995: figs. 8A, 9A, 10A; Kuntner 2005, 2006a & b), exhibits little spiraling, and may not be homologous to the tegular conductor (Kuntner et al. in prep.). The condition in "metines" is diverse (Levi 1980; Hormiga et al. 1995: figs. 13A–H; Alvarez-Padilla in prep.). The conductor and the embolus of *Sancus* are closely associated: the conductor is grooved to hold the embolus in place and the coiling conductor closely follows the coiling of the embolus, so it seems to fit the first tetragnathid synapomorphy.

Character 61: Cymbial basal process apical denticles. 0: absent. 1: present (Figs 11–14). The feature is present in *Sancus*, absent in other tetragnathid genera with a CBP (*Dolichognatha*, *Meta*, *Chrysometa*, *Metellina*) and inapplicable for the remaining taxa. A cymbial denticulate process is typical of *Pimoa* (Pimoidae; Hormiga 1994: fig. 11). Although somewhat similar to the *Sancus* cymbial basal process, the cymbial process of *Pimoa* is positioned further apically on the cymbium and has no association with the paracymbium. We agree that *Pimoa* lacks the CBP (or paracymbium secondary process) and therefore this character is inapplicable in *Pimoa*.

Character 62: Epigynal transverse bar. 0: absent. 1: present (Figs. 6–9, TB). The feature

Table 2.—Coding of morphological and behavioral characters for both *Sancus* species.

S. bilineatus	001??11000?0000-0001101111001100000001000??????????????????111
S. acoreensis	0011111000?0000-0001101111001100000001000??????????????????111

occurs in *Sancus*, but is absent in all other terminals or inapplicable for haplogyne taxa.

Character 63: Epigynal ventral depression. 0: absent. 1: present (Figs. 6, 8, VD). The feature occurs in *Sancus*, but is absent in all other terminals or inapplicable for haplogyne taxa.

Phylogenetic analysis.—The matrix analyzed here had a total of 24 taxa (Table 1) scored for 63 characters. The parsimony analyses were performed using the computer programs NONA version 2.0 (Goloboff 1993) and PAUP*4.0b.10 (Swofford 2002). In NONA we used search parameters 'hold 1000', 'mult*500', 'max*', and 'sswap', under 'amb–' and 'amb =='. In PAUP we used random taxon addition for 500 replicates and TBR branch swapping. Winclada 1.00.08 (Nixon 2002) was used to display and manipulate trees and matrices for NONA. The multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch 1971). Successive character weighting (Farris 1969) was performed in PAUP based on the maximum value of the rescaled consistency index, base weight of 1. The bootstrap values were calculated in Winclada with 1000 iterations, each iteration with the search parameters 'hold 500', 'mult*50', 'max*'. Bremer support or decay index values (Bremer 1988, 1994) were calculated in NONA using the command 'bs10' and 'hold 100000'.

TAXONOMY

Family Tetragnathidae Menge 1866
Genus *Sancus* Tullgren 1910

Sancus Tullgren 1910: 152. Type species, by monotypy, *Sancus bilineatus* Tullgren.

Sancus: Petrunkevitch 1928: 142; Roewer 1942: 922; Bonnet 1958: 3928; Brignoli 1983: 226; Dippenaar-Schoeman & Jocqué 1997: 292, 338; Platnick 2004.

Leucognatha Wunderlich 1992: 359. Type species, by original designation, *Leucognatha acoreensis* Wunderlich NEW SYNONYMY.

Diagnosis.—*Sancus* can be diagnosed from all other tetragnathids by the combination of the following characters: denticulated male cymbial basal process (Figs. 11–14), sclerotized epigynum with a ventral depression and a transverse bar (Figs. 6–9), and absence of femoral trichobothria.

Description.—*Female:* General somatic morphology as in Figs. 1–3, 5. Cephalothorax with a narrow and low head region and elevated thoracic region (Figs. 1, 2, 5). Carapace glabrous. Carapace color (in alcohol) yellow to brown with two conspicuous lateral white lines (Figs. 2, 5). Sternum roughly heart-shaped, brown (Fig. 3). Labium as long as wide, rebordered (Fig. 3). Endites 2.5 times as long as wide. Anterior eye row slightly recurved, posterior eye row straight (Figs. 2, 5). Lateral eyes on a tubercle, almost juxtaposed, not widely separated from the medians (Figs. 1, 2, 5). Tapeta in secondary eyes present, canoe shaped (observed in *S. acoreensis* but not in *S. bilineatus* due to the specimen age). Chelicerae massive (Figs. 1, 3), with three prolateral and four (two large and two small) retrolateral teeth; cheliceral furrow not denticulated. Cheliceral boss (condyle) absent. Legs fairly short (see measurements below), with few spines. Femoral trichobothria absent. Leg formula 1-2-4-3. Abdomen cylindrical (Figs. 1–3, 5). Dorsum with silvery spots and with (*S. bilineatus*) or without (*S. acoreensis*) white lateral longitudinal lines. Venter with two longitudinal white lines and two paired white spots around the spinnerets (Fig. 3). Booklung covers smooth.

Epigynum (Figs. 6–9) is a well sclerotized ventral plate with an anterior depression (VD, Fig. 6, 8), a posterior transverse bar (TB, Figs. 6–9) and a caudal plate (CP, Figs. 7, 9). Internal epigynum morphology as in Fig. 10. Copulatory openings in the shape of slits laterally under the bases of the transverse bar (Fig. 10). The spermathecae wide apart, oval and well sclerotized (Fig. 10). Fertilization ducts arise from posterior part of spermathecae (Fig. 10).

Male: General somatic morphology illustrated in *S. bilineatus* (Fig. 4), resembles the female. Pedipalp (Figs. 11–14) with a single long patellar macroseta (Fig. 12). Palpal tibia long, with prolateral trichobothria (Fig. 12).

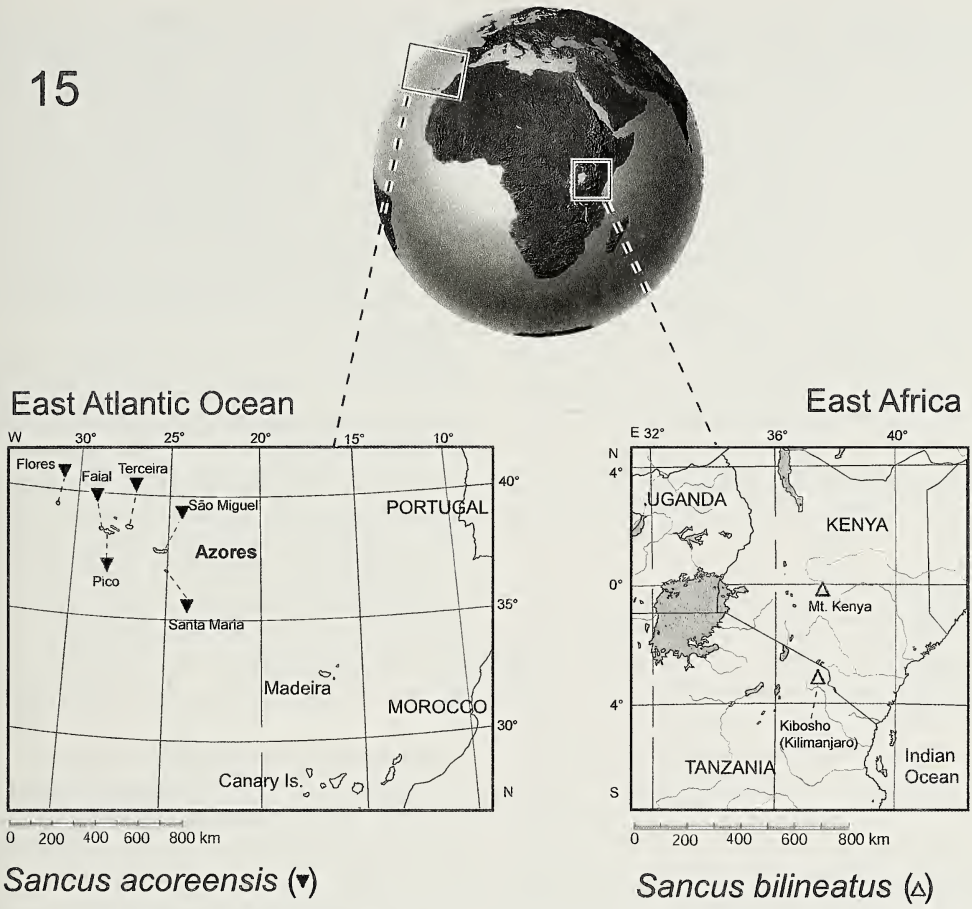


Figure 15.—World *Sancus* distribution. The genus is known from the Azores in the Atlantic Ocean (*S. acoreensis*) and from the mountains of eastern Africa (*S. bilineatus*).

Cymbium long, tapering apically (Figs. 11, 12). Cymbial basal process present, with apical denticles (Figs 11–14). Paracymbium hook shaped (Figs 11–12), with a small mid-anterior process (Figs. 12–14), and no setae. Subtegulum as large as the globular tegulum (Fig. 12). Sperm duct without a switchback. Conductor (Figs. 11, 12), arising from the distal part of the tegulum, has a sclerotized and a membranous part, both holding the embolus in position. Embolus (Figs. 11, 12) sclerotized and wide, with no modifications.

Composition.—Two species: *Sancus bilineatus* Tullgren 1910 and S. *acoreensis* (Wunderlich 1992) new combination.

Comment on species diagnoses.—The two *Sancus* species are best diagnosed by somatic features (size, abdomen shape and folium pattern) and less so by the genitalic morphology. While the ventral epigynal view is diagnostic (Figs. 6, 8), the inner (dorsal) epigynum is uniform in both species. The difference between the palps of the species is subtle (detail of the paracymbial apophysis, see Figs. 13, 14).

Distribution.—East Africa, Azores (Fig. 15; also see Discussion).

Natural History.—Largely unknown (but see Ecology of each species).

Sancus bilineatus Tullgren 1910
Figs. 1–4, 6, 7, 10–13

Sancus bilineatus Tullgren 1910: 152, plate 3, figs. 87, 88 (♂ ♀ description (from Kilimanjaro). Syntypes in SMNH; examined; see comments below); Petrunkevitch 1928: 142; Roewer 1942: 922; Bonnet 1958: 3928; Brignoli 1983: 226; Platnick 2004.

Material examined.—We examined two males, three females and ten juveniles from

SMNH labeled "*Sancus bilineatus* Tullgr., Kilimandjaro, Kiboscho, Colleg. Lj. Sjst. Determ. A. T-n." Without a doubt these specimens are a part of the type series of *S. bilineatus*. Tullgren (1910:152) reported the type series collected during an expedition led by Y. Sjöstedt to the German East African territories as: "*Kilimandjaro*: Kiboscho, 3,000 Mtr., Febr. (18 ♂, ♀)" [= Kibosho, Tanzania, 3°14′S; 37°18′E]. The 15 syntypes available to us may represent only a part of the type series. Female chelicerae and two left male palps had been removed before our examination, yet the preserved material is in good condition.

Other material examined.—Kenya: 1 ♀, Mt. Kenya [approximate coordinates 0°08′S; 37°18′E], 16 Aug. 1970, D. Messersmith (USNM).

Diagnosis.—Females of *S. bilineatus* differ from those of *S. acoreensis* by the larger size (see variation), by the oval abdomen shape (Fig. 2), by the presence of longitudinal white lines on dorsum (Fig. 2), and by the epigynum with a large, well defined and well sclerotized anterior depression (Fig. 6). Males of *S. bilineatus* differ from those of *S. acoreensis* by the larger size (see variation), by the details of the paracymbium, which has a blunt apophysis (Fig. 13), and by the palpal tibial length, which is 2.5 times longer than wide (at its widest point).

Description.—*Female (syntype):* Habitus as in Figs. 1–3. Total length 6.26. Cephalothorax 2.13 long, 1.75 wide, 0.75 high; yellow. Sternum 1.12 long, 0.94 wide; brown, darker at margins. Abdomen 4.56 long, 2.5 wide, 2.1 high; pale gray covered with white-silvery spots; dorsum with three longitudinal white lines (Fig. 2). Venter dark brown with two longitudinal white lines and four white spots around the spinnerets (Fig. 3). AME diameter 0.10. PME 0.12, ALE 0.08, PLE 0.08. AME separation 0.12, PME separation 0.13, AME-ALE separation 0.18. PME-PLE 0.16. Clypeus height 0.13. Legs yellow with white coxal spots. Leg I length 9.9, Leg II 8.4, Leg III 4.0, Leg IV 7.1, pedipalp length 2.3. Epigynum (Figs. 6, 7): Anterior depression deep and round, as wide as the transverse bar.

Male (syntype): Habitus as in Fig. 4. Total length 3.6. Cephalothorax 1.68 long, 1.25 wide, 0.47 high; color as in female. Sternum 0.87 long, 0.7 wide; color as in female. Abdomen 2.18 long, 1.19 wide, 0.95 high; pale gray covered with white-silvery spots; dorsum with two longitudinal white lines (Fig. 4). AME diameter 0.10. PME 0.08, ALE 0.06, PLE 0.07. AME separation 0.08, PME separation 0.09. AME-ALE separation 0.14. PME-PLE separation 0.13. Clypeus height 0.1. Chelicerae teeth and leg pigmentation as in female. Leg I length 9.2, Leg II 7.0, Leg III 3.1, Leg IV 5.6, pedipalp 2.1. Pedipalp as in Figs. 11–13.

Variation.—Female total length ranges from 4.8 (Mt. Kenya) to 6.3 (Kilimanjaro), cephalothorax length from 1.4 (Mt. Kenya) to 2.4 (Kilimanjaro) (n = 4). The epigynal caudal plate of the females from Kilimanjaro is narrow and only slightly notched (Fig. 7), while the caudal plate of the female from Mt. Kenya resembles that of *S. acoreensis* (Fig. 9). Male total length from 3.04–3.55, cephalothorax length from 1.68–1.90. The cymbial basal process can have four to six denticles and the number varies even within individuals.

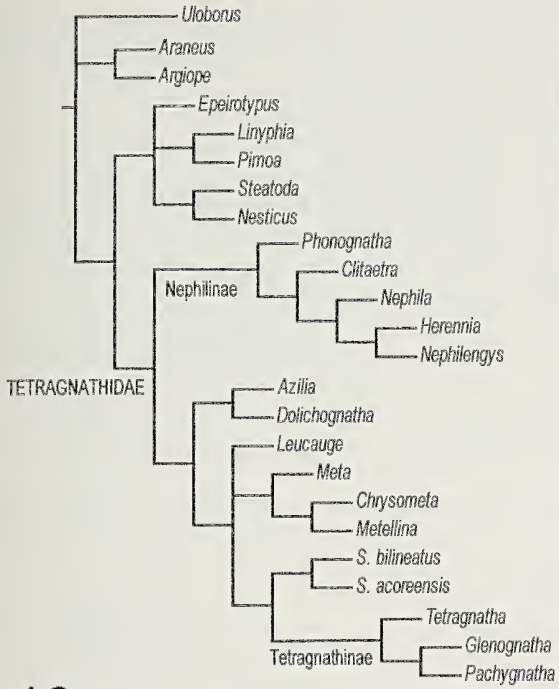
Distribution and ecology.—Known from the high altitude (3000 m) type locality on the southern slope of Mount Kilimanjaro, Tanzania and the unspecified locality on Mt. Kenya, Kenya (Fig. 15).

Sancus acoreensis (Wunderlich 1992)
NEW COMBINATION
Figs. 5, 8, 9, 14

Leucognatha acoreensis Wunderlich 1992: 360, figs. 315–326 (♂♀ description (from Azores); male and female paratypes deposited in USNM; examined); Platnick 2004.

Material examined.—A male and a female paratype of *Leucognatha acoreensis* Wunderlich, with no specific locality label (but see Distribution) was donated by J. Wunderlich, deposited in USNM. No additional material was available for examination.

Diagnosis.—Females of *S. acoreensis* differ from those of *bilineatus* by the smaller size (see variation), by the egg-shaped abdomen (Fig. 5), by the absence of longitudinal white lines on dorsum (Fig. 5), and by the epigynum with a small, poorly defined and weakly sclerotized anterior depression (Fig. 8). Males of *S. acoreensis* differ from those of *bilineatus* by the smaller size (see variation), the detail of the paracymbium, which has a pointed



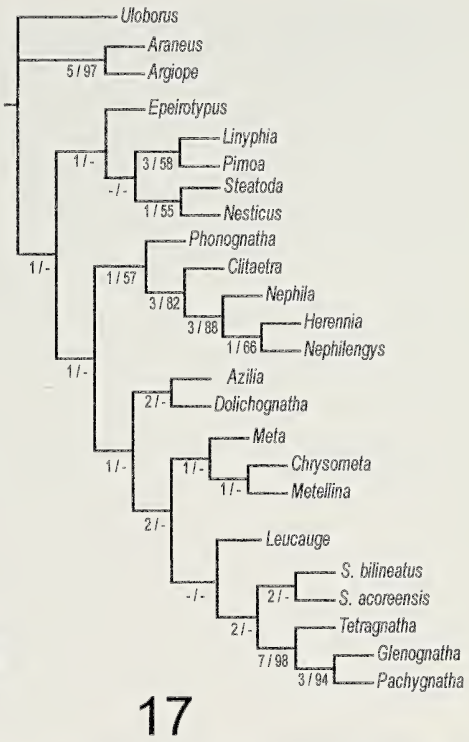


Figure 16.—Strict consensus of the six shortest cladograms (unweighted parsimony analysis). Family and subfamily names follow Hormiga et al. (1995). *Sancus bilineatus* and *S. acoreensis* form a clade sister to tetragnathines.

Figure 17.—Preferred tetragnathid phylogeny with *Sancus* (a single successively weighted cladogram identical to one of the six fundamental cladograms). Branch support values given as Bremer/bootstrap, reported for values 1 and more for Bremer and for 50% and more for bootstrap.

apophysis (Fig. 14) and the tibial length, which is 1.7 times as long as wide.

Description.—*Female (paratype):* Total length 3.9. Cephalothorax 1.56 long, 1.14 wide, 0.55 high; dark brown. Sternum 0.79 long, 0.78 wide; light brown, darker at margins. Abdomen 1.36 long, 1.66 wide, 1.7 high; dark gray covered with silver and golden spots (Fig. 5). AME diameter 0.10. PME 0.09, ALE 0.08, PLE 0.08. AME separation 0.10, PME separation 0.10. AME-ALE separation 0.08. PME-PLE separation 0.12. Clypeus height 0.10. Legs light brown. Leg I length 8.7, Leg II 7.0, Leg III 3.8, Leg IV 5.6, pedipalp length 1.9. Epigynum as in Figs. 8, 9: Anterior depression 0.8 times as wide as the transverse bar. Epigynal caudal plate wide and deeply notched (Fig. 9).

Male (paratype): Total length 2.98. Cephalothorax 1.29 long, 0.90 wide, 0.44 high; color as in *S. bilineatus*. Sternum 0.7 long, 0.64 wide; color as in female. Abdomen 1.72 long, 1.0 wide, 1.04 high; dark gray covered with silvery spots and two longitudinal white-golden lines. AME diameter 0.09. PME 0.07, ALE 0.07, PLE 0.08. AME separation 0.09, PME separation 0.1. AME-ALE separation 0.12. PME-PLE separation 0.11. Clypeus height 0.09. Cheliceral teeth and leg pigmentation as in female. Leg I length 8.7, Leg II 6.7, Leg III 3.4, Leg IV 5.4, pedipalp length 1.6. Pedipalp as in *S. bilineatus* except for the diagnostic characters (see above).

Variation (from Wunderlich 1992).—Female total length ranges from 3.8–4.3, cephalothorax length from 1.45–1.55. Male total length from 2.5–3.2, cephalothorax length from 1.2–1.5.

Distribution.—Azores (Fig. 15): São Miguel, Santa Maria, Fajal, Pico, Terceira, Flores (Wunderlich 1992).

Ecology.—In Azores the spiders live in

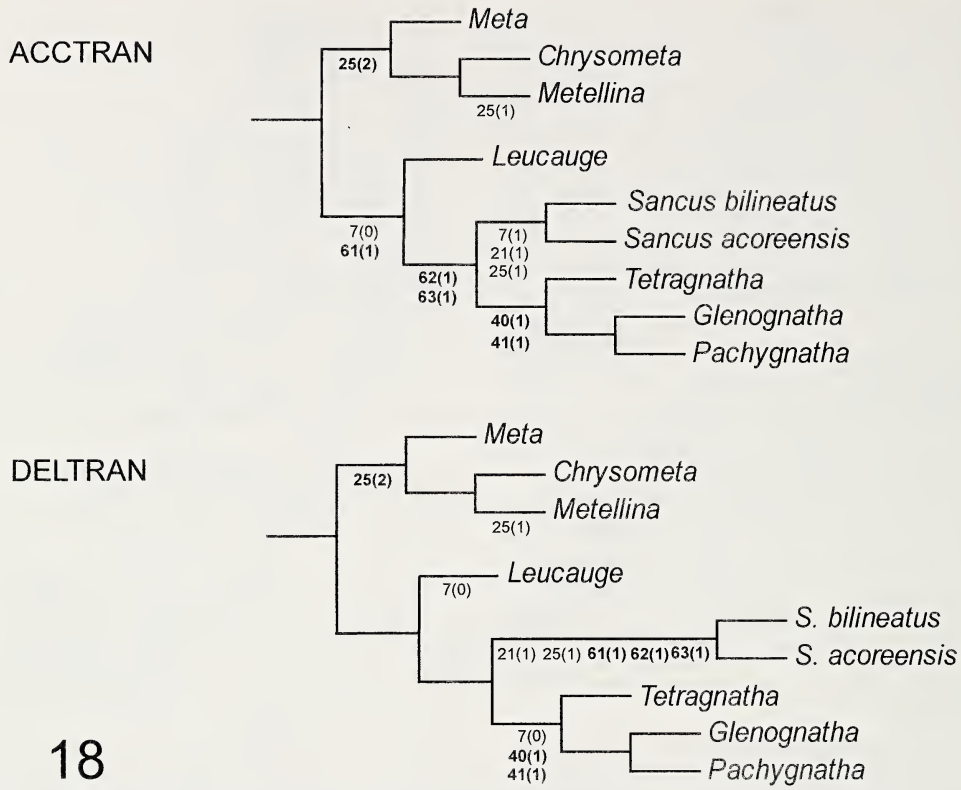


Figure 18.—Alternative optimizations of *Sancus* synapomorphies and other relevant characters and states (in parentheses) on the preferred phylogeny. Bolded are non-homoplasious characters. Delayed transformation (DELTRAN) is the preferred and more logical optimization (see text for details).

sunny to shaded upper vegetation layers near lakes (Wunderlich 1992:360). They were collected by beating vegetation and thus their webs are not known (Wunderlich in litt.).

PHYLOGENETICS

Heuristic searches in NONA produced two trees of minimal length under amb-, representing a subset of six minimal length trees in NONA under amb= and in PAUP. All minimal length topologies (length 136, CI = 0.56, RI = 0.72) have in common the placement of *Sancus* within Tetragnathidae, as well as the monophyly of *Sancus* and of Tetragnathidae. These results are congruent with those of Hormiga et al. (1995). Figure 16 shows the strict consensus of the six shortest trees. *Sancus* is recovered as sister to the tetragnathine clade (as defined by Hormiga *et al.* 1995) containing the genera *Tetragnatha* Latreille 1804, *Glenognatha* Simon 1887 and *Pachygnatha* Sundevall 1823. The six trees conflict in the placement of *Leucauge* White 1841, which is sister either to *Sancus* + tetragnathines (Fig. 17) or sister to *Meta* C.L. Koch 1836, *Metellina* Chamberlin & Ivie 1941 and *Chrysometa* Simon 1894, as well as in the position of *Epeirotypus* O. P.-Cambridge 1894 relative to the sheet-web builders. Successive weighting resulted in one stable topology after a single iteration, identical to one of the most parsimonious cladograms under equal weights (Fig. 17). Bremer support and bootstrap support values are mapped on this preferred phylogeny.

The diagnostic characters and synapomorphies (Fig. 18) of the genus *Sancus* (under DELTRAN optimization; see justification below) are the CBP apical denticles (61/1), the epigynal transverse bar (62/1) and the epigynal ventral depression (63/1). Another diagnostic character, lack of dorsal femoral trichobothria (7/1) serves as synapomorphy under ACCTRAN (Fig. 18). In addition, unambiguous synapomorphies of *Sancus* (homoplasious on the cladogram) are mesal cymbium

orientation (21/1) and procurved CBP (25/1) (see Character analysis).

DISCUSSION

Monotypic genera are problematic because they contain no grouping information and therefore are not phylogenetic hypotheses (Zujko-Miller 1999). Platnick (1976, 1977) also argued that monophyly cannot apply to monotypic genera. In some cases, taxonomists have no choice but to retain monotypic genera (e.g. Kuntner 2002), for example if the sister species or clade is unknown or unresolved. By synonymizing *Leucognatha* with *Sancus* we rid tetragnathid systematics of two monotypic genera.

Alternative optimizations and synapomorphies.—Delayed transformation (DELTRAN) optimizes three out of four diagnostic *Sancus* characters as synapomorphies for the genus (Fig. 18). The accelerated transformation alternative (ACCTRAN) optimizes the CBP denticles (character 61) as a synapomorphy for *Leucauge* + (*Sancus* + tetragnathines) (Fig. 18). However, the CBP itself (character 25) is primitively absent at this node. Since the CBP denticles are an attribute of the CBP, any optimization in which the denticles arise before the process is illogical, an artifact resulting from the inapplicable coding of the CBP denticles (character 61) in *Leucauge* and tetragnathines, which lack the CBP. Since the presence of the CBP is an unambiguous synapomorphy of *Sancus*, the DELTRAN alternative is more reasonable, implying the evolution of the CBP denticles (along with the CBP) in the common ancestor of *Sancus*.

ACCTRAN optimizes the two new epigynal characters (62, 63) as synapomorphies of *Sancus* + Tetragnathinae. However, tetragnathines are haplogyne, meaning they lack the epigynum (40/1) and fertilization ducts (41/1), both unambiguous synapomorphies of the clade (Fig. 18). Thus, for tetragnathines, the two new epigynal characters are inapplicable. The ACCTRAN optimization implicitly assumes tetragnathine ancestor had the *Sancus* epigynal characters but lost them (along with the epigynum itself), an unwarranted presumption. In this case, DELTRAN is a simpler explanation of the data.

The presence of dorsal femoral trichobothria (character 7/0) served as a synapomorphy for *Leucauge* + tetragnathines in Hormiga et al. (1995). In this analysis the optimization of this homoplasious character is ambiguous (Fig. 18). ACCTRAN resolves the presence of trichobothria as a synapomorphy for *Leucauge* + (*Sancus* + tetragnathines) and the absence as a synapomorphy of *Sancus*. On the other hand, DELTRAN favors two separate origins (Fig. 18) and thus implies that trichobothria in *Leucauge* may not be homologous to the ones in tetragnathines.

Phylogenetic placement with comments on tetragnathid relationships.—This paper establishes the phylogenetic placement of *Sancus*, not new phylogenetic relationships of the tetragnathid genera. The preferred phylogeny (Fig. 17) agrees with the phylogeny found by Hormiga et al. (1995), and *Sancus* groups with tetragnathines. Of course, we basically re-ran the Hormiga et al. (1995) data, so such congruence is not surprising, even though we think some homology statements should be reassessed. We will present these new hypotheses in future papers on nephiline and metine systematics.

Three unambiguous synapomorphies support the group *Sancus* + Tetragnathinae: 1) long and finger-like paracymbium (Figs. 11–14); 2) presence of an anterior paracymbial apophysis (Figs. 13, 14); 3) spiraled reservoir course (homoplasious). One unambiguous but weak synapomorphy supports *Leucauge* + (*Sancus* + tetragnathines): posterior gut caeca (character 11 of Hormiga et al. 1995), but we did not score the feature for *Sancus* because specimens are too rare to dissect.

The tetragnathid phylogeny, as currently understood (Fig. 17), must be considered preliminary and interpreted cautiously. Hormiga et al. (1995) did not present branch support statistics, but most nodes are poorly supported (Fig. 17; Bremer = 1, bootstrap < 50%). Bootstrapping collapsed 11 out of 20 nodes and tetragnathid monophyly collapsed. Nephilinae, especially distal nephilines (*Clitaetra* (*Nephila* (*Herennia* + *Nephilengys*), and Tetragnathinae are well supported (also in Hormiga et al. 1995). On the other hand, current work disputes the placement of the nephiline clade as tetragnathids (Kuntner 2003; Kuntner 2005, 2006a & b) and some genera, traditionally classified as nephilines, have been transferred to Araneidae (Kuntner 2002; Kuntner & Hormiga 2002).

Wunderlich (1992:359) placed *Leucognatha*

(= *Sancus*) in Leucauginae, but did not provide synapomorphies for the subfamily. All *Leucauge* species possess characteristic rows of fourth femoral trichobothria (Levi 1980: figs. 50, 51, 67). Similar condition can be found in tetragnathid genera *Opadometa* Archer 1951, *Tylorida* Simon 1894, *Mesida* Kulczynski 1911 and *Orsinome* Thorell 1890 (none of them placed phylogenetically), but not in *Sancus*. Femoral trichobothria of tetragnathines, though present, are not in rows and may not be homologous to the *Leucauge* condition (Fig. 18; see above). We will test and discuss homology of femoral trichobothria in *Leucauge* and tetragnathines and possible monophyly of 'leucaugines' and 'metines' elsewhere.

Behavior.—*Sancus* behavior and web architecture are unknown. Our prediction based on the phylogenetic outcome is that *Sancus* builds orb webs with an open hub and few radii, which are more horizontal than vertical. *Leucauge* and most *Tetragnatha* species build such webs (e.g. Levi 1980; own data). *Sancus acoreensis* was collected adjacent to bodies of water (Wunderlich 1992), which is typical for *Tetragnatha*.

Biogeography.—*Sancus* is now known from the Azores in the Atlantic Ocean and two mountain peaks (Kilimanjaro and Mt. Kenya) in equatorial eastern Africa (Fig. 15). The two areas are more than 7,500 km apart, in very different climatic regimes, latitudes and elevations, and are habitat islands. The Azores are 1,370 km from Europe and 1,530 km from Africa. The type series of *S. bilineatus* says 3,000 m on Kilimanjaro; the other collection simply says Mt. Kenya. We are not aware of any other comparable taxon distribution.

This unusual distribution is probably an undersampling artifact. However, we tried but failed to find more *Sancus* material in African collections. *Sancus* (= *Leucognatha*) is apparently also absent from Madeira and the Canary Islands (Wunderlich 1992: 359; see also Fig. 15), which lie between the Azores and the mainland Africa; nor does the genus occur in the Mediterranean.

If not artifactual, the distribution might be explained either by extinction of *Sancus* in intervening Africa or dispersal and divergence into the two clearly diagnosable species we see today. An undiscovered African population of *S. acoreensis* might also exist and have been introduced to the Azores. We expect more records of *Sancus* in the future from Africa, Macaronesia, and perhaps from the Mediterranean, and hope this paper will facilitate such discoveries.

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THREE NEW SPECIES OF *PHOLCUS* (ARANEAE, PHOLCIDAE) FROM THE CANARY ISLANDS WITH NOTES ON THE GENUS *PHOLCUS* IN THE ARCHIPELAGO

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ABSTRACT. Over the last decade, numerous papers focusing on the fauna of the Canary Islands have reported that many spectacular species radiations have taken place, leading to a very high level of endemicity in this archipelago. The species of the genus *Pholcus* are a very good example of such a fascinating process. The Canary Islands harbor the highest number of endemic species of this genus. Therefore, in order to obtain a detailed picture of the diversity and the phylogeny of the Canarian *Pholcus*, a complete taxonomic revision is required. The present work is the second contribution to achieve this goal. Three new species of *Pholcus* are described: *Pholcus bimbache*, *P. anachoreta* and *P. corniger*. The first endemic species of *Pholcus* from El Hierro (*P. bimbache*) is reported; *P. anachoreta* is the only *Pholcus* species found on the Montaña Clara Islet; and *P. corniger* is the second and most troglomorphic species known from Tenerife.

Keywords: Araneae, Pholcidae, *Pholcus* new species, taxonomy, Canary Islands

The Canary Islands are situated about 100 km off the northwestern coast of Africa. This volcanic archipelago was formed during various volcanic episodes and is nowadays composed of seven main islands and several islets. All of them are situated almost on a straight line with an east-west orientation, with the age of the islands decreasing towards the east. The estimated ages of the islands are: Fuerteventura 20–22 My, Lanzarote 15–19 My, Gran Canaria 14–16 My, Tenerife 11.6–14 My, La Gomera 10–12 My, La Palma 1.6–2 My and El Hierro 0.8–1 My (Anguita & Hernán 1975; Ancochea et al. 1990; Coello et al. 1992).

The older islands, Fuerteventura and Lanzarote, are lower in elevation due to the effects of erosion. As a result of their low height they receive less moisture from the northeast trade winds than the other, higher islands. This, and the proximity of the Sahara Desert, renders them the driest islands in the archipelago, with most of their habitats being dry lowlands. The remainder of the Canary Islands have higher mountains, reaching an elevation of 3717 m (Teide, Tenerife). This high elevation combined with the trade winds (humid from the northeast and dry from the northwest), causes a thermic inversion that forms a cloud belt between 600 and 1000 m. These clouds are almost permanent on the northern slopes, favoring the growth of a characteristic subtropical forest named laurel forest.

Differences in humidity and elevation between and within islands are the main reasons for the development of a large variety of habitats. The so-called hypogean environment also contributes to changes in the diversity of habitats. In the case of the Canaries it is formed by lava tubes and the MSS (mesocavernous shallow stratum) (Oromí et al. 1986; Medina 1991). This high diversity of ecological niches and the initial emptiness of habitats provide the best conditions for species radiations.

The spider genus *Pholcus* Walckenaer 1805 is a good example of this process. The 114 species that it comprises are distributed almost all around the world. However, it is interesting to note that there are no indigenous *Pholcus* species in Central and South America and only a few are known from North America.

Before the present study, eighteen species of *Pholcus* had been reported from the Canary

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Islands. This represents more than 15% of the total number of species of this genus. If we add to them the five species from Madeira (another Macaronesian island), this ratio reaches more than 19%. At the same time, the area of these islands represents an extremely small part of the total area of the generic distribution, providing clear evidence of a species radiation on the Canary Islands.

Apart from the cosmopolitan *P. phalangioides* (Fuesslin 1775), the remaining species of *Pholcus* recorded from the Canary Islands are endemic to this archipelago. Two of them have been collected from more than one island: *P. ornatus* Böesenberg 1895 has the broadest distribution, occurring on all the islands except Lanzarote and Fuerteventura; and *P. fuerteventurensis* Wunderlich 1991 is found on Fuerteventura and Gran Canaria. *Pholcus knoeseli* Wunderlich 1991, *P. malpaisensis* Wunderlich 1991, *P. mascaensis* Wunderlich 1987, *P. baldiosensis* Wunderlich 1991, *P. roquensis* Wunderlich 1991, *P. intricatus* Dimitrov & Ribera 2003 and *P. tenerifensis* Wunderlich 1987 are endemic to the island of Tenerife. *Pholcus multidentatus* Wunderlich 1987, *P. calcar* Wunderlich 1987, *P. corcho* Wunderlich 1987, *P. edentatus* Campos & Wunderlich 1995 and *P. helenae* Wunderlich 1987 are known only from the island of Gran Canaria, while *P. gomerae* Wunderlich 1980, *P. gomeroides* Wunderlich 1987 and *P. sveni* Wunderlich 1987 are endemic to La Gomera.

In the present work, three new endemic species of *Pholcus* are described. *Pholcus bimbache* is the first endemic *Phoclus* species from El Hierro; *P. anachoreta* is endemic to the Montaña Clara islet and *P. corniger* is the second and most troglomorphic species of this genus known from this archipelago. With these three new species the number of Canarian endemic species of *Pholcus* reaches twenty, eighteen of which are mono-insular endemics, indicating that the genus has a higher diversity in the Canary Islands than previously suspected.

Pholcus corniger is the most troglomorphic species of *Pholcus* known from the Canaries. While in *P. baldiosensis*, the other troglomorphic species, the reduction of the eyes is incomplete, in *P. corniger* they are totally absent. This species, unfortunately, may be extinct due to the destruction of its habitat in Cueva de San Miguel, where residual waters are thrown out of houses nearby. This seems to be still a common practice in the Canaries, affecting numerous volcanic tubes and small caves. Estimating how many species suffer from this particular activity and how many are brought to extinction will be a difficult task. Taking into account the high vulnerability of both cave faunas and island ecosystems, Canarian authorities and the Spanish government should implement more active and efficient measures to eliminate these type of activities.

METHODS

Specimens were examined under a Wild Heerbrugg (12–100X) stereomicroscope. The female vulva was removed and treated with 50% solution of lactic acid in order to render the remaining soft tissues transparent. After observation and drawing the vulva were washed in distilled water and stored in 70% ethyl alcohol. All measurements are in millimeters. The total body length is the sum of the prosoma and the opisthosoma omitting the pedicel. The specimens are deposited in the Departament de Biologia Animal, Universitat de Barcelona (CCRUB). The numbers of the collection are given in brackets.

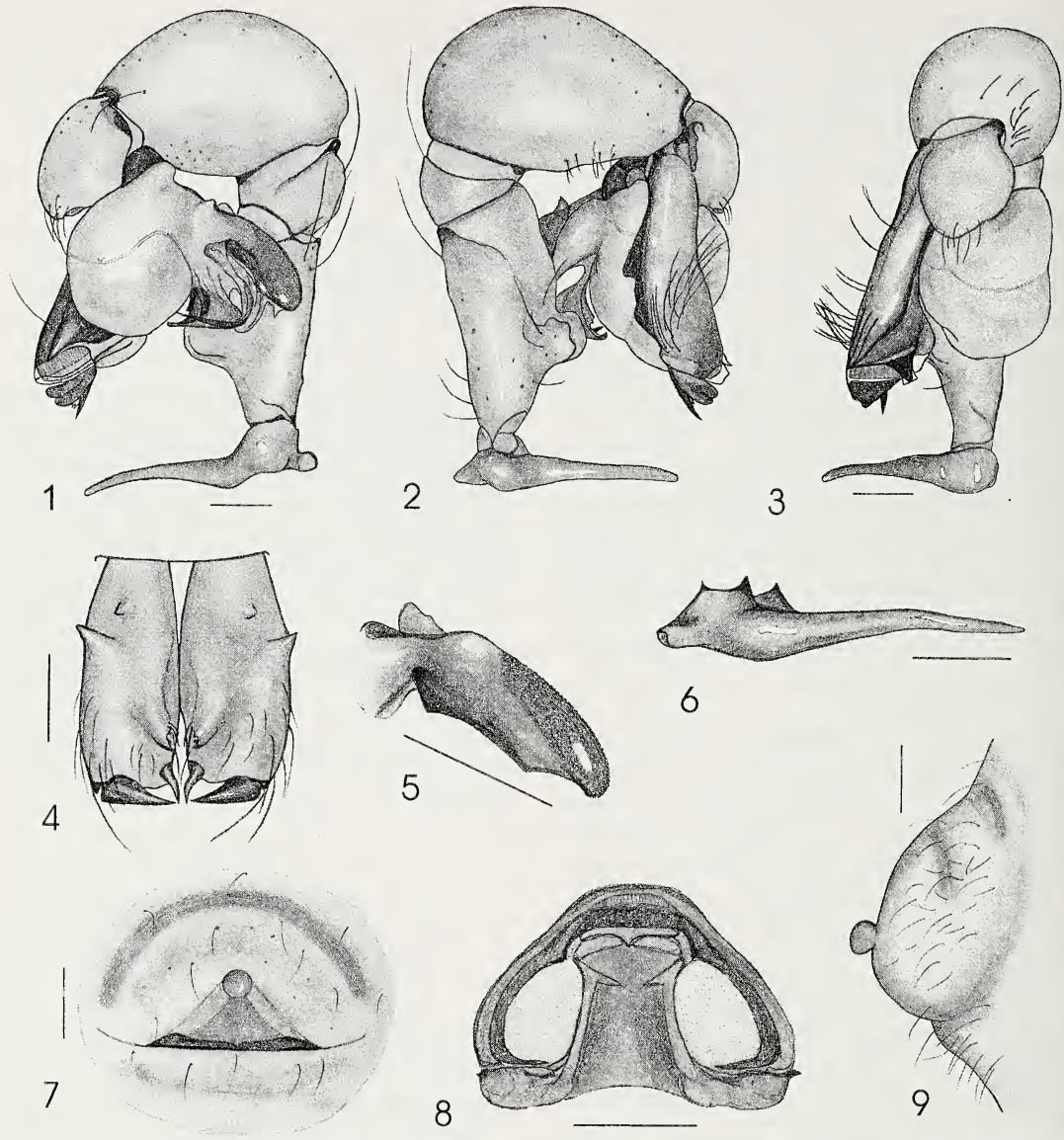
TAXONOMY

Family Pholcidae C.L. Koch 1851
Genus *Pholcus* Walckenaer 1805
Pholcus bimbache new species
Figs. 1–9

Material examined.—Holotype male, Cueva del Juaclo de las Moleras, Frontera, El Hierro, Canary Islands, 27°43′N, 18°08′W, 7 November 1991, C. Ribera (CCRUB 3523–140). Paratypes: Canary Islands: 1 female, same locality and date as holotype, C. Ribera (CCRUB 3524–140) (drawings and description of the female are based on this specimen); 1 male, 2 females and 8 juveniles (CCRUB 3522, 3525 to 3527–140) same locality and date as holotype; 1 male and 1 juvenile, same locality, 4 February 2000, N. Mercader & E. Muñoz (CCRUB 4505–170).

Etymology.—The species is named after the original inhabitants of El Hierro island, the so-called "Bimbaches".

Diagnosis.—*Pholcus bimbache* can be distinguished from similar Canarian species (*P. sveni* and *P. gomerae*) by the less pronounced callosity of the procursus, the narrower base



Figures 1–9.—*Pholcus bimbache* new species: 1. Male palp, prolateral view; 2. Male palp, retrolateral view; 3. Male palp, frontal view; 4. Male chelicerae; 5. Uncus; 6. Trochanter of the male palp; 7. Epigynum, ventral view; 8. Vulva, dorsal view; 9. Epigynum, lateral view. Scale 0.2 mm.

of the uncus (Fig. 5), the longer claw-shaped apophysis of the appendix and the long, almost straight trochanteral apophysis (Fig. 6) of the male palp (Figs. 1–3); also, by the shape of the apophyses of the male chelicerae (Fig. 4). The diagnostic characters of the female are the shape of the epigynum and the large oval pore plates of the vulva (Figs. 7–9).

Description.—*Male (holotype):* Prosoma yellowish with well marked cephalothoracic junction and fovea. Ocular area elevated. Thorax with brown marking, wider than long, which starts at the fovea and extends to the posterior margin of the prosoma. It has three lighter zones dividing it into four darker radial lobes. Sternum brown-yellowish with borders slightly darker brown. Distance between AME equal to their diameter. Distance AME-ALE slightly more than two times the diameter of AME; AME-PME three times the diameter of AME. Anterior eye line frontal view slightly

recurved. Posterior eye line dorsal view recurved. Clypeus high with yellowish color. Chelicerae (Fig. 4) yellow-brownish; cheliceral apophyses brownish with cylindrical shape finishing with small darker outgrowths; upper margin of the proximolateral apophyses does not reach the lower margin of the frontal prominence. A few dark bristles are placed near the base of the cheliceral apophyses. Palps (Figs. 1–3) with yellow-brownish color, trochanter with long retrolateral apophysis (Fig. 6), femur large with ventral bulge, procursus with dark process of the apical apophysis. Opisthosoma elongated, almost cylindrical, whitish with small darker transversal zone in the genital area.

Female (paratype): All characters as in male except: less elevated ocular area, distance between AME slightly less than their diameter, distance AME-ALE slightly less than two times the diameter of the AME, AME-PME two and half times the diameter of the AME. Chelicerae without apophyses. Genital zone without pigmentation except the sclerotized zone of the epigynum. By transparence some parts of the vulva can be observed. Epigynum and vulva as in (Figs. 7–9).

Measurements.—*Male (holotype):* Prosoma 1.2 (1.2) wide, 1.3 (1.3) long; opisthosoma 1.1 (1.5) wide and 2.5 (3.0) long. Total body length 3.8 (4.3). Legs: I, femur 8.7(9.2), patella 0.5(0.5), tibia 8.1(9.5), metatarsus 13.2(14.3), tarsus 2.0(2.2), total 32.5(37.5); II 6.5(7.0), 0.5(0.5), 6.0(6.5), 9.0(8.5), 1.3(1.5), 23.3(24.0); III 5.0(5.0), 0.5(0.5), 4.0(4.2), 6.2(7.0), 1.0(1.0), 16.7(17.7); IV 6.3(7.0), 0.5(0.5), 5.8(6.2), 8.0(9.0), 1.2(1.1) 21.8(23.9). In brackets male paratype no. 3522–140. Palp: femur 0.60, patella 0.18, tibia 0.50, tarsus 0.20, total 1.48. Procursus 0.8.

Female: Prosoma 1.3 wide, 1.2 long; opisthosoma 1.5 wide, 3.5 long; total body length 4.7. Legs: I, femur 9.0, patella 0.7, tibia 8.2, metatarus 14.0, tarsus 1.2, total 33.1; II 6.5, 0.7, 8.6, 9.2, 1.2, 23.6; III 5.0, 0.7, 4.5, 6.5, 1.0, 17.7; IV 7.0, 0.7, 5.0, 9.0, 1.2, 22.9. Palp femur 0.40, patella 0.14, tibia 0.19, tarsus 0.3, total 1.03.

Distribution.—This species is endemic to El Hierro, and is only known from the type locality.

Remarks.—*Pholcus bimbache* appears to be related to members of the so-called Tenerifensis group (Wunderlich 1987, 1991; Dimitrov & Ribera 2003) composed of ten species (seven in Tenerife and three in Gomera). Here we should note that the term "Tenerifensis group" is used as merely descriptive and does not imply any phylogenetic relationship. All these species are characterized by the claw–shaped apophysis of the appendix, and by the shape of both the uncus and the lamella of the procursus. *Pholcus sveni* Wunderlich 1987 is the most similar species. *Pholcus bimbache* can be distinguished from it by the longer and more curved claw–shaped apophysis, the shape of the procursus and the morphology of both the epigynum and the vulva. The presence of this species on El Hierro Island emphasizes the close faunistic relationships between Tenerife, La Gomera and El Hierro.

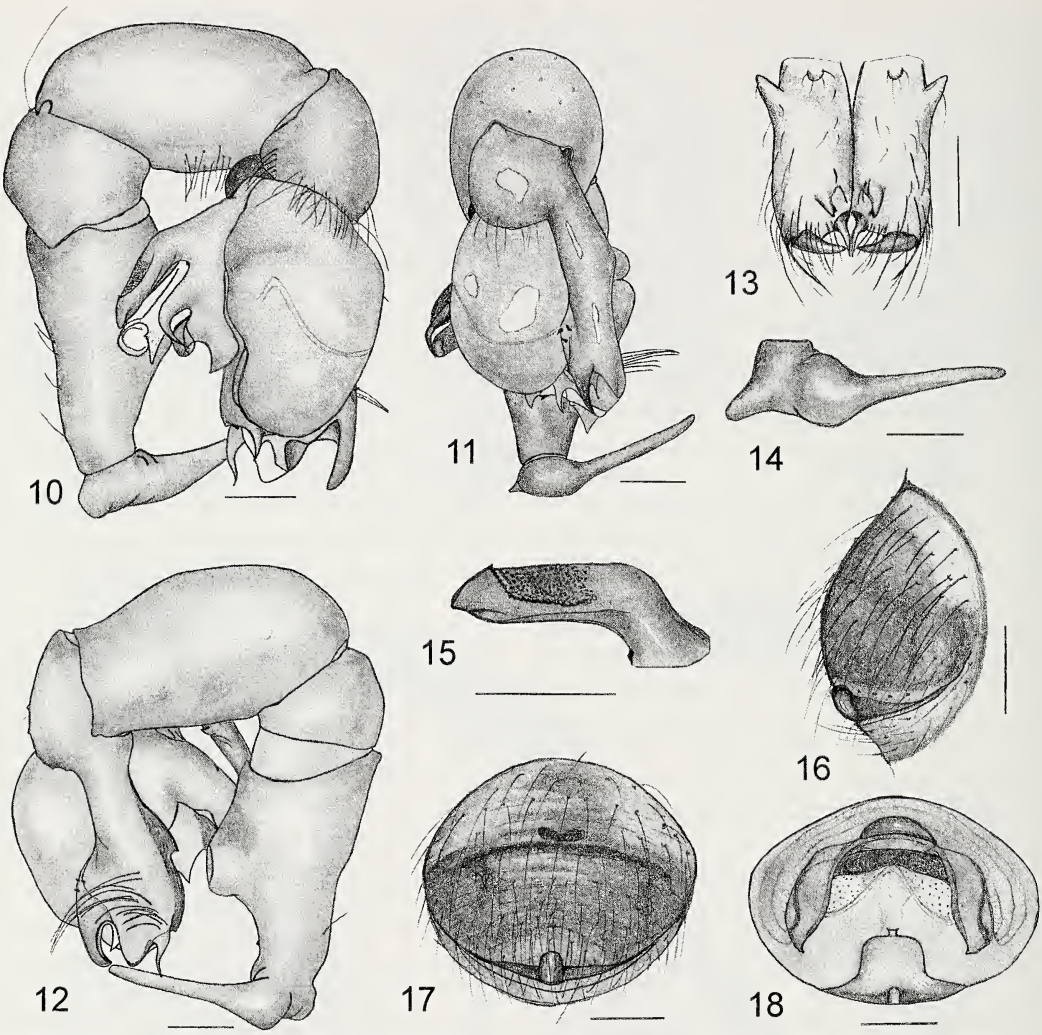
Pholcus anachoreta new species
Figs. 10–18

Material examined.—Holotype male, Montaña Clara islet, Canary Islands, 29°18′N, 13°31′W, 24 April 1994, C. Ribera (CCRUB 2459–99). Paratypes: Canary Islands: 1 male, 1 female, same locality, 23–27 November 2002, A.J. Pérez (CCRUB 4502, 4503–170); 1 juvenile, from the same locality, 27 January 2002, P. Oromí (CCRUB 4504–170).

Etymology.—The name comes from the Greek word "anachoretes" meaning person who lives in a lonely place dedicated to contemplation. This word was adopted in the Latin as anachoreta–ae keeping the male gender. Named after the remoteness and isolation of the type locality.

Diagnosis.—*Pholcus anachoreta* is easily distinguished from canarian congeners by the serrated keel of the uncus (Fig. 15), the morphology of the apex of the procursus (number and shape of the apophyses and lamellas) and the cheliceral apophyses (Fig. 13). The female can be distinguished from the most similar canarian species (*P. fuerteventurensis* and *P. edentatus*) by the lower sclerotized plate of the epigynum (Figs. 16, 17) and the more arced ridges of the valve (Fig. 18).

Description.—*Male (holotype):* Prosoma whitish without a clearly marked fovea and practically indistinguishable cephalothoracic junction. The prosoma does not carry hairs except for its borders and the intraocular area. Ocular area elevated. Sternum with a whitish coloring. Clypeus high and whitish. Chelic-



Figures 10–18.—*Pholcus anachoreta* new species: 10. Male palp, prolateral view; 11. Male palp, frontal view; 12. Male palp, retrolateral view; 13. Male chelicerae; 14. Trochanter of the male palp; 15. Uncus; 16. Epigynum, lateral view; 17. Epigynum, ventral view; 18. Vulva, dorsal view. Scale bar 0.2 mm.

erae (Fig. 13) whitish; cheliceral apophyses darker with conical shape and group of 2–3 thick bristles placed near the base. The proximolateral apophyses (proximal teeth) and the frontal prominence show the same coloring as the rest of the chelicerae. The upper margin of the proximolateral apophyses is higher than the lower margin of the frontal prominence. Distance between AME less than their diameter. The rest of the eyes situated in two elevated triads. AME around 50% of the size of the other eyes. Anterior eye line frontal view slightly recurved. Posterior eye line dorsal view recurved. Palps as in Figs. 10–12. Trochanter (Fig. 14) with long curved retrolateral apophysis, femur with ventral bulge, procursus very complex with many apical lamellae and with three distal dorsal spines. Uncus (Fig. 15) very characteristic with serrated keel. Opisthosoma elongated and cylindrical with whitish color, dorsally darker. A longitudinal zone with darker pigmentation starting from the genital area and followed by two tear-shaped spots is observed ventrally.

Female (paratype): Prosoma: all characters as in male except for the cheliceral apophyses, which are absent. Sizes and distribution of the eyes as in the male but the elevation of the

ocular area is less conspicuous. Opisthosoma cylindrical with yellowish coloring. The genital zone is darker, with brownish pigmentation. Dorsally with two parallel lines of dark spots. The whole opisthosoma is covered with short and regularly distributed hairs. Epigynum and vulva as in Figs. 16–18.

Measurements.—*Male (type):* Prosoma 1.2 wide, 1.0 long; opisthosoma 1.0 wide, 3.1 long; total body length 4.1. Legs: I, femur 9.5, patella 0.4, tibia 12.0, metatarsus 16.0, tarsus 2.0, total 39.9; II 6.2, 0.4, 6.0, 10.0, 1.0, 23.6; III 5.0, 0.4, 4.2, 7.0, 1.0, 17.6; IV 7.0, 0.4, 6.0, 6.5, 0.8, 20.7. Palp femur 0.8, patella 0.2, tibia 0.7, tarsus 0.3, total 2.0. Procursus 0.75

Female: Prosoma 1.9 wide, 1.5 long; opisthosoma 1.8 wide, 4.0 long; total body length 5.5. Legs: I, femur 8.3, patella 0.5, tibia 8.0, metatarsus 12.9, tarsus 1.9, total 31.6; II 6.4, 0.5, 5.6, 9.6, 1.5, 23.6; III 4.9, 0.5, 4.9, 7.3, 0.9, 18.5; IV 6.8, 0.5, 5.6, 8.8, 1.7, 23.4. Palp femur 0.34, patella 0.10, tibia 0.24, tarsus 0.24, total 0.92.

Distribution.—This species appears to be endemic to Montaña Clara and is known only from type locality, although it might occur in the neighboring islets of Graciosa and Alegranza and in Lanzarote island considering their geographical vicinity.

Remarks.—The structure of the procursus of this species is similar to that of *P. edentatus* Campos & Wunderlich 1995 and *P. fuerteventurensis* Wunderlich 1992. Similar finger-like lamellae in the procursus allow the three species to be distinguished from the rest of the Canarian *Pholcus*. Despite of this remarkable similarity the procursus and the uncus are very different and therefore very useful for specific identification.

Pholcus corniger new species
Figs. 19–32

Material examined.—Holotype male, Cueva de San Miguel, San Miguel de Abona, Tenerife, Canary Islands, 28°06′N, 16°36′W, 1 January 1991, P. Oromi (CCRUB 4500–170). Paratype: Canary Islands: 1 female from the same locality, 1 January 1991, P. Oromi (CCRUB 4501–170).

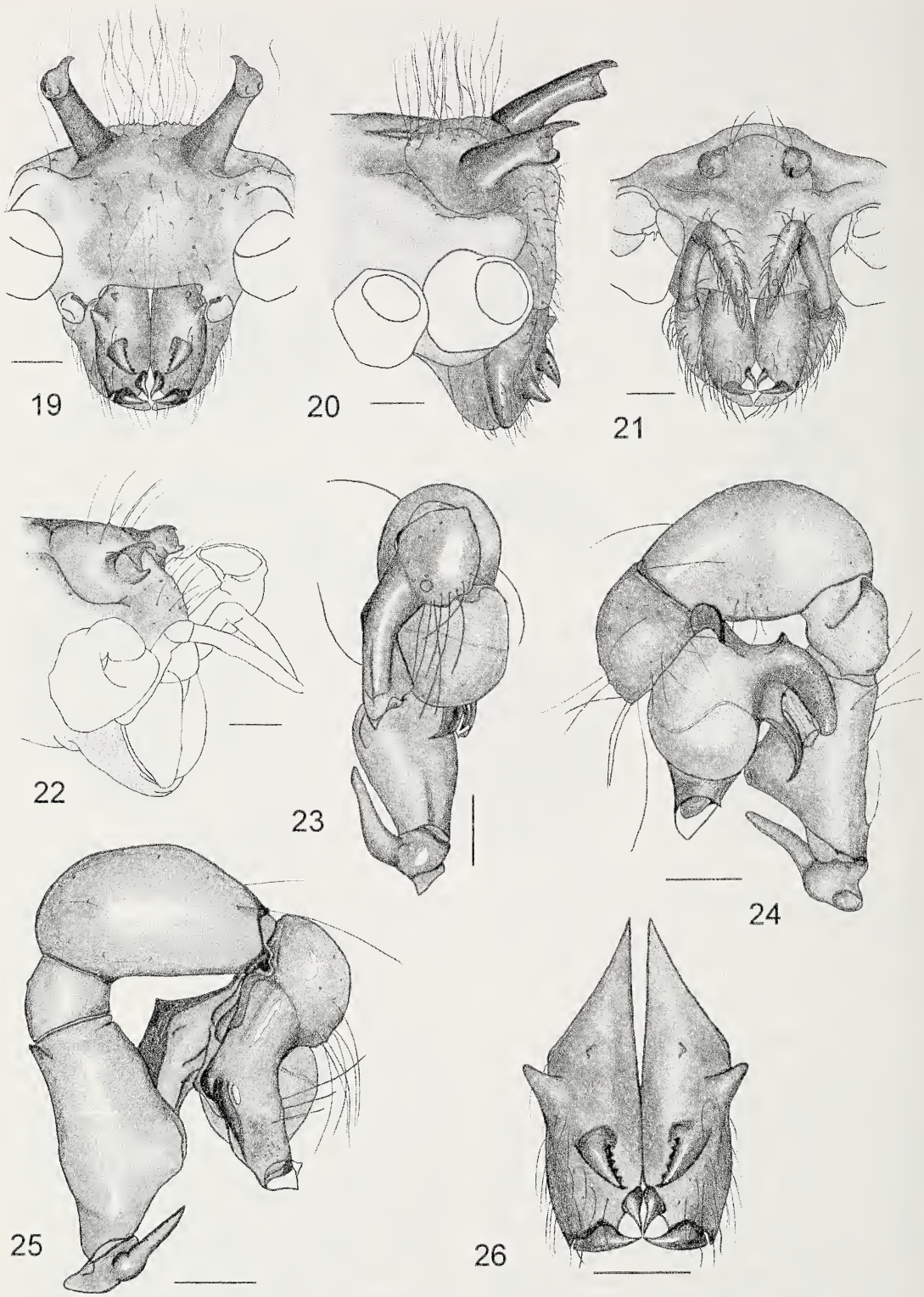
Etymology.—The specific name refers to the shape of the elevated ocular area reminding horns. The word "corniger" in Latin means "with horns".

Diagnosis.—*Pholcus corniger* can be easily distinguished from the rest of canarian *Pholcus* species by the simplified structure of the procursus with single membranous lamella on its apex, the presence of six teeth and the absence of basal bristles on the cheliceral apophyses (Fig. 26). The female is differentiated by the elevated conically shaped epigynum (Figs. 27–29). This species can be easily distinguished by the total reduction of the eyes (both in male and female) and the shape of the elevated ocular area that reminds horns (Figs. 19–22).

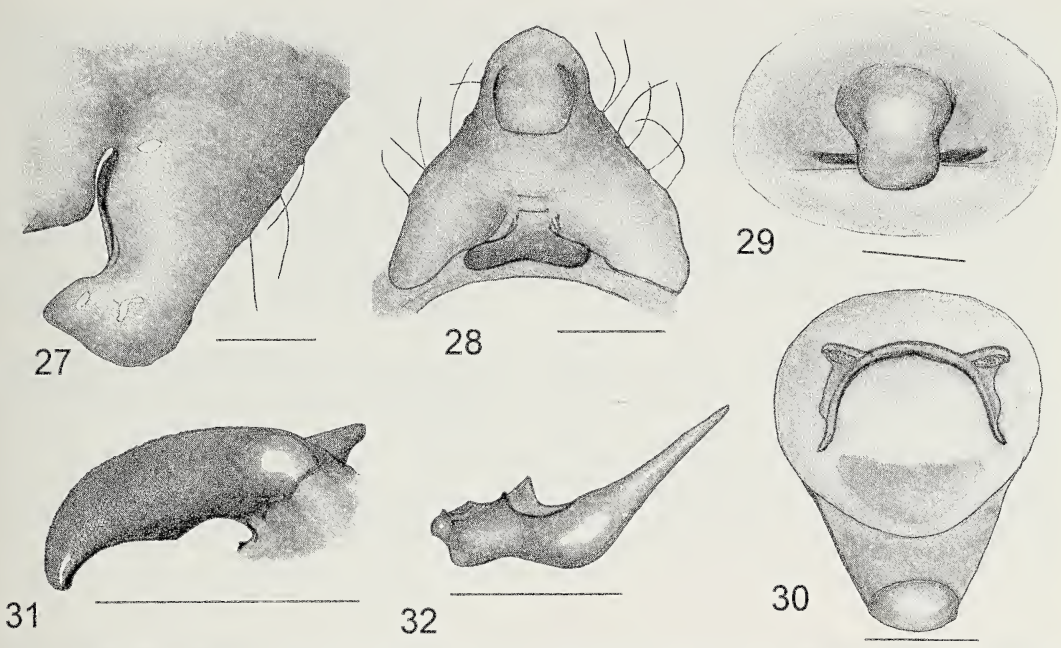
Description.—*Male (holotype):* Prosoma with an ochre-yellow coloring and well-marked fovea and cephalic furrow. Eye area elevated with characteristic shape and brown coloring (Figs. 19–20), with group of hairs between the ocular elevations. Clypeus high, yellowish with brownish spot in the center and almost transparent at the edges. Sternum yellowish. Chelicerae yellow-brownish, with brown apophyses carrying six dark brown teeth without bristles at the base (Fig. 26). Frontal prominence small. The upper margin of the proximolateral apophyses roughly reaching the lower margin of the frontal prominence. Eyes completely missing. Palps as in Figs. 23–25. Uncus as in Fig. 31. Trochanter (Fig. 32) with retrolateral apophysis, femur with ventral bulge. The procursus is very characteristic, conspicuously different from those of the remaining species of Canarian *Pholcus*. While in all the other species the apical part of the procursus is very complex and carries one or various apophyses and lamellar processes, in *P corniger* it is much simpler and ends with a single membranous lamella. This lamella extends along all the apex of the procursus. Opisthosoma cylindrical with pale yellowish color.

Female (paratype): Like the male, although the elevations of the ocular area are much smaller and colored like the rest of the prosoma (Figs. 21, 22). Prosoma lighter. Clypeus almost transparent. The genital area is not pigmented except for the sclerotized parts of the epigynum. Epigynum and vulva as in Figs. 27–30. As in the male, eyes are absent.

Measurements.—*Male (holotype):* Prosoma 1.1 wide and 1.0 long; opisthosoma 1.0 wide and 2.5 long. Total body length 3.5. Legs: I, femur 7.0, patella 0.3, tibia 7.0, metatarsus 11.5, tarsus 1.3, total 27.1; II 5.5, 0.3, 5.2, 8.0, 1.2, 20.2; III 4.0, 0.3, 3.9, 5.3, 1.0,



Figures 19–26.—*Pholcus corniger* new species: 19. Male prosoma, frontal view; 20. Male prosoma, lateral view; 21. Female prosoma, frontal view; 22. Female prosoma, lateral view; 23. Male palp, frontal view; 24. Male palp, prolateral view; 25. Male palp, retrolateral view; 26. Male chelicerae. Scale bar 0.2 mm.



Figures 27–32.—*Pholcus corniger* new species: 27. Epigynum, lateral view; 28. Epigynum, caudal view; 29. Epigynum, ventral view; 30. Vulva, dorsal view; 31. Uncus; 32. Trochanter of the male palp. Scale bar 0.2 mm.

14.5; IV 6.5, 0.3, 5.0, 7.0, 1.0, 19.8. Palp femur 0.50, patella 0.10, tibia 0.50, tarsus 0.28, total 1.38. Procursus 0.4

Female: Prosoma 1.1 wide, 1.0 long; opisthosoma 1.1 wide, 2,2 long; total body length 3.2. Legs: I, femur 7.0, patella 0.3, tibia 6.5, metatarsus 11.0, tarsus 1.8, total 26.6; II 6.2, 0.3, 5.0, 7.2, 1.1, 19.8; III 4.0, 0.3, 3.8, 5.0, 0.8, 13.9; IV 6.0, 0.3, 5.0, 7.0, 1.0, 19.3. Palp femur 0.24, patella 0.07, tibia 0.19, tarsus 0.30, total 0.80.

Distribution.—Endemic to the island of Tenerife, only known from the type locality.

Remarks.—Determining the closest relatives is difficult for this species. Taking into account the shape of the uncus, this species can be associated to the Tenerifensis group (see above). On the other hand, though, the epigynum of the female is very different from those of the Tenerifensis group, and it looks more similar to that of *P. baldiosensis* Wunderlich 1992 (the other troglomorphic species). Unfortunately, we cannot determine whether the male of *P. baldiosensis* is in fact similar to the Tenerifensis group since it still remains unknown.

Taking in account the characteristic features of the epigynum and the procursus, which are remarkably different from those of the other Canarian *Pholcus* species, *P. corniger* could possibly be a member of a different group, or it could form a subgroup (with *P. baldiosensis*) of the Tenerifensis group. In order to yield an answer to this question, a detailed phylogenetic study must be performed.

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A NEW SPECIES OF *CUPIENNIUS* (ARANEAE, CTENIDAE) COEXISTING WITH *CUPIENNIUS SALEI* IN A MEXICAN MANGROVE FOREST

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ABSTRACT. The new species *Cupiennius chapanensis* is described from a mangrove forest in the coastal regions of Chiapas, México. The most noticeable characteristic of the species is the bright red coloration of the chelicerae, given by a covering of long setae on the anterior surface; because of this coloration, it has been previously confused with *Phoneutria fera* Perty 1833. It is generally similar to *Cupiennius getazi* Simon 1891, but lacks the spotted pattern on the ventral surface of the femora, together with other differences in genitalic morphology. *Cupiennius salei* Keyserling 1877 was also found on the same forest during the wet season, while *C. chiapanensis* appeared in the dry season. Adults of both species were never collected at the same time. This is also the first record of *C. salei* at the sea level, being previously considered a highland species.

RESUMEN. Se describe *Cupiennius chiapanensis* nueva especie, la décima del género. Fue recolectada del manglar de la costa de Chiapas, México. La característica más notoria es la coloración roja brillante de sus quelíceros, dada por una cubierta de sedas largas en el frente del quelícero. Esta coloración ha provocado que se le confunda con *Phoneutria fera* Perty 1833 en tres referencias que se documentan. En general, es similar a *Cupiennius getazi* Simon 1891, pero no exhibe el patrón moteado en la superficie ventral de los fémures, además de otras diferencias en su estructura genital que se discuten. Se encontró también en el mismo bosque a *Cupiennius salei* Keyserling 1877 durante la época de lluvias, mientras que *C. chiapanensis* apareció durante la época de secas. Los adultos de ambas especies nunca fueron recolectados en la misma época. Este también es el primer registro de *C. salei* a nivel del mar, pues era considerada una especie de tierras altas.

Keywords: Mangrove forest, *Cupiennius*, wandering spiders, taxonomy, new species

The genus *Cupiennius* Simon 1891 is comprised of nine species distributed throughout Mexico, Central America and Cuba, while *Cupiennius celerrimus* Simon 1891 is found from Venezuela to Brazil. The latest revision of the genus (Lachmuth et al. 1985) regards the terminal apophysis of the male bulb, and the internal epigynal structure as diagnostic characteristics among the species; the external coloration is often taken into account for some species. In a later work, *C. remedius* Barth & Cordes 1998 was reported as the only species known to share habitat with *C. salei* Keyserling 1877 (Barth & Cordes 1998).

During a study on the spider fauna of a mangrove forest in the reserve "La Encrucijada", Chiapas, México, specimens of *C. salei* and a different species of the same genus were collected in exactly the same localities, but in different seasons. This other species displays sufficient differences to be considered as a new species. Several references to this same spider have been found in several publications and web pages (Browning 1989; Alvarez del Toro 1992; Spider Homepage 2000) where it has been incorrectly referred to the genus *Phoneutria* Perty 1833.

In the present paper, this new species is described, the tenth of the genus and the second besides *C. salei* to be reported from Mexico. Some aspects concerning the occurrence of both species in a mangrove forest are discussed.

METHODS

The specimens were collected during three expeditions to the reserve "La Encrucijada", in Chiapas, México, in April 2002, September 2002 and April 2003, on the island "Solo Tú" (15°04′28″N, 92°45′49″W) and in the path

called "La Vida Sigue", next to the monitoring station (15°04′06″N, 92°45′20″W). The plant coverage at the sites corresponds to a mangrove forest, where *Rhizophora mangle* (red mangrove) is the dominant species, associated with *Laguncularia racemosa* (white mangrove). The understory is mainly composed of ferns (*Acrosticum aureum*) and "piñuela" *Bromelia plumieri* (Rico-Gray 1990).

A total of 21 specimens were examined, 13 females and eight males. All measurements are given in millimeters, maximum and minimum; the numbers within parentheses correspond to the mean. Body length was considered to be the distance from the anterior edge of the carapace to the posterior edge of the opisthosoma, carapace length from its anterior to its posterior edge, as well as the opisthosoma length, including spinnerets. Carapace width was taken at the third leg pair; opisthosoma width was taken at the middle. The general description was based upon dried specimens, since those wet in alcohol appear darker and the setae covering carapace and legs are not clearly visible; in over- dried specimens the chelicerae color may look paler. The holotype and paratype were those complete specimens closer to the mean. All type specimens are deposited in the National Arachnid Collection (CNAN), Laboratorio de Acarología, Instituto de Biología, UNAM, México.

Only the most common abbreviations were used in the description: AME = anterior median eyes, PME = posterior median eyes, PLE = posterior lateral eyes, RTA = retrolateral tibial apophysis. For male and female genitalia the names used in Lachmuth et al. (1985) were kept as close as possible. For the male bulb: embolus = Em; terminal apophysis = TAp; embolar apophysis = EAp; conductor = Co; embolar base = StE. For the female epigynum: median plate (septum) = MP; lateral plate = LP; seminal receptacle = R; seminal duct = SD.

TAXONOMY

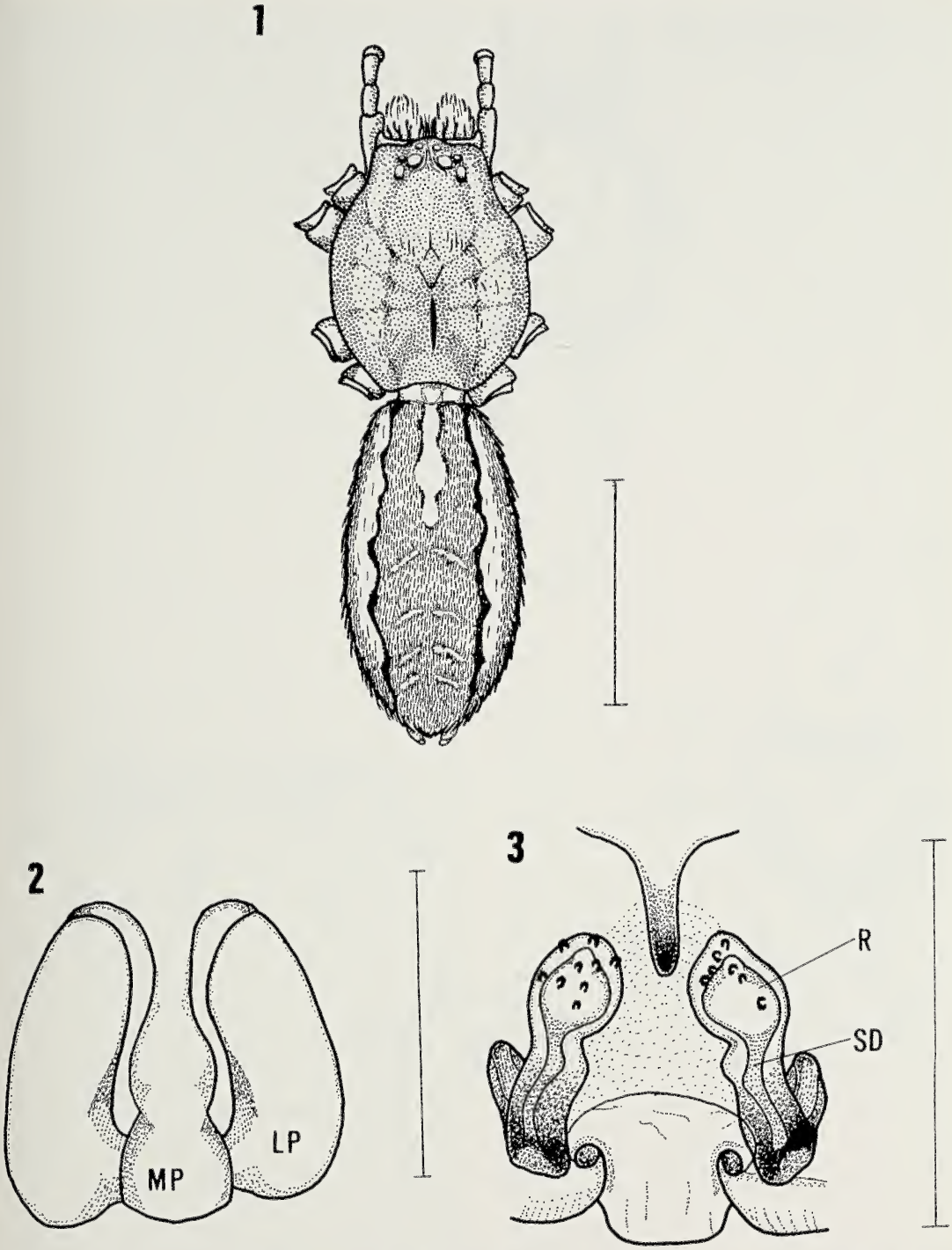
Family Ctenidae Keyserling 1877
Genus *Cupiennius* Simon 1891
Cupiennius chiapanensis new species

Type material.—Mexico: *Chiapas:* Holotype female, from the island "Solo Tú", 15°04′28″N, 92°45′49″W, 17 April 2003, Y. García Martínez (CNAN). Allotype male, from the path "La Vida Sigue", next to the monitoring station of the reserve "La Encrucijada", 15°04′06″N, 92°45′20″W, 10 April 2003, F. Medina (CNAN). Paratypes: 9 females from the path "La Vida Sigue" and 3 females from the island "Solo Tu"; 6 males collected from "La Vida Sigue" and 1 male from "Solo Tú".

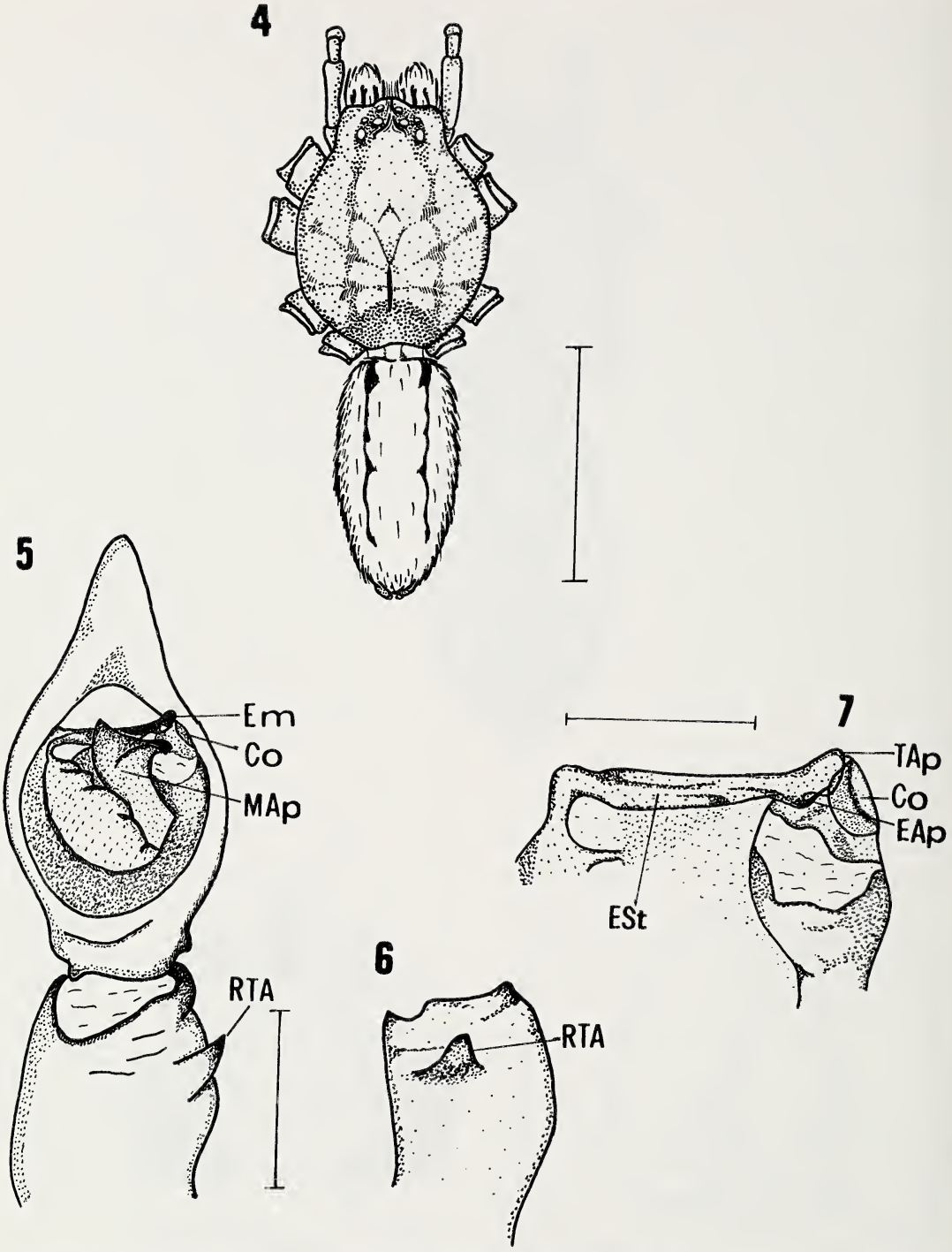
Etymology.—The specific epithet refers to the state where the species was found.

Diagnosis.—*Cupiennius chiapanensis* is distinguished from other species of the genus by the characteristic color of the chelicerae which are mostly covered by bright red setae in females and pale red setae in males. The female has the epigynal lateral plates curved on the inner edge; the septum is thinner in its upper part and wider below, rounded in the middle and square at the end (Fig. 2); the seminal receptacles are spherical with a small distal hump and bits of cuticle adhered to the surface (Fig.3). The male pedipalp has the RTA triangular viewed from the front, and square viewed from the side (Fig. 6); the bulb is quite similar to that of *Cupiennius getazi* (Lachmuth et al. 1985, fig. 3), but the terminal apophysis has the upper edge gently sloping rather than almost square; the embolar apophysis is longer and thinner; the conductor is larger, overlapping with the terminal apophysis and the embolar base has clearly visible keels through the upper and lower edges of its extension (Fig. 7).

Description.—*Female:* Total length 21.9–27.0 mm (25.3); carapace length 9.4–13.1 mm (10.8), width 9.0–10.5 mm (9.7); opisthosoma length 11.0–15.0 mm (13.4), width 6.4–8.9 mm (8.2). Leg I: femur 10.9–16.8 (12.2), patella 4.4–5.7 (5.3), tibia 10.2–12.7 (11.3), metatarsus 9.1–13.2 (11.2), tarsus 3.0–5.0 (4.1). Leg II: femur 10.7–13.5 (11.9), patella 4.3–5.9 (5.2), tibia 9.9–13.1 (10.8), metatarsus 9.3–13.8 (11.2), tarsus 3.2–4.3 (3.9). Leg III: femur 8.1–12.9 (9.9), patella 4.3–5.9 (5.2), tibia 6.0–10.3 (8.1), metatarsus 6.7–12.2 (8.8), tarsus 2.5–4.2 (3.4). Leg IV: femur 10.5–13.7 (11.6), patella 3.7–5.5 (4.6), tibia 8.3–11.6 (9.6), metatarsus 10.9–15.1 (12.5), tarsus 3.2–4.8 (3.9). Pedipalp: femur 4.1–5.7 (4.7), patella 1.8–2.5 (2.1), tibia 3.3–4.0 (3.5), tarsus 3.6–4.6 (3.9). *Prosoma:* Carapace orange-brown with a darker brown median band that begins behind PME, reaching posterior edge;



Figures 1–3.—*Cupiennius chiapanensis* new species, female. 1. Dorsal aspect of body, scale = 1.0 cm; 2. Ventral view of epigynum, scale = 1.0 mm; 3. Dorsal view of epigynum, scale = 1.0 mm. MP = median plate, LP = lateral plate, R = seminal receptacle, SD = seminal duct.



Figures 4–7.—*Cupiennius chiapanensis* new species, male. 4. Dorsal aspect of body, scale = 1.0 cm; 5. Ventral view of left pedipalp, scale = 1.0 mm; 6. Retrolateral view of left pedipalp tibia; 7. Embolar area, scale = 0.5 mm. Em = embolus, Co = conductor, MAp = median apophysis, RTA = retrolateral tibial apophysis, TAp = terminal apophysis, EAp = embolar apophysis, ESt = embolar base.

surface covered by short, white setae, except for small spots over ocular area and behind the PLE, where short black setae cover the spot. Long, white setae along the entire carapace edge, those on the anterior lateral edge red colored. Ocular area slightly elevated, long black setae below AME and in between them with long white setae between the PME and PLE and between each other. Fovea longitudinal with two long, erected setae on anterior edge and divergent black lines of short setae leading up to the edge of the carapace. Endites black with long white setae along anterior edge, with white border; long black setae curved downwards coming from the lateral endite edge. Labium trapezoidal, black colored with anterior border white and covered with long black setae. Sternum light brown with black border, covered with long black setae mixed with short white setae. Coxae the same color as sternum. *Opisthosoma:* General color brown-grayish, covered with long, thick white setae. Median black band with winding edge on dorsum in which there is a shorter white band that reaches up to less than half its length, dorsal pattern as illustrated (Fig. 1). Sides of opisthosoma dark and covered with long brown setae. Ventral surface light brown, with a median longitudinal black band, beginning in the epigastric furrow and ending at the spinneret circled area. Anterior spinnerets light brown with white apical band, posterior spinnerets darker and slightly longer and thinner. Epigynum with the common structure in the genus, two lateral plates and a median plate or septum. Septum thin anteriorly and wider posteriorly, rounded in the middle, then constrained and ending in a square shape. Lateral plates curved on their inner side, linked to the septum by their upper lateral edge, on the dorsal side (Fig. 2). Seminal receptacles spherical, with a small anterior mound and dark bits of cuticle adhered to their surface, similar to the "porose area" described for other lycosoid families by Griswold (1993), the diameter less than half of duct length. Ducts straight, elbowed on the last two thirds (Fig. 3). *Chelicerae:* General color black, covered with long bright setae on their front surface, up to three quarters of their length, with a few scattered black long setae. Interior border of chelicerae with long white setae, fangs black. *Pedipalps:* General color dark brown, covered with white setae. *Legs:* General color dark brown, covered with short white setae, in living spiders the legs look much darker than the rest of the body. Coxae with long black setae on ventral surface, all trochanters notched with a median transverse band of long black setae. Femora densely covered with long black setae with white tip, mixed with short white setae. Femur I with three dorsal spines, 3 prolateral and 3 retrolateral, and dorsum covered with short white setae concentrated in two bands on anterior half. Femur II with two bands of white setae. Femur III without complete bands, only spots visible on dorsum. Femur IV without bands. Patellae dark brown covered with white short setae, mixed with some long black ones, without spines. Tibiae dorsally darker and devoid of setae, with one prolateral spine, one retrolateral and three pairs of ventral spines; ventral surface covered with short white setae. Metatarsi without setae on dorsum, with an irregular row of trichobothria, two pairs of dorsal spines, 3 prolateral, 3 retrolateral and two pairs of ventral spines. Scopula covering the whole ventral surface of metatarsi, except the posterior edge. Tarsi dorsally covered with dense scopula, mixed with tarsal tufts, three tarsal claws, dorsum covered with short white setae and one or two trichobothria.

Male: Total length 7.6–23.6 mm (20.4); carapace length 8.3–10.8 mm (9.5), width 7.8–18.9 mm (9.8), opisthosoma length 8.6–11.9 mm (10.3), width 4.5–16.0 mm (7.2). Leg I: femur 10.9–12.3 (11.7), patella 4.2–5.5 (4.8), tibia 10.6–13.1 (11.8), metatarsus 11.3–14.2 (12.8), tarsus 4.1–5.0 (4.6). Leg II: femur 11.3–12.7 (12.1), patella 4.5–5.9 (5.1), tibia 10.8–12.5 (11.4), metatarso 10.8–13.5 (12.6), tarsus 3.8–4.6 (4.3). Leg III: femur 9.7–11.5 (10.4), patella 3.4–4.5 (3.9), tibia 7.0–8.7 (8.0), metatarsus 8.8–10.2 (9.5), tarsus 3.1–4.2 (3.6). Leg IV: femur 10.8–11.5 (11.3), patella 3.8–5.2 (4.2), tibia 9.3–10.8 (10.0), metatarsus 11.4–13.4 (12.4), tarsus 3.5–4.5 (4.2). Pedipalp: femur 3.1–5.0 (4.4), patella 1.7–2.6 (2.0), tibia 2.8–4.0 (3.5), tarsus 2.9–3.8 (3.2).

Prosoma: Carapace color orange-brown, with a median darker band, beginning behind the PME and reaching the posterior edge. Surface entirely covered with short grayish setae that leave only two parallel black lines delineating the median band. Long white setae along the margin, those on the anterior lateral border orange colored. Ocular area slightly el-

evated, with white setae above the posterior eyes and between the median eyes. Fovea longitudinal. *Opisthosoma:* General color dark gray, covered with light brown setae, except some small spots where the setae have come off, without any pattern but a pair of parallel black lines that follow from the carapace (Fig. 4). Ventral surface light gray with a median black band originating at the epigastric furrow and ending at the circled spinneret area. *Chelicerae:* General color black, covered with pale red setae on most of their surface, up to two thirds their length, with some scattered long black setae, interior border with long white setae, fangs black. Endites and labium dark brown with long black setae. Sternum and coxae light brown, covered with grayish short setae. *Pedipalps:* General color same as the carapace, dorsally covered with short grayish setae, femur with one dorsal and three apical spines, patella with one apical prolateral spine, tibia with two dorsal spines and long white setae on its lateral borders. RTA short with square shape in lateral view and triangular in ventral view (Fig. 5). Cymbium dark brown, covered with short black and white setae, bulb in agreement to the general structure of the genus and very similar to that of *C. getazi* (Fig.5). Median apophysis with the upper side rounded and the lateral process sharp and curved downwards. Embolus ending close to the conductor; embolar apophysis slender, hook shaped, and the tip covered with the terminal apophysis, which is slightly ovoid and the upper edge slopes down to the embolar base; conductor rounded and directed outwards, bent downwards on its distal portion, covering part of the embolus (Fig.7). *Legs:* Same color as the carapace covered with light grayish setae, with no visible bands, only dark spots on dorsum. Femur with spines similar to those of the female. All legs covered with light setae, except dorsal surfaces of tibiae and metatarsi. Dorsal irregular row of trichobothria on metatarsi; tarsi with no visible trichobothria. Ventral surface of metatarsi covered with scopula, not as dense as in the female, and beginning at the second third of its length. Tarsi completely covered with scopula and claw tufts, three tarsal claws. Other structures as in the female.

Distribution.—This species has only been collected from the mangrove forest of "La Encrucijada", municipality of Acapetahua, Chiapas state, México.

DISCUSSION

The first external characteristic indicating that *Cupiennius chiapanensis* could represent a distinct species was the striking red color of the chelicerae, which couldn't have been overlooked in any other description and is an invariable feature of every adult which is not lost when kept in alcohol at least after one year; therefore, it is herein regarded as a diagnostic character. This red color probably led to the confusion of this spider with *Phoneutria fera*, in two photographic references. The first one is from a web site from Australia (Spider Homepage 2000), where some pictures were sent by a photographer and incorrectly identified; the other is from a book on tarantulas where it is regarded as "the Brazilian huntsman spider" (Browning 1989:67). A third reference was found in the book "Arañas de Chiapas", where it is stated that the spider probably belongs in *Phoneutria* due to the color of the chelicerae (Alvarez del Toro 1992, plate 63). *Cupiennius salei* sometimes shows red setae on the chelicerae too, as can be observed in color drawings (Cambridge 1900) and even in living spiders, however, they don't fully cover the front of the chelicerae, so the characteristic dark longitudinal bands of this species prevail.

Barth & Cordes (1998) consider the coloration of the sternum and coxae as a character to separate some of the species of the genus, pointing out that external body pattern could allow the identification of even subadult specimens. The ventral pattern of *C. chiapanensis* is similar to that of *C. valentinei* Petrunkevitch 1925, which is the only other species with a ventral black median band. The rest of the coloration, including the dorsal opisthosomal pattern, is very similar to *C. getazi*, which however shows a distinctive spotted ventral surface of the femora, that is not present in this new species. *Cupiennius chiapanensis* is also similar to *C. getazi* in the shape of the seminal receptacles and ducts, but the small distal mound and the granules all over the surface of the receptacles, together with the external shape of the epigynum, set them apart.

Before this study, only *Cupiennius remedius* was known to share habitat with *C. salei*,

in the highlands of Guatemala (Barth & Cordes 1998). Here, *C. chiapanensis* is the second species to exist in the same place as *C. salei*, but at different times. During the wet season, between September and October 2002, 35 adults of *C. salei* were collected at exactly the same sites where 18 of *C. chiapanensis* had been obtained in the dry season, including females carrying egg sacs attached to their spinnerets. Adults of both species at the same time were never found. Juveniles, on the other hand, are morphologically very similar, so their identification was not possible. In this study, the first report of *C. salei* at a lower altitude than 800 msnm is given, for it was formerly considered to be a highland species (Barth & Seyfarth 1979).

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HAVE YOU SEEN MY MATE? DESCRIPTIONS OF UNKNOWN SEXES OF SOME NORTH AMERICAN SPECIES OF LINYPHIIDAE AND THERIDIIDAE (ARANEAE)

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ABSTRACT. The previously unknown sexes of 13 species of Linyphiidae and Theridiidae are described and illustrated for the first time. These include the following members of the Linyphiidae: *Centromerus furcatus* (Emerton) female, *Cheniseo sphagnicultor* Bishop & Crosby female, *Coloncus siou* Chamberlin male, *Dismodicus alticeps* Chamberlin & Ivie female, *Floricomus praedesignatus* (Bishop & Crosby) female, *Glyphesis idahoanus* (Chamberlin) male, *Gnathonaroides pedalis* (Emerton) female, *Lepthyphantes intricatus* (Emerton) female, *Scyletria inflata* Bishop & Crosby female, *Sisicus penifusifer* Bishop & Crosby female, *Walckenaeria clavipalpis* Millidge male; and two members of the Theridiidae: *Thymoites minnesota* Levi female and *Robertus crosbyi* (Kaston) male. Synonymy, new records, and comments on distribution, habitat and taxonomy are also given. The generic placement of *Glyphesis idahoanus* (Chamberlin) and *Glyphesis scopulifer* (Emerton) is confirmed.

Keywords: taxonomy, Canada, U.S.A., undescribed sexes, distribution, museum collection

Recently, Paquin & Dupérré (2003) published an identification guide to the known and suspected spiders of Québec. In the treatment of these species, we came across several for which only one sex was known. The other sex of these species is described below. We also give the synonymy, new distribution data and provide relevant taxonomic and ecological comments. The failure to recognize matching sexes may result in situations where a female is known under a certain name and the male under another, therefore leaving the false impression that only one sex is known. Such cases, however possible, are not common and for most species in which only one sex is known, there may be rather simple and direct explanations. Firstly, the species is quite rare and it happens that only one sex was collected. Secondly, differences in either microhabitat selection or behavior of males and females may result in one sex being overlooked. For instance, approximately one hundred males are known for *Maro amplus* Dondale & Buckle 2001, but so far, the female remains unknown (Dondale & Buckle 2001). In other cases, such as *Nesticus* Thorell 1869 (Nesticidae), the ratio of specimens collected in the field largely favors females and juveniles while mature males are rarely encountered (M. Hedin pers. comm., pers. obs.). Similar observations were made by Gertsch (1992) for the genus *Cicurina* Menge 1871 (Dictynidae). Thirdly, in most cases the undescribed sex has been collected and properly assigned to a species but awaits formal description. Most species treated in this paper belong to this last category.

We have collected both sexes of some species [*Gnathonaroides pedalis* (Emerton 1923), *Centromerus furcatus* (Emerton 1882), *Lepthyphantes intricatus* (Emerton 1911), *Dismodicus alticeps* Chamberlin & Ivie 1947, *Scyletria inflata* Bishop & Crosby 1938, *Coloncus siou* Chamberlin 1949, *Sisicus penifuscifer* Bishop & Crosby 1938, *Thymoites minnesota* Levi 1964], in the same pitfall sample, or together in the field, thus allowing the association. Most other records were sorted together in vials belonging the Canadian National Collection. These associations were

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made over the years by C.D. Dondale and J.H. Redner from samples in which both sexes were collected together.

METHODS

Specimens were examined in 70% ethanol under a SMZ-U Nikon dissection microscope. A Nikon Coolpix 950 digital camera attached to the microscope was used to take a photograph of the structure. The digital photo was then used to trace proportions and the illustration was detailed and shaded by referring back to the structure under the microscope. Female genitalia were excised using a sharp entomological needle and transferred to lactic acid to clear non-chitinous tissues. A temporary lactic acid mount was used to examine the genitalia under an Olympus BX40 microscope, and was photographed and illustrated as explained above. All measurements were made using a micrometric ruler fitted on the eyepiece of the microscope. When available, 5 specimens were measured for the description. Calculation for the location of TmI follows Denis (1949).

Most of the specimens studied were from the Canadian National Collection of Insects and Arachnids, Ottawa, Canada (CNC). In addition, material from several other collections was examined. The collection is indicated in brackets and unless specified otherwise, the specimens are deposited in the CNC. Abbreviations used: AG = Collection of Alice Graham; CMB = Collection of C.M. Buddle; CPAD = Collection of Paquin-Dupérré; DJB = Collection of D.J. Buckle; DSU = Dickinson State University, North Dakota (currently at Texas A&M International University); HAC = Collection of H.A. Carcamo; MCZ = Museum of Comparative Zoology, Harvard University; MLC = Collection of Maxime Larivée; RF = Collection of Robert Fimbel; RGH = Collection of R.G. Holmberg; RPC = Collection of Roger Pickavance; RSM = Royal Saskatchewan Museum; UASM = University of Alberta, Strickland Museum. Latitude and longitude given for each locality should be considered approximate.

TAXONOMY

Family Linyphiidae Blackwall 1859

Genus *Centromerus* Dahl 1886

Centromerus furcatus (Emerton 1882)

Figs. 1–3

Microneta furcata Emerton 1882:76, pl. 24 fig. 5.
Centromerus furcatus (Emerton): van Helsdingen 1973:27, figs. 22–24; Jennings et al. 1988:61; Bélanger & Hutchinson 1992:50; Buckle et al. 2001: 105; Paquin et al. 2001:16; Paquin & LeSage 2001:96; Paquin & Dupérré 2003:137, figs. 1503–1506.

Material examined.—U.S.A.: *Maine:* Piscataquis County Soubunge Mountain [45°58′N, 69°12′W], 1♂, 1 ♀ (CNC); CANADA: *Newfoundland:* Eastern Blue pond [50°27′N, 57°07′W], 1 ♂, 1 ♀ (CNC); Crabbes River [48°13′N, 58°52′W], 2 ♀ (CNC); Barachois Brook [48°27′N, 58°26′W], 1 ♀ (CNC); Lloyd's Lake [48°23′N, 57°31′W], 2 ♀ (CNC); Highlands River [48°11′N, 58°53′W], 1 ♀ (CNC); Big Falls [47°05′N, 54°03′W], 1 ♀ (CNC); Pasadena [49°01′N, 57°36′W], 1 ♂, 6 ♀ (CNC); *New Brunswick:* Green River 30 mi N Edmunston [47°19′N, 65°27′W], 2 ♂ (CNC); *Québec:* Parc de la Gaspésie Mont Albert [48°56′N, 66°10′W], 1 ♀ (CNC); 24 mi S of Ste-Anne-des-Monts [48°52′N, 65°58′W], 3 ♂ (CNC); Abitibi Lac Duparquet [48°30′N, 79°13′W], 1 ♂, 1 ♀ (CPAD).

Description.—*Female (n = 5):* Total length: 1.35 ± 0.08 mm; carapace length: 0.63 ± 0.03 mm; carapace width: 0.47 ± 0.02 mm; carapace smooth, shiny, light yellow to yellow with a tinge of orange, lightly shaded with gray along radiating lines; carapace margin more strongly shaded, 3–4 erect setae along midline; sternum yellow, strongly shaded with gray, margin darker. Chelicerae yellow with a tinge of orange, promargin with 3 large teeth, retromargin with 5 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, off-white, lightly suffused with gray, densely covered with long semi-erect setae. Legs light yellow to yellow with a tinge of orange, tibia I-IV with two dorsal macrosetae; metatarsus I with dorsal trichobothrium, TmI 0.28–0.33, TmIV absent. Epigynal plate flat, protruding, wider than long; scape short, broad, straight or widening slightly toward the tip, cochlear present (Figs. 1, 2); spermathecae bean-shaped (Fig. 3).

Distribution.—Eastern species, southernmost record from New Hampshire (Buckle et al. 2001).

Habitat.—Collected in coniferous habitat, in moss and forest litter.

Genus *Cheniseo* Bishop & Crosby 1935
Cheniseo sphagnicultor Bishop & Crosby 1935
Figs. 4, 5

Cheniseo sphagnicultor Bishop & Crosby 1935a: 263, pl. 21 figs. 64–69; Buckle et al. 2001:110; Paquin et al. 2001:16; Paquin & Dupérré 2003: 96, figs. 883–886.

Acartauchenius sphagnicultor (Bishop & Crosby): Aitchison-Benell & Dondale 1992:221; Dondale & Redner 1994:36; Bélanger & Hutchinson 1992: 22.

Material examined.—CANADA: *Nova Scotia:* Cape Breton National Park French Lake [46°44′N, 60°52′W], 1 ♀ (CNC); Cape Breton National Park North Mount [46°53′N, 60°35′W], 2 ♂ (CNC); *Québec:* Gatineau Park Hopkin's Hole [45°34′N, 75°57′W], 1 ♂ (CNC); *Ontario:* Alfred [45°33′N, 76°52′W], 1 ♂, 1 ♀ (CNC); Mer Bleu 8 miles E. of Ottawa [45°24′N, 75°30′W], 8 ♂, 3 ♀ (CNC); Upper Rock Lake 30 km N Kingston [44°30′N, 76°24′W], 1 ♂ (CNC); Crieff Bog 3 km W Puslinch [43°26′N, 80°05′W], 1 ♂ (CNC); Wylde Lake Bog 8 km E Arthur [43°50′N, 80°22′W], 7 ♂, 1 ♀ (CNC); Brucedale conservation area nr Port Elgin [44°26′N, 81°24′W], 1 ♀ (CNC); *Manitoba:* Riding Mountain National Park Swanson Spring [50°53′N, 100°15′W], 6 ♂, 1 ♀ (CNC).

Description.—*Female (n = 5):* Total length: 0.98 ± 0.07 mm; carapace length: 0.43 ± 0.05 mm; carapace width: 0.33 ± 0.04 mm; carapace smooth, shiny, light brown to dark brown, radiating lines and carapace margin with diffuse gray pattern, cephalic region occasionally ornamented by a dark gray marking forming a trident (or psi, Ψ); 3 long erect setae along midline; sternum light brown to dark brown strongly shaded with gray. Chelicerae yellow to light brown, promargin with 1 large tooth and 5 small teeth, retromargin with 4–5 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, light to dark gray, densely covered with short semi-erect setae. Legs light yellow with a tinge of orange, tibia I-IV with one dorsal macroseta; metatarsus I with dorsal trichobothrium, TmI 0.38–0.47, TmIV absent. Epigynum with plate resembling an hexagon; median lobe, broad, pointed, extending in pale area; copulatory openings small, round, situated at anterior end of the median lobe (Fig. 4); spermathecae round, widely separated, flanking the median lobe (Figs. 4, 5).

Distribution.—Species restricted to the eastern portion of North America, W to Manitoba.

Habitat.—This species has been collected in coniferous forest litter but seems mainly associated with sphagnum bogs.

Genus *Coloncus* Chamberlin 1949
Coloncus siou Chamberlin 1949
Figs. 6–8

Coloncus siou Chamberlin 1949:525 figs. 48, 49; Levi & Levi 1955:36; Bélanger & Hutchinson 1992:27; Buckle et al. 2001:110; Paquin et al. 2001:16; Paquin & Dupérré 2003:97, figs. 891–893.

Material examined.—U.S.A.: *Massachusetts:* Barnstable County: Quisset [41°43′N, 70°39′W], 10 ♂, 8 ♀ (CNC); *North Dakota:* Dunn County: Lake Ilo [47°20′N, 102°39′W], 1 ♂ (DSU); Canada: *Québec:* Gatineau Park King Mountain [45°29′N, 75°52′W], 1 ♂ (CNC); *Saskatchewan:* 10 km S Cadillac [49°30′N, 107°50′W], 22 ♂, 4 ♀ (RSM); Grasslands National Park West Block [49°07′N, 107°26′W], 55 ♂, 27 ♀ (DJB); North Battleford [52°47′N, 108°17′W], 5 ♂, 2 ♀ (DJB); Morse [50°30′N, 106°53′W], 15 ♂, 2 ♀ (RSM); 22 km W Hazlet [50°24′N, 108°36′W], 1 ♂ (RSM); 5 mi NE Saskatoon [52°11′N, 106°34′W], 18 ♂ (DJB); 21 km N Scotsguard [49°43′N, 108°09′W], 1 ♂ (RSM);

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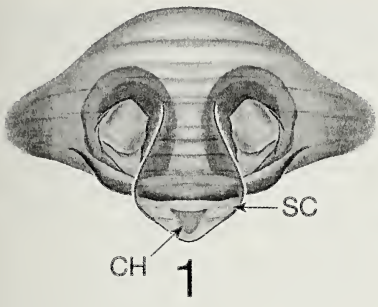
Figures 1–10.—Linyphiid genitalic structures: 1—3.*Centromerus furcatus*: 1. Epigynum, ventral view; 2. Epigynum, lateral view; 3. Spermathecae, dorsal view. 4, 5. *Cheniseo sphagnicultor*: 4. Epigynum, ventral view; 5. Spermathecae, dorsal view. 6–8. *Coloncus siou*: 6. Palpal tibia of male, dorsal view; 7. Palpal cymbium, lateral view; 8. Palpus of male, ventral view. 9, 10. *Dismodicus alticeps*: 9. Epigynum, ventral view; 10. spermathecae, dorsal view. Abbreviations used: CH = Cochlea, CO = Copulatory Opening, CY = Cymbium, E = Embolus, ML = Median Lobe, MPr = Median Process, PTA = Palpal Tibia Apophysis, SC = Scape, S = Spermatheca.



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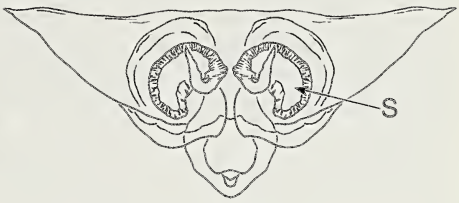

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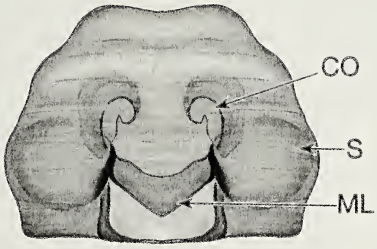

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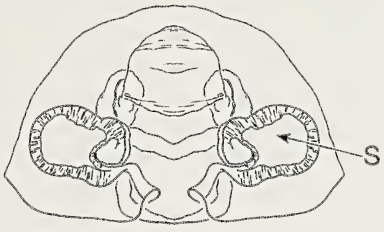

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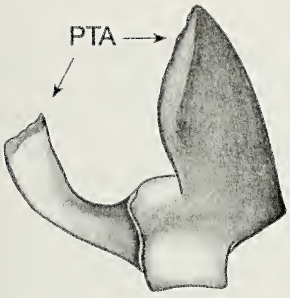

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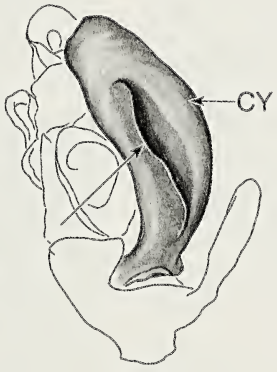

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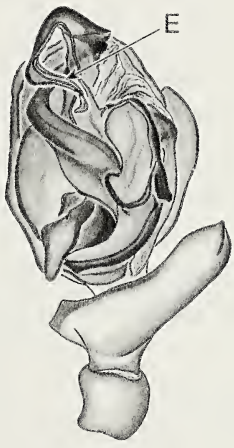

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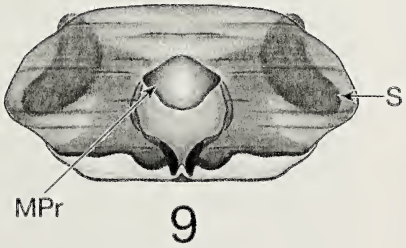

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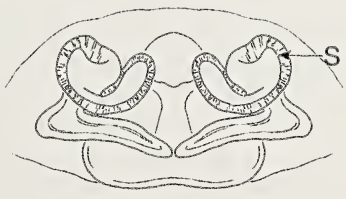

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24 km N Shaunavon [49°53′N, 108°30′W], 7 ♂, 1 ♀ (RSM); ~10 km NE Simmie [49°59′N, 108°00′W], 9 ♂, 1 ♀ (RSM); *Alberta:* Lethbridge [49°42′N, 112°49′W], 2 ♂ (DJB); Suffield [50°12′N, 111°10′W], 25 ♂, 6 ♀ (DJB).

Description.—*Male (n = 5):* Total length: 1.58 ± 0.11 mm; carapace length: 0.66 ± 0.03 mm; carapace width: 0.54 ± 0.04 mm; carapace smooth, shiny, light brown to brown with diffused gray markings along midline and radiating line, carapace margin with dark gray markings; 6 short erect setae along midline; sternum brown strongly shaded with gray, margin darker. Chelicerae yellow to light brown, paler basally and apically, promargin with 3 large teeth and 1 small tooth, retromargin with 2 small teeth. Cheliceral stridulatory organ easily visible with ~20 ridges. Abdomen unicolor, dark gray, sparsely covered with long erect setae. Legs light yellow with a tinge of brown, coxae lightly shaded with gray; tibia I-IV with one dorsal macroseta; metatarsus I with dorsal trichobothrium, TmI 0.40–0.48, TmIV absent. Palpal tibia with two apophyses (Fig. 6); cymbium with large, deep, longitudinal, retrolateral groove (Fig. 7); paracymbium concealed behind palpal tibia apophysis; embolus flat, ribbon like, curving twice at almost a right angle (Fig. 8).

Distribution.—Apparently a northern species. It has been found from Alberta to Québec to the North and in North Dakota and Massachusetts (Buckle et al. 2001).

Habitat.—This species appears to inhabit forest litter and moss in the east of its distribution, and prairie in the west.

Remarks.—Five species are listed in the genus *Coloncus* (Buckle et al. 2001). One species, *C. americanus*, was described by Chamberlin & Ivie (1944), the remaining by Chamberlin (1949). Four of these species were described from females only and appear very similar based on available illustrations. *Coloncus cascadeus* Chamberlin 1949 was briefly described from both male and female, but no illustrations of the genitalia were provided. The description and illustration of the male of *Coloncus siou* given here will hopefully bring attention to the genus and result in a re-examination of the five species, which may prove to be synonyms. On the other hand, *C. siou* is associated with forest and moss in the East, but specimens collected in Saskatchewan, Alberta, Montana and North Dakota are found in prairie habitats (Buckle unpub.). It is presently unclear whether this indicates a broad habitat selection for *C. siou*, or that more than one species is present. A revision of the genus is necessary to clarify these questions. The name *Coloncus siou* has been used for the species found in the East to remain consistent with Buckle et al. (2001).

As mentioned in Buckle et al. (2001) and Paquin et al. (2001), the date of Chamberlin's paper "On some American spiders of the Family Erigonidae" is erroneously cited as 1948. The paper was published in 1949 as stated on page 570 of the volume 41 of the Annals of the Entomological Society of America.

Genus *Dismodicus* Simon 1884
Dismodicus alticeps Chamberlin & Ivie 1947
Figs. 9, 10

Dismodicus alticeps Chamberlin & Ivie 1947:34 figs. 29–31; Hackman 1954:28, figs. 69–71; West et al. 1984:86; Bélanger & Hutchinson 1992:28; Aitchison-Benell & Dondale 1992:222; Marusik et al. 1993:76; Hutchinson 1994:168; Dondale et al. 1997:83; Buckle et al. 2001:112. Paquin et al. 2001:17; Paquin & Dupérré 2003:99, figs. 918–921.

Material examined.—U.S.A.: *North Dakota:* Benson County: Wood Lake [47°54′N, 98°53′W], 1 ♂, 2 ♀ (DSU); Bottineau County [County record only], 1 ♂, 2 ♀ (DSU); Rolette County [County record only], 1 ♀ (DSU); Rolette County: Fish Lake [48°06′N, 99°33′W], 1 ♂ (DSU); CANADA: *Newfoundland:* Noel Pauls Brook [48°49′N, 56°18′W], 1 ♀ (CNC); *Nova Scotia:* Cape Breton Highlands National Park North of Paquet Lake [46°48′N, 60°41′W], 4 ♂ (CNC); Cape Breton Highlands National Park New Ross Lunenburg County [44°44′N, 64°27′W], 2 ♂ (CNC); Cape Breton Highlands National Park Sweet's Cove [44°44′N, 64°27′W], 1 ♂, 12 ♀ (CNC); Hebbville [44°21′N, 64°32′W], 2 ♀ (CNC); Cape Blomidon [45°13′N, 64°22′W], 1 ♀ (CNC); Kentville [45°05′N, 64°30′W], 3 ♀ (CNC); *New Brunswick:* Fredericton Lincoln [45°54′N, 66°35′W], 2 ♀ (CNC); Green River 30 mi N Edmunston [47°19′N, 68°09′W], 1 ♀ (CNC); Kouchibouguac National Park [46°51′N, 64°58′W], 4 ♀ (CNC); *Québec:* Lac Roddick [46°15′N, 75°53′W], 1 ♀ (CNC); La Rivière-du-Nord, Saint-Hippolyte, Station

biologie Université de Montréal [45°59′N, 74°00′W], 4 ♂, 4 ♀ (CPAD); *Ontario:* Shirleys Bay 15 km w of Ottawa [45°22′N, 75°53′W], 1 ♀ (CNC); Algonquin Provincial Park Lake Opeongo [45°42′N, 78°23′W], 3 ♂, 6 ♀ (CNC); Algonquin Provincial Park Lake Opeongo Deer Island [45°42′N, 78°23′W], 5 ♀ (CNC); Petawawa [45°54′N, 77°20′W], 2 ♂, 3 ♀ (CNC); Iroquois Falls [48°46′N, 80°41′W], 1 ♀ (CNC); *Manitoba:* Riverton [50°59′N, 96°59′W], 14 ♂, 22 ♀ (CNC); 15 km SW Swan River [51°58′N 101°W], 2 ♀ (DJB); South Indian Lake [56°47′N, 98°56′W], 1 ♀ (CNC); Seddon's Corner [50°03′N, 96°17′W], 4 ♀ (CNC); Pine Falls [50°33′N, 96°13′W], 1 ♂, 5 ♀ (CNC); Rennie [49°51′N, 95°33′W], 2 ♂, 2 ♀ (CNC); Agassiz Provincial Park [49°59′N, 96°09′W], 3 ♀ (CNC); Telford [49°50′N, 95°23′W], 1 ♂, 3 ♀ (CNC); Darwin [49°55′N, 95°49′W], 4 ♂, 4 ♀ (CNC); Glenlea [49°38′N, 97°08′W], 1 ♀ (CNC); Eardley Lake [52°31′N, 96°06′W], 1 ♀ (CNC); Spuce Woods Provincial Forest [49°46′N, 99°21′W], 3 ♀ (CNC); Ninette [49°20′N, 99°33′W], 1 ♂ (CNC); Riding Mountain National Park [50°39′N, 99°58′W], 1 ♀ (CNC); *Saskatchewan:* Lady Lake [52°02′N, 102°37′W], 4 ♂, 3 ♀ (DJB, RGH); Anglin Lake [53°44′N, 105°56′W], 3 ♂, 2 ♀ (DJB); Fort Carlton [52°52′N, 106°32′W], 1 ♀ (DJB); Besnard Lake [55°25′N, 106°00′W], 1 ♂, 2 ♀ (DJB); *Alberta:* Winfield [52°58′N, 114°26′W], 2 ♀; Fox Lake Reservation [58°26′N, 114°33′W], 1 ♂, 1 ♀ (DJB); Wentzel Lake [59°02′N, 114°28′W], 2 ♂, 1 ♀ (UASM); Steele Lake [54°40′N, 113°38′N], 2 ♂ (DJB); Athabasca [54°43′N, 113°17′W], 1 ♀ (DJB); Baptiste Lake [54°45′N, 113°35′W], 1 ♂, 2 ♀ (DJB); Marguerite Crag and Tail Provincial Park [57°43′N, 110°20′W], 1 ♀ (UASM); 90 km NW Peace River [56°42′N, 118°29′W], 2 ♀ (DSU); *British Columbia:* Little Prairie Lake [54°57′N, 120°11′W], 1 ♀ (CNC); Babine Lake Johnson Bay [54°45′N, 126°00′W], 9 ♀ (CNC); Atlin [59°34′N, 133°42′W], 2 ♀ (CNC); *Northwest Territory:* Martin River [61°55′N, 121°34′W], 1 ♀ (CNC); Maunoir Lake [67°29′N, 124°55′W], 1 ♀ (CNC); Wrigley [63°16′N, 123°36′W], 2 ♂, 2 ♀ (CNC); *Yukon Territories:* Kathleen Lake Kluane National Park [60°34′N, 137°17′W], 5 ♀ (CNC); Gravel Lake 58 mi E Dawson [63°48′N, 137°53′W], 2 ♀ (CNC); 13 mi E Dawson [64°03′N, 139°25′W], 2 ♀ (CNC); Old Crow [67°35′N, 137°53′W], 1 ♂, 2 ♀ (CNC).

Description.—*Female (n = 5):* Total length: 2.14 ± 0.46 mm; carapace length: 0.86 ± 0.09 mm; carapace width: 0.67 ± 0.05 mm; carapace smooth, shiny, yellow to light orange, radiating lines light brown, cephalic region of the carapace occasionally ornamented by a gray marking forming a trident (or psi, Ψ); 5 short erect setae along midline; sternum yellow to light orange with dusky gray margins. Chelicerae yellow to light orange, promargin with 4 large teeth, retromargin with 3–4 large teeth; cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, gray to dark gray, densely covered with semi-erect setae. Coxae, femora and patella yellow to light orange, tibia, metatarsi and tarsi light orange to dark brown, tibia I-IV with one dorsal macroseta; metatarsus I with dorsal trichobothrium, TmI 0.68–0.82, TmIV present. Epigynum with plate distinctly wider than long, posterior end of plate rising and recurving into a median process, tapered toward midline (Fig. 9); spermathecae c-shaped, beanlike, widely separate, situated near the anterior end of the epigynal plate (Figs. 9, 10).

Distribution.—Widespread species, apparently boreal.

Habitat.—This species has been recorded from several habitats, but mainly on coniferous vegetation and in forest litter.

Genus *Floricomus* Bishop & Crosby 1925

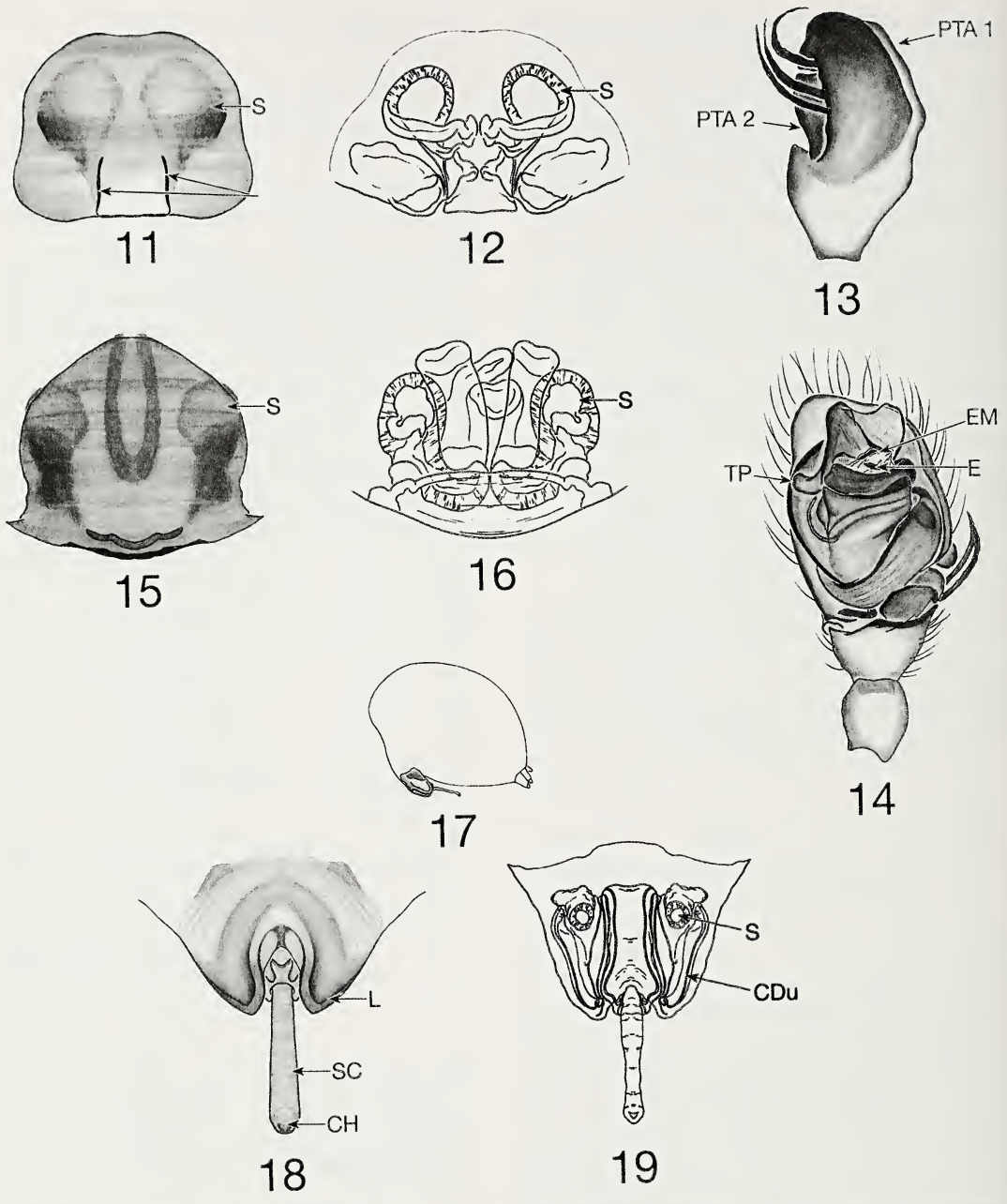
Floricomus praedesignatus Bishop & Crosby 1935

Figs. 11, 12

Floricomus praedesignatus Bishop & Crosby 1935b:38, pl. 6 figs. 22–24; Hormiga 1994:32 figs. 19e, f; Bélanger & Hutchinson 1992:31; Buckle et al. 2001:119; Paquin et al. 2001:17; Paquin & Dupérré 2003:105, figs. 1042–1045.

Material examined.—U.S.A.: *North Carolina:* Jackson County: Blue Ridge Park [36°53′N, 80°95′W], 1 ♂ (CNC); CANADA: *Québec:* Pink Lake Gatineau Park [45°28′N, 75°48′W], 1 ♀ (CNC).

Description.—*Female (n = 1):* Total length: 1.39 mm; carapace length: 0.58 mm; carapace width: 0.50 mm; carapace smooth, shiny, cephalic region and cervical groove dark brown shaded with gray; thoracic region light brown with radiating line slightly shaded with gray; carapace margin strongly shaded;



Figures 11–19.—Linyphiid structures: 11, 12. *Floricomus praedesignatus*: 11. Epigynum, ventral view; 12. Spermathecae, dorsal view. 13, 14. *Glyphesis idahoanus*: 13. Palpal tibia of male, dorsal view; 14. palpus of male, ventral view. 15, 16. *Gnathonaroides pedalis*: 15. Epigynum, ventral view; 16. Spermathecae, dorsal view. 17–19. *Lepthyphantes intricatus*: 17. Abdomen, lateral view; 18. Epigynum, ventral view; 19. Spermathecae, dorsal view. Abbreviations used: CH = Cochlea, CDu = Copulatory Ducts, E = Embolus, EM = Embolic Membrane, L = Lobe, PTA = Palpal Tibia Apophysis, SC = Scape, S = Spermatheca, TP = Tail Piece.

sternum dark brown suffused with gray, margin darker. Chelicerae light brown, promargin with 1 large tooth and 5 small teeth, retromargin with 5 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, dark gray, densely covered with semi-erect setae. Legs light orange with a tinge of brown, tibia I without dorsal macrosetae, tibia II-IV with one such seta; metatarsus I with dorsal trichobothrium, TmI 0.45; TmIV absent. Epigynum with plate inconspicuous, slightly convex, bearing two longitudinal fissures (Fig. 11); spermathecae rounded, and separated by less than half of their width (Figs. 11, 12).

Distribution.—Based on the few records known, this is an eastern species.

Habitat.—*Floricomus praedesignatus* has been collected in forest litter.

Genus *Glyphesis* Simon 1926

Glyphesis idahoanus (Chamberlin 1949)

Figs. 13, 14

Tapinocyba idahoana Chamberlin 1949:551 figs. 129, 130; West et al. 1988:82.

Glyphesis idahoana (Chamberlin): Aitchison-Benell & Dondale 1992:222; Bélanger & Hutchinson 1992:31; Dondale & Redner 1994:37.

Glyphesis idahoanus (Chamberlin): Buckle et al. 2001:119; Paquin et al. 2001:17; Paquin & Dupérré 2003:106, figs. 1050–1052.

Material examined.—CANADA: *Québec:* Les Buissons [49°06′N, 68°23′W], 1 ♀ (CNC); Lac Roddick [46°15′N, 75°53′W], 5 ♂, 2 ♀ (CNC); *Ontario:* Richmond [45°11′N, 75°50′W], 1 ♀ (CNC); Schaffeys Locks [44°35′N, 76°19′W], 1 ♀ (CNC); ~10 km W Carleton Place [45°08′N, 76°09′W], 1 ♂, 2 ♀ (CNC); Alfred [45°33′N, 76°52′W], 1 ♀ (CNC); *Manitoba:* Dauphin [51°09′N, 100°03′W], 1 ♂ (CNC); *Saskatchewan*: Grasslands National Park West Block [49°07′N, 107°26′W], 1 ♂ (DJB); *British Columbia:* Oliver [49°11′N, 119°33′W], 2 ♀ (CNC).

Description.—*Male (n = 5):* Total length: 1.32 ± 0.09 mm; carapace length: 0.51 ± 0.03 mm; carapace width: 0.47 ± 0.03 mm; carapace smooth, shiny, dark brown with radiating line and margin strongly shaded with gray, cephalic region ornamented by a dark gray inverse pear shape marking, 3 long erect setae along midline; sternum dark brown strongly shaded with gray. Chelicerae yellow to light brown, promargin with 3 large and 2 small teeth, retromargin with 4 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, dark gray, densely covered with short semi-erect setae. Legs yellow, coxae lightly shaded with gray, tibia I-IV with one dorsal macroseta; metatarsus I with dorsal trichobothrium, TmI 0.44–0.48, TmIV absent. Palpal tibia with one cuplike apophysis, dark brown to black, long, broad with 3 thick serrate setae (Fig. 13); second apophysis black, short, half hidden behind the cuplike apophysis; tail piece rather small, rounded; embolus thick, stout, hidden behind embolic membrane (Fig. 14).

Distribution.—Widespread species in Canada: from British to Quebec (Buckle et al. 2001).

Habitat.—This species has been recorded from litter near ponds, sphagnum and salt marshes.

Remarks.—This species was originally placed in the genus *Tapinocyba* Simon 1884 by Chamberlin (1949:551) based on the female genitalia. In defining the genus *Glyphesis*, Simon (1926:350) gave a diagnostic feature in the male palpal tibia bearing several strong setae (see Simon 1926, fig. 605). The male of *T. idahoana* has the same character as that illustrated by Simon for the type species *G. servulus* (Simon 1881). The species was placed in *Glyphesis* by Aitchison-Benell & Dondale (1992), without indication that this was a new combination, and subsequent authors have followed this placement. The examination and illustration of the male palp of the species confirm the generic placement in *Glyphesis*, along with *Glyphesis scopulifer* (Emerton 1882), which has the same tibial character (see Paquin & Dupérré 2003:106, fig. 1054). Holm (1968) proposed that *G. scopulifer* was a junior synonym of *G. servulus* (the type species), but this synonymy has been rejected (Buckle et al. 2001).

Genus *Gnathonaroides* Bishop & Crosby 1938

Gnathonaroides pedalis (Emerton 1923)

Figs. 15, 16

Araeoncus pedalis Emerton 1923:239, fig. 2.

Gnathonaroides pedale (Emerton): Jennings et al. 1988:61, Peck 1988:1202, Bélanger & Hutchinson 1992:32.

Gnathonaroides pedalis (Emerton): Bishop & Cros-

by 1938:84, pl. 6 figs. 65, 66; Levi & Field 1954: 447; Buckle et al. 2001:120; Paquin et al. 2001: 17; Paquin & Dupérré 2003:106, figs. 1056–1058.

Material examined.—U.S.A.: *New Hampshire:* Somerswort [43°15′N, 70°51′W], 1 ♂ (CNC); *Vermont:* Mounts Mansfield [44°32′N, 72°48′W], 2 ♂ (CNC); *Maine:* Piscataquis County: Soubunge Mountain [45°58′N, 69°12′W], 1 ♂ (CNC); CANADA: *Nova Scotia:* Cape Breton Highland National Park Lone Shieling [46°48′N, 60°57′W], 1 ♂ (CNC); Bridgewater [49°17′N, 122°54′W], 10 ♂ (CNC); *New Brunswick:* Acadia forest 10 mi E of Fredericton [45°56′N, 66°40′W], 5 ♂ (CNC); Kouchibouguac National Park [46°51′N, 64°58′W], 1 ♀ (CNC); *Québec:* Lac Roddick [46°15′N, 75°53′W], 1 ♂ (CNC); Mont-Albert, La Haute-Gaspésie, Parc de la Gaspésie, Ruisseau Cap Seize [48°59′N, 66°21′W], 1 ♂ (CNC); Maskinongé, Sainte-Angèle-de-Prémont [46°21′N, 73°03′W], 1 ♂ (CNC); Drummondville [45°53′N, 72°29′W], 1 ♀ (CNC); Lac Duparquet Abitibi [48°30′N, 79°13′W], 3 ♂, 3 ♀ (CPAD); *Ontario:* 7 km W Carleton Place [45°08′N, 76°09′W], 4 ♂ (CNC); Eastman Farm Chatterton [44°15′N, 77°29′W], 4 ♂ (CNC); El Dorado Gold Mine [44°45′N, 78°06′W], 1 ♂ (CNC); Guelph [43°33′N, 80°15′W], 1 ♂ (CNC); Ancaster [43°13′N, 79°59′W], 2 ♂, 1 ♀ (CNC); Rait [48°50′N, 89°56′W], 1 ♂ (CNC); *Manitoba:* Onanole [50°37′N, 99°58′W], 3 ♂, 1 ♀ (CNC); Riding Mountain National Park Clear Lake [50°40′N, 100°00′W], 1 ♂ (CNC); *Saskatchewan:* Lady Lake [52°02′N, 102°37′W], 1 ♂ (DJB); *Alberta:* Edmonton [53°33′N, 113°20′W], 3 ♂ (DJB); George Lake 16 km W Busby [53°57′N, 114°06′W], 1 ♂ (CMB).

Description.—*Female (n = 3):* Total length: 1.19 ± 0.13 mm; carapace length: 0.56 ± 0.05 mm; carapace width: 0.40 ± 0.05 mm; carapace smooth, shiny, light yellow, cephalic region light yellow with a tinge of orange, radiating lines and midline with diffused gray patterns; 5 long erect setae along midline; sternum yellow shaded lightly with gray, margin darker. Chelicerae yellow to light brown, promargin with 4 large teeth and 1 small tooth, retromargin with 5 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, off-white, densely covered with long semi-erect setae. Legs yellow with a tinge of orange, tibia I-III with two dorsal macrosetae and tibia IV with one dorsal seta; metatarsus I with dorsal trichobothrium, TmI 0.35–0.38, TmIV absent. Epigynal plate conspicuous, somewhat pentagonal, with two longitudinal dark bands converging below the middle of the plate, transversal band present near the posterior margin; posterior margin darker, more sclerotized (Fig. 15); spermathecae rounded, widely separated, situated at edge of lateral margin (Figs. 15, 16).

Distribution.—*Gnathonaroides pedalis* occurs in northern North America east of the Rockies. Buckle et al. (2001) report the species from New York and Maine.

Habitat.—This species has been found in various habitats including fields and grass, but it is mainly associated with forest litter, spruce litter and duff. Specimens from Lac Duparquet (Abitibi, Québec) have been collected under snow during winter.

Remarks.—External characters of the epigynum of *G. pedalis* are quite subtle and difficult to recognize. Thus, it is not surprising that the female has not been described as it has probably been classified in many collections as 'undet. Linyphiidae'.

Genus *Lepthyphantes* Menge 1866
Lepthyphantes intricatus (Emerton 1911)
Figs. 17–19

Microneta complicata Banks 1892:47, pl. 2, fig. 50 (preoccupied by *Lepthyphantes complicata* Emerton 1911); Banks 1916:77, pl. 10, fig. 14; Levi & Field 1954:446, figs. 22, 23 (male; not female, = *Centromerus cornupalpis*).

Bathyphantes intricata Emerton 1911:397, pl. 3 figs. 7, 7a–d.

Centromerus intricatus (Emerton): Freitag et al. 1969:1329.

Lepthyphantes intricatus (Emerton): Ivie 1969:6; van Helsdingen 1973:7 (synonymy with *Microneta complicata* Banks 1892); Koponen 1987: 285; West et al. 1988:79; Jennings et al. 1988:61; Bélanger & Hutchinson 1992:53; Aitchison & Sutherland 2000:638, 644; Buddle *et al.* 2000: 427–431; Buckle et al. 2001:128; Paquin et al. 2001:18; Paquin & LeSage 2001:98; Paquin & Dupérré 2003:141, figs. 1559–1561.

Material examined.—U.S.A.: *Maine:* Piscataquis County: Soubunge Mountain [45°58′N, 69°12′W], 1 ♂ (CNC); *Montana:* 5 mi N Whitefish [48°24′N, 114°20′W], 1 ♂, 2 ♀ (DJB); *New Mexico:* Los Alamos [35°51′N,

106°18′W], 1 ♂ (DJB); *New York:* Hamilton County: ~10 km ESE Brandreth [43°56′N, 74°51′W], 4 ♂, 2 ♀ (RF); CANADA: *New Brunswick:* Green River 30 mi N Edmunston [47°19′N, 68°09′W], 1 ♂, 3 ♀ (CNC); *New Scotia:* Cape Breton Highlands National Park [46°48′N, 60°57′W], 3 ♂ (CNC); Cape Breton Highlands National Park Lone Shieling [46°48′N, 60°57′W], 2 ♂, 2 ♀ (CNC); Cape Breton Highlands National Park MacKenzie Mountain [46°46′N, 60°49′W], 3 ♂, 1 ♀ (CNC); Cape Breton Highlands National Park North Mountain [46°53′N, 60°35′W], 4 ♂, 14 ♀ (CNC); Cape Breton Highlands National Park Paquet Lake [46°48′N, 60°41′W], 3 ♂, 1 ♀ (CNC); *Ontario:* Fathom Five National Park Bear Rump Island [45°17′N, 81°40′W], 1 ♂ (CMB); 30 mi E Dryden [49°47′N, 92°45′W], 1 ♂ (CNC); Grundy provincial Park [45°56′N, 80°32′W], 1 ♀ (CNC); 56 mi N Hurket [49°20′N, 88°53′W], 1 ♀ (CNC); 20 mi E Kenora [49°49′N, 94°26′W], 2 ♂ (CNC); Long Point Squires Ridge [42°34′N, 80°15′W], 1 ♀ (CNC); 75 mi W Marathon [48°52′N, 87°35′W], 1 ♂ (CNC); 22 mi S Pickle Lake [51°28′N, 90°12′W], 1 ♀ (CNC); Raith [48°50′N, 89°56′W], 1 ♂ (CNC); Spencerville [44°51′N, 75°33′W], 1 ♀ (CNC); Tillsonburg [42°51′N, 80°44′W], 1 ♀ (CNC); Turkey Point [42°42′N, 80°19′W], 1 ♀ (CNC); Walsingham [42°41′N, 80°32′W], 1 ♂ (CNC); Wawa [47°59′N, 84°47′W], 6 ♂, 25 ♀ (CNC); *Québec:* Gatineau Park King Mountain [45°29′N, 75°52′W], 1 ♂, 3 ♀ (CNC); Lac Roddick [46°15′N, 75°53′W], 1 ♀ (CNC); 24 mi S Ste-Anne-des-Monts [48°52′N, 65°58′W], 1 ♂ (CNC); Lac Duparquet Abitibi [48°30′N, 79°13′W], 3 ♂, 3 ♀ (CPAD); La Haute-Gaspésie, Parc de la Gaspésie; Mines Madeleine [48°57′N, 66°01′W], 1 ♂ (CNC); La Rivière-du-Nord, Saint-Hippolyte, Station biologie Université de Montréal [45°59′N, 74°00′W], 1 ♂ (CPAD); Antoine-Labelle, Lac Saguay, hwy 117 [46°32′N, 75°09′W], 1 ♂ (CPAD); Val-d'Or, Vallée-de-l'Or, Louvicourt, hwy 117, km 491 [48°04′N, 77°23′W], 2 ♂, 1 ♀ (CPAD); *Manitoba:* Dauphin [51°09′N, 100°03′W], 1 ♂ (CNC); Riding Mountain National Park North Gate [50°53′N, 100°15′W], 1 ♂, 4 ♀ (CNC); Riding Mountain National Park East Escarpment [50°53′N, 100°15′W], 1 ♂ (CNC); Riverton [50°59′N, 96°59′W], 1 ♂, Wallace Lake [51°00′N, 95°21′W], 1 ♂, 3 ♀ (CNC); *Saskatchewan:* Anglin Lake [53°44′N, 105°56′W], 8 ♂, 12 ♀ (DJB); Besnard Lake [55°25′N, 106°00′W], 4 ♂ (DJB); *Alberta:* Blood Indian Reserve 148A [49°03′N, 113°42′W], 1 ♂ (DJB); Waterton National Park [49°04′N, 113°47′W], 7 ♂, 1 ♀ (DJB); Waterton Lakes National Park Cameron Lake [49°01′N, 114°04′W], 2 ♂, 1 ♀ (CNC); Baptiste Lake [54°45′N, 113°35′W], 3 ♂, 3 ♀ (DJB); 19 km N of Calling Lake [55°15′N, 113°12′W], 2 ♂ (DJB); Edmonton [53°33′N, 113°28′W], 1 ♂, 1 ♀ (DJB); 25 km sw Rocky Mountain House [52°22′N, 114°55′W], 6 ♂, 3 ♀ (HAC, DJB); ~20 km s Slave Lake 3 ♂, 1 ♀, [55°23′N, 115°13′W], (CMB); *British Columbia:* Babine Lake [54°45′N, 126°00′W], 1 ♀ (CNC); Cougar Canyon Ecological Reserve Vernon [50°09′N, 119°19′W], 1 ♂ (CNC); 15 mi NE Kamloops [50°40′N, 126°19′W], 1 ♀ (CNC); Pinkut Creek [54°27′N, 125°27′W], 1 ♀ (CNC); Lumby [50°15′N, 118°58′W], 1 ♂ (CNC); Vance Creek Ecological Reserve Vernon [50°17′N, 118°57′W], 1 ♂ (CNC).

Description.—*Female (n = 5):* Total length: 2.94 ± 0.23 mm; carapace length: 1.11 ± 0.09 mm; carapace width: 0.89 ± 0.06 mm; carapace smooth, shiny, light orange to orange-brown with radiating line and midline shaded with gray; carapace with diffuse gray margins; 2 long erect setae along midline; sternum light orange shaded with gray. Chelicerae light orange to orange-brown, promargin with 3 large teeth, retromargin with 4–7 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, light to dark gray, sparsely covered with long erect setae. Legs light orange to orange-brown, tibia I-IV with two dorsal macrosetae; metatarsus I with dorsal trichobothrium, TmI 0.26–0.35, TmIV absent. Epigynum with plate deeply notched, dividing into two protruding lobes; scape long, narrow, slightly widening toward the tip, cochlear present at tip (Figs. 17, 18); spermathecae small, copulatory ducts long, following the folding of the epigynum (Fig. 19).

Distribution.—Widespread boreal species (see also Buckle et al. 2001).

Habitat.—This common species has been collected in forested habitat, under rocks and logs, mainly in deciduous litter and occasionally in coniferous stands.

Remarks.—Ivie (1969) was the first to

place *M. intricatus* in *Lepthyphantes*. In his 1973 paper, however, van Helsdingen overlooked Ivie's paper and erroneously treated it as a new combination.

While *L. intricatus* is similar to other *Lepthyphantes* in its general morphology, the form of both palp and epigynum differ sufficiently from that of *L. minutus*, the type species of *Lepthyphantes*, and from other species of *Lepthyphantes*, sens lat., as to very likely justify its placement in a new genus. This transfer, however, is best left for a future revisional study.

Genus *Scyletria* Bishop & Crosby 1938
Scyletria inflata Bishop & Crosby 1938
Figs. 20, 21

Scyletria inflata Bishop & Crosby 1938:89, pl. 7 figs. 72–74; Bélanger & Hutchinson 1992:38; Aitchison-Benell & Dondale 1992:224; Buckle et al. 2001:141; Paquin et al. 2001:19; Paquin & Dupérré 2003:118, figs. 1233–1235.

Material examined.—CANADA: *Newfoundland:* The Arches [50°06′N, 57°40′W], 1 ♀ (CNC); *Nova Scotia:* Cape Breton Highlands National Park N of Paquet Lake [46°48′N, 60°41′W], 1 ♀ (CNC); Cape Breton Highlands National Park Lone Shieling [46°48′N, 60°57′W], 1 ♂ (CNC); Cape Breton Highlands National Park Pleasant Bay [49°49′N, 60°48′W], 1 ♂ (CNC); *New Brunswick:* Priceville 12 mi NW Boiestown [46°31′N, 66°17′W], 1 ♀ (CNC); Green River 30 mi N Edmunston [47°19′N, 68°09′W], 4 ♂, 1 ♀ (CNC); 25 km SW Bathurst [47°37′N, 65°37′W], 1 ♀ (CNC); Fredericton [45°56′N, 66°40′W], 1 ♂ (CNC); *Québec:* Îles-de-la-Madeleine Grosse-Île [47°37′N, 61°31′W], 1 ♀ (CNC); St-Méthode [48°43′N, 72°24′W], 1 ♀ (CNC); St-Hippolyte [45°31′N, 73°41′W], 2 ♂ (CNC); Baie-James; Jamésie [49°43′N, 79°17′W], 2 ♀ (CPAD); *Ontario:* Spruce River Sturgeon Lake 42 mi N of Hurkett [50°23′N, 92°30′W], 1 ♀ (CNC); *Manitoba:* Duck Mountain National Park Cowan Creek [52°01′N, 100°38′W], 1 ♀ (CNC); Riding Mountain National Park Swanson spring [50°53′N, 100°15′W], 1 ♂ (CNC); Riding Mountain National Park Jackfish Creek [50°45′N, 100°14′W], 4 ♂, 2 ♀ (CNC); Fort Churchill [58°45′N, 94°04′W], 2 ♂ (CNC); *Saskatchewan:* Lady Lake [52°02′N, 102°37′W], 13 ♂, 7 ♀ (DJB); *Alberta:* Wentzel Lake [59°02′N, 114°28′W], 2 ♂, 1 ♀ (UASM); Cypress Hills Provincial Park Elkwater Lake [49°40′N, 110°17′W], 2 ♀ (CNC); Athabasca [54°43′N, 113°17′W], 2 ♂ (DJB); Baptiste Lake [54°45′N, 113°35′ W], 5 ♂, 5 ♀ (DJB); George Lake 16 km W Busby [53°57′N, 114°06′W], 1 ♂ (AG); Winagami Provincial Park [55°36′N, 116°40′W], 1 ♀ (DJB); *Northwest Territories*: Harris River Fort Simpson [61°51′N, 121°20′W], 1 ♂ (CNC).

Description.—*Female (n = 5):* Total length: 1.65 ± 0.16 mm; carapace length: 0.68 ± 0.05 mm; carapace width: 0.48 ± 0.05 mm; carapace smooth, shiny, light brown to dark brown with diffused gray patterns along radiating lines and midline; carapace margin darker strongly shaded with gray; 4–5 erect setae along midline; sternum dark brown to almost black, shaded with gray. Chelicerae yellow to light brown, promargin with 4–5 large teeth, retromargin with 4–5 denticles. Cheliceral stridulatory organ visible, weak, ~13 ridges. Abdomen unicolor, gray to dark gray, densely covered with short semi-erect setae. Legs light brown to brown, tibia I-III with two dorsal macrosetae and tibia IV with one dorsal seta; metatarsus I with dorsal trichobothrium, TmI 0.43–0.56, TmIV absent. Epigynum with plate extended posteriad over the epigastric furrow, wider than long, divided in two rounded blunt prominences (Fig. 20); spermathecae small, widely separated, situated near the anterior margin of the epigynal plate (Figs. 20, 21).

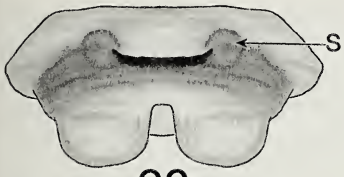
Distribution.—This species is widely distributed in northern North America and is also found in New York and North Carolina in the east (Buckle et al. 2001).

Habitat.—*Scyletria inflata* has been recorded from a wide range of habitats: moss and litter in coniferous forest, moss and algal mats near beaches, riparian vegetation, in conifers and river banks.

Remarks.—The female illustrated under the name *Cephalethus birostrum* Chamberlin & Ivie 1947: fig. 21 (now placed in *Savignia*) appears very similar to *S. inflata*.

Genus *Sisicus* Bishop & Crosby 1938
Sisicus penifusifer Bishop & Crosby 1938
Figs. 22, 23

Sisicus penifusiferus Bishop & Crosby 1938:62, pl. 2 figs. 12, 13; Levi & Field 1954:448; Drew 1967:172; West et al. 1984:87; Jennings et al.



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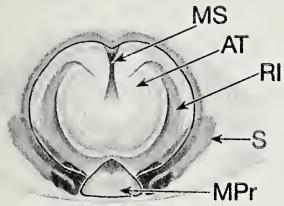

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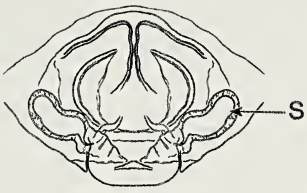

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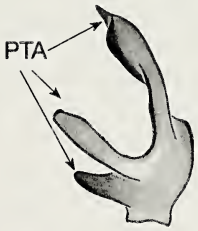

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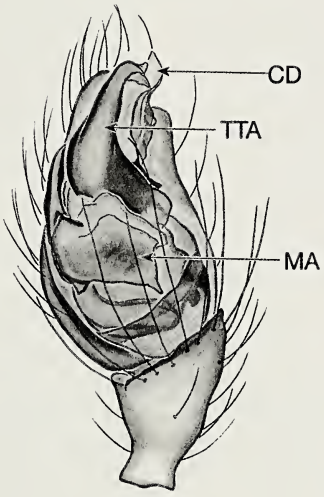

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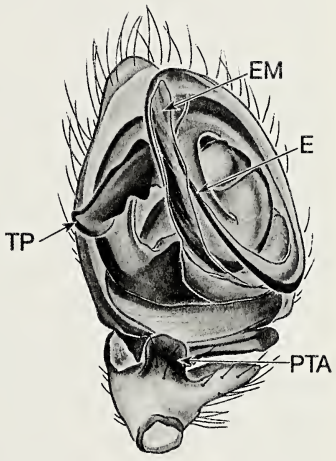

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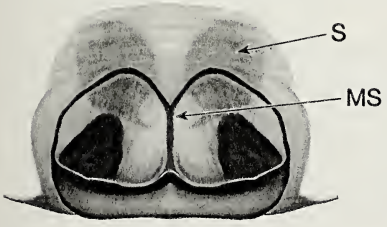

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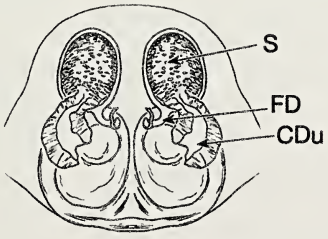

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Figures 20–30.—Linyphiid and theridiid structures: 20, 21. *Scyletria inflata*: 20. Epigynum, ventral view; 21. Spermathecae, dorsal view. 22, 23. *Sisicus penifusifer*: 22. Epigynum, ventral view; 23. Spermathecae, dorsal view. 24–26. *Walckenaeria clavipalpis*: 24. Carapace of male, lateral view; 25. Palpal tibia of male, dorsal view; 26. Palpus of male, ventral view. 27, 28. *Robertus crosbyi*: 27. Palpus of male, cymbium and tibia, dorsal view; 28. Palpus of male, ventral view. 29, 30. *Thymoites minnesota*: 29. Epigynum, ventral view; 30. Spermathecae, dorsal view. Abbreviations used: AT = Atrium, CD = Conductor, CDu = Copulatory Ducts, E = Embolus, EM = Embolic Membrane, FD = Fertilization Ducts, MA = Median Apophysis, MPr = Median Process, MS = Median Septum, PTA = Palpal Tibia Apophysis, RI = Rim, S = Spermatheca, TTA = Theridiid Terminal Apophysis, TP = Tail piece.

1988:61; Aitchison-Benell & Dondale 1992:224; Bélanger & Hutchinson 1992:38.

Sisicus penifusifer Bishop & Crosby: Buckle et al. 2001:142; Paquin et al. 2001:19; Paquin & Dupérré 2003:148, figs. 1639–1640.

Material examined.—CANADA: *Newfoundland:* Lloyds River [48°32′N, 57°13′W], 2 ♀ (CNC); Trout River w of Badger [48°59′N, 56°02′W], 2 ♂, 4 ♀ (CNC); Pasadena [49°01′N, 57°36′W], 3 ♀ (CNC); *Nova Scotia:* Cape Breton Highlands National Park Franey Mountain [46°41′N, 60°28′W], 2 ♂, 2 ♀ (CNC); Cape Breton Highlands National Park MacKenzie Mountain [46°46′N, 60°49′W], 3 ♀ (CNC); Cape Breton Highlands National Park Lone Shieling [46°48′N, 60°57′W], 1 ♂, 4 ♀ (CNC); Cape Breton Highlands National Park Beulack Ball Falls [46°44′N, 60°38′W], 1 ♂, 1 ♀ (CNC); Cape Breton Highlands National Park Black Brook [46°44′N, 60°38], 2 ♀ (CNC); Bridgewater [49°17′N, 122°54′W], 5 ♂ (CNC); *New Brunswick:* Fredericton [45°56′N, 66°40′W], 2 ♂, 2 ♀ (CNC); Kouchibouguac National Park [46°51′N, 64°58′W], 7 ♀ (CNC); *Québec:* Forillon National Park [48°54′N, 64°21′W], 1 ♀ (CNC); Gatineau Park King Mountain [45°29′N, 75°52′W], 1 ♀ (CNC); Cedarville [45°01′N, 72°13′W], 1 ♀ (CNC); Maskinongé, Sainte-Angèle-de-Prémont [46°21′N, 73°03′W], 1 ♀ (CNC); Baie-James, Jamésie, Val Paradis [49°16′N, 79°08′W], 3 ♀ (CPAD); Pontiac, Les Collines-de-l'Outaouais, 2 km North of Eardley [45°34′N, 76°05′W], 1 ♂ (CPAD); Abitibi-Ouest, Duparquet [48°30′N, 79°14′W], 1 ♂, 1 ♀ (CPAD); Kazabazua, La Vallée-de-la-Gatineau, Lac Danford [45°57′N, 76°08′W], 1 ♀ (CPAD); *Ontario:* Huntsville [45°20′N, 79°13′W], 1 ♀ (CNC); Ottawa [46°16′N, 75°45′W], 1 ♀ (CNC); Kinburn [43°23′N, 76°11′W], 5 ♀ (CNC); Christie Lake [44°49′N, 76°25′W], 1 ♀ (CNC); Gower [45°08′N, 75°43′W], 1 ♂ (CNC); *Manitoba:* Turtle Mountain [49°03′N, 100°08′W], 5 ♀ (CNC); *Saskatchewan:* Beaver Creek 15 mi S Saskatoon [51°55′N, 106°43′W], 1 ♂, 1 ♀ (CNC); *Alberta:* Edmonton [53°33′N, 113°28′W], 2 ♂, 1 ♀ (CNC); *British Columbia:* Gold Stream Park Vancouver Island [48°28′N, 123°33′W], 1 ♂, 1 ♀ (CNC); Burton [49°59′N, 117°53′W], 3 ♀ (CNC).

Description.—*Female (n = 5):* Total length: 1.08 ± 0.11 mm; carapace length: 0.49 ± 0.04 mm; carapace width: 0.33 ± 0.04 mm; carapace smooth, shiny, light yellow to light brown, sometimes with diffused gray markings; 5–6 erect setae along midline; sternum light yellow slightly shaded with gray. Chelicerae yellow to light brown, promargin with 4–5 large teeth, retromargin with 5 denticles. Cheliceral stridulatory organ not visible with stereomicroscope. Abdomen unicolor, off-white to light yellow, densely covered with long semi-erect setae. Legs light yellow to light brown, tibia I-II with two dorsal macrosetae and tibia III-IV with one dorsal seta; metatarsus I with dorsal trichobothrium, TmI 0.27–0.38, TmIV absent. Epigynum with atrium broad, deep, almost round; median septum slender, short, extending one-half length of atrium; presence of a rim along side of atrium; (Fig. 22); posterior end of epigynal plate rising, recurving into a median triangular process; spermathecae elongated reaching one-half length of atrium (Figs. 22, 23).

Distribution.—Widespread species in Canada, from British Columbia to Québec and the northern states of USA.

Habitat.—*Sisicus penifusifer* has been mainly collected in forest litter (deciduous and coniferous), under logs, in duff and moss.

Remarks.—The original description of the species includes a description and illustrations of the male, but also a short description of the female which is not mentioned by Platnick (2004). Bishop & Crosby (1938) did not, however, include any illustrations of the female epigynum which is shown here for the first time.

Genus *Walckenaeria* Blackwall 1833

Walckenaeria clavipalpis Millidge 1983

Figs. 24–26

Walckenaeria clavipalpe Millidge 1983:135, figs. 95, 117, 118.

Walckenaeria clavipalpis Millidge: Paquin et al. 2000:272; Paquin & LeSage 2001:101; Buckle et al. 2001:149; Paquin et al. 2001:20; Paquin & Dupérré 2003:125, figs. 1319–1322.

Material examined.—CANADA: *Newfoundland:* Gros Morne National Park Stanford River [49°41′N, 57°44′W], 1 ♀ (RPC); Gros Morne National Park east 1 ♀Main River West [49°41′N, 57°44′W], 3 ♂ (RPC); Port-au-Choix [50°42′N, 57°22′W], 2 ♂, 1 ♀ (RPC); *Québec:* Réserve faunique des Laurentides [47°41′N, 70°51′W], 1 ♂, 1 ♀

(MLC); La Haute-Gaspésie, Parc de la Gaspésie; Mines Madeleine [48°57′N, 66°01′W], 2 ♂ (CNC).

Description.—*Male (n = 1):* Total length: 2.55 mm; carapace length: 1.05 mm; carapace width: 0.85 mm; carapace dark brown, radiating lines and cephalic groove darker brown, midline shaded with black; sternum dark brown, margin darker; cephalic horn absent (Fig. 24). Chelicerae brown, promargin with 3 large teeth and 1 small tooth, retromargin with 2–3 denticles. Cheliceral stridulatory organ easily visible, well developed, ~11 ridges widely separated. Abdomen unicolor, dark gray, densely covered with medium length semi-erect setae. Legs orange, tibia I-II with two dorsal macrosetae and tibia III-IV with one dorsal seta; metatarsus I with dorsal trichobothrium, TmI 0.49, TmIV absent. Palpal tibia with four apophyses (3 dorsal, 1 ventral) (Fig. 25); tail piece long, apex billhook shaped; embolus long, coiled, covering 3/4 of the genital bulb length; embolic membrane long, narrow, covering 3/4 of the genital bulb length (Fig. 26).

Distribution.—This rare species was known only from Mt Whiteface (New York) (Millidge 1983), the type locality, and the Gaspésie Park (Québec). Based on these records, the species was tentatively placed in the Alpine-Appalachian category (*sensu* LeSage & Paquin 2001) by Paquin et al. (2000). The records given here provide additional support for this placement as both localities confirm the alpine and Appalachian affinities of the species.

Habitat.—Coniferous forest litter on the summits of North-East North America; ~500 m and higher.

Family Theridiidae Sundevall 1833
Genus *Robertus* O. Pickard-Cambrdidge 1879
Robertus crosbyi (Kaston 1946)
Figs. 27, 28

Ctenium crosbyi Kaston 1946:7, fig. 52.
Robertus crosbyi (Kaston 1946): Brignoli 1983: 411; Aitchison-Benell & Dondale 1992:219, Bélanger & Hutchinson 1992:81; Paquin et al. 2001: 24; Paquin & Dupérré 2003:218, figs. 2435–2437.

Material examined.—CANADA: *Québec:* Rivière-du-Loup, Île Verte [47°50′N, 69°32′W], 6 ♂, 6 ♀ (CNC); Pontiac, Les Collines-de-l'Outaouais, Parc de la Gatineau, Lac Brown [45°36′N, 75°55′W], 1 ♂ (CNC); Îles-de-la-Madeleine [47°24′N, 61°47′W], 1 ♀ (CNC); *Manitoba:* Riding Mountain National Park [46°41′N, 60°28′W], 1 ♀ (CNC); *Alberta:* Athabasca [54°45′N, 113°35′W], 1 ♀ (DJB).

Description.—*Male (n = 3):* Total length: 2.31 ± 0.06 mm; carapace length: 1.13 ± 0.07 mm; carapace width: 0.92 ± 0.06 mm; carapace smooth, shiny, light brown to dark brown, cephalic groove slightly darker, radiating lines shaded with gray; sternum brown shaded with gray, margin darker. Chelicerae dark. Abdomen unicolor, light gray to dark gray, sparsely covered with long erect setae. Legs light brown. Palpal tibia with one apophysis, cymbium with one lateral apophysis lacking apical setae (Fig. 27). Theredíid terminal apophysis elongated, narrowing into a hook bearing an additional process; median apophysis bearing two basal points, median apophysis projecting toward the apex of the palpus and curving behind the terminal apophysis; conductor sinuate, projecting apically (Fig. 28).

Distribution.—In the original description, Kaston (1946) lists only two records from New York. Based on the few records available, this is a widespread but rarely collected species.

Habitat.—*Robertus crosbyi* seems associated with salt marshes, sea wrack, lakeshore litter and mosses in boggy areas.

Genus *Thymoites* Keyserling 1884
Thymoites minnesota Levi 1964
Figs. 29, 30

Thymoites minnesota Levi 1964:467, figs. 74–76; Levi & Randolph 1975:47; Bélanger & Hutchinson 1992:85; Dondale et al. 1997:78; Paquin et al. 2001:24; Paquin & Dupérré 2003:224 figs. 2509–2511.

Material examined.—U.S.A.: *North Dakota:* Bottineau County [county record only], 1 ♀ (DSU); CANADA: *Nova Scotia:* Lockeport [43°42′N, 65°07′W], 1 ♂ (CNC); *New Brunswick:* Sackville [45°55′N, 63°23′W], 1 ♂ (CNC); *Québec:* Saint-Jean-sur-Richelieu, Le Haut-Richelieu, L'Acadie [45°18′N, 73°20′W], 1 ♂, 1 ♀ (CPAD); Rivière-du-Loup, Île Verte [47°50′N, 69°32′W], 4 ♂ (CNC); Îles-de-la-Madeleine [47°24′N, 61°47′W], 1 ♂ (CNC); *Ontario:* Wawa

[47°59′N, 84°47′W], 1 ♀ (CNC); *Saskatchewan:* Lady Lake [52°02′N, 102°37′W], several ♂, several ♀ (MCZ, DJB); St-Denis [52°09′N, 106°07′W], 1 ♂, 1 ♀ (DJB); *Manitoba:* 9 mi W Souris [49°37′N, 100°15′W], 1 ♀ (CNC); *Alberta:* Waterton Lake National Park [49°01′N, 114°04′W], 1 ♂, 2 ♀ (CNC); Wentzel Lake [59°02′N, 114°28′W], 1 ♂ (UASM); 5 mi S Armena [53°07′N, 112°57′W], 1 ♀ (AG); Baptiste Lake [54°45, 113°35], 1 ♂ (DJB); 7 km W Bittern Lake [53°01′N, 113°03′W], 1 ♂ (AG); *Northwest Territories:* Yellowknife [62°27′N, 114°21′W], 1 ♂ (CNC); *Yukon Territory:* Old Crow [67°35′N, 137°53′W], 1 ♀ (CNC).

Description.—*Male (n = 5):* Total length: 2.18 ± 0.32 mm; carapace length: 0.77 ± 0.01 mm; carapace width: 0.76 ± 0.02 mm; carapace shiny, yellow with a tinge of orange, gray to black band along midline and along the second half of carapace margin; chelicerae light yellow to yellow; sternum yellow with a tinge of orange, margin shaded with gray. Abdomen unicolor, off-white or off-white with random pattern of white pigment, sparsely covered with decumbent setae; ventral side of abdomen often with a gray to black triangular mark above the spinnerets and two oval markings on each side of the epigynum. Legs yellow-orange. Epigynal plate with atrium, deep, divided in two by a complete median septum; posterior margin of plate rising and forming a ledge connecting with the median septum (Fig. 29); copulatory ducts large, spermathecae oval, situated at anterior margin of the epigynal plate (Figs. 29, 30).

Distribution.—Widespread northern species.

Habitat.—*Thymoites minnesota* has been recorded from limestone outcrops, moss, freshwater sedge marshes, salt marshes, and a male and female were collected in a pitfall trap in a cultivated field in L'Acadie (Québec).

DISCUSSION

Couples *in copula* are rarely used as a reference for matching the sexes of a given species. Usually, we rely on the co-occurrence of two sexes in the same sample, or the occurrence of an unmatched sex in a precise region or habitat in which only one species of a given genus is known. Although these practices may lead to incorrect matches of sexes, most associations were done using these simple methods, resulting in a very low number of misassociations. In almost all the present cases, at least one couple was collected together in a given sample, thereby, facilitating the correct associations between the sexes. Also, the fauna of the Québec region is well known, therefore limiting the possibilities of a mismatch (see Bélanger & Hutchinson 1992; Paquin et al. 2001).

Knowledge of spider fauna is highly dependent on museum collections that gathered specimens from several types of surveys and biodiversity studies. In the present case, examination of material preserved in museums and private collections allowed us to fill some gaps for species descriptions. The accessibility of such material was essential to this study. Museum specimens provide not only precious information about specimens, but may also be used to orient further collecting to discover an unknown sex or to collect fresh specimens for DNA studies.

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CAPTURE EFFICIENCY AND PRESERVATION ATTRIBUTES OF DIFFERENT FLUIDS IN PITFALL TRAPS

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ABSTRACT. Pitfall traps are widely used to capture arthropods. The type of fluid employed in the traps can affect size and condition of the catch. Direct comparisons of different fluids allow entomologists to avoid suboptimal solutions, and facilitate comparisons between studies using different fluids. We compared capture efficiency and preservation attributes between five fluids in a field experiment with special respect to spiders (Araneae) and ground beetles (Coleoptera, Carabidae). Catches in pure water, ethanol-water and ethanol-glycerin were less well preserved than in brine or ethylene glycol-water. Brine and ethanol-glycerin showed low capture efficiencies, presumably because their high specific density made arthropods float and thereby facilitated escape. Only the mixture of ethylene glycol and water combined good preservation attributes with high capture efficiency, and therefore represented the best solution.

Keywords: Brine, ethanol, ethylene glycol, glycerin, pitfall traps

Originally described by Barber (1931), pitfall traps continue to be among the most widely employed sampling methods for ground-dwelling arthropods, particularly spiders (Araneae) and ground beetles (Coleoptera, Carabidae). Consisting of cups sunk into the ground flush with the surface, pitfall traps are inexpensive, easy to use and operate round-the-clock, resulting in large, species-rich samples (Clark & Blom 1992). A variety of liquids are employed to retain, kill and preserve the arthropods. Solutions of formalin and water were once common, but have been largely abandoned because of health hazards (van den Berghe 1992). Pure water is an alternative (Waage 1985), but mixtures with ethanol, glycerin, ethylene glycol or brine are often preferred because their conservation attributes are presumably better (Holopainen 1992; Teichmann 1994). The use of different preservatives also affects sampling efficiency and thereby complicates comparisons between studies. As only a few replicated field studies have been published that compare different preservatives, informed recommendations remain difficult (Weeks & McIntyre 1997; Lemieux & Lindgren 1999). Here, we compared sampling efficiencies and conservation attributes of five commonly used fluids in a field experiment.

METHODS

The preservatives compared in this study were (tap) water, brine (saturated solution of NaCl in water), 2:1 mixture of ethanol and water, 3:1 mixture of ethanol and glycerin, and 1:3 mixture of ethylene glycol (automobile antifreeze) and water. An unscented detergent was added to all liquids to break the surface tension and accelerate wetting and killing of arthropods (Topping & Luff 1995). The traps consisted of 0.2 liter plastic cups with an opening of 7.0cm diameter. They were protected from rain with 25 × 25cm acrylic glass roofs. Two cm from the top of the cup, pieces of 2cm mesh hardware cloth were inserted to hold off vertebrates (Hall 1991). Forty of these traps were installed in a fallow on calcareous soil near Göttingen, Germany, in a grid with 5m distance between traps. Seventy ml of each of the five preservatives described above were added to the traps with eight replicates in a Latin square design. The traps were operated for seven days starting on 2 May 2003. Upon withdrawal, catches were transferred to polyethylene bottles and stored at 4°C for another week. Then, the volume of remaining liquid was recorded after pouring it

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Table 1.—Differences between fluids in the percentage of damaged spiders (with detached legs, palps or opisthosomae), the amount of liquid retrieved, numbers of individuals (N), species (S) or genera (G) captured. Means ± SE. One-way ANOVA, or Kruskal-Wallis ANOVA when variance homogeneity was not met (Hymenoptera N and springtail N). Means preceded by different capitals are significantly different at $P < 0.05$.

Tested variable	Water	Brine	Ethanol-water	Ethanol-glycerin
Damaged spiders [%]	^{A}28.9 ± 3.7	^{B}9.0 ± 1.6	^{A}38.1 ± 6.0	^{A}33.3 ± 4.0
Liquid [ml]	^{B}46.8 ± 1.0	^{A}52.6 ± 1.4	^{D}8.8 ± 1.2	^{C}29.6 ± 0.9
Arthropod N	87.8 ± 9.7	63.9 ± 8.6	79.0 ± 7.2	68.5 ± 10.8
Spider N	^{A}45.8 ± 5.1	^{C}23.5 ± 3.2	^{AB}40.0 ± 4.8	^{BC}30.0 ± 4.8
Spider S	7.5 ± 0.6	5.9 ± 0.5	6.5 ± 0.7	6.0 ± 0.4
Ground beetle N	18.0 ± 2.8	11.6 ± 2.2	14.3 ± 1.4	14.0 ± 3.8
Ground beetle G	^{AB}4.4 ± 0.3	^{B}3.9 ± 0.3	^{A}5.1 ± 0.3	^{B}3.8 ± 0.4
Hymenoptera N	4.3 ± 1.0	17.3 ± 9.8	8.1 ± 4.4	3.5 ± 1.2
Springtail N	^{AB}2.6 ± 0.6	^{B}1.5 ± 0.5	^{AB}2.8 ± 0.8	^{A}8.3 ± 2.0
Diptera N	^{A}6.5 ± 1.1	^{B}1.6 ± 0.5	^{B}3.5 ± 0.7	^{B}2.6 ± 0.7

through gauze, and the arthropods were transferred to 80% ethanol. The condition of the catch was noted with particular attention to signs of decomposing processes, such as the percentage of spiders with detached body parts (legs, palps or opisthosomae). All arthropods were identified to order. Spiders were further identified to species, and ground beetles to genera. The number of genera was used as a surrogate of ground beetle species richness (Báldi 2003). The weather during the sampling period was dry and sunny, with an average temperature of 14.7 °C (2.9°–30.0°), mean wind velocity of 3.4 m/s (daily average 1.4–6.4), and 8.5 hours of sunshine per day (0.5–14.2). Rain (1.5mm) occurred only on the last of the seven sampling days (data supplied by Deutscher Wetterdienst, Offenbach, Germany).

RESULTS

The condition of the samples differed markedly between preservatives. The percentage of spiders that had lost body parts was nearly three times as high in water, ethanol-water and ethanol-glycerin as in brine and ethylene-glycol (Table 1). Additionally, all ethanol-water and two out of eight brine samples developed mold after one week in the refrigerator. Most liquid was retrieved from the traps filled with ethylene glycol and brine, representing 77% and 75% of the initial volume, respectively. Significantly less liquid was retrieved from traps filled with water (67%), ethanol-glycerin (42%) and ethanol-water (13%) at the end of the experiment (Table 1).

The overall catch was 1522 spiders (comprising 1232 Lycosidae, 248 Tetragnathidae, and 42 individuals from six other families), 607 ground beetles, 336 Hymenoptera (96% ants, Formicidae), 127 springtails (Collembola), 122 dipterans and 289 other arthropods. While the total number of arthropods was not significantly different between liquids, the number of spiders, springtails and dipterans, and the number of ground beetle genera showed significant treatment effects (Table 1). Thirty-five percent fewer spider individuals were captured in brine and ethanol-glycerin compared to the three remaining liquids. The number of ground beetle genera was 25% lower in brine and ethanol-glycerin than in ethanol-water and ethylene glycol. The number of dipterans was 6.5 times as high in water as in ethylene glycol, with intermediate values in the three remaining liquids, and 7.3 times as many springtails were captured in ethanol-glycerin than in brine and ethylene glycol.

DISCUSSION

Both preservation attributes and sampling efficiency differed between the fluids compared in this study. High losses of volume from ethanol-glycerin and ethanol-water suggest that the ethanol had largely evaporated during one week of exposure. The development of mold in ethanol-water catches gives additional indication that most of the ethanol, and thereby the conservation attributes of the solution, had disappeared. The mold presumably also kept back an additional part of the remaining liquid, explaining why markedly

Table 1.—Extended.

Glycol	$F_{4,35}$	P	χ^2	P
^{B}14.7 ± 3.7	9.5	<0.001		
^{A}53.6 ± 3.2	118	<0.001		
75.8 ± 7.8	1.1	0.38		
^{ABC}37.0 ± 6.1	3.2	0.026		
7.3 ± 0.6	1.6	0.18		
18.0 ± 2.4	1.1	0.38		
^{A}5.0 ± 0.4	3.6	0.015		
8.5 ± 5.8			2.0	0.73
^{B}0.8 ± 0.4			10.8	0.028
^{C}1.0 ± 0.4	9.3	<0.001		

less than the deployed amount of water could be retrieved, while losses from the pure water traps were minor. Water and brine catches smelled offensive, and water attracted high numbers of dipterans, which are further signs for the decay occurring in these catches. High percentages of spiders had lost body parts in the water, ethanol-water and ethanol-glycerin catches, indicating softening of the cuticle due to decomposition and/or chemical processes. Ground beetles appeared to be less vulnerable to decomposition than spiders (Holopainen 1992), and a certain degree of softening may even be desired because it facilitates mounting of specimens or preparation of genitalia. However, in other ground beetle studies, ethylene glycol was found to be preferable to brine because of its better conservation attributes (Lemieux & Lindgren 1999; Vennila & Rajagopal 2000). Therefore, a non-volatile preserving component like ethylene glycol is recommended to reliably prevent decomposition in pitfall traps exposed for one week or longer.

Numbers of spider individuals and beetle genera were lower in ethanol-glycerin and brine than in the three remaining liquids. Such differing sampling efficiencies can be ascribed to attraction or deterrence by the preservative (Teichmann 1994; Weeks & McIntyre 1997). However, the differences observed in our study suggest an additional mechanism. Arthropods usually float in liquids whose specific gravity (SG) is distinctly higher than that of water (SG = 1.0). Reduced capture efficiencies in ethanol-glycerin and brine may hence be due to arthropods floating at the surface, which facilitated escape of newly trapped individuals falling on top of them. Brine (SG = 1.18–1.20) and glycerin (SG = 1.26) were the liquids with the highest specific gravities employed in this study, and the specific gravity of the ethanol-glycerin mixture presumably rose to similar values as brine, once most of the ethanol (SG = 0.80) had evaporated. Arthropods may also float in pure ethylene glycol (SG = 1.11), but sink in 1:3 mixtures with water, as has been confirmed with wolf spiders in the laboratory (MHS personal observation). Hence, diluting ethylene glycol with water not only reduces expenses, but may also improve capture efficiency.

In conclusion, ethylene glycol had better conservation attributes and/or higher sampling efficiencies for spiders and ground beetles than brine, pure water, or any combination containing ethanol. If there are no specific purposes like DNA preservation (Gurdebeke & Maelfait 2002) or attraction of slugs and snails (to ethanol), mixtures of ethylene glycol and water remain the first choice preservative for pitfall traps. As ethylene glycol is potentially hazardous to wildlife, a bitter agent should be added, or physical obstacles employed to avoid access by vertebrates (Hall 1991; van den Berghe 1992). To date, only propylene glycol appears to be a comparably adequate, yet more expensive alternative (Weeks & McIntyre 1997).

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DESCRIPTION AND ECOLOGY OF A NEW SOLIFUGE FROM BRAZILIAN AMAZONIA (ARACHNIDA, SOLIFUGAE, MUMMUCIIDAE)

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ABSTRACT. Three regions of Brazilian Amazonia within the state of Rondônia were searched for the presence of solifuges by means of pitfall traps. A new solifuge, *Mummucia taiete*, was found at two sites inside Vilhena region, which are "Cerrado" enclaves surrounded by Amazonian forest. This new species is described here and is the seventh from Brazil. Populations of *M. taiete* from these two sites were compared regarding some autoecological parameters. Results showed populations from the two sites are similarly diurnal and male biased, as observed in *M. mauryi* and *M. coaraciandu*. On the other hand, these populations differ in density and juvenile/adult ratio.

RESUMO. Três regiões da Amazônia brasileira pertencentes ao Estado de Rondônia foram investigadas quanto à presença de Solifugae por meio de armadilhas "pitfall". Um novo solífugo, *Mummucia taiete*, foi encontrado dois locais no município de Vilhena, que são enclaves de Cerrado circundados por floresta Amazônica. Esta nova espécie de Solifugae é descrita aqui e é a sétima do território brasileiro. Populações de *Mummucia taiete* desses dois locais foram comparadas quanto a alguns parâmetros autoecológicos. Resultados indicam que as populações se assemelham pelos hábitos diurnos e pelo maior número de machos, como observado para outras espécies como *Mummucia mauryi* and *Mummucia coaraciandu*.Por outro lado, essas populações diferem em densidade e na razão jovens/adultos.

Keywords: Solpugida, sun-spiders, camel-spiders, taxonomy

The arachnid order Solifugae is distributed over the Americas, Africa and Eurasia, currently comprising about 1,100 species (Harvey 2002). However, South American distributional maps exhibit the presence of only six species in Brazil with large empty areas (Rocha & Cancello 2002b). That is mostly due to the lack of studies as shown by recent novel species descriptions (Xavier & Rocha 2001; Martins et al. 2004). We hereby describe a new species from "Cerrado" enclaves, surrounded by Amazonian forest, in Vilhena region, situated in southwestern Brazilian Amazonia and provide notes on the habitat and abundance of this species.

"Cerrado" is the Brazilian savannah-like vegetation, the largest domain after Amazon forest (Silva & Bates 2002). This vegetation occupies a large continuous area in central Brazil and many isolated remnants or "islands" in the Atlantic and Amazon forests biomes (Silva & Bates 2002; Prance 1996). The Cerrado comprises mainly open vegetation types such as grasslands, open-scrublands and woodlands. Cerrado has been nominated as an important world biodiversity hotspot due to its diversity and high incidence of endemism (Myers et al. 2000). Solifuges are arthropod predators common in arid and semi-arid lands (Muma 1967). Besides the functional similarity between solifuges and spiders, the former resemble scorpions in relation to thermal tolerance (Cloudsley-Thompson 1962), which enable them to be typical desert inhabitants (Cloudsley-Thompson 1977). They present an extreme wide foraging mode (*sensu* Pianka 1966) differentiating them from other arachnids, including wandering spiders. Solifuges are also prodigal excavators in order to meet various needs (Muma 1966a), and the role played by them in trophic webs of drier ecosystems should not be underestimated.

METHODS

We surveyed nine Cerrado enclaves in the state of Rondônia, northwestern Brazil, with three study sites in each region: Vilhena, Pimenta Bueno and Guajará-Mirim. We used 50 pitfall traps set 100 cm apart from each other at three sites. These traps were 500 ml plastic cups sunk in the soil so that the top of the cup remains at the soil level, with 9 cm diameter, filled with a 200 ml mixture of 9 parts of 80% G.L. alcohol and 1 part of 0.8% formaldehyde. The traps were provided with a protective cover consisting of a 20 cm diameter white plastic plate fixed with sticks 5–8 cm height above the traps. The traps were opened for seven days.

On all nine study sites we searched both during morning and night hours for arachnids. We also inspected 20 liter pitfall traps (used for herpetological surveys) at all three Vilhena sites plus two P. Bueno sites. Night collecting was a one hour search per collector over each of 12 quadrats (30 × 5 meters) set up on each site. The surveys were conducted on the following dates: Vilhena (30 August–14 September 1999) and P. Bueno (11–29 July 2000) during the dry season and (southern hemisphere) winter, whereas the G.-Mirim surveys were conducted during summer (wet season, 12–21 January 2001). The material studied is deposited in the Instituto Butantã, São Paulo, Brazil (IBSP) and the Universidade Nacional de Brasília, Brasília-DF, Brazil (UNB).

Cheliceral teeth are named according to Muma (1951), where sizes of cheliceral teeth are ordered with Roman numerals, such that I is larger than II, etc. The telotarsal spination formulae are used as in Maury (1982). The nomenclature of podomeres is in accordance with Shultz (1989).

TAXONOMY

Family Mummuciidae Roewer 1934
Genus *Mummucia* Simon 1879
Mummucia taiete new species
Figs. 1–8

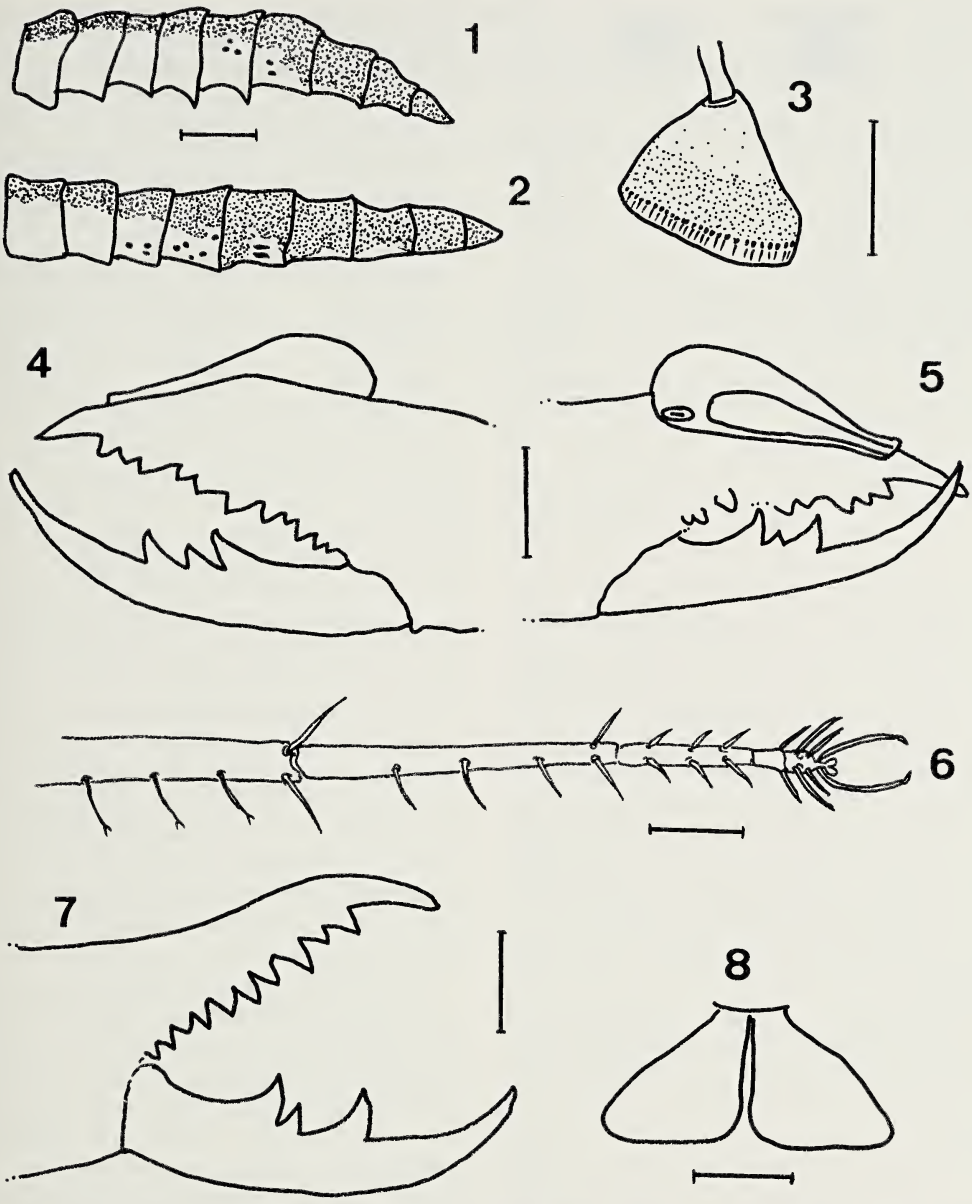
Types.—Holotype male, Vilhena (12° 41′39″S, 60°05′53″W), State of Rondônia, Brazil, 30 August–14 September 1999, M.C. Carvalho (IBSP). Paratypes: 4 males and 5 females, same data as holotype (IBSP); 1 male and 1 female, same data as holotype (UNB).

Etymology.—The specific name "taiete" is from Tupi, ancient South American Indian language, and means "very good teeth", and is to be treated as a noun in apposition.

Diagnosis.—*Mummucia taiete* is the only species of Mummuciidae with the last three distal pleurites almost totally dark-brown (Figs. 1, 2).

Description.—*Male:* Coloration in 80% ethanol: Prosoma. Propeltidium white, with a central brown blotch, with the dorsal grooves between propeltidium and lateral lobes dark-brown. Ocular tubercle dark-brown. Peltidium white. Parapeltidium, mesopeltidium and metapeltidium similar to opisthosomal tergites. Chelicerae pale-brown, three longitudinal white stripes on ectal face joined dorsally above the fondal teeth. Pedipalps and legs brown, with slightly darker ends. Malleoli as in Fig. 3. Opisthosoma: Lateral borders of tergites white, with wide dark-brown stripe on the central half, which is darker near the posterior border of the tergites. Brown bifid setae with brown sockets when they are in white area of the tergites, and white sockets when in the dark-brown area. Pleurites (Figs. 1, 2) with dark-brown and pale-brown areas, being the three last distal almost entirely dark-brown. Sternites pale-brown, lateral borders slightly darker. First and second post-spiracular sternites with about 15 brown spots which include the sockets of some bifid bristles. All vestitural bristles and bifid bristles are translucent pale-brown.

Morphology and chaetotaxy: Prosoma. Propeltidium with some scattered bifid setae, slightly wider than long (Table 1) and separated from lateral lobes by dorsal grooves. Ocular tubercle prominent with bifid setae anteriorly oriented. Distance between the two eyes slightly more than one eye diameter. Peltidium narrow, with a transverse row of bifid setae. Parapeltidium smooth. Mesopeltidium wider than long, semicircle-shaped, with several bifid setae on posterior border. Metapeltidium wider than long, with several bifid setae. Chelicerae (Figs. 4, 5): stridulatory apparatus on mesal face with six parallel narrow grooves; ectal face with several short bristles and several setae, bifid or acuminate; movable finger with one anterior, one intermediate and one principal tooth, graded in size from distal to proximal II, III, I. Fixed finger with three anterior teeth, one intermediate and one principal tooth, graded in size from distal to prox-



Figures 1–8.—*Mummucia taiete* new species, holotype male unless stated otherwise: 1. Left pleurites; 2. Left pleurites of male paratype; 3. Left malleolus V; 4. Left chelicera, mesal view; 5. Left chelicera, ectal view; 6. Left leg IV; 7. Right chelicera, ectal view, of female paratype; 8. Genital operculum of female paratype.

imal III, V, II, IV, I. The three anterior teeth placed in a slightly prominent projection so that they are not completely aligned with other teeth. Six ectal fondal teeth graded in size from distal to proximal I, II, V, III, IV, VI, being third and sixth ectal teeth from distal to proximal occasionally vestigial or absent. Three mesal fondal teeth graded I, II, III, the first distal separated from the others by a diastema; flagellum (Figs. 4, 5) thin, translucent drop-shaped vesicle, laterally flattened and with a longitudinal ectal opening. Pedipalp: tarsi immovable, without spines, densely covered by differentially sized bifid bristles, with some very long setae on basitarsi and tibiae (about twice the length of pedipalpal tibia). Legs: with several differentially sized bifid bristles and some bifid setae. Some very long

Table 1.—Morphometric characters of *Mummucia taiete*, in millimeters (except propeltidium length/width ratio).

Morphometric character	Holotype	Males (n = 5)	Female paratype	Females (n = 5)
Total length	9.20	8.00–9.20	12.00	10.00–12.00
Cheliceral length	2.50	1.80–2.50	2.80	2.50–2.80
Cheliceral width	0.90	0.70–0.90	1.00	0.84–1.00
Propeltidium length	1.72	1.30–1.72	1.63	1.56–1.63
Propeltidium width	2.03	1.60–2.03	2.25	2.19–2.25
Propeltidium length/width ratio	0.85	0.81–0.85	0.72	0.71–0.72
Pedipalpus length	6.88	6.50–6.88	6.40	5.84–6.40
Leg I	5.75	5.75–6.00	5.50	5.20–5.50
Leg IV	11.88	9.20–11.88	8.96	8.00–8.96

dorsal setae (about twice the length of basitarsus IV). Leg I thin, without claws and spines. Legs II and III: tibiae with a distal pair of ventral spines; basitarsus with three retrolateral spines and 1.1.2 ventral spines; telotarsi two-segmented with 2.2.2/2.2 ventral spines. Leg IV (Fig. 6): tibia with an anterior row of 1.1.1 ventral bifid spines and a distal pair of ventral spines; basitarsus with 1.1.1.2 ventral spines; telotarsi three-segmented, with 2.2.2/2/2.2 ventral spines. Opisthosoma. Tergites with rounded borders, covered by bifid setae and bifid bristles. Sternites densely covered by bifid bristles. Posterior border of second post-spiracular sternite with a row of about 50 ctenidia. Morphometric dimensions in Table 1.

Female: Similar to male, but with the following particular features. Morphology and chaetotaxy: Prosoma. Eyes separated by twice their diameter. Chelicerae (Fig. 7): stridulatory apparatus with 8 parallel narrow grooves. Movable finger with 1 anterior, 1 intermediate and 1 principal teeth graded in size from distal to proximal I, III, II. Fixed finger with three anterior teeth, one intermediate and one principal tooth, graded in size from distal to proximal III, V, I, IV, II. Five ectal fondal teeth graded in size from distal to proximal I, II, IV, III, V. Genital operculum prominent, fan-shaped, round-bordered, with central longitudinal opening (Fig. 8). Morphometric characters in Table 1.

Remarks.—According to Maury (1998), it is impossible to reliably distinguish the genera of Mummuciidae, so the most conservative decision is to consider the new species described here as belonging to the typical genus *Mummucia* until more precise information about the taxonomy and phylogeny of the group become available. The same decision was adopted in the description of *Mummucia mauryi* Rocha 2001 (Xavier & Rocha 2001) and *M. coaraciandu* Pinto-da-Rocha & Rocha 2004 (Martins et al. 2004).

The cheliceral dentition of *M. taiete* and *M. coaraciandu* are quite similar; remarkably this feature is generally species-specific in Solifugae (Maury 1984; Rocha 2002). These two species can only be distinguished by the coloration of the posterior three pleurites, which are almost totally dark-brown in *M. taiete* whereas they are predominantly pale-brown in *M. coaraciandu.*

The color pattern of the pleurites are known for four species of Mummuciidae and may be considered as species-specific. The mummuciids *Metacleobis fulvipes* Rower 1934 (Rocha & Cancello 2002a), *Mummucia mauryi* (Xavier & Rocha 2001), *Mummucia coaraciandu* (Martins et al. 2004), *Gaucha fasciata* Mello-Leitão 1924 (Maury 1970; Rocha, unpub. data) present distinct patterns of pleurite coloration, with slight intraspecific variation. Unfortunately, pleurite coloration has not been studied in the remaining 15 species of Mummuciidae.

It is not known if the coloration difference between *M. coaraciandu* and *M. taiete* suggests that they are two actual and reproductively isolated species. Alternatively, this distinction could be merely a geographical polymorphism due to low gene flow between the populations (putative species), since they are isolated by about 1300 km and by several rivers, ecosystems and other barriers. Any-

Table 2.—Characteristics of two Cerrado enclaves near Vilhena, Rondônia state, Brazil where *M. taiete* was collected (data from Colli, G.R. in prep.). Cerrado "stricto sensu" = a woodland; Cerrado field = open scrubland.

	Area (Km^2)	Cerrado "stricto sensu"	Antropic field	Cerrado field	"forest"
Site 1	73.15	83.9%	8.2%	7.6%	0.3%
Site 2	10.06	85.2%	9.4%	5.4%	0%

how, pleurite coloration is indeed diagnostic for *M. coaraciandu* and *M. taiete* and fits at least the definition of the typological concept of a species.

ECOLOGICAL RESULTS AND DISCUSSION

We recorded the occurrence of *M. taiete* at only two study sites in the Vilhena region with densities of 29.65 individuals/m^2/day at site 1 and 17.52 individuals/m^2/day at site 2. Both sites are Cerrado enclaves with similar vegetation cover (Table 2). Total number of individuals captured: $n_{site1} = 66$; $n_{site\ 2} = 39$. These figures show both the high density and mobility of this species. The observed frequency distributions of the number of *M. taiete* caught in 50 pitfall traps fit the Poisson distribution in both areas (Kolmogorov-Smirnov one-sample test, K = 0.368, $P < 0.01$, $n = 50$) showing a random distribution pattern of *M. taiete* movements. We found no solifuges in the other seven study sites. Data from other arachnids will appear elsewhere (Carvalho et al. in prep.).

We found a decreasing activity in *M. taiete* in the early morning hours when we arrived at the sites between 7:30–8:30 a.m., when many live individuals were found in the 20 l pitfall traps. This suggests that activity may begin at dawn (no individuals were seen during the night surveys) (Maury 1984; Xavier & Rocha 2001; Martins et al. 2004). The sex-ratio (operational) was biased toward males ($\chi^2 = 4.694$, d.f. = 1, $P < 0.05$; with Yates correction; data from both areas were pooled after perform heterogeneity chi-square analysis: $\chi^2 = 0.29$, d.f. = 1, N.S.; Chi-square analysis with Yates correction Ho = 1:1; site #1: $\chi^2 = 3{,}368$, d.f. = 1, N.S.; site #2: $\chi^2 = 0.941$, d.f. = 1, N.S.), probably due to higher male activity (Muma 1975, 1980; Xavier & Rocha 2001; Martins et al. 2004) or to early male maturity (Muma 1966b). The occurrence of one or both of these factors could explain the male biased sex-ratio we found in the pitfall trap data (Fig. 9). We tested the null hypothesis of an 1:1 juvenile/adult ratio and Site 1 seems to have a young, rapidly expanding population (χ^2 with Yates correction test: $\chi^2 = 11.045$, d.f. = 1, $P < 0.001$, $n = 66$) and site 2 a relatively slow growth population ($\chi^2 = 0.41$, d.f. = 1, N.S., N = 39) (Fig. 10). This difference in the dynamic of these populations may reflect constraints due to the smaller size of Site 2. This survey was conducted at the end of the dry season, thus juveniles would

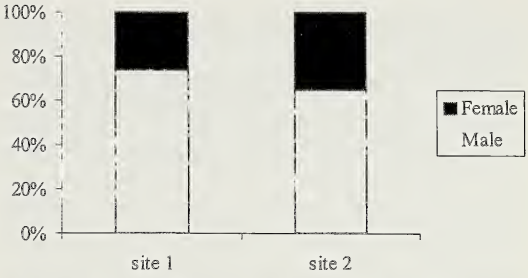


Figure 9.—Operational sex-ratio of *M. taiete* is male biased (χ^2 with Yates correction = 4.694, d.f. = 1, $P < 0.05$, $n = 36$; data from both areas were pooled after perform heterogeneity chi-square analysis). Mature individuals were captured in two Cerrado enclaves near Vilhena, Rondônia state, Brazil. ($n_{site1} = 19$, $n_{site\ 2} = 17$). Capture effort: 50 pitfall traps (9 cm diameter, 1 meter apart) were exposed for one week.

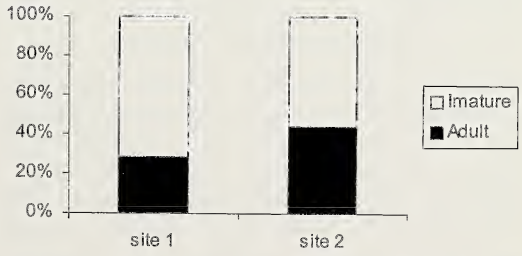


Figure 10.—Proportion of juveniles in *M. taiete* populations from two Cerrado enclaves near Vilhena, Rondônia state, Brazil. Individuals were caught by 50 pitfall traps (9 cm diameter, 1 meter apart) exposed for one week in each site. (χ^2 with Yates correction test Ho = 1:1, site 1: $\chi^2 = 11.045$, d.f. = 1, $P < 0.001$, $n_{site1} = 66$; site 2: $\chi^2 = 0.41$, d.f. = 1, N.S., $n_{site\ 2} = 39$).

reach maturity after the onset of the rainy season.

Both sites have white sandy soil and this may facilitate colonization by *M. taiete* due to the excavation behavior of Solifugae. Similar soil features appear to be favorable for *M. coaraciandu*, another solifuge from Brazilian Cerrado, which is more abundant in sites with sandy soils (Martins et al. 2004). Accordingly to these observations, Dean & Griffin (1993) suggest that sandy soils are a key factor determining the occurrence of many solifuge species. However, two other P. Bueno sites (Sites 12 & 12A) also have white sandy soils and may potentially be colonized by *M. taiete*. Prance (1996) observes that savannahs on white sandy soil have a high incidence of endemism among plant species. All three G. Mirim sites are rock outcrops and seem unlikely to be colonized by *M. taiete* (Colli unpub. data, for details of vegetation structure and physical characteristics for all nine sites; we use here the same site labels as Colli). *Mummucia taiete* may be a distribution-restricted species with high density populations in Cerrados of white sandy soils with a particular combination of Cerrado types allowing direct incidence of solar radiation in patches of bare soil surface. It is worth noting that these two sites are the most similar regarding vegetation cover compared to the other seven sites surveyed (Colli et al. unpub. data).

The data presented here coupled with the above-mentioned characteristics derived from the literature suggest that Solifugae deserve further investigation as a key predator of arthropod fauna in the Brazilian Cerrados, a poorly known biodiversity hotspot.

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TWO NEW PURSE-WEB SPIDERS OF THE GENUS *ATYPUS* (ARANEAE, ATYPIDAE) FROM KOREA

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ABSTRACT. Two new species of the genus *Atypus*, *Atypus sternosulcus* new species from Andong and *A. suwonensis* new species from Suwon, are newly described from Korea.

Keywords: Purse-web, *Atypus sternosulcus*, *Atypus suwonensis*, Asia, taxonomy

Spiders of the genus *Atypus* are known as purse-web spiders as they construct silk-lined tunnels in the ground that extend above the soil surface, usually against the vertical side of a tree or rock. The tube is covered with sand and debris and is difficult to detect. Males are active mostly from June to August, and females then guard their egg sacs during August and September (Schwendinger 1990). Mating takes place inside the tube and the spiders stay together for several months, after which the male dies or is eaten by the female (Im & Kim 2000). Females of these primitive spiders may live for several years.

Worldwide, 19 species of the genus *Atypus* have been recorded from the United States, Europe and south-east Asia (Platnick 2004). Three species have been described from Korea: *A. coreanus* Kim 1985, *A. magnus* Namkung 1986 and *A. quelpartensis* Namkung 2001 (Kim 1985; Namkung 1986, 2001). Atypid spiders are characterized by a male sternum with marginal ridges, a short, straight and spike-like embolus, a straight conductor and a distally widened vulva with bulbous or pyriform receptacula and with two lateral patches of pores on the genital atrium (Gertsch & Platnick 1980). Kraus & Baur (1974) utilized various taxonomic characters to distinguish between the European species, such as the segmentation of the posterior spinnerets, features of the patellar membrane, morphology of sigilla I and IV, and the male palpal conductor, palpal furrow and male metatarsal spines. Schwendinger (1990) noted and discussed the granular texture on the male chelicerae and front legs, and the cymbial pit for distinguishing species.

METHODS

This paper describes two new atypid spiders, *Atypus sternosulcus* from Giran stream, Andong, Gyeongsangbuk-do and *Atypus suwonensis* from Suwon, Gyeonggi-do in Korea. Male specimens of all Korean atypid spiders were examined, and we reviewed published descriptions to compare taxonomic characters (Kim 1985; Yaginuma 1986; Schwendinger 1990; Chen & Zhang 1991; Song *et al.* 1999; Namkung 1986, 2001). The specimens examined were: *A. karschi*: 1 ♂, 15 August 1995, Kumamoto, Kyusu, Japan, Kim and J. Namkung; *A. coreanus*: 1 ♂, 17 May 1982, Mt. Ungil, Gyeonggi-do, Korea, J. Namkung; *A. magnus*: 1 ♂, 7 June 1986, Jigdong, Gyeonggi-do, Korea, J. Namkung; *A. quelpartensis*: 1 ♂, 4 July 1989, Jungmun, Jeju island, Korea, J. Namkung (Table 1).

The external morphology of the specimens was observed and illustrated utilizing a stereoscopic microscope, and metric characters were measured with an ocular micrometer. All measurements are given in mm. Leg measurements are given in the order of femur, patella + tibia, metatarsus and tarsus, in parentheses. Abbreviations used in this paper are: AER = anterior eye row; PER = posterior eye row; AME = anterior median eye; ALE = anterior lateral eye; PME = posterior median eye; PLE = posterior lateral eye; MOQ = median oc-

Table 1.—Comparisons of taxonomic characters of male of some Asian atypid spiders.

Species	PLS, number of segments	Leg patella, retrolateral face	Sigilla I	Sigilla IV	Conductor, bend in upper corner	Furrow on palpal femur	Spines on metatarsus IV	Granules on femur I (II)	Distribution
A. karschi	4	pigmented	marginal	oval	strong	shallow	present	domed (domed)	Japan China Taiwan
A. heteropthecus	4	white	remote from margin	oval	medium	shallow	absent	domed (domed)	China
A. coreanus	4	pigmented	marginal	oval	strong	deep	present	domed (domed)	Korea
A. magnus	4	pigmented	marginal	oval	strong	deep	present	smooth (smooth)	Korea Russia
A. quelpartensis	4	white	remote from margin	oval	strong	deep	present	smooth (smooth)	Korea
A. sternosulcus	4	white	marginal	suboval	strong	shallow	present	domed (smooth)	Korea
A. suwonensis	4	white	remote from margin	oval	strong	shallow	present	smooth (smooth)	Korea

ular quadrangle; ALS = anterior lateral spinnerets; PMS = posterior median spinnerets; PLS = posterior lateral spinnerets. The specimens studied are lodged in the deposited in the Laboratory of Insect Ecology, Seoul National University, Seoul, Korea (SNU).

TAXONOMY

Family Atypidae Thorell 1870
Genus *Atypus* Latreille 1804
Atypus sternosulcus new species
Figs. 1–7

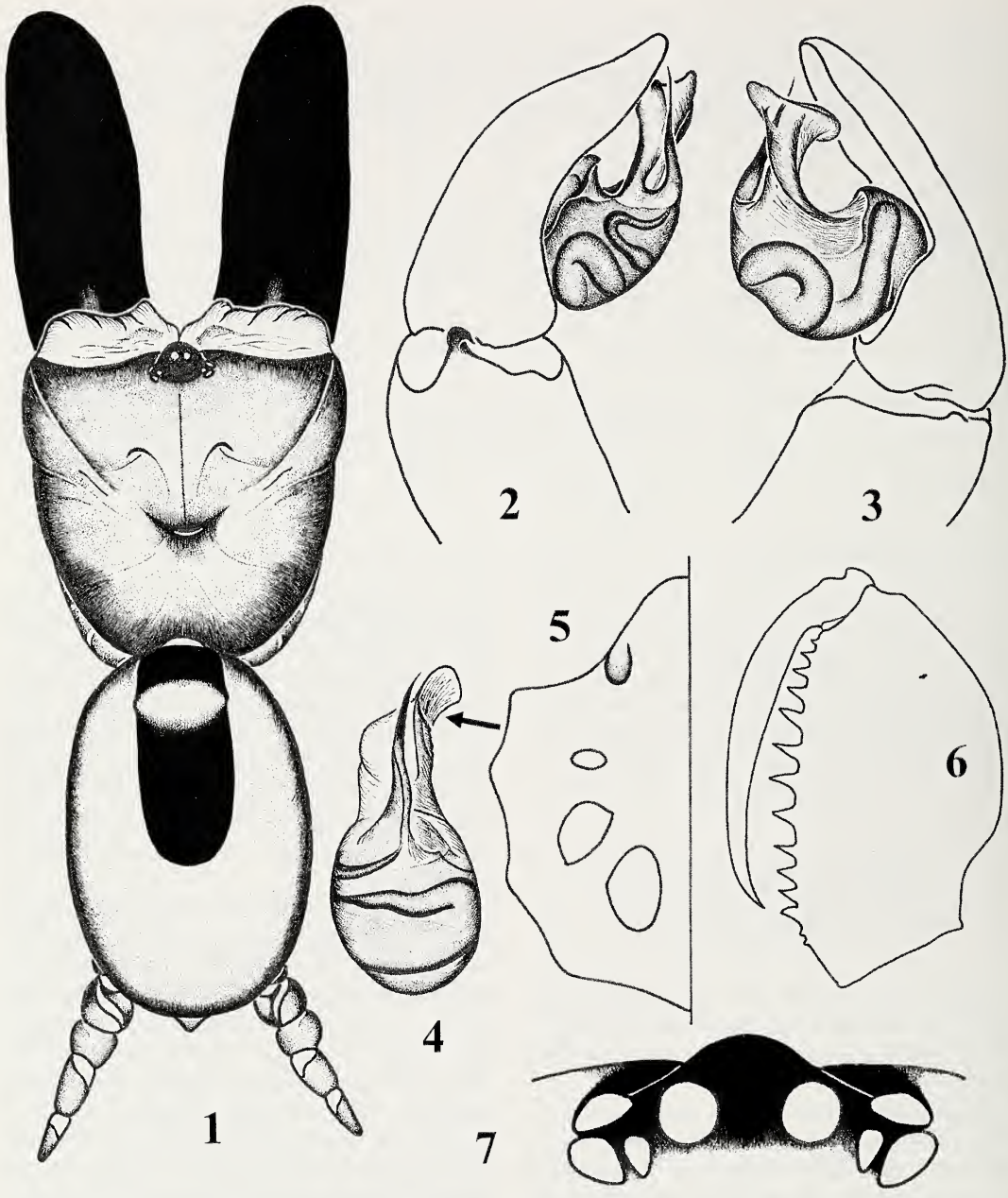
Type.—Holotype male, Giran stream, Andong, Korea (36°31′01″ N, 128°50′31″E), 3 June 2003, S.T. Kim, H.S. Kim, M.P. Jung and J.H. Lee (SNU).

Etymology.—The specific name is a combination of 'stern' from Greek meaning breast and Latin 'sulcus', a furrow or pit, referring to the pit on the sternum of the male holotype.

Diagnosis.—This species is similar to *A. karschi* Dönitz 1887 in general appearance, but differs as follows: the coloration of the abdomen; the chelicera with 12 teeth and 2 denticles on promargin (Fig. 6), instead of 13 in *A. karschi* (Yaginuma 1986, fig. 1e) and their alignment; the shape of vestigial and pitted anterior sternal sigilla (Fig. 5) (*A. karschi*: Yaginuma 1986, fig. 1b); and the shape of upper lateral edge of conductor (Figs. 2–4) (*A. karschi*: Yaginuma 1986: fig. 1p).

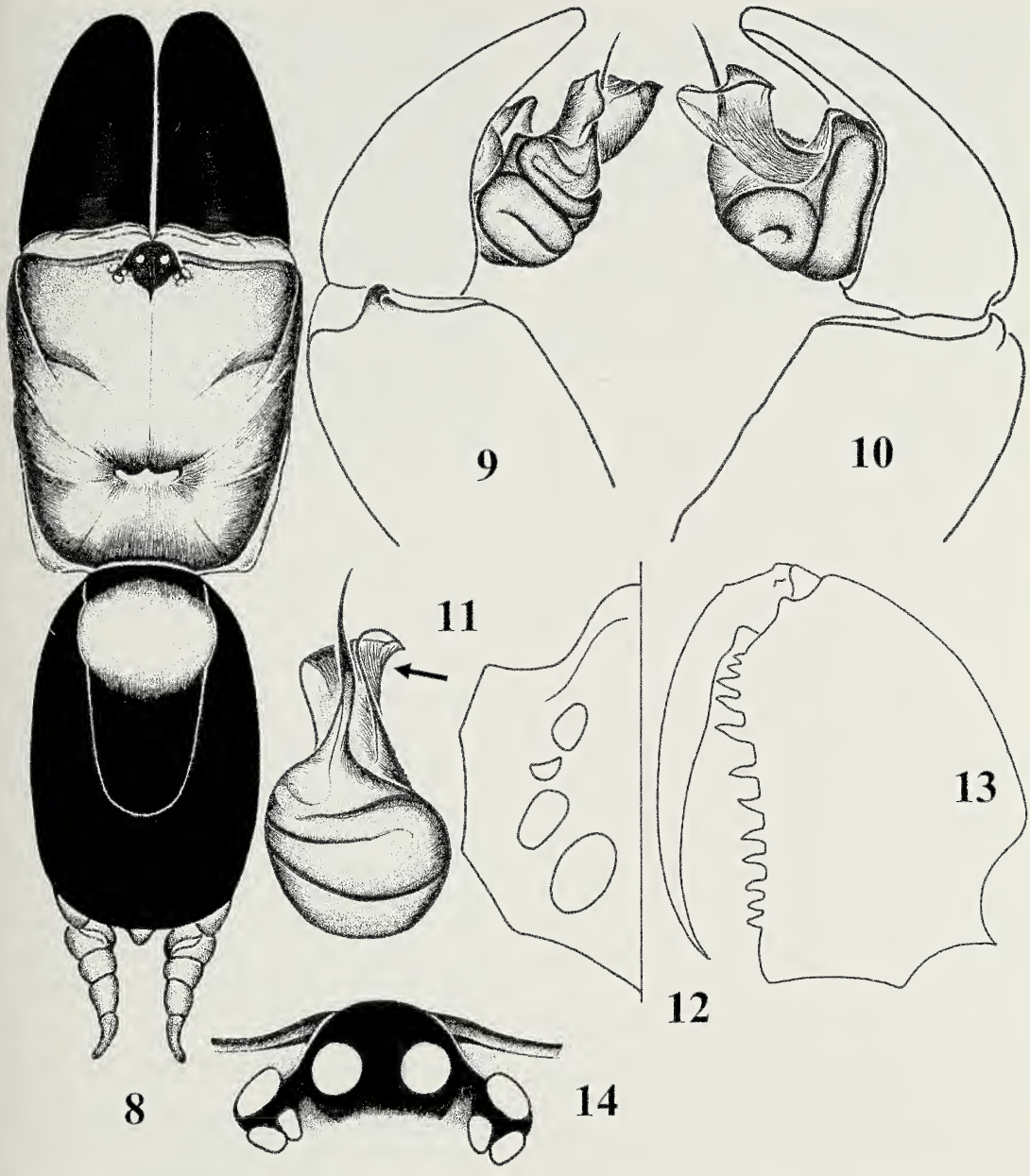
Description.—*Male:* Total length 16.5 (including chelicerae and excluding spinnerets). Body length 11.7. Carapace 5.1 long, 4.7 wide. Abdomen 6.6 long, 4.2 wide. Chelicerae 5.0 long, 1.7 wide. Endite 2.7 long, 1.9 wide. Labium 0.3 long, 1.1 wide. Sternum 3.4 long, 3.1 wide. AER 1.2, PER 1.3. Leg measurements; I: 14.9 (4.7, 4.5, 3.5, 2.2); II: 12.7 (3.7, 3.9, 3.0, 2.1); III: 12.0 (3.4, 3.5, 2.8, 2.3), IV: 15.2 (4.5, 4.4, 3.5, 2.8); pedipalp 5.8 (2.4, 2.3, -, 1.1).

Carapace lustrous and quadranglar, reddish brown with narrow black border, gently narrowed posteriorly; cephalic region dark reddish brown and elevated, lateral margins with black stripes; thoracic region reddish brown, flat, gently rounded on both sides, emarginated posterior margins bearing conspicuous pleurites. Median groove broad weakly U-shaped and deeply imprinted, behind midpoint of carapace, occupying about 1/6 of carapace width at that point; cervical and radial furrows distinct and deeply imprinted (Fig. 1). Eye tubercle black, 0.7 long and 0.8 wide. AER and PER slightly recurved when viewed from above. Eye sizes and interdistances: AME 0.26, ALE 0.23, PME 0.17, PLE 0.20; AME-AME 0.20, AME-ALE 0.07, AME-PLE 0.23, PME-PME 0.63, PME-PLE almost touching, PLE-PLE 0.83, ALE-PLE-PME contiguous. MOQ 0.5 long, front width 0.7 and back width 0.9 (Fig. 7). Chelicerae dark reddish brown, well developed with deep longitudinal furrow at base of retrolateral surface; 12 teeth and 2



Figures 1–7.—*Atypus sternosulcus* new species: 1. Body, dorsal view; 2. Left palp, prolateral view; 3. Left palp, retrolateral view; 4. Left palpal bulb, ventral view; 5. Sternum, left half; 6. Left chelicera, retrolateral view; 7. Eyes, dorsal view, Upper corner of conductor indicated by arrow.

denticles on promargin of cheliceral furrow (Fig. 6); prolateral and retrolateral surface with distinct granular texture. Sternum dark reddish brown with ridges at margins. Four pairs of sigilla deeply imprinted. Anterior sigilla vestigial and deeply pitted between labium and endite. Sigilla sizes and interdistances: I 0.3 long and 0.2 wide, almost touching at margin, II 0.2 long and 0.3 wide, 0.6 from margin, III 0.6 long and 0.3 wide, 0.5 from margin, IV 0.7 long and 0.5 wide, 0.4 from margin; I-I 1.1, II-II 1.5, III-III 1.3, IV-IV 0.5, I-II 0.6, II-III 0.3, III-IV 0.2 (Fig. 5). Endite and labium dark reddish brown. Legs 4123, dark reddish brown and armed with short spines; prolateral side of femur I with granular tex-



Figures 8–14.—*Atypus suwonensis* new species. 8. Body, dorsal view; 9. Left palp, prolateral view; 10. Left palp, retrolateral view; 11. Left palpal bulb, ventral view; 12. Sternum, left half; 13. Left chelicera, retrolateral view; 14. Eyes, dorsal view, Upper corner of conductor indicated by arrow.

ture; tarsi light reddish brown and pseudosegmented; retrolatral membranous area on patella I without pigments; trichobothria in two distally convergent rows on basal 2/3 tibiae I-IV (left): 4 + 6, 5 + 6, 5 + 5, 6 + 6 and in single row on distal half of metatarsi I-IV: 3, 3, 3, 4. Abdomen suboval and dull grayish brown; dorsal scutum (3.8 long and 2.0 wide) blackish gray enclosing dull blackish gray tergite (Fig. 1); lung patches light grayish brown. Spinnerets light blackish gray. ALS 0.5; PMS 0.9; PLS 4 segmented: basal joint 0.6, median 0.7, subapical 0.7, apical 0.5. Pedipalp dark reddish brown; palpal cymbium without basal pit; palpal femur without furrow; bulb small and globe-like; embolus short and stout,

spine-shaped; upper distal corner of conductor slightly bent upwards (Figs. 2–4).

Female: Unknown.

Distribution.—Korea (Giran stream, Andong, Gyeongsangbuk-do).

Ecological remarks.—The sole specimen was collected in a pitfall trap near a stream beside a hillock.

Atypus suwonensis new species
Figs. 8–14

Type.—Holotype male, Seodung-dong, Suwon, Korea (37°15′41″N, 126°59′16″E), 24 June 2000, T.W. Kim (SWU).

Etymology.—The specific name is an adjective referring to the type locality.

Diagnosis.—This species is similar to *Atypus coreanus* Kim 1985 in general appearance, but differs as follows: the alignment of cheliceral promarginal teeth (Fig. 13) (*A. coreanus*: Kim 1985: 6, figs. 1–3); the shape of upper lateral edge of conductor (Figs. 9–11) (*A. coreanus*: Kim 1985: p. 6, fig. 7; Namkung 2001; p. 25, figs. b–c).

Description.—*Male:* Total length 14.7 (including chelicerae and excluding spinnerets). Body length 10.6. Carapace 5.0 long, 4.9 wide. Abdomen 5.6 long, 3.6 wide. Chelicerae 4.8 long, 1.8 wide. Endite 2.8 long, 1.7 wide. Labium 0.3 long, 1.1 wide. Sternum 3.7 long, 3.4 wide. AER 1.3, PER 1.4. Leg measurements; I: 13.7 (4.6, 4.2, 3.0, 1.9); II: 12.0 (3.7, 3.6, 2.5, 2.2); III: 10.8 (3.2, 3.1, 2.6, 1.9), IV: 14.2 (4.1, 3.9, 3.6, 2.6); pedipalp 5.3 (2.1, 2.1, -, 1.1).

Carapace lustrous and quadranglar, reddish brown with narrow black border, gently narrowed backward; cephalic region dark reddish brown and elevated, margined by black stripes; thoracic region reddish brown and flat, gently rounded on both sides, emarginated posterior margins bearing conspicuous pleurites. Median groove weakly W-shaped and deeply imprinted, positioned at about 2/3 of carapace length, occupying about 1/5 of carapace width at that point; cervical and radial furrows distinct and deeply imprinted (Fig. 8). Eye tubercle black, 0.8 long and 0.7 wide. AER and PER slightly recurved from the above. Eye sizes and interdistances: AME 0.26, ALE 0.23, PME 0.17, PLE 0.18; AME-AME 0.20, AME-ALE 0.10, AME-PLE 0.26, PME-PME 0.73, PME-PLE almost touching, PLE-PLE 1.02, ALE-PLE-PME contiguous. MOQ 0.6 long, front width 0.7 and back width 1.0 (Fig. 14). Chelicerae dark reddish brown, well developed with deep longitudinal furrow at base of retrolateral surface; 12 teeth on promargin of cheliceral furrow (Fig. 13); prolateral and retrolateral surface with distinct granular texture. Sternum dark reddish brown with ridges at margins. Four pairs of sigilla deeply imprinted. Sigilla sizes and interdistances: I 0.6 long and 0.4 wide, 0.7 from the margin, II 0.3 long and 0.4 wide, 0.6 from the margin, III 0.6 long and 0.4 wide, 0.5 from the margin, IV 0.7 long and 0.6 wide; I-I 0.9, II-II 1.4, III-III 1.4, IV-VI 0.4, I-II 0.06, II-III 0.03, III-IV 0.09 (Fig. 12). Endite and labium dark reddish brown. Legs 4123, dark reddish brown and armed with short spines; prolateral side of femur I with granular texture; tarsi light reddish brown and pseudosegmented; retrolatral membranous area on patella I without pigments; trichobothria in two distally convergent rows on basal 2/3 tibiae I-IV (left): 6 + 7, 6 + 6, 5 + 5, 6 + 6 and in single row on distal half of metatarsi I-IV: 4, 3, 3, 7. Abdomen suboval and dull black; dorsal scutum (4.0 long and 2.1 wide) blackish brown enclosing yellowish brown tergite (Fig. 8); lung patches light grayish brown. Spinnerets light blackish gray. ALS 0.5; PMS 0.9; PLS 4 segmented: basal joint 0.6, median 0.8, subapical 0.7, apical 0.6. Pedipalp dark reddish brown; palpal cymbium without basal pit; palpal femur without furrow; bulb small and globe like; embolus short and stout spine-shaped; upper distal corner of conductor conspicuously bent upwards (Figs. 9–11).

Female.—Unknown.

Distribution.—Korea (Suwon, Gyeonggi-do).

Ecological remarks.—The sole specimen was collected in a pitfall trap.

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COPULATORY BEHAVIOR AND WEB OF *INDICOBLEMMA LANNAIANUM* FROM THAILAND (ARACHNIDA, ARANEAE, TETRABLEMMIDAE)

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ABSTRACT. The present study reports for the first time on the behavior prior to, during and after the copulation of a member of the haplogyne spider family, Tetrablemmidae and describes the web of this species. Prior to copulation, male and female of *Indicoblemma lannaianum* from Thailand sometimes avoided each other or the female scared the male away, apparently by vigorous vibrations of her body. When first copulations were initiated, they lasted from 1.21 to 3.8 h with an average of 2.25 ± 0.71 h (n = 17). Some females accepted a second male for mating 3–9 days after first mating. There was no significant difference between the duration of first and second copulations but significantly more trials were needed to induce the second copulations. In the copulatory position, the male was inverted and faced in the same direction as the female. He seized the female's opisthosoma with apophyses on his chelicerae which fit into grooves on a female's ventral plate in this way building a locking mechanism during copulation. The pedipalps were inserted alternately. The web of *I. lannaianum* consisted of a longish narrow sheet, which was made of many short threads forming a zigzag pattern and additional long oblique threads overdrawing the sheet and functioning as signal threads.

Keywords: Haplogynae, copulation, locking mechanism, courtship

Spiders show an impressive array of various copulatory patterns and positions (e. g., Gerhardt 1933; von Helversen 1976; Foelix 1996; Huber & Eberhard 1997). Although there have been numerous studies on the mating of a variety of spiders, the copulatory behavior of many species still remains unknown. Bristowe and Gerhardt described the mating behavior of several entelegyne species, and of haplogynes including members of the families Scytodidae, Pholcidae, Segestriidae, Dysderidae and Oonopidae (Bristowe 1929–1931; Gerhardt 1926–1930, 1933). In addition to Gerhardt's comprehensive work (reviewed by Huber 1998a), the most detailed descriptions of reproductive biology and copulatory mechanisms in haplogynes are given for the family Pholcidae (Uhl 1993a, 1993b, 1998; Uhl et al. 1995; Huber 1994, 1995, 1997, 1998b, 2002; Huber & Eberhard 1997; Yoward 1998; Senglet 2001; Schäfer & Uhl 2002). However, studies on the copulatory behavior of many haplogynes are still missing. This is especially true for members of the family Tetrablemmidae as their behavior has not yet been observed in detail.

Tetrablemmids are armored spiders which mainly live as soil-dwellers in the litter habitat of tropical rain forests (Shear 1978; Lehtinen 1981; Burger 2005). They show a characteristic pattern of abdominal sclerotization, and the carapace or the chelicerae of males are often strongly modified (Shear 1978; Lehtinen 1981; Schwendinger 1989, 1994). The family Tetrablemmidae is systematically placed as sister group of the Dysderoidea (Coddington & Levi 1991; Platnick et al. 1991).

The diminutive size (body length less than 2 mm) of most tetrablemmids and the fact that many species are hard to find make behavioral observations difficult. In the present study we investigate the mating behavior of a tetra-

blemmid spider and compare the copulation duration of first and second copulations. We also describe avoidance behaviors of males and females, female aggressive behavior prior to copulation, and we provide details of the web of this species.

METHODS

Specimens of the tetrablemmid *Indicoblemma lannaianum* Burger 2005 were collected in the primary evergreen hill forest of Doi Suthep, 1600 m elevation, near Chiang Mai (18°48′ N, 98°59′ E) in northern Thailand, from 11–21 July 2003 by sieving. Types are deposited in the Geneva Natural History Museum, Switzerland and the Natural History Museum of Bern, Switzerland. *Indicoblemma lannaianum* inhabits the middle humid leaf litter layer alongside little streams. Sixty-four females and forty-four males were caught and kept singly in little snap cap glass jars (3 cm diameter and 5 cm height) with ground gypsum, which was moistened every day by one or two drops of water so that the air humidity was almost saturated. The spiders were fed Collembola (*Folsomia candida* Willem). All spiders were mature when collected and thus their mating history is unknown.

For the mating behavior studies, the spiders were used one or two days after they were collected. Copulations were observed with a binocular microscope (Wild M3; 6.4×, 16×, 40×) and partially photographed using a digital camera (Canon Power Shot G2). All sixty-four females and forty-four males were used for the mating observations. For each pairing, the male was carefully removed from his glass jar with a paint-brush and placed into the female's jar. The spiders were left together for 30–60 min. If no copulation was initiated during that time, the male was put back in his own glass jar and another male was offered to the female after a recovery period of 30 min. 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. Post-copulatory behavior was observed for 15 minutes in each case.

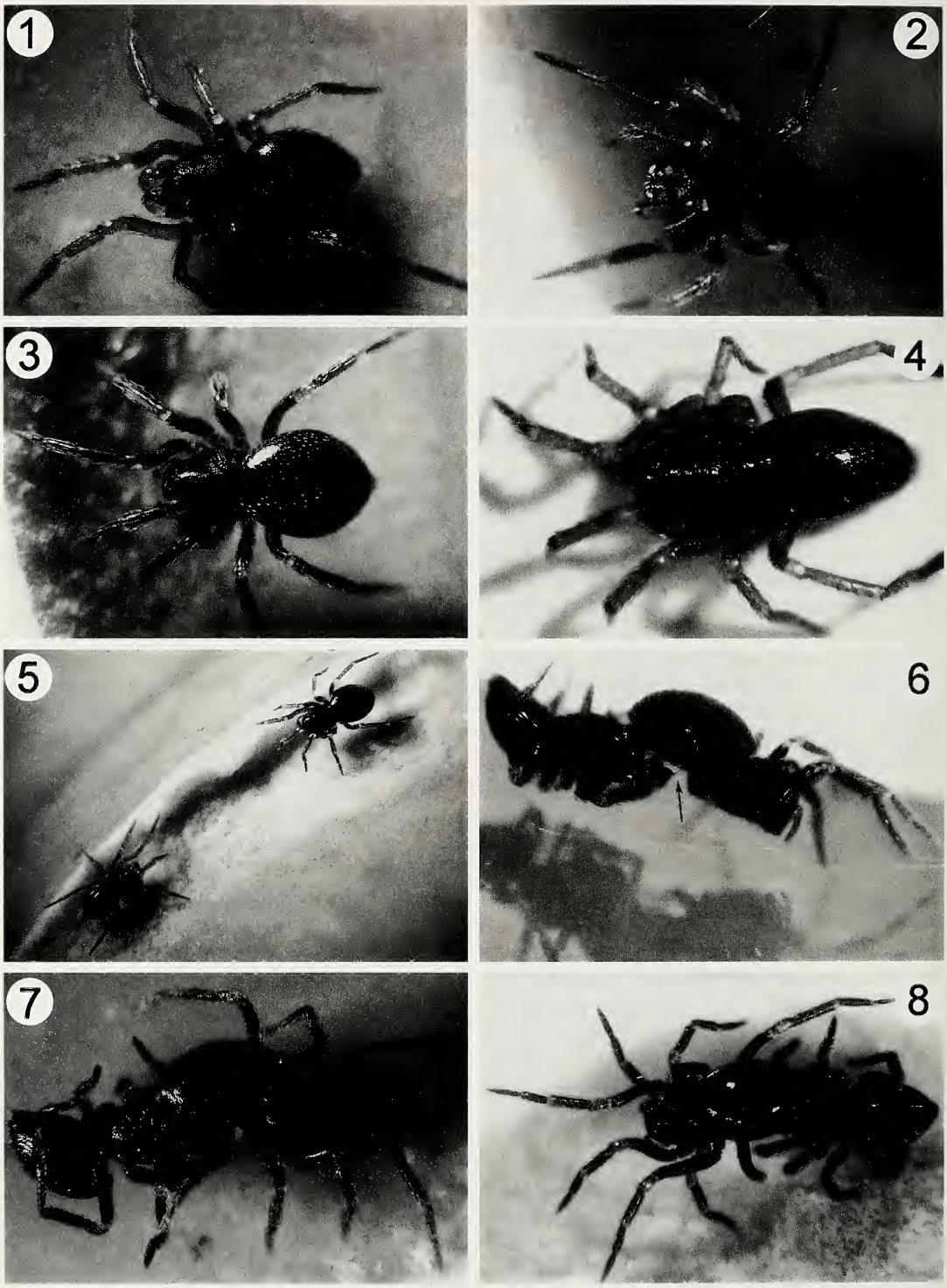
Eleven females which had copulated once were given the opportunity to mate a second time. One day after a female had copulated in the lab for the first time, different males were offered to her one after another (1–3 males per day). When a female copulated for the second time no more males were offered. If a female did not accept a second male within 14 days, the procedure was stopped and the female was considered as single mated.

Only the six females that had mated twice were included in the statistical comparison of first and second copulations. To compare first and second copulations, two-tailed Wilcoxon Sign-Rank-tests for paired data were applied. We tested for a difference in copulation duration and for a difference in the number of trials needed until successful first and second copulations took place. We used nonparametric statistics because most of our groups to test differed significantly from a normal distribution [duration of second copulations (Shapiro Wilk W-test; $W = 0.775621$, $P < 0.0351$); number of trials for the first ($W = 0.639893$, $P < 0.0014$) and second copulations ($W = 0.763674$, $P < 0.0270$)]. Averages are given ± standard deviation.

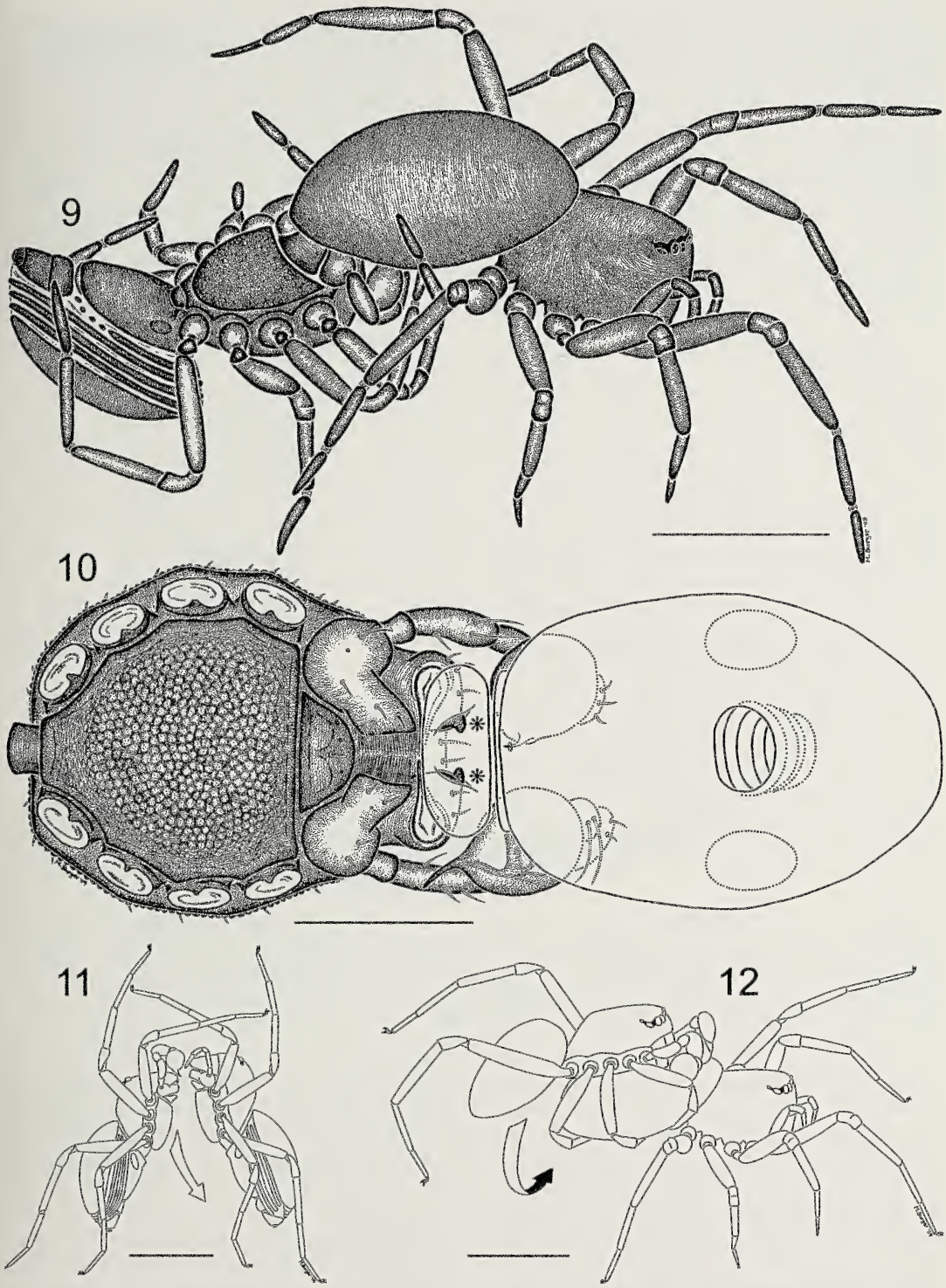
RESULTS

Pre-copulatory behavior.—When a male (Figs. 1, 2) was placed in the female's jar (Figs. 3, 4), both spiders usually walked around and appeared to meet each other accidentally. A male who came into contact with the threads of a female's web appeared to commence searching for the female. The female then reacted by turning towards him. No male was ever seen filling his pedipalps with sperm prior to copulation. Sometimes males and females stood immobile at a distance of about 3–5 mm facing each other for 8–10 minutes before contacting (Fig. 5). When the spiders met frontally, the male either grasped the female directly and took the copulatory position (Figs. 6–10) or he pushed her back and upwards with his front legs. In the latter case both of them palpated each other with their front legs for a few seconds before the male took the copulatory position by going backwards along the ventrum of the female (Fig. 11). When the male approached the female from the side or from behind he jumped at her and gripped her back with his chelicerae. If the female kept running around, the male grasped her opisthosoma with his legs (Fig. 12). Before mating, the male crept under her from the side and took the copulatory position (Figs. 6–10).

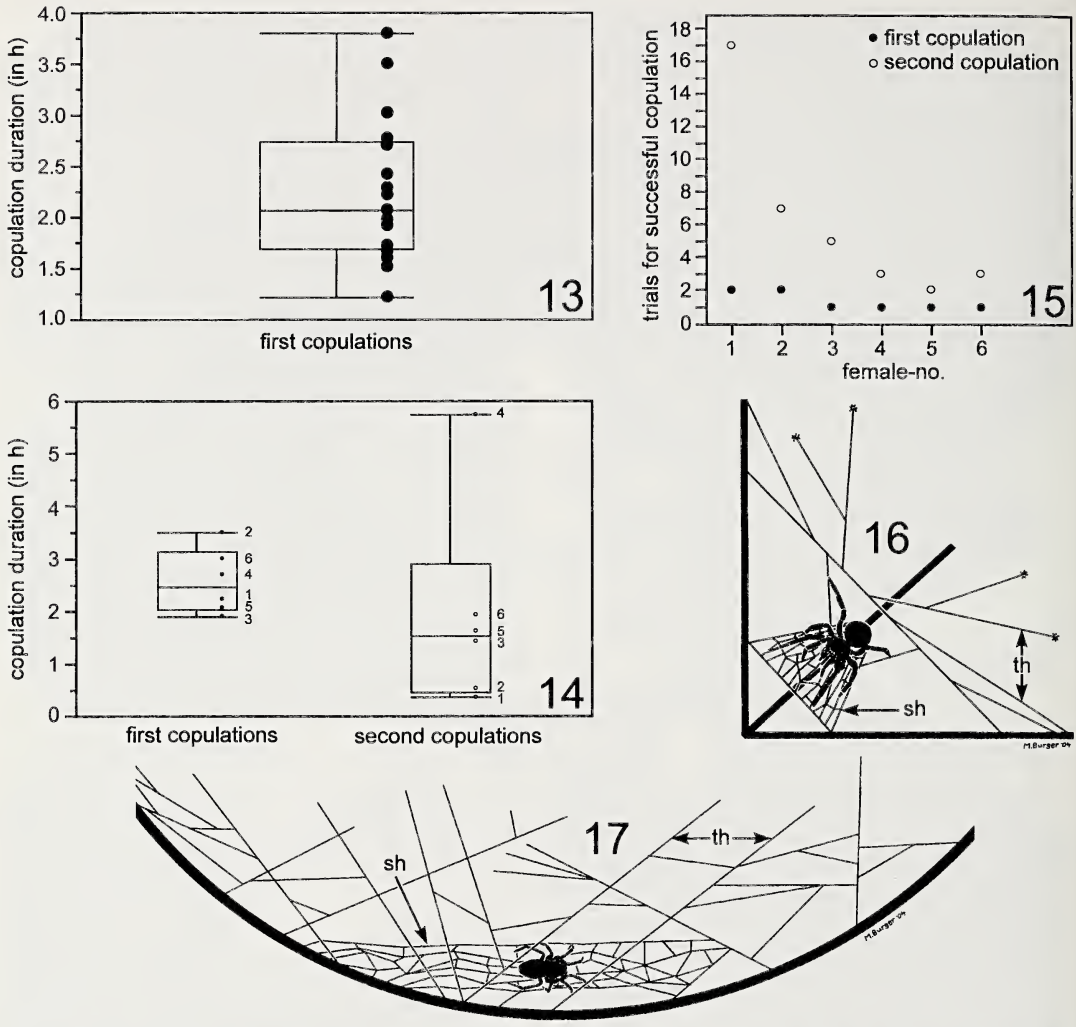
Locking mechanism.—When the male was



Figures 1–8.—*Indicoblemma lannaianum*, male and female. 1. Male, dorsal view; 2. Male in web, anterior dorsal view, arrow pointing to signal thread; 3, 4. Female, dorsal view; 5. Male (left side) facing the female prior to copulation; 6. Male (left side) and female in copula, arrow pointing to embolus of male pedipalp; 7. Male (left side) and female in copula; 8. Male (right side) and female in copula.



Figures 9–12.—*Indicoblemma lannaianum* prior and during copulation. 9. Male (left side) and female in copula; 10. Male (prosoma on the left side, ventral view) grasping the female (ventral plates in optical cut, dorsal view) with apophyses on his chelicerae during copulation (asterisks); 11. Male (left side) and female palpating each other with the front legs prior to copulation before the male moves into the copulatory position (arrow); 12. Male (left side) grasping the female's opisthosoma prior to copulation before creeping under her (arrow) and taking the copulatory position. Scale bars = 0.5 mm (9, 11, 12), 0.2 mm (10).



Figures 13–17.—Copulation durations, trials for successful copulations and web of *Indicoblemma lannaianum*. 13. Copulation duration of first copulations (n = 17); 14. Copulation duration of first and second copulations (n = 6; numbers beneath box-plots indicate female-no. corresponding to Fig. 15); 15. Number of trials needed for each female to induce successful first and second copulation; 16, 17. Web. Abbreviations: sh = horizontal sheet, th = oblique signal threads.

in the copulatory position, he only used apophyses on his chelicerae to grasp grooves on a ventral plate of the female's opisthosoma (asterisks in Fig. 10). The tips of his legs were not used to hold the female's opisthosoma (Figs. 6–9). In this position the male often bent and stretched his legs in quick succession.

Avoidance behavior.—We observed three types of behavior that appeared to be avoidance behavior: (i) Sometimes, when put together, the two spiders ran quickly in different directions. (ii) After facing each other and staying motionless for several minutes, the female or the male (or both) sometimes turned around and walked away without copulating. (iii) After having palpated each other with the front legs (once or several times in quick succession), the spiders sometimes walked away from each other.

Female aggressive behavior.—We sometimes observed that when a male approached a female (or had faced her for some time or had already come into contact with her) she seemed to scare him away by vigorous vibrations of her body, especially the front legs. Such apparent female aggressive behavior was observed 18 times.

Copulatory behavior.—Seventeen out of 64 females accepted a male for copulation (first copulations). Forty-one trials were necessary to induce successful first copulations. Those first copulations lasted from 1.21 to 3.8 h (median = 2.06; lower quartile = 1.7; upper quartile = 2.74; Fig. 13). Eleven of the 17 females that had copulated once were tested to see if they would accept a second mate. Six of them accepted a second male for copulation 3–9 days after first copulation (average 4.3 ± 2.3). The second copulations lasted from 0.36 to 5.75 h (median = 1.53; lower quartile = 0.48; upper quartile = 2.89; Fig. 14). There was no significant difference between the duration of first and second copulations ($T = -4.5$; $df = 5$; $P < 0.44$; Fig. 14).

For the females that mated twice, eight trials were necessary to induce successful first copulations whereas 37 trials totally were necessary to induce successful second copulations (Fig. 15). The numbers of trials needed to induce successful first and second copulations significantly differed ($T = 10.5$; $df = 5$; $P < 0.031$; Fig. 15).

In the copulatory position (Figs. 6–10) the male was inverted and faced in the same direction as the female. His legs did not touch the female's opisthosoma. The male only used his chelicerae to grasp the female (see "locking mechanism" above). After copulation had begun, all his legs stayed motionless and slightly bent. The male rested on the patellae of his legs III and IV and on the anterior dorsal part of his opisthosoma.

During copulation both spiders remained calm and almost motionless. From time to time the female could take a few steps and slightly change her position. The palps were inserted alternately (arrow in Fig. 6, Fig. 10). Towards the end of copulation, some females started to run around or tried to knock off the male using their legs. In all cases, the male sprang away from the female when copulation was finished by turning a somersault.

Post-copulatory behavior.—After their separation, the spiders mostly walked away from each other. In some cases, they remained close together and showed intense self-grooming. The male often ran his pedipalps through his chelicerae. When the spiders met a second time by walking around after copulation, they either both ran quickly in different directions and kept out of each other's way, or they palpated each other with the front legs for a few seconds before they separated again (see "avoidance behavior" above). Sometimes the female scared away the male (see "female aggressive behavior" above).

Uncertain cases.—In some pairings, after the male had seized the female's opisthosoma with his chelicerae (or had already taken the copulatory position), the female ran until the male loosened his hold and let her go. Sometimes the female pushed her legs against the male's legs and she seemed trying to knock the male off. Such male-female interactions were observed five times and lasted from 1.5–10.62 minutes (average 5.33 ± 3.42). These uncertain cases were not counted as copulations and consequently not included for the analyses shown above.

Web characterization and function.—The web inhabited by *I. lannaianum* consisted of a longish narrow horizontal sheet which was made of many short threads forming a zigzag pattern (sh in Figs. 16, 17). The sheet should be attached along dry leaves and small branches on the ground. Long oblique additional threads functioning as signal threads overlaid the sheet and were partly connected with it (th in Figs. 16, 17). The spiders often stayed in contact with these threads (arrow in Fig. 2, Fig. 16). They immediately reacted to a prey touching the threads and successfully captured it. No particular retreat for the spider was observed.

DISCUSSION

Pre-copulatory behavior.—The main reasons for a male to court before copulation are probably to identify himself as a mate of the same species, to avoid being mistaken for prey or to stimulate the female and convince her of his quality (Eberhard 1985, 1996; Foelix 1996; Huber 1997; Huber & Eberhard 1997; Bartos 1998). In many haplogyne spiders the male courtship behavior prior to copulation is restricted to abdominal vibrations or simple leg and palp movements (Bristowe 1929; Gerhardt 1929; Dabelow 1958; Uhl et al. 1995; Huber 1994, 1995, 1998b, 2002; Huber & Eberhard 1997; Bartos 1998; Senglet 2001). In pholcids, males often keep on moving their pedipalps during copulation (copulatory courtship) (Gerhard 1927; Uhl et al. 1995; Huber 1994, 1995, 1998b, 2002; Huber & Eberhard 1997; Schäfer & Uhl 2002). Other

forms of male courtship behavior are tapping or jerking the female's web (Bartos 1998), cutting threads of the female's web (Uhl et al. 1995; Bartos 1998; Senglet 2001), or spreading the chelicerae (Jackson & Pollard 1982). In exceptional cases male pholcids even perform gustatorial courtship (Huber 1997).

Males of *I. lannaianum* showed several behaviors that could have some sort of pre-copulatory courtship function. Some males palpated the female and pushed her backwards or the male bent and stretched his legs in quick succession before copulation started. The grasping of the female's opisthosoma by cheliceral apophyses could also have a courtship function (Huber 1999). In 5% of the cases, distinctive female aggressive behavior was observed: the male may have been ready to copulate, but the female prevented any further interaction by scaring him away. This behavior is a striking indication for pre-copulatory female choice as those females often mated with other males afterwards. Similar female aggressive behavior in haplogynes was observed in certain pholcids prior to copulation (Huber 1994, 1995; Huber & Eberhard 1997; Bartos 1998) or after copulation (Bartos 1998; Senglet 2001). The fact, that significantly more trials were needed for successful copulation if females had already mated (Fig. 15) could indicate that females become choosier with increasing copulation number as suggested by Schäfer & Uhl (2002) for *Pholcus phalangioides* Fuesslin, 1775. Nevertheless copulations also seemed to take place without pronounced pre-copulatory courtship as sometimes males just grasped the females forcefully with their chelicerae and took the copulatory position directly.

Locking mechanism.—A cheliceral locking mechanism (by apophyses or modified cheliceral hairs) during copulation in haplogyes was reported for certain scytodids (Dabelow 1958) and pholcids (Huber 1994, 1995, 1998b, 2002; Uhl et al. 1995; Senglet 2001). Lehtinen (1981) proposed that some tetrablemmids use apophyses on their chelicerae to grasp corresponding grooves on a ventral plate of the female during copulation. The present study confirms this suggestion for the first time by live observations.

Copulation duration.—Copulation duration is quite variable among different spiders. Elgar (1995) suggested that haplogynes have shorter copulations because of the simplicity of their copulatory apparatus. However, studies have shown that the copulatory organs of some haplogynes are in fact quite complex (e. g., Uhl 2000; Burger et al. 2003), and little is known about the copulation duration of many haplogynes. A few of the haplogyne spiders investigated so far copulate longer than one hour (Gerhardt 1927–1929, 1933; Uhl 1993a; Bartos 1998; Senglet 2001; Schäfer & Uhl 2002). The longest copulation known for a haplogyne spider was longer than 5 hours in the oonopid *Silhouettella loricatula* (Roewer 1942) (sub *Dysderina loricata*) (Bristowe 1930).

It seems obvious that the function of a prolonged copulation in general cannot be explained by prolonged sperm transfer only (Eberhard 1985; Suter & Parkhill 1990). During long copulations, apparent risks are accepted, which should favor brief mating (e. g. increased danger from predators or interruption by another male or by the female before sperm transfer is completed; Eberhard 1996). Copulation duration may correlate with the amount of transferred sperm (Engqvist & Sauer 2003) and/or with fertilization success (Andres & Rivera 2000) but Schäfer & Uhl (2002) showed that longer copulations do not indicate higher fertilization rates in their study. The prolonged copulation duration in *I. lannaianum* could be explained by sperm competition hypotheses such as sperm precedence (Suter & Parkhill 1990; Elgar 1998) and/or by hypotheses of sexual selection by cryptic female choice (the male could initiate processes in the female during copulation which increase his chances of siring her offspring; Eberhard 1985, 1996). The prolonged copulation could also serve as mate guarding. By guarding the female, a male can restrict access to females from other males (Sillén-Tullberg 1981; Wynn & Vahed 2004) and consequently guard and protect his own transferred ejaculate (Schöfl & Taborsky 2002). These are all hypotheses yet to be tested but it appears that *I. lannaianum* could be a good species for testing these ideas.

The second copulation of female no. 4 (Fig. 14) seemed to last disproportionately long when compared to the other second copulations. Excluding it from the analysis would result in a trend towards a decreased duration of the second copulations. Schäfer & Uhl

(2002) suggested that shorter second copulations resulted from a stronger conflict of interest between the sexes over paternity in second matings.

Copulatory position.—The evolution of the mating positions in spiders was discussed by von Helversen (1976). The most plesiomorphic copulatory position is the one taken by most mygalomorphs and haplogynes like *Oonops* (Gerhardt 1930), *Segestria* or *Filistata* (Gerhardt 1928, 1929): the male approaches the female frontally, pushes her body back and upwards and inserts his pedipalps simultaneously or alternately (von Helversen 1976). Among different spider groups, a change from the plesiomorphic to a derived copulatory position took place convergently: the male rests on the ventral side of the female and both partners face in the same direction. This position is seen in the oonopids *Silhouettella* (Bristowe 1930) and *Xestaspis* (Gerhardt 1933).

Indicoblemma lannaianum takes the derived copulatory position. The behavior before some copulations could be a remnant of the one shown by spiders that take the plesiomorphic position: the male pushes the female back and they palpate each other with the front legs for a few seconds (Fig. 11) before he goes backwards along the ventrum of the female and takes the derived copulatory position (Figs. 6–10).

Web characterization and function.—The web of *I. lannaianum* resembles the only web known so far of a tetrablemmine spider. In *Brignoliella vulgaris* Lehtinen 1981, it is a small dense sheet attached along the surface of large dry leaves (Lehtinen 1981). Schwendinger (1989) described the web constructed by *Perania nasuta* Schwendinger 1989, a member of the subfamily Pacullinae. It is a loose sheetweb in which the spider hangs upside down at night.

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PREY CHOICE BY *NESTICODES RUFIPES* (ARANEAE, THERIDIIDAE) ON *MUSCA DOMESTICA* (DIPTERA, MUSCIDAE) AND *DERMESTES ATER* (COLEOPTERA, DERMESTIDAE)

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ABSTRACT. *Nesticodes rufipes* is widely distributed in tropical and subtropical regions, being strongly associated with humans. However, few behavioral and ecological studies have investigated interspecific interactions between these spiders and insects of medical and veterinary importance. Here, we have investigated prey choice by *N. rufipes* when two different prey species, *Musca domestica* and *Dermestes ater*, were offered simultaneously. We also quantified the capture of these prey types by this predator in a poultry house and analyzed the association between prey-choice with physical characteristics of the prey. Finally, we discuss whether there is an antagonistic intraguild interaction in such a system composed of *N. rufipes* (top predator), *D. ater* (predator of larvae of *M. domestica* and prey of *N. rufipes*) and *M. domestica* (*N. rufipes*' prey). We found that *Musca domestica* were more abundant than *D. ater* in *N. rufipes* webs in the poultry house. Spiders given a choice of adults of *M. domestica* plus adults of *D. ater*, and also on adults plus larvae of *M. domestica*, preyed more on adult flies than on the other prey types. This preference was probably associated with the lesser mass and shorter lengths of adult flies. Our experiments demonstrated that the predation impact of *N. rufipes* on *D. ater* is low when compared to *M. domestica*. This result provides evidence that an antagonistic interaction between these predators does not occur, suggesting that they are in fact acting either synergistically or additively on *M. domestica* prey.

Keywords: Prey selection, housefly, spider predation, poultry house

Many spiders eat a wide variety of prey species (usually insects), and they usually present a sedentary foraging behavior (Wise 1993), suggesting that selection for habitat, not for prey, should be the rule. However, several prey capture specializations can be seen (Greenstone 1979; Riechert & Luczak 1982; Uetz 1992; Alderweireldt 1994; Onkonbury & Formanowicz 1997; Nyffeler 1999; Toft 1999), and some may have been an important influence on the evolution of insect defense behavior (Uetz 1990). It has been recognized that the choice of habitat (patch) in spiders is of primary importance through its effect on feeding rates, growth and reproduction (Riechert 1981; Morse & Stephens 1996). Nevertheless, once in a feeding patch, spiders typically are confronted with an array of potential prey species. Indiscriminate feeding is not advantageous because prey vary enormously in quality due to toxicity or nutrient content. Thus, active prey selection by spiders serves to find the optimal compromise between three "nutritional goals": to maximize energy intake, to balance nutrient composition of the body, and to minimize toxin consumption (Toft 1999).

Prey selection has been defined by Hassell (1978) as follows: "Preference for a particular prey is normally measured in terms of the deviation of the proportion of that prey attacked from the proportion available in the environment." A common form of prey specialization shown by spiders is on prey size (Uetz 1992), evidenced by some studies comparing the prey of spiders to that available in the environment (Uetz & Hartsock 1987; Uetz 1990).

Spiders are major components of the generalist predator guild that characterizes intermediate trophic levels in many terrestrial systems (Moulder & Reichle 1972; Manley et al. 1976; Spiller & Schoener 1996). Theory suggests that prey suppression by multiple predator species can lead to a variety of outcomes depending on the nature of the predator-predator interaction. Predator effects can be en-

hanced when predators interact either additively or synergistically (Finke & Denno 2002). Antagonistic interactions, on the other hand, result in diminished prey suppression, either because one predator disrupts the foraging behavior of another predator (Moran et al. 1996), or consumes the other predator (Polis & Holt 1992; Rosenheim 1998; Wise & Chen 1999).

Nesticodes rufipes (Lucas 1846) (Araneae, Theridiidae) (referred to as *Theridion rufipes* in references) is widely distributed in tropical and subtropical regions, extending to temperate zones, and these spiders construct irregular webs with a disordered aspect (González 1989). Its exact distribution is not easy to determine, since it is strongly associated with humans (Downes 1988; González & Estévez 1988; González 1989). Behavioral and ecological studies considering predation by *N. rufipes* are scarce. Fox (1998) highlighted the strategic importance of these spiders to the natural control of *Aedes aegypti* (Diptera, Culicidae), since the spiders incorporate a paralyzing substance in the webs, which paralyzed the mosquitoes through contact, increasing their capture efficiency. Barreto et al. (1987) also mentioned the importance of *N. rufipes* as predators of *Rhodnius prolixus* (Hemiptera, Reduviidae).

Musca domestica (Linnaeus 1758) (Diptera, Muscidae) has a cosmopolitan distribution and high synanthropic indices (Smith 1986; Ferreira & Lacerda 1993), being also of considerable medical and veterinary importance (Harwood & James 1979; Smith 1986; Levine & Levine 1991). This species lives in human dwellings, poultry houses, supermarkets and garbage, growing on a wide variety of substrates such as food and vertebrate excrement (Axtell & Arends 1990; Bowman 1995). Although there are some chemical techniques aimed to control *M. domestica* in poultry houses, the negligent human behavior related to the correct application of chemicals has intensified the search for potential natural enemies of houseflies in order to diminish chemical applications (Cunha & Lomônaco 1996). Therefore, the understanding of the strength of interspecific interactions between *M. domestica* and its predators is of major importance.

Dermestes beetles grow in organic matter, such as carrion and dung that accumulate in poultry houses (Cloud & Collison 1986). *Dermestes ater* (DeGeer 1774) (Coleoptera, Dermestidae) feeds and scavenges on animal products. However, sometimes it feeds on other insects, thus acting as a predator (Veer et al. 1996). For example, *D. ater* causes serious economic damage to sericiculture, because the beetles feed on high numbers of *Bombyx mori* (Lepidoptera, Bombycidae) (Kumar et al. 1988; Bai & Mahadevappa 1996).

According to Lomônaco & Prado (1994), *M. domestica* (91. 82%) and *Chrysomya putoria* (Diptera: Calliphoridae) (6.47%) were the most abundant fly species sampled in a poultry house located in the city of Uberlândia (MG), Brazil. These authors also observed that *D. ater* was one of the most frequent natural enemies of larvae and pupae of *M. domestica* in that system. As *M. domestica* (adults) and *D. ater* (adults and larvae) are usually seen in *N. rufipes* webs in poultry houses, and *D. ater* attacks and feeds on *M. domestica*, it is of major importance to understand the strength of interspecific interactions among these animals in such a system.

Here, we investigated prey choice by *N. rufipes* when two different prey species, *D. ater* and *M. domestica*, were provided at the same time as primary food sources. We also quantified the capture of these prey species by this predator in a poultry house, comparing the results with the prey choice experiment. Correlations of prey choice with physical characteristics of prey types are also presented. Finally, we discuss whether there is evidence of antagonistic intraguild interactions in such a system composed of *N. rufipes* (top predator), *D. ater* (intermediate predator and prey of *N. rufipes*), and *M. domestica* (*N. rufipes*' prey).

METHODS

Field observations.—An experimental poultry house located in the city of Botucatu-SP (Brazil) (22°52′20″S; 48°26′37″W) was chosen to collect insects captured by *N. rufipes* webs. From September 2001 to August 2002, all poultry house parts (walls, door crevices, wood supports, chicken cages, etc.) were examined monthly. When a web site containing *N. rufipes* was found, all arthropod carcasses caught in the web were removed and put into small glass tubes for identification. Spiders were never removed from their web

sites in order not to diminish their abundance, and we did not distinguish males from females, or even spiderlings from adults, that were inhabiting the webs. The carcasses were then taken to the laboratory where prey were identified. We recorded from each web the species of prey and also the respective month of collection. Voucher specimens (spiders and insects) from this study are deposited in the Invertebrate Collection of the Department of Parasitology, Unesp (Botucatu-SP), Brazil.

We compared which prey species were captured throughout the year by plotting the total number of flies and beetles (adults + larvae) captured monthly. In the same plot, we included the number of web sites observed by month.

Rearing of prey species.—While visiting the poultry house, we collected larvae of houseflies and adults of *D. ater* from small samples of chicken feces deposited below the cages and put them into small glass tubes. All insects were then taken to the laboratory where larvae of *M. domestica* were reared in vials containing wet ground animal ration (25 °C under 12 h light). After pupation, vials were kept in cages of nylon mesh on a wood frame (30 cm × 30 cm × 30 cm) where water and sugar were provided for adults. Adults of *D. ater* were kept in plastic boxes (15 cm × 45 cm × 30 cm) (25 °C under 12 h light) with large pieces of cotton which allows females to lay their eggs. Wet cotton and fish (sardines) were added weekly as water and food sources, respectively.

Prey choice.—Forty-five adult females of *N. rufipes* were captured in several buildings located on the campus of the University of the State of São Paulo (Botucatu, Brazil) from January–March 2003, and kept individually in clear plastic containers [10.5 cm × 11.5 cm (900 ml)] in the laboratory (25 °C under 12 h light). All spiders were of similar size range (15 mm). Before the prey choice experiments were carried out, a nylon mesh (10 cm × 3 cm) was internally fixed in each container in order to allow spiders to build their webs. All spiders were fed with both houseflies and dermestid beetles for a month (insects were randomly offered twice a week) in order to attain similar nutritional status.

After twenty-four hours of food deprivation (sufficient time for spiders to build their webs), fifteen containers with spiders received five larvae (third instar) and five adults of *M. domestica* each. Another fifteen containers received five larvae (fifth instar) of *D. ater* and five adults of *M. domestica* each, and the remaining containers received five adults of *D. ater* and five adults of *M. domestica* each.

Before adding the different prey types into the spider containers, flies were immobilized by chilling in a freezer for three minutes. After that, flies were removed and put in a Petri dish together with the other insects [*D. ater* (larvae or adult) or larvae of *M. domestica*)] previously removed from their laboratory rearing cages. When flies began to move, all ten insects were carefully dropped in the bottom of a spider container, without touching the spider web. This procedure prevented flies from being captured quickly due to their superior flying ability and it insured that flies could be easily separated prior to the experiments. In the first two minutes (approximately) inside the spider containers, flies just walked and then started flying. Prey consumption evaluation started twenty-four hours following the introduction of the insects.

The number of prey eaten by spiders was recorded according to the combination of prey types, and an analysis of variance (ANOVA) (Zar 1999) was computed comparing the mean proportions [arcsin ($\sqrt{\text{proportion}}$)] of adults of *M. domestica* consumed, since it was common for all combinations of prey. A Least Significant Difference test (LSD) was computed comparing the pairs of transformed mean proportions of adults of *M. domestica* consumed between the different prey combination treatments (adults + larvae of *M. domestica*, adults of *M. domestica* + larvae of *D. ater*, and adults of *M. domestica* + adults of *D. ater*). To test the hypothesis that prey choice was random, we compared the measured proportion of prey captured to the probability that prey capture was random (i.e. 50% chance of capturing house flies). We did this by constructing *t*-tests on the arcsin ($\sqrt{\text{proportion}}$) transformed data, which compared the mean transformed value to arcsin ($\sqrt{0.5}$).

Size of prey.—After the prey-choice experiments, many larvae (fifth instar) and adults of *D. ater* as well as larvae (third instar) and adults of *M. domestica* were randomly removed from their respective rearing cages

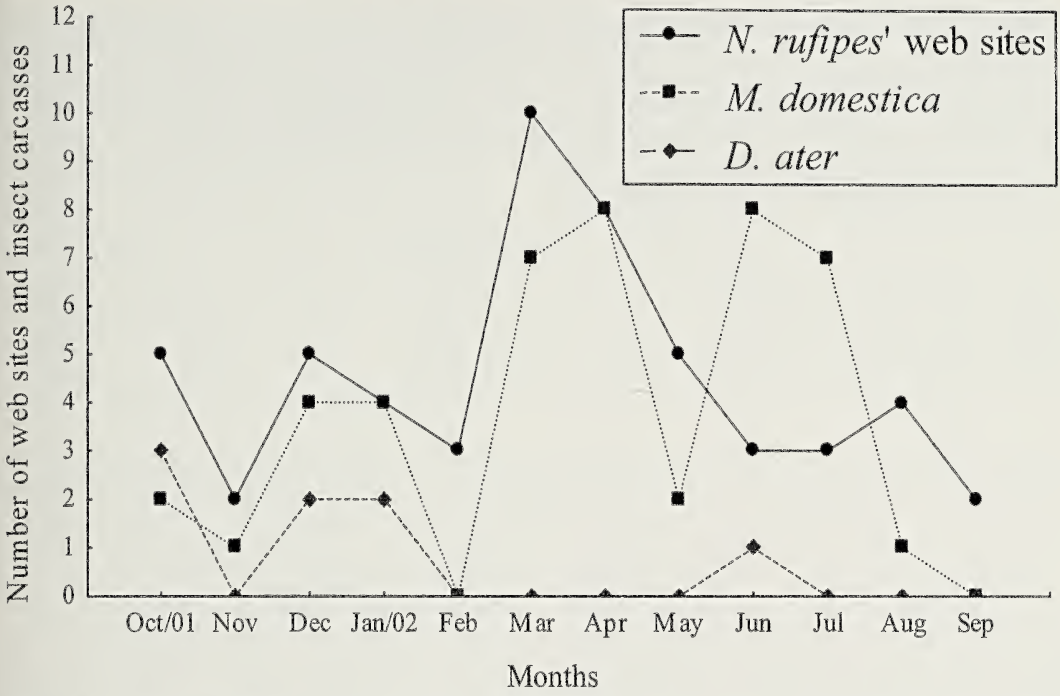

Figure 1.—Number of *M. domestica* (adults) and *D. ater* (adults plus larvae) carcasses collected from October 2001 to September 2002 in a poultry house located in Botucatu (SP), Brazil. The number of web sites observed is also included.

and, from there, twenty insects from each prey type were again randomly removed. These insects were first killed with ether solution (90%) and then measured (body length measured from anus to head without measuring wings for adult flies) by using a graduated micrometric ocular coupled to a stereoscopic microscopy and weighed with a semi-analytical scale. Student's *t*-tests were computed comparing pairs of mean weights and lengths for each combination of prey types. Thus, we tested whether the lighter and shorter prey were also the more preferable ones.

RESULTS

Musca domestica carcasses were much more abundant than *D. ater* (adults + larvae) on *N. rufipes* webs for most of the 12 months of collection (Fig. 1). The spiders in the poultry house ate more 5.5 times as many flies (n = 44) than dermestid beetles (n = 8) over the course of the year-long study (Fig. 1). Spiders captured a total of sixteen species of prey. Insects from orders Coleoptera (48.36%) and Diptera (34.02%) represented 82.38% of all prey captured, and for all months sampled *M. domestica* was predominant as prey, since it represented 24.59% of the insects captured, followed by the coleopterans *Alphitobius diaperinus* (Tenebrionidae) (20.90%), *Aphodius* (Scarabaeidae) (10.25%), *Gnathocerus* (Tenebrionidae) (6.15%), and *D. ater* (3.28%). All dipterans except *M. domestica* represented only 9.4% of prey. Even though several prey were captured, in figure 1 we present data only related with the arthropod species studied here.

In the prey choice experiments, the number of adult flies consumed by spiders was significantly different when different combinations of prey types were offered (df = 2; MS = 0.808; F = 4.185; P = 0.023), and the combination of adults of *M. domestica* plus adults of *D. ater* showed the highest average proportion of adult flies consumed (Table 1).

The Student's *t*-tests showed that when spiders were placed in cages with adults of *M. domestica* plus adults of *D. ater*, or with adults of *M. domestica* plus larvae of *M. domestica*, spiders were selective and took more adult flies than the other prey (Table 1). Although the combination of adults of *M. do-*

Table 1.—Mean proportion of spiders that fed on adults of *M. domestica* given different combinations of potential prey. Student's *t*-tests were used to test for significance of difference using the transformed mean proportions [arcsin ($\sqrt{}$proportion)] of adults of *M. domestica* consumed and the probability of 50% [arcsin ($\sqrt{0.5}$)] of consumption. *Significant at $P < 0.01$. In addition, proportions followed by different letters differed statistically from each other [Least Significant Difference (*LSD*) test] at $P < 0.05$. n = Number of observations for each group. $n = 14$ and $n = 13$ means that one and two spiders did not feed on any prey during experimentation, respectively.

Combination of prey types	Mean proportion (± SD)	n	*t*	*P*
Adults × Larvae of *M. domestica*	0.73 ± 0.44 a	13	3.45	*0.002**
Adults of *M. domestica* × Larvae of *D. ater*	0.71 ± 0.80 a	15	1.86	0.074
Adults of *M. domestica* × Adults of *D. ater*	0.96 ± 0.26 b	14	13.0	*0.000**

mestica plus larvae of *D. ater* presented a nonsignificant result for adult flies consumed ($P = 0.074$), a strong tendency of spiders to consume more flies was evidenced (Table 1).

Adults of *M. domestica* weighed less when compared to the other prey offered to spiders, and it also had smaller body size since Student's *t*-tests were significant for all comparisons in all combinations of prey (Figs. 2, 3).

DISCUSSION

The preference of *N. rufipes* for adults of *M. domestica* might be associated with their smaller mass and shorter lengths, probably because it would facilitate their being killed and handled by spiders. Prey activity would also explain why spiders captured disproportionately more adults of *M. domestica* than the other prey types (Table 1). According to Provencher & Coderre (1987), prey activity is believed to influence functional responses and switching of spiders for some prey. Although all prey species were highly active in the experimental containers, only adults of *M. domestica* could do a three-dimensional exploration in the container, since it flew over all

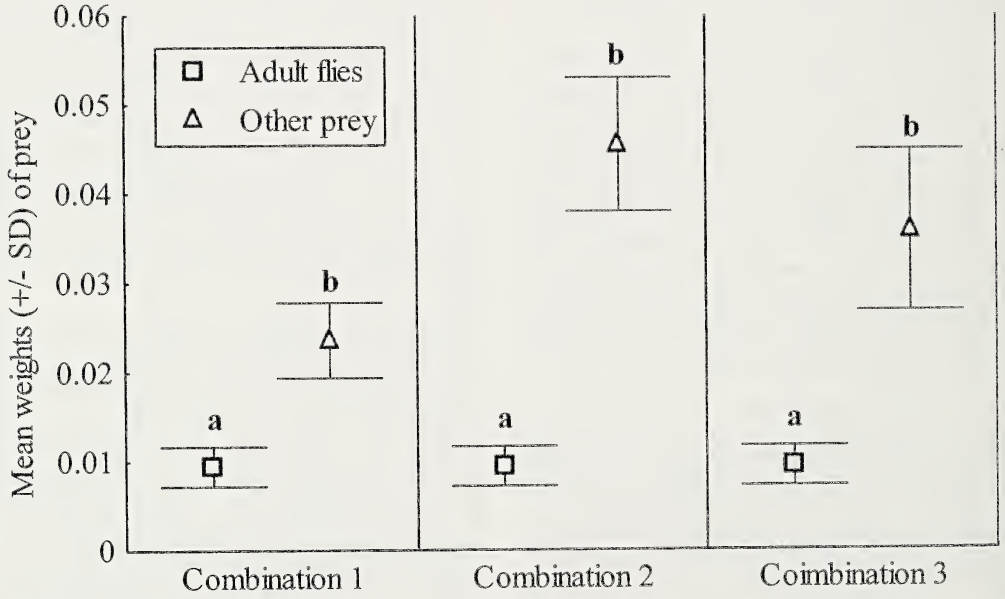

Figure 2.—Comparisons of mean weights (grams) of prey according to different combinations of prey types. A Student's *t*-test was computed for each combination and all analyses were statistically significant (All analyses had n = 20 and 38 degrees of freedom). Combination 1: adults + larvae of *M. domestica* (*t*-value = −13.27; $P < 0.01$); Combination 2: adults of *M. domestica* + larvae of *D. ater* (*t*-value = −20.60; $P < 0.01$); Combination 3: adults of *M. domestica* + adults of *D. ater* (*t*-value = −12.69; $P < 0.01$).

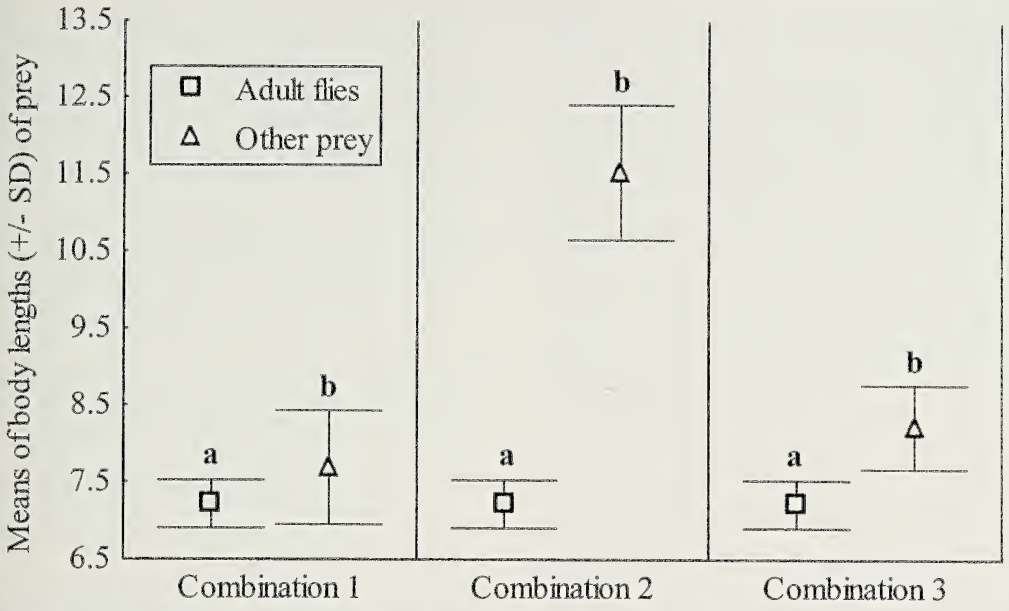

Figure 3.—Comparisons of mean lengths (mm) of prey according to different combinations of prey types. A Student's *t*-test was computed for each combination and all analyses were statistically significant (All analyses had n = 20 and 38 degrees of freedom). Combination 1: adults + larvae of *M. domestica* (*t*-value = −2.65; $P < 0.05$); Combination 2: adults of *M. domestica* + larvae of *D. ater* (*t*-value = −20.71; $P < 0.01$); Combination 3: adults of *M. domestica* + adults of *D. ater* (*t*-value = −7.15; $P < 0.01$).

areas of the container, probably increasing its frequencies of encountering the predator. The other prey types only walked intensively in the bottom of the container with the exception of adults of *D. ater*, which occasionally flew. The higher rate of consumption of adults of *M. domestica* when this prey was offered concomitantly with adults of *D. ater* (Table 1) is possibly associated with the rigidity of beetle exoskeletons, which may increase their rate of escape from spider attacks.

We observed that all spiders actively captured their prey rather than passively waiting for prey to fall randomly in their webs (sit-and-wait strategy). This behavior was possible because the available time given to spiders to build their webs (24 hours) was insufficient to enable them to weave large and dense webs. Large webs would allow spiders to catch prey only by a prey-web contact. Hence, the way that we set up the experiments ensured that webs were just used by spiders to increase their area of attack, forcing them to actively choose a prey type. It is important to state that all spiders wove webs in all parts of the containers, including the bottom, enabling them to capture all prey available. Thus, we conclude that preference of spiders for housefly adults was determined by prey behavior and physical characteristics of prey (length and weight) in addition to active spider prey choice.

Finke & Denno (2002) studied the combined impact of two salt-marsh-inhabiting invertebrate predators, the mirid *Tytthus vagus* (Heteroptera, Miridae) and the wolf spider *Pardosa littoralis* Banks 1896 (Araneae, Lycosidae), on suppression of their shared prey, the planthopper *Prokelisia dolus* (Hemiptera, Delphacidae), in simple and complex habitats. They observed that in simple habitats, the predators interacted antagonistically, due to intraguild predation of mirids by spiders, and predation pressure on the planthopper population was relaxed. However, for structurally complex habitats this antagonistic interaction was dampened by providing a refuge for mirids from spider predation. Our experiments demonstrated that the predation impact of *N. rufipes* on *D. ater* is low when compared to that on *M. domestica* (Fig. 1), and it provides some evidence that an antagonistic interaction between these predators (and scavenger) may not occur, suggesting that they are in fact act-

ing either synergistically or additively on *M. domestica* prey.

Considering that more than a hundred of pathogens are associated with *M. domestica*, such as those causing typhoid fever, cholera, tuberculosis, parasitic helminthiasis and protozoosis (Harwood & James 1979; Smith 1986; Levine & Levine 1991; Chavasse et al. 1999; Fischer 1999), synergistic and additive interactions between *D. ater* and *N. rufipes* have important practical implications since it may increase the likelihood of a natural suppression of housefly populations established in poultry houses. However, functional response studies of *D. ater* and *N. rufipes* on larvae and adults of *M. domestica*, respectively, are encouraged in order to understand the actual contribution of these predators in diminishing natural or experimental housefly populations.

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A REVIEW OF PHOLCID SPIDERS FROM TIBET, CHINA (ARANEAE, PHOLCIDAE)

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ABSTRACT. The pholcid spiders from Tibet, China, are reviewed. Seven species belonging to three genera are recorded. A new genus, *Tibetia*, is established, and four new species, *Pholcus medog*, *P. zham*, *Belisana gyirong* and *B. mainling* are described. And two new combinations are formed: *Tibetia everesti* (Hu & Li 1987) is transferred from *Pholcus*, and *Belisana yadongensis* (Hu 1985) is transferred from *Spermophora*.

Keywords: Taxonomy, new species, new combination, Asia

The spider family Pholcidae currently contains 75 genera and 868 species (Platnick 2004) throughout the world. Members of the family vary in habitus, size and life style. Also, the pholcids are among the most common spiders occurring in houses. These spiders have elongate or globose abdomens and frequently very long and thin legs (about 4–20 times as their body length) with false segments in tarsi, and are thus called daddy-long-legs, although in a few pholcid species, the legs are quite short (only about 1 mm). The overall coloration of pholcids is quite variable, but the legs are often characteristically annulated. The eye region is more or less elevated, bearing eight or six eyes. If the smallest AMEs are present, the others are in two triads. The presence of the cheliceral stridulatory organs is variable. The male chelicerae are frequently equipped with pairs of special apophyses which are often species-specific in morphology and the pedipalps are conspicuously large and strong (Huber 1995, 1999) and their complex morphology has been well demonstrated by Uhl et al. (1995). Externally the female genitalia are usually relatively simple, but the internal morphology is very complicated (Huber 1998).

Pholcids spin messy, loose and irregular webs, and the males and females often hang inverted in the same webs. The females carry the spherical egg cluster under their chelicerae. When disturbed or under threat of attack, most pholcid species violently vibrate within their webs to scare off antagonists. Also solitary species on firm ground can shake their bodies in such a rhythm that they virtually disappear from the human eye (Saaristo 2001). Many pholcid species are pantropical and synanthropic. They live in dark recesses, such as within houses and other buildings, in caves, under rocks and loose bark, as well as in leaf litter.

Previously, only three pholcid species belonging to two genera have been recorded from the Tibetan region of China (Hu 1985; Hu & Li 1987; Hu 2001): *Spermophora yadongensis* Hu 1985, *Pholcus everesti* Hu & Li 1987 and *Pholcus affinis* Schenkel 1953.

After examination of pholcid specimens collected from Tibet in 2002 and 2003, we here deal with seven species of this family belonging to three genera, including a new genus, *Tibetia*, and four new species: *Pholcus medog*, *P. zham*, *Belisana gyirong* and *B. mainling*. Also, two new combinations are proposed: *Belisana yadongensis* (Hu 1985) (transferred from *Spermophora*), *Tibetia everesti* (Hu & Li 1987) (transferred from *Pholcus*). Additionally, the common species, *Pholcus manueli* Gertsch 1937 (senior synonym of *Pholcus affinis* Schenkel 1953, by Senglet 2001) is listed.

METHODS

This paper is mostly based on material collected from Tibet by staff members from Hebei University, with the exception of *Pholcus manueli* Gertsch 1937. Terminology is standard for Araneae. Carapace length was mea-

sured from the anterior face of the ocular area to the rear margin of the carapace medially, excluding the clypeus. Total length is the sum of carapace and abdomen length, regardless of the petiole. The measurements of legs are presented as follows: total length (femur + patella plus tibia + metatarsus + tarsus). The left male pedipalp is used for illustrations. Epigyna were cleared in a warm solution of potassium hydroxide (KOH), transferred to water and temporarily mounted for drawing.

All measurements are given in millimeters. Type specimens are deposited in the College of Life Sciences, Hebei University (HU).

The following abbreviations are used: ALE = anterior lateral eyes; AME = anterior median eyes; PLE = posterior lateral eyes; PME = posterior median eyes; MOA = median ocular area; AME-ALE = distance between AME and ALE; ALE-PLE = distance between ALE and PLE; AME-AME = distance between AMEs; PME-PLE = distance between PME and PLE; PME-PME = distance between PMEs.

TAXONOMY

Family Pholcidae C.L. Koch 1851
Genus *Pholcus* Walckenaer 1805

Pholcus Walckenaer 1805: 80; Simon 1893: 470–471; Huber 2000: 77; Huber 2001: 108–111; Hu 2001: 81.

Type species.—*Aranea phalangioides* Fuesslin 1775, by subsequent designation.

Diagnosis.—Medium to large-sized pholcids with cylindrical opisthosoma, mostly with AMEs present. The most useful characters that distinguish *Pholcus* from other genera are the projections of the bulb, traditionally called the uncus, the appendix and the embolus. Other characters are the conservative male chelicerae (a pair of dark frontal apophyses and a pair of light lateral apophyses), the shape of the procursus (usually with ventral boss), and the knob or worm-shaped apophysis on the often roughly triangular or oval epigynum (Huber 2001).

Remarks.—The genus *Pholcus*, with more than 110 species mainly from the pan-Pacific region and Africa, is the largest pholcid genus. Most nominal species seem to be correctly placed, although they are poorly revised at the specific level. The real taxonomic problem is its relationship to other genera of the *Pholcus* group(see Huber 2001).

Pholcus manueli Gertsch 1937

Pholcus manueli Gertsch 1937: 1, figs. 6–7; Senglet 2001: 62, figs. 60–66.

Pholcus affinis Schenkel 1953: 23, figs. 12a–b; Song et al. 1999: 52, figs. 11H, 22D–G; Hu 2001: 81, figs. 7.1–4 (first synonymized with *P. manueli* by Senglet in 2001).

Type material.—*Pholcus manueli*: the type specimens from New Jersey are deposited in the American Museum of Natural History, New York (not examined).

Pholcus affinis: 1 male paratype from Tcheuly of China is deposited in the Natural History Museum of Basel, Switzerland, examined by Senglet (2001); other type material unknown.

Material examined.—None from Tibet.

Description.—See Gertsch (1937) and Hu (2001).

Distribution.—China: Tibet (Gyirong), Hebei, Zhejiang, Jiangsu, Sichuan, Shannxi, Shanxi, Inner Mongolia, Liaoning, Jilin; Russia, Japan, U.S.A.

Remarks.—Judging from the figures drawn by Hu (2001), we are confident that this species is correctly identified and it is confirmed from Tibet.

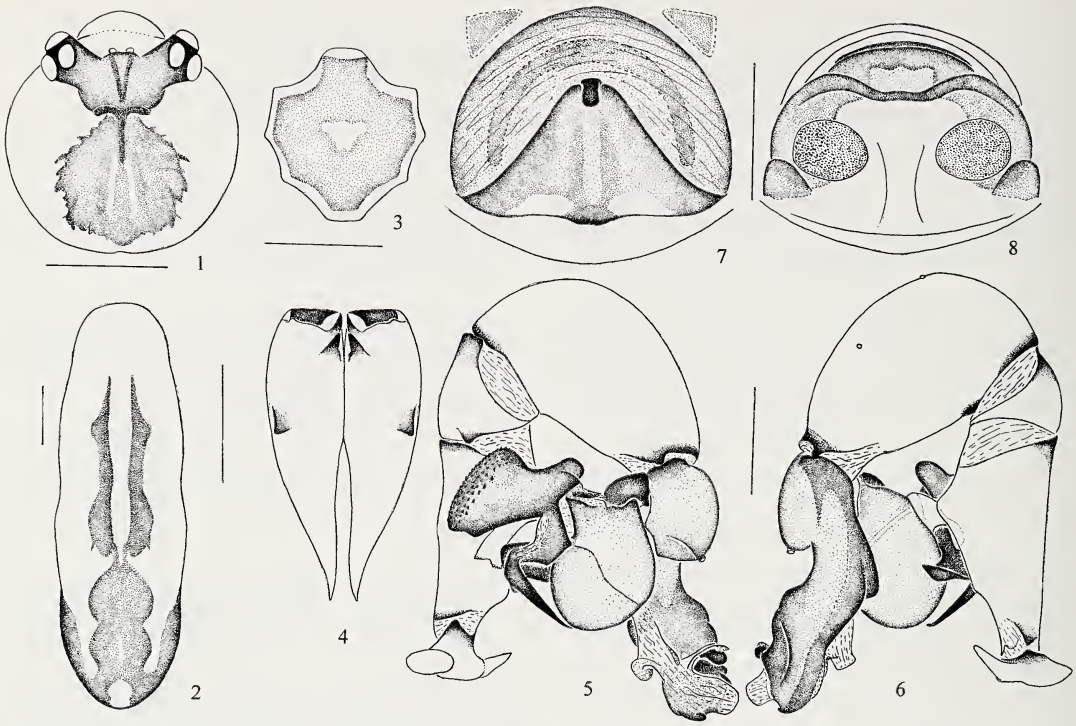
Pholcus medog new species
Figs. 1–8

Material examined.—CHINA: *Tibet*: Holotype male, Medog County (29°12′N, 95°18′E), 17 August 2003, Feng Zhang (HU). Paratypes: 5 females, 2 males, same data as holotype; 1 ♀, 1 ♂, Medog County, 10 August 2003, Feng Zhang (HU); 1 ♀, 3 juveniles, Baibung Town (29°12′N, 95°06′E), Medog County, 13 August 2003, Feng Zhang (HU).

Etymology.—The species name is a noun in apposition derived from the type locality.

Diagnosis.—This species resembles *P. podophthalmus* Simon 1893 (Song et al. 1999: 58, figs. 24O–V), but can be readily distinguished from the latter by the shape of uncus, the bifurcate appendix of the male pedipalp and the color pattern of the carapace.

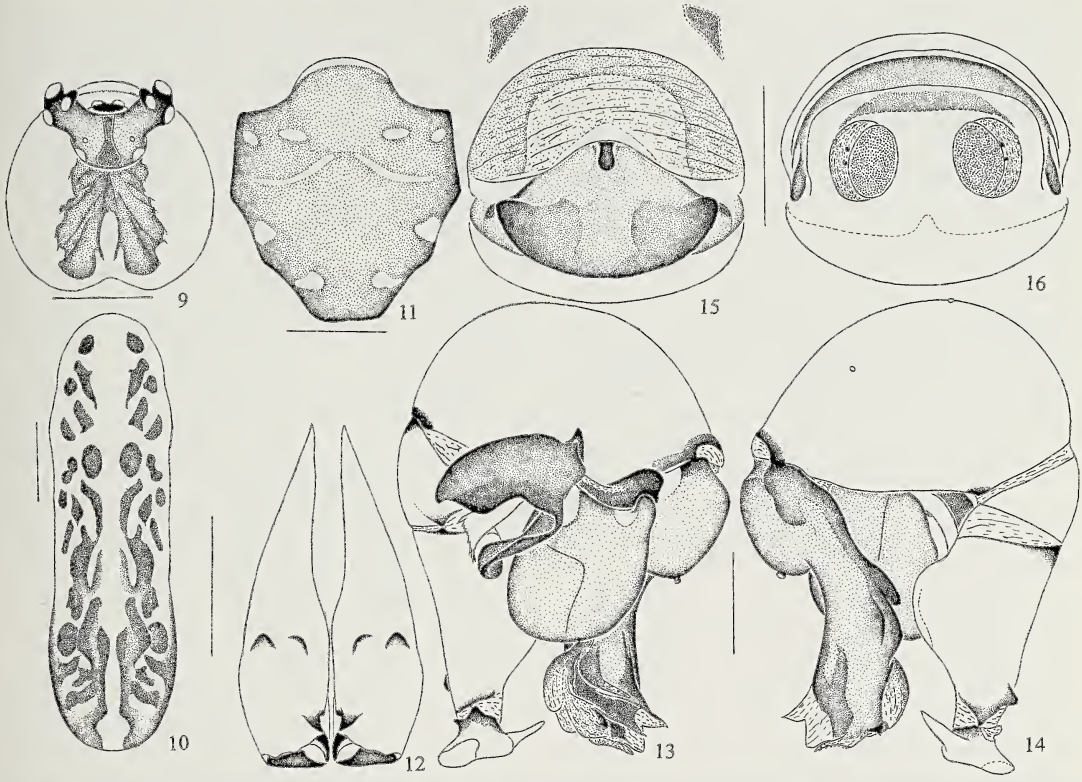
Description.—*Male (holotype):* Total body length 6.25: cephalothorax 1.17 long, 1.71 wide; abdomen 5.08 long, 1.40 wide. Prosoma shape as in Fig 1. Carapace short, broad and



Figures 1–8.—*Pholcus medog*, new species: 1. male prosoma, dorsal view; 2. male opisthosoma, dorsal view; 3. male sternum, ventral view; 4. male chelicerae, frontal view; 5. left pedipalp, prolateral view. 6. same, retrolateral view; 7. epigynum, ventral view; 8. same, dorsal view. Scale lines: 1 mm (1–3), 0.5 mm (4–8).

almost circular, ochre, with brown mark broadly connecting to ocular area. Cephalic region raised, with two brown slender central marks, ocular area dark yellow. Clypeus 0.43 high, ochre, without marks. Except AMEs, other six eyes in two triads, each triad on the top of a relatively longer eye stalk. Distance AME-AME 0.05. Diameter AME 0.09, ALE 0.26, PME 0.18, PLE 0.23. Chelicerae shaped as in Fig. 4, with pair of black apophyses distally and pair of unsclerotized rounded apophyses proximolaterally. Labium light yellow. Endites gray. Sternum (Fig. 3) dark gray, with irregular yellow patches centrally. Legs exceedingly long and slender, femora, patellae and tibiae ochre, with dark rings, metatarsi and tarsi brown. Measurements of legs: I 52.51 (13.05 + 13.50 + 22.95 + 3.01); II 34.23 (9.00 + 9.21 + 14.4 + 1.62); III 23.47 (6.49 + 6.30 + 9.23 + 1.45); IV 32.11 (8.89 + 8.68 + 12.83 + 1.71). Leg formula: 1243. Abdomen cylindrical, pale ochre, dorsum with large brown pattern as in Fig. 2, venter with central long brown stripe. Spinnerets yellowish brown. Uncus of male pedipalp large and slightly triangular, heavily sclerotized and provided with many teeth on the edge; appendix spilt into two parts; embolus lying between the uncus and appendix, soft and transparent (Fig. 5); procursus with ventral boss (Fig. 6).

Female: In general very similar to male. Total body length 4.86–6.23. One specimen measured: total length 5.95: cephalothorax 1.45 long, 1.53 wide; abdomen 4.50 long, 1.31 wide. Clypeus 0.55 high. Both eye rows recurved. Except AMEs, other six eyes in two triads, each triad on a slightly elevated tubercle. Distance AME-AME 0.05, AME-ALE 0.13, PME-PME 0.30, PME-PLE 0.04. Diameter AME 0.08, ALE 0.18, PME 0.15, PLE 0.17; MOA 0.26 long, front width 0.19, back width 0.56. Measurements of legs: I 40.81 (10.07 + 10.21 + 18.00 + 2.53); II 24.53 (6.75 + 6.03 + 10.13 + 1.62); III 17.58 (4.97 + 4.82 + 6.66 + 1.13); IV 24.08 (6.93 + 6.53 + 9.00 + 1.62). Leg formula: 1243. Epigynum roughly triangular, with a knob-shaped apophysis on the top of it (Fig. 7).



Figures 9–16.—*Pholcus zham*, new species: 9. male prosoma, dorsal view; 10. male opisthosoma, dorsal view; 11. male sternum, ventral view; 12. male chelicerae, frontal view; 13. left pedipalp, prolateral view; 14. same, retrolateral view; 15. epigynum, ventral view; 16. same, dorsal view. Scale lines: 1 mm (9, 10), 0.5 mm (11–16).

Habitat.—Untidy webs are made under cliff or rock crevices. Generally, a male and a female hang upside down in the same web.

Distribution.—Known from Medog County, Tibet.

Pholcus zham new species
Figs. 9–16

Material examined.—CHINA: *Tibet*: Holotype male, Zham Town (27°54′N, 85°54′E), Nyalam County, 30 August 2002, Feng Zhang and Zhi-Sheng Zhang (HU). Paratypes: 6 females, same data as holotype (HU).

Etymology.—The species name is a noun in apposition derived from the type locality.

Diagnosis.—This new species resembles *P. medog* (Figs. 1–8), but can be readily distinguished from the latter by: the shape of the uncus, the non-bifurcate appendix of male pedipalp and the chelicerae with two pairs of unsclerotized apophyses centrally.

Description.—*Male (holotype):* Total body length 6.33: cephalothorax 1.56 long, 1.73 wide; abdomen 4.77 long, 1.26 wide. Prosoma shape as in Fig. 9. Carapace short, broad and almost circular, ochre, with brown mark broadly connecting to ocular area. Cephalic region raised, with a brown longitudinal mark centrally, ocular area yellow. Clypeus 0.80 high, ochre, without marks. Except AMEs, other six eyes in two triads, each triad on the top of a relatively longer eye stalk. Distance AME-AME 0.07. Diameter AME 0.11, ALE 0.22, PME 0.16, PLE 0.17. Chelicerae shaped as in Fig. 12, with pair of black apophyses distally, and two pairs of unsclerotized rounded apophyses proximolaterally and proximocentrally respectively. Labium light yellow. Endites gray. Sternum (Fig. 11) dark gray, with roughly 5 pairs of irregular yellow patches on it. Legs exceedingly long and slender, femora, patellae and tibiae ochre, with dark rings, metatarsi and tarsi brown. Measurements of legs: I 56.61 (13.77 + 13.95 + 25.65

+ 3.24); II 36.90 (9.76 + 10.04 + 14.85 + 2.25); III 24.57 (7.02 + 6.75 + 9.45 + 1.35); IV 32.91 (9.59 + 8.83 + 12.83 + 1.66). Leg formula: 1243. Abdomen cylindrical, pale ochre, dorsum with many brown spots as in Fig. 10, venter with central long brown stripe. Spinnerets yellowish brown. Uncus of male pedipalp large and slightly rectangular, heavily sclerotized and provided with many scales on the edge; sclerotized appendix hook-shaped and rod-like; embolus lying between the uncus and appendix, soft and transparent (Fig. 13); and procursus with ventral boss (Fig. 14).

Female: In general very similar to male. Total body length 7.36–8.82. One specimen measured: total length 8.82: cephalothorax 1.70 long, 1.72 wide; abdomen 4.32 long, 1.48 wide. Clypeus 0.49 high. Both eye rows recurved. Except AMEs, other six eyes in two triads, each triad on a slightly elevated tubercle. Distance AME-AME 0.06, AME-ALE 0.12, PME- PME 0.33, PME-PLE 0.08. Diameter AME 0.10, ALE 0.22, PME 0.14, PLE 0.21; MOA 0.31 long, front width 0.27, back width 0.58. Measurements of legs: I (12.96 + 13.95 + 25.61 + 3.19); II (9.45 + 9.54 + 14.37 + 2.21); III (6.75 + 6.44 + 9.00 + 1.26); IV (9.72 + 8.82 + 12.96 + 1.74). Leg formula: 1243. Epigynum roughly triangular, with a knob-shaped apophysis on the top of it (Fig. 15).

Habitat.—Untidy webs are made under rocks.

Distribution.—Known only from type locality in Nyalam County, Tibet.

Tibetia new genus

Type species.—*Pholcus everesti* Hu & Li 1987.

Etymology.—The generic name refers to Tibet, the Xizang Autonomous Region. The gender is feminine.

Diagnosis.—The genus *Tibetia* is similar to several other genera (*Wugigarra* Huber 2001, *Trichocyclus* Simon 1908, *Physocyclus* Simon 1893 and *Artema* Walckenaer 1837) through the possession of the peculiar set of structures on the procursus (dorsal apophysis and ventral pocket). It can be distinguished from *Wugigarra* by the absence of a characteristic worm-shaped process on the male bulb (Figs. 21–22) and the absence of stridulatory files in females, and the epigynum with a median depression (Figs. 23, 51); from *Trichocyclus* by the absence of a weak zone dorsally on male cymbium (Fig. 56), and the median depression of the female epigynum; from *Physocyclus* by the bulbal apophysis and the shape of the procursus (Fig. 56), the absence of embolus on the bulb (only the sperm duct opening be seen) (Fig. 52) and the shape of the epigynum (Figs. 23, 51); and from *Artema* by the epigynal depression centrally (Fig. 23, 51), the absence of embolus and the shape of bulbal apophysis.

Additionally, the new genus also differs from the *Holocneminus* Berland 1942 (Berland 1942, figs. 5a–f), which is apparently widely distributed in eastern Asia, by the absence of stridulatory files in the female, and the normal tarsus of female pedipalp (not strongly dilated) (Fig. 52).

Description.—See description of single species below.

Remarks.—Judging from the known distribution of *Physocyclus*, it appears that *Physocyclus* is a New World genus, with the exception of the pantropical *Physocyclus globosus*, while the new genus is found only in Tibet. Thus the two genera appear to be allopatric in distribution.

Tibetia everesti (Hu & Li 1987) new combination
Figs. 17–24, 51–56

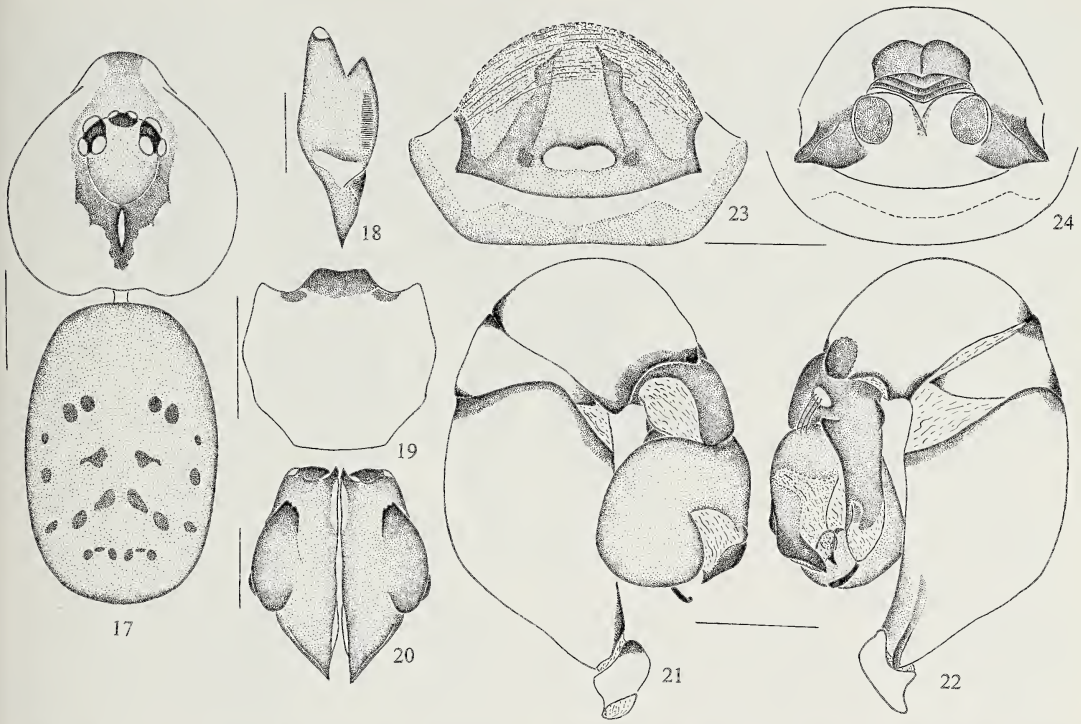
Pholcus everesti Hu & Li 1987: 260, fig. 8; Song, Zhu & Chen 1999: 57; Hu 2001: 82, fig. 8. 1–7.

Type material.—Hu & Li (1987) described both sexes from Nyingchi and Namling Counties, Tibet. The type specimens are deposited in Shandong University, China, not examined.

Material examined.—CHINA: *Tibet*: 5 ♀, 2 ♂, Zetang Town (29°12′N, 91°42′E), Nedong County, 25 August 2002, Ming-Sheng Zhu and Feng Zhang (HU); 1 ♀, 1 ♂, Rigaze City (29°12′N, 88°48′E), 6 September 2002, Jun-Xia Zhang (HU); 1 ♀, Nyingchi County (29°30′N, 94°18′E), 21 August 2003, Feng Zhang (HU); 1 ♀, 1 ♂, Bayi Town (29°36′N, 94°12′E), Nyingchi County, 2 August 2003, Ming-Sheng Zhu and Zhi-Sheng Zhang (HU); 1 ♀, Lhasa City (29°36′N, 91°06′E), 30 July 2002, Ming-Sheng Zhu and Jun-Xia Zhang (HU).

Diagnosis.—See generic diagnosis above.

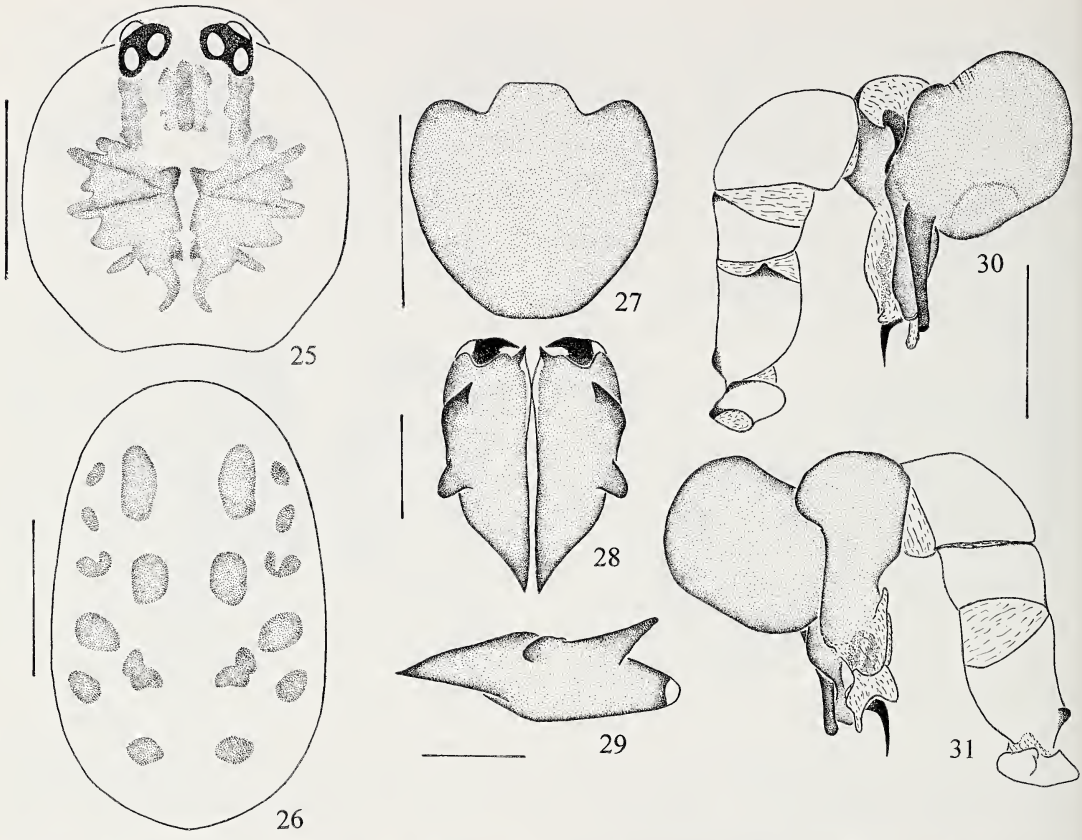
Description.—*Male:* Total body length



Figures 17–24.—*Tibetia everesti*, new species: 17. male, dorsal view; 18. male left chelicerae, retrelateral view; 19. male sternum, ventral view; 20. male chelicerae, frontal view; 21. left pedipalp, prolateral view; 22. same, retrolateral view; 23. epigynum, ventral view; 24. same, dorsal view. Scale lines: 0.5 mm (17, 19), 0.3 mm (21–24), 0.2 mm (18, 20).

1.63–2.24. One specimen measured: total length 2.24: cephalothorax 0.81 long, 1.15 wide; abdomen 1.43 long, 1.00 wide. Prosoma shape as in Fig 17. Carapace oval, wider than long, with distinct thoracic groove and brown mark centrally. Cephalic region slightly raised, ocular area light yellowish. Clypeus 0.30 high, unmodified, yellowish, with light brown marks. Except AMEs, other six eyes in two traids, on a moderately elevated ocular area. Distance AME-AME 0.04, AME-ALE 0.04, PME-PME 0.13, PME-PLE 0.03. Diameter AME 0.06, ALE 0.10, PME 0.13, PLE 0.10. MOA 0.22 long, front width 0.16, back width 0.29. Chelicerae (Figs. 20–21) with stridulatory ridges and pair of large black apophyses proximolaterally. Labium gray. Endites pale. Sternum (Fig. 19) yellowish, without patches on it. Legs long, yellow, with dark rings subdistally on femur, patella plus tibia proximally, and tibia subdistally. Measurements of legs: I 11.15 (3.33 + 3.42 + 3.50 + 0.90); II 9.50 (2.75 + 2.97 + 3.06 + 0.72); III 8.70 (2.39 + 3.06 + 2.57 + 0.68); IV 10.31 (3.42 + 3.06 + 3.15 + 0.68). Leg formula: 1243. Abdomen globular, gray, with black spots dorsally. Spinnerets whitish yellow. Procursus (Fig. 22) relatively simple and with dorsal apophysis, ventral pocket indistinct; bulb (Fig. 21) consisting of the proximal globular part and the distal sclerotized apophysis, without embolus, but the sperm duct opening can be seen (Fig. 52).

Female: In general very similar to male. Total body length 1.88–2.34. One specimen measured: total length 2.34: cephalothorax 0.86 long, 1.04 wide; abdomen 1.50 long, 1.04 wide. Clypeus 0.33 high. Both eye rows recurved. Distance AME-AME 0.03, AME-ALE 0.03, PME-PME 0.14, PME-PLE 0.02. Diameter AME 0.05, ALE 0.10, PME 0.10, PLE 0.10. MOA 0.20 long, front width 0.13, back width 0.29. Measurements of legs: I lost; II 8.02 (2.52 + 2.45 + 2.46 + 0.59); III 6.85 (2.03 + 2.07 + 2.16 + 0.59); IV 8.97 (2.88 + 2.70 + 2.70 + 0.69). Epigynum roughly rectangular, with a depression centrally (Fig. 23).



Figures 25–31.—*Belisana gyirong*, new species: 25. male prosoma, dorsal view. 26. male opisthosoma, dorsal view. 27. male sternum, ventral view. 28. male chelicerae, frontal view. 29. male left chelicera, retrolateral view. 30. left pedipalp, prolateral view. 31, same, retrolateral view. Scale lines: 0.5 mm (25–27), 0.3 mm (30–31), 0.2 mm (28–29).

Distribution.—Known only from several localities in Tibet.

Belisana Thorell 1898

Belisana Thorell 1898: 278; Simon 1903: 988; Simon 1909: 81; Deeleman-Reinhold 1986: 46–47; Huber 2001: 124–126.

Type species.—*Belisana tauricornis* Thorell 1898, by original designation

Diagnosis.—Small-sized, pholcids with roughly globular or higher-than-long opisthosoma. Six eyes in two triads, AMEs absent, and eyes not elevated. Distance between PMEs less than two times diameter of PME. The genitalic structure is somewhat similar to that of *Spermophora* (Deeleman-Reinhold 1986), but can be distinguished from *Spermophora* by the distance between the PMEs which is less than two times the diameter of PME, but is more than three times the diameter of PME in *Spermophora*.

Remarks.—The distinction between *Belisana* and *Spermophorides* requires further clarification (see Huber 2001).

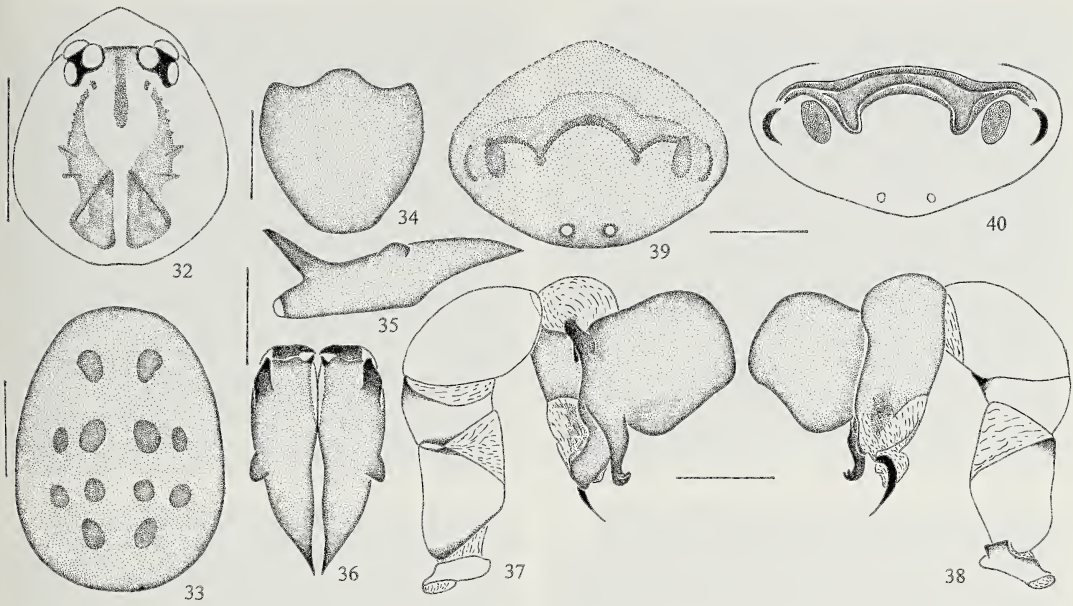
Belisana gyirong new species
Figs. 25–31

Material examined.—CHINA: *Tibet*: Holotype male, Gyirong Town (28°24′N, 85°12′E), Gyirong County (28°54′N, 85°12′E), 2 September 2002, Ming-Sheng Zhu and Jun-Xia Zhang (HU). Paratype: 1 male, same data as holotype (HU).

Etymology.—The species name is a noun in apposition derived from the type locality.

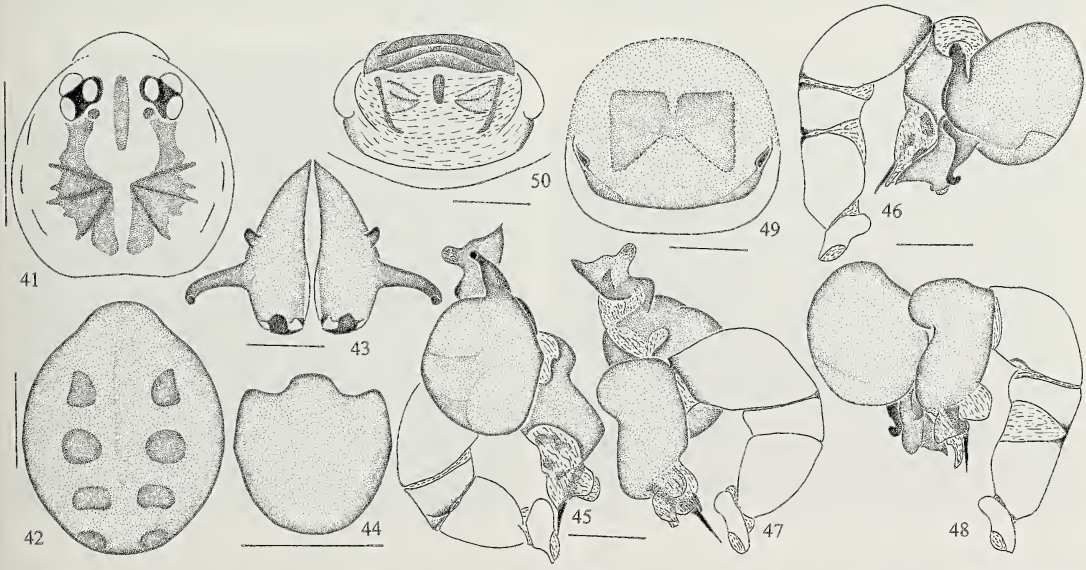
Diagnosis.—This new species resembles *B. yadongensis* (Hu 1985), but can be readily distinguished from the latter by the long apophysis of the bulb and the subdistal apophyses of chelicerae bending internally.

Description.—*Male (holotype):* Total length of body 2.23: cephalothorax 0.86 long,

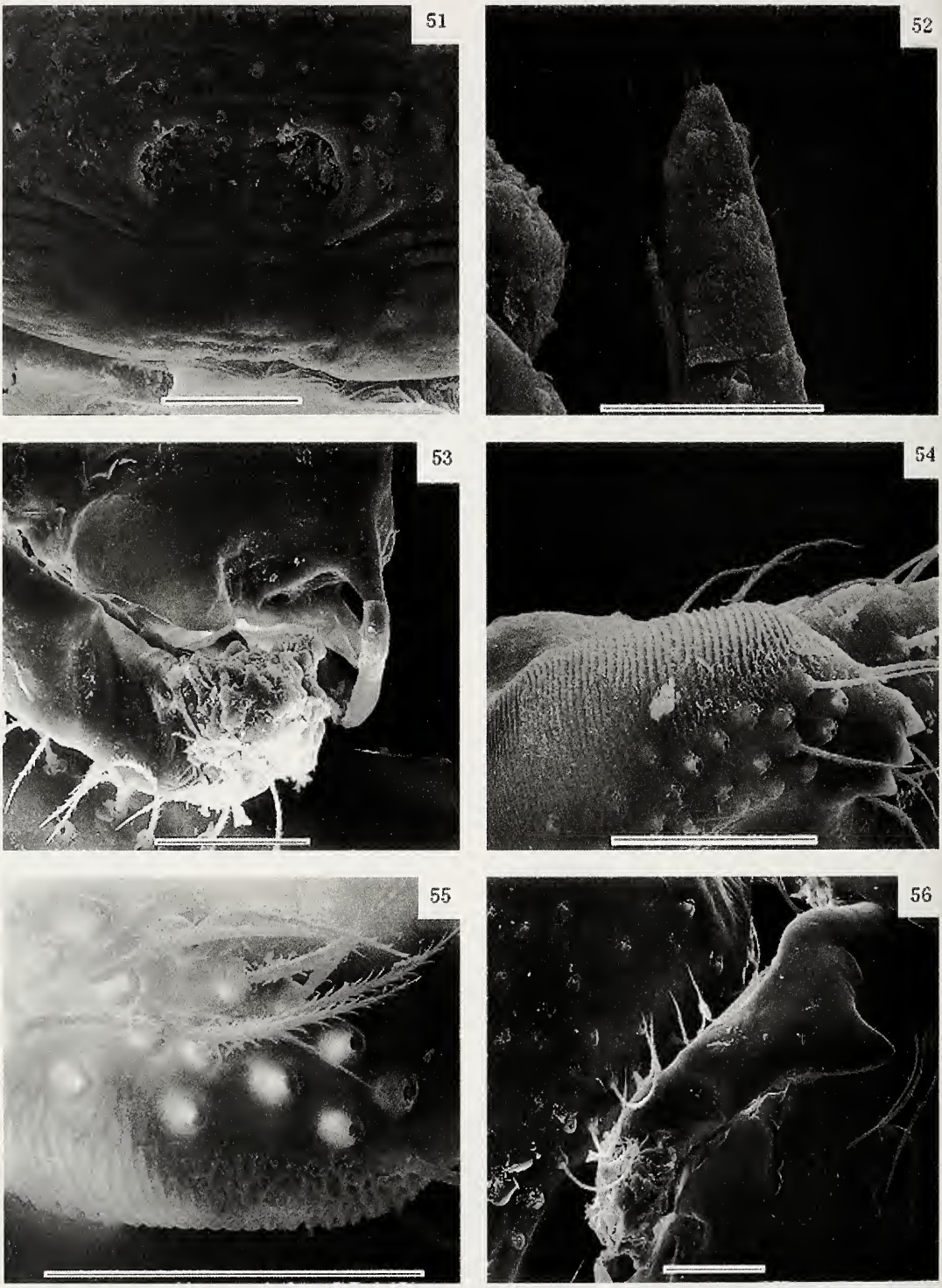


Figures 32–40.—*Belisana mainling*, new species: 32. male prosoma, dorsal view; 33. male opisthosoma, dorsal view; 34. male sternum, ventral view; 35. male left chelicera, retrolateral view; 36. male chelicerae, frontal view; 37. left pedipalp, prolateral view; 38, same, retrolateral view; 39. epigynum, ventral view; 40. same, dorsal view. Scale lines: 0.5 mm (32–33), 0.3 mm (34), 0.2 mm (35–40).

0.91 wide; abdomen 1.37 long, 0.87 wide. Prosoma shape as in Fig. 25. Carapace oval, slightly longer than wide, without thoracic groove, with brown mark on each side of carapace. Cephalic region not raised. Ocular area light yellowish, with an ochre mark centrally. Clypeus 0.22 high, unmodified, without marks. Six eyes in two triads. Distance PME-



Figures 41–50.—*Belisana yadongensis*: 41. male prosoma, dorsal view; 42. male opisthosoma, dorsal view; 43. male chelicerae, frontal view; 44. male sternum, ventral view; 45, 46. left pedipalp, prolateral view; 47, 48. same, retrolateral view; 49. epigynum, ventral view; 50. same, dorsal view. Scale lines: 0.5 mm (41–42, 44), 0.2 mm (43, 45–50).



Figures 51–56.—*Tibetia everesti*, new species: 51. epigynum, ventral view, showing copulatory opening; 52. tip of female pedipalp; 53. male right palpal organ, showing sperm duct opening; 54. male right chelicera, showing the end of black apophysis proximolaterally; 55. male right chelicera, showing stridulatory ridges; 56. male right pedipalp, showing shape of the procursus.

PME 0.09. Diameter ALE 0.09, PME 0.09, PLE 0.09. Chelicerae (Figs. 28–29) with pair of simple, black and long apophyses subdistally and pair of rounded light apophyses proximolaterally. Labium and endites whitish. Sternum yellowish, without patches on it. Measurements of legs: I 19.06 (5.22 + 5.72 + 5.89 + 2.23); II 13.66 (3.38 + 4.05 + 4.95 + 1.28); III 9.18 (2.70 + 2.61 + 3.15 + 0.72); IV11.21 (3.33 + 3.15 + 3.83 + 0.90). Leg formula: 1243. Abdomen (Fig. 26) almost globular, whitish with black spots dorsally. Bulb consisting of proximal globular part and distal sclerotized apophysis (Fig. 30).

Female: Unknown.

Distribution.—Known only from the type locality in Tibet.

Belisana mainling new species
Figs. 32–40

Material examined.—CHINA: *Tibet*: Holotype male, Mainling County (29°12′N, 94°06′E), 19 August 2002, Ming-Sheng Zhu and Jun-Xia Zhang (HU). Paratypes: 2 females, same data as holotype (HU).

Etymology.—The species name is a noun in apposition derived from the type locality.

Diagnosis.—This new species resembles *B. yadongensis* (Hu 1985), but can be readily distinguished from the latter by the tip of the bulbal apophysis with two pointed apiculi, the internal structure of epigynum, and the apophyses subdistally of chelicerae bending internally.

Description.—*Male (holotype):* Total length of body 2.18: cephalothorax 0.73 long, 0.78 wide; abdomen 1.45 long, 1.05 wide. Prosoma shape as in Fig. 32. Carapace oval, wider than long, without thoracic groove, with brown mark on each side of carapace. Cephalic region not raised. Ocular area light yellowish, with a ochre bar centrally. Clypeus 0.23 high, unmodified, without marks. Six eyes in two triads. Distance PME-PME 0.10. Diameter ALE 0.09, PME 0.08, PLE 0.08. Chelicerae (Figs. 35–36) with pair of simple black long apophyses subdistally and pair of rounded light apophyses proximolaterally. Labium and endites whitish. Sternum (Fig. 34) yellowish, without patches on it. Measurements of legs: I 10.13 (2.56 + 2.83 + 3.51 + 1.23); II 7.45 (2.03 + 2.18 + 2.49 + 0.75); III 5.89 (1.57 + 1.93 + 1.71 + 0.68); IV 6.63 (1.87 + 1.92 + 2.16 + 0.68). Leg formula: 1243. Abdomen (Fig. 33) almost globular, white with black spots dorsally. Bulb consisting of the proximal globular part and the distal sclerotized apophysis (Fig. 37).

Female: In general very similar to male. Total body length 1.58–1.66. One specimen measured: total length 1.66: cephalothorax 0.67 long, 0.70 wide; abdomen 0.99 long, 0.58 wide. Clypeus 0.19 high. Distance PME-PME 0.08. Diameter ALE 0.08, PME 0.08, PLE 0.08. Measurements of legs: I 8.07 (2.23 + 2.38 + 2.45 + 1.01); II 5.90 (1.79 + 1.76 + 1.69 + 0.66); III 4.04 (1.16 + 1.14 + 1.19 + 0.55); IV 5.35 (1.73 + 1.53 + 1.48 + 0.61). Leg formula: 1243. Epigynum roughly oval (Fig. 39).

Distribution.—Known only from the type locality in Tibet.

Belisana yadongensis (Hu 1985) new combination
Figs. 41–50

Spermophora yadongensis Hu 1985: 148, figs. 1–10; Song et al. 1999: 65; Hu 2001: 85, figs. 10.1–10.

Type material.—Hu (1985) described both sexes from Yadong County, Tibet. The type specimens are deposited in Shandong University, China, not examined.

Material examined.—CHINA: *Tibet*: 19 ♀, 11 ♂, Yadong County (27°24′N, 88°54′E), 3 September 2002, under stone heap, Feng Zhang and Zhi-Sheng Zhang (HU); 2 ♀, 1 ♂, Xiayadong Town, Yadong County, 4 September 2002, Feng Zhang and Zhi-Sheng Zhang (HU).

Description.—*Male:* Total body length 1.39–1.71. One specimen measured: total body length 1.71: cephalothorax 0.70 long, 0.67 wide; abdomen 1.01 long, 0.78 wide. Prosoma shape as in Fig. 41. Carapace oval, slightly longer than wide, without thoracic groove, with brown mark on each side of carapace. Cephalic region not raised. Ocular area light yellowish, with an ochre bar centrally. Clypeus 0.18 high, unmodified, without marks. Six eyes in two triads. Distance PME-PME 0.12. Diameter ALE 0.08, PME 0.06, PLE 0.07. Chelicerae shaped as in Fig. 43, with pair of simple large black apophyses subdistally and pair of rounded light apophyses proximolaterally. Labium and endites whitish. Sternum yellowish, without patches on it. Legs light ochre, without dark ring and spine.

Measurements of legs: I 9.91 (2.48 + 2.80 + 3.42 + 1.21); II 7.16 (1.94 + 2.16 + 2.34 + 0.72); III 5.66 (1.52 + 1.89 + 1.67 + 0.58); IV 6.36 (1.80 + 1.87 + 2.07 + 0.62). Leg formula: 1243. Abdomen almost globular, whitish with black spots dorsally. Bulb consisting of the proximal globular part and the distal sclerotized apophysis.

Female: In general very similar to male. Total body length 1.63–1.88. One specimen measured: total body length 1.84: cephalothorax 0.67 long, 0.67 wide; abdomen 1.17 long, 0.92 wide. Clypeus 0.17 high. Distance PME-PME 0.13. Diameter ALE 0.08, PME 0.08, PLE 0.06; Measurements of legs: I 7.84 (2.12 + 2.25 + 2.48 + 0.99); II 5.66 (1.63 + 1.65 + 1.70 + 0.68); III 4.37 (1.30 + 1.28 + 1.31 + 0.48); IV 5.59 (1.70 + 1.62 + 1.62 + 0.65). Leg formula: 1243. Epigynum roughly rectangular.

Distribution.—Only found in Yadong County, Tibet.

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MAINOSA, A NEW GENUS FOR THE AUSTRALIAN 'SHUTTLECOCK WOLF SPIDER' (ARANEAE, LYCOSIDAE)

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ABSTRACT. A new monotypic genus, *Mainosa*, is described to accommodate the Australian 'shuttlecock wolf spider', *Mainosa longipes* (L. Koch 1878) (= *Lycosa mainae* McKay 1979, new synonymy) as the type species. The male of this species is described for the first time. *Mainosa longipes* differs from other wolf spiders in having a the distinct color pattern of the abdomen, with white transverse bars and lines on a dark surface, and unusually long legs in males. Its genital morphology confirms *M. longipes* as a member of the subfamily Lycosinae. *Mainosa longipes* inhabits areas in South Australia and Western Australia with dry sandy soils in *Acacia* litter, where it constructs palisades around the entrance of its burrow. It appears to reproduce in winter.

Keywords: Lycosinae, Australia, turret-building, palisade, taxonomy

Australia has long been recognized for its unique fauna and flora. Two main reasons for Australia's large number of endemic species are the long period of time it has been in geographic isolation and its comparatively stable geological history (Hopper et al. 1996). Australia is thought to have split from the southern supercontinent Gondwana in the Late Paleocene, about 65 million years ago (e.g. Heatwole 1987), and some regions in Western Australia have not been subject to major geological changes in the form of glaciation or continental uplifts (mountain building) since the Triassic more than 250 million years ago (e.g., Heatwole 1987; Hopper et al. 1996). Consequently, the spider fauna of Australia is very diverse and recent estimates suggest that some 20,000 species exist (Yeates et al. 2003).

Wolf spiders belong to one of the predominant spider families in Australia. The presence of large areas of open woodland, inland diffuse waterways (including salt lakes) and expansive arid and semi-arid regions that are all favored habitat areas of this family seems to account for this dominance (Main 1976, 1981). Recent studies have shown that the Australian and New Zealand wolf spider faunas contain some unique elements, such as the genera *Artoria* Thorell 1870, *Anoteropsis* L. Koch, 1878, *Tetralycosa* Roewer 1960, *Notocosa* Vink 2002 and *Venatrix* Roewer 1960 (Framenau 2002, 2005; Framenau et al. 2006; Framenau & Vink 2001; Vink 2002).

As part of his monumental monograph on Australian spiders *Die Arachniden Australiens,* L. Koch (1878) described the female of a wolf spider species with a very unusual color pattern of white transverse bars on an otherwise blackish-brown abdomen, *Anoteropsis longipes* L. Koch 1878. The type material of this species, part of the 'Bradley Collection', is considered lost (Framenau 2005). More than 100 years later, McKay (1979) described *Lycosa mainae* McKay 1979 from Western Australia with a very similar color pattern, also solely based on a single female and some immature spiders (Fig. 1). Earlier, Main (1976) had described the burrow of this spider and called this species the 'shuttlecock wolf spider' as these lycosids construct a palisade of litter around their burrow, reminiscent of a badminton shuttlecock (Fig. 2). A comparison of L. Koch's (1878) and McKay's (1979) descriptions of *A. longipes* and *L. mainae* strongly suggests that both species are actually the same. After the examination of more than 15,000 Australian records of wolf spiders, I have found no other species that even remotely resembles that described by L. Koch (1878) and McKay (1979).

An exhaustive investigation of the spider collection of the Western Australian Museum revealed some additional material of this species, including two males that match the females of *A. longipes* and *L. mainae*. The ped-

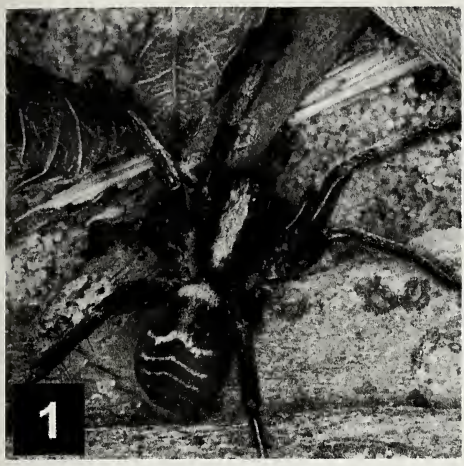


Figure 1.—Penultimate female of *Mainosa longipes* from Lorna Glen Station, Western Australia (WAM T58395). The body length of this specimen is 10.5 mm.

Figure 2.—Female of *Mainosa longipes* at the entrance of its burrow near Murchison Station, Western Australia (photograph courtesy of Fred and Jean Hort, Swan View).

ipalp structure clearly identifies it as a member of the subfamily Lycosinae (sensu Dondale 1986). Consequently, the species cannot be a member of the genus *Anoteropsis*, as recently postulated in a revision of this genus (Vink 2002), since *Anoteropsis* is considered member of an unnamed subfamily very different to the Lycosinae (Framenau et al. 2006). This species has also no somatic or genitalic similarities with *Lycosa* Latreille 1804, a putatively Mediterranean genus in which *L. mainae* was originally described (see e.g. Zyuzin & Logunov 2000).

Here, *L. mainae* is considered a junior synonym of *A. longipes*. A new endemic Australian genus, *Mainosa*, is erected to accommodate the unusual 'shuttlecock wolf spider' from Western Australia and South Australia, as it is not possible to place it in any other currently described genus within the Lycosidae.

METHODS

Descriptions are based on specimens preserved in 70% ethyl alcohol. A female epigynum was cleared in lactic acid overnight for examination of the internal genitalia. The illustrations of epigyna and male pedipalps omit the setae for clarity. The morphological nomenclature follows Framenau & Vink (2001) and Framenau (2002). All measurements are in millimetres (mm). Since juvenile spiders can be clearly identified by the distinct color pattern, the species distribution is documented based on both mature and immature specimens.

Abbreviations.—*Eyes:* anterior (AE), anterior median (AME), anterior lateral (ALE), posterior (PE), posterior median (PME), posterior lateral (PLE). *Measurements (adult spiders, if not otherwise stated):* total length (TL), carapace length (CL) and width (CW), abdomen length (AL) and width (AW). *Collections*: QM = Queensland Museum, Brisbane; WAM = Western Australian Museum, Perth.

SYSTEMATICS

Subfamily Lycosinae Sumderall 1833
Mainosa new genus

Type species.—*Anoteropsis longipes* L. Koch 1878.

Etymology.—The genus is named in honor of Barbara York Main. Barbara's contribution to Australian arachnology is legendary, and after two years at the Western Australian Museum, I still have not finished sorting through her part of the immense wolf spider collection. It also preserves McKay's (1979) acknowledgment of Barbara's contribution to the naming of *L. mainae*. The gender is feminine.

Diagnosis.—*Mainosa* can be distinguished from all other known wolf spiders by the unique coloration of the abdomen, consisting

of white transverse bars and lines on a brown to black surface (Fig. 1). In addition, males have unusually long legs, with a large ratio of leg length to carapace width (WAM T62713; leg 1 = 7.0; leg 2 = 6.4; leg 3 = 6.13; leg = 8.6). For example this leg ratio is twice as large as the average for the species within the Australian lycosine genus *Venatrix* (leg 1 = 3.6; leg 2 = 3.2; leg 3 = 3.0, leg 4 = 4.2; data for 17 species derived from Framenau & Vink 2001).

Description.—Medium sized wolf spiders (TL 6–15 mm). Males smaller than females. Carapace elevated in head region, more pronounced in males than females (Fig. 3). Row of AE narrower than row of PME. Row of AE slightly procurved (Fig. 4). Caput flanks steep in males (Fig. 4), but a gentle slope in females. Spiders overall very dark, reddish-brown to black, however, the carapace has white setae medially resulting in a distinct median band in live specimens (Fig. 1). Abdomen with distinct light transverse bars and lines on a dark surface (Fig. 1). Chelicerae with three promarginal and three retromarginal teeth. Leg formula IV>I>II>III. Males with very long and thin legs, each at least 6 times as long as the carapace width. Females with dense scopulae on the tarsi of all legs, metatarsi I-III and the apical two thirds of tibiae I+II. Triangular median apophysis of male pedipalp directed retrolaterally and without ventral process (Fig. 5). Bulb rotated slightly clockwise, so that the large subtegulum is situated prolaterally (rather than basally) and the base of the embolus apically (rather than apicoprolateral) (Fig. 5). Terminal apophysis sickle-shaped (Fig. 7). Female epigyum with inverted T-shaped median septum, of which the longitudinal part is indistinct and the lateral edges of the posterior transverse part are slightly bent anteriorly (Figs. 8, 10).

Included species.—*Mainosa longipes* (L. Koch 1878).

Distribution.—As for species (Fig. 11).

Mainosa longipes (L. Koch 1878), NEW COMBINATION
(Figs. 1–11)

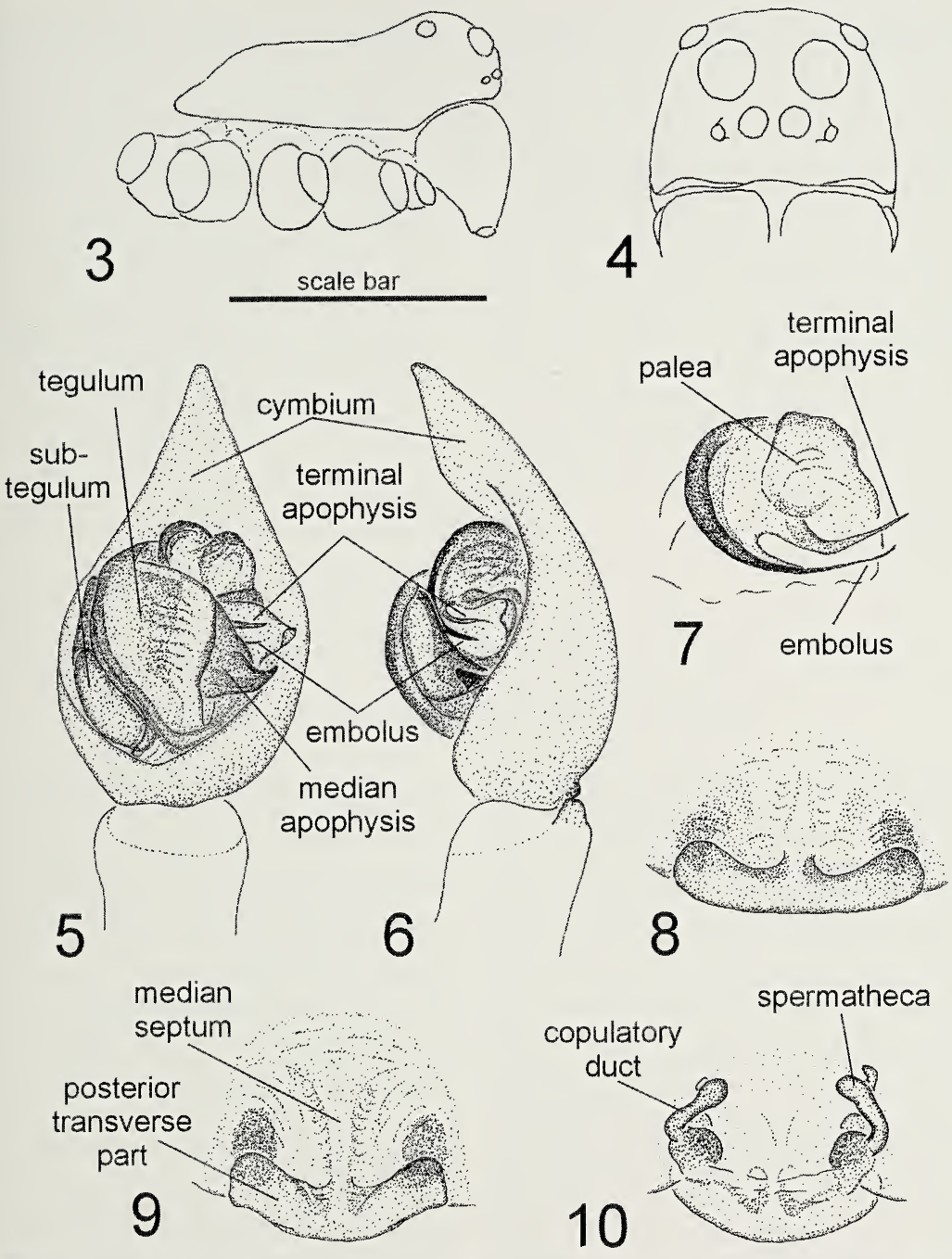
Anoteropsis longipes L. Koch 1878: 973–974, plate 85, figs. 2, 2a.

Lycosa maini McKay 1979: 260–263, figs. 7a–e; McKay, 1985b: 80. NEW SYNONYMY.

Lycosa mainae McKay.- Platnick 1989: 372.

Types.—*Anoteropsis longipes:* holotype female, Australia, locality not given in L. Koch (1878), Bradley Collection (presumed lost, see Framenau in press; not examined). *Lycosa mainae*: holotype female, Western Australia, 88 km N. of Murchison River, 27°42′S, 114°09′E, 30 January 1969, on red soil with mulga, *Acacia aneura*, in turret burrow, R.J. McKay (WAM 69/115), examined. Paratypes: AUSTRALIA: *Western Australia*: 1 immature female, Billabong Roadhouse, near Shark Bay turn-off, 26°49′S, 114°36′E, 5 December 1972, R.J. McKay (QM W4668); 1 juvenile, 5 miles N. of Menzies, 29°41′S, 121°02′E, 1 September 1954, FN24, B.Y. Main (WAM 68/821); 2 penultimate females, Mount Magnet area, 28°05′S, 117°52′E, station 7, 323 mile peg Mt Magnet, 7–8 December 1968, R.J. McKay, J. Gilbert, J. Ayres (WAM 69/1031, 69/1036); 1 juvenile, Murchison, 19 km N., 29°38′S, 115°57′E, 20 February 1962, A.R. Main (WAM 68/820); 2 juveniles, Norseman, 76 km N., 31°33′S, 121°47′E, 26 December 1968, W.H. Butler (WAM 69/105–6); 1 juvenile, 220 mile peg, Paynes Find, 29°15′S, 117°41′E, 8 December 1968, R.J. McKay, J. Gilbert, P. Snowball (WAM 68/819); 1 juvenile, Tarin Rock Reserve, 33°06′S, 118°11′E, 22 May 1971, palisade burrows on loam and litter, A. Baynes (WAM 71/1859); 1 penultimate female, 1 penultimate male, Wubin, 32 km N.E., 30°06′S, 116°37′E, 14 July 1968, in large turret burrow, R.J. McKay, J. Gilbert, J. Ayres (WAM 68/817–8). All paratypes examined.

Other material examined.—AUSTRALIA: *South Australia*: 1 penultimate ♂, Dublin, 34°27′S, 138°21′E, 16 May 1986, B.Y. Main, FN11 (WAM T62718); 1 juvenile, Mallabie Shed Tank, 18 miles W., 31°28′S, 130°20′E, 23 December 1952, B.Y. Main, FN40 (WAM T62719). *Western Australia*: 1 juvenile, Arnolds Tank (PWD tank 488), N. of Wialki, 28°39′S, 122°36′E, 24 April 1957, A.R. Main, FN1, BYM 1957/A10, palisade, thick litter under *Acacia* (WAM T46842); 1 ♂, Francois Peron National Park, 25°52′31″S, 113°32′59″E, 24 August–10 November 1994, wet pitfall traps, A. Sampey et al., WAM/CALM Carnarvon Survey (WAM T48038); 1 juvenile, Francois Peron National Park, 1.6km NW of Monkey Mia Road, 25°50′20″S, 113°36′23″E, 18 January–23 May 1994, wet pitfall traps, M.S. Harvey et al., WAM/CALM



Figures 3–10.—*Mainosa longipes* (L. Koch, 1878): Male from 'Sieda', near Grass Patch, Western Australia (WAM T62713): 3. Carapace, lateral view; 4. Eyes, frontal view; 5. Left pedipalp, ventral; 6. Left pedipalp, retrolateral; 7. Apical part of bulb. Female holotype of *Lycosa mainae*, 88 km N. of Murchison River, Western Australia (WAM 69/115): 8. Epigynum, ventral view; 9. Epigynum, dorsal view. Female from Nerren Nerren, Western Australia (WAM 94/1940): 10. Epigynum, ventral view. Scale bar: (3) 2.70 mm, (4) 1.44 mm, (5–6) 0.66 mm, (7) 0.42 mm, (8–10) 0.80 mm.

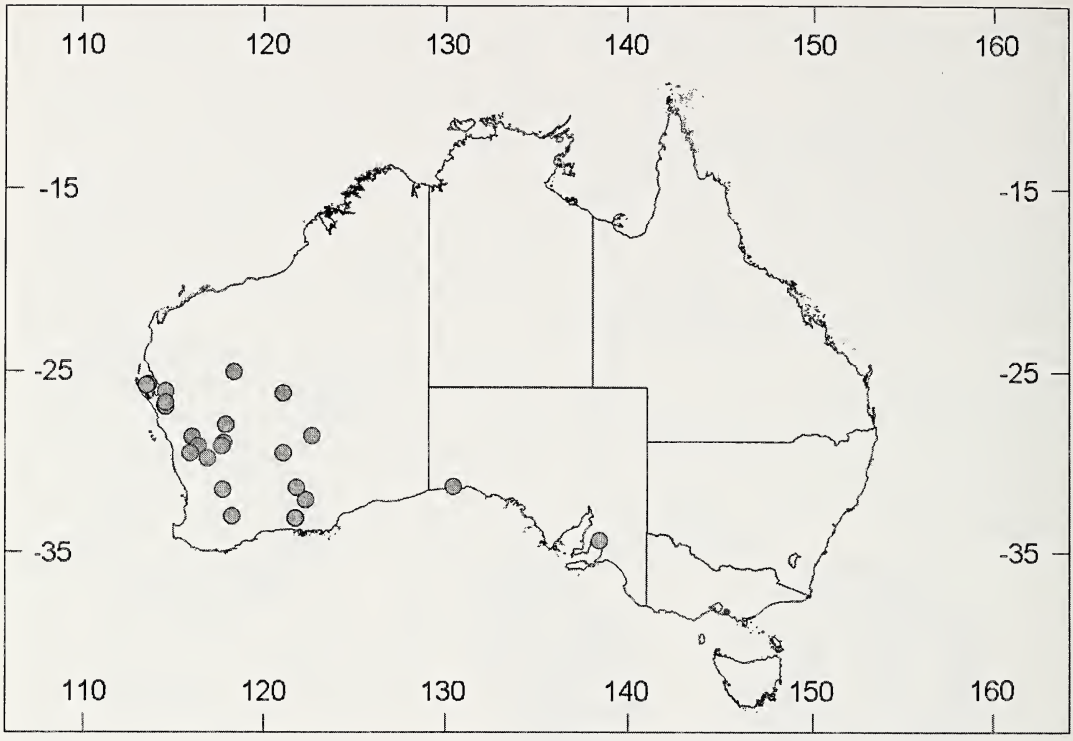


Figure 11.—Records of *Mainosa longipes* (L. Koch 1878).

Carnarvon Survey, site PE4 (WAMT62720); 1♂, 'Sieda', near Grass Patch, Fitzgerald Location 41, 33°13′56″S, 121°46′00″E, 20 September 1988, A.F. Longbottom, in house on desk near telephone, S233 (WAM T62713); 1 juvenile, Grass Patch, E. of, Fitzgerald Location 71, 33°13′S, 121°43′E, 17 December 1980, A.F. Longbottom, web-lined burrow amongst leaf litter, S62 (WAM T53625); 1 juvenile, Gutha, 15 miles N., 28°44′S, 116°01′E, 18 August 1953, B.Y. Main, palisade in *Acacia* litter, no silk, FN5 (WAM T53473); 1 penultimate ♀, Kellerberrin, 31°33′S, 117°43′E, 1 April 1993, G.T. Smith, leaves on entrance, M17 (WAM T62714); 1 penultimate ♀, Lorna Glen Station, 26°19′S, 121°02′E, 28 April 2004, K.E.C. Brennan, G. Owen, M. Moir, P.R. Langlands (WAM T58395); 1 juvenile, Morawa, S.E., nature reserve on Lochada Road, 29°15′29″S, 116°21′43″E, 12 October 1999, B.Y. Main, dug from burrow with palisade (WAM T62716); 1 ♀, Nerren Nerren Station, 4.0km E of Nerren Nerren boundary fence, E of North West Coastal Highway, 27°00′21″S, 114°32′29″E, 15 October 1994, J.M. Waldock, J. Riley, dug from burrow with palisade, WAM/CALM Carnarvon Survey, site NE 4 (WAM 94/1940); 1 penultimate ♀, Nerren Nerren Station, 5.9km E of Nerren Nerren boundary fence, E of North West Coastal Highway, 27°03′28″S, 114°36′25″E, 18 October 1994, J.M.Waldock, WAM/CALM Carnarvon Survey, site NE5 (WAM 94/1941); 1 juvenile, Norseman, 29.2 miles E., on Eyre Highway, 32°12′S, 122°17′E, 8 December 1953, B.Y. Main, FN8 (WAM T46843); 1 ♀, North West Coastal Highway, 20.3km E, on Woodleigh—Byro Road, 22°12′31″S, 114°34′35″E, 12 October 1994, M.S. Harvey et al., WAM/CALM Carnarvon Survey, site WO2, from burrow with Acacia leaves palisade (WAM T62730); 1 juvenile, Oudabunna Station, 15.9km S. of Wydgee Homestead, 29°04′S, 117°45′E, 8 August 1982, B.Y. Main, FN13 (WAM T62715); 1 penultimate ♀, Paynes Find, 29°15′S, 117°41′E, 1 August 1982, B.Y. Main, FN14 (WAM T62717).

Diagnosis.—*Mainosa longipes* displays a unique color pattern among known wolf spiders. The abdomen is dark brown to black, with white transverse bars and lines in the posterior half of the abdomen (Fig. 1), less distinct in males.

Description.—*Male (based on WAM*

T62713): Carapace: head region strongly elevated (Fig. 3); overall dark brown, medially in front of fovea slightly lighter; indistinct dark radial pattern; covered with mainly silver-white setae, that are particularly dense between eyes and towards the carapace margins; some black setae between median and lateral bands on carapace flanks; one long brown bristle between AME, six long brown bristles below AE; clypeus high, more than one diameter of AME (Fig. 4). Eyes: row of AE shorter then row of PME; row of AE procurved (Fig. 4). Sternum: light brown with dense, black pigmentation; covered with brown bristles, which are longer towards the margin. Labium: brown; front end truncate and white. Chelicerae: dark brown with a dark longitudinal band; a few white setae and, medially, a few long brown bristles; three retromarginal teeth, with the apical slightly smaller; three promarginal teeth, with the median largest. Pedipalp (Figs. 5–7): embolus long and slender with its tip pointing slightly apically, terminal apophysis sickle-shaped (Fig. 7). Abdomen: very dark grey with indistinct light lanceolate heart mark in anterior half, its front end a more distinct orange patch; orange-whitish transverse bar medially and some thin transverse orange-whitish lines in posterior half; white setae medially in a band that widens posteriorly, otherwise brown setae; venter uniformly dark brown, laterally with irregular light spots; spinnerets yellow brown. Legs: leg formula IV > I > II > III; uniformly dark brown, coxae ventrally yellow-brown; spination of leg I: femur: 2 dorsal, 1 apicoprolateral; tibia: 3 ventral pairs, 2 prolateral; metatarsus: 3 ventral pairs, 1 retrolateral, 1 apicoventral, 1 apicoprolateral, 1 apicoretrolateral.

Female (based on holotype of L. mainae WAM 69/115): Carapace: very dark reddish-brown with indistinct radial pattern; most setae rubbed off, some silver-white setae on carapace flanks and between eyes. Eyes: row of AE shorter than row of PME, row of AE slightly procurved. Sternum: brown, long brown setae of increasing length and density towards margins. Labium: as in male. Chelicerae: black, few brown setae medially, dentition as in male. Epigynum (Figs. 8–10): ventral view: longitudinal part of median septum indistinct, but with distinct posterior transverse part of which the lateral ends are bent forward; no anterior hoods (Figs. 8, 9); dorsal view: small spermathecae with dorsal appendix (Fig. 10). Abdomen: very dark brown with a wide light-brown patch anteriorly; white transverse bars in posterior half; covered in brown setae, whitish setae in transverse bars, some longer light brown setae in area of lanceolate heart mark. Venter as in male; spinnerets brown. Legs: leg formula IV > I > II > III; uniformly dark brown, apical segments somewhat darker; dense scopulae on tarsi, metatarsi and apical two thirds of tibiae of leg I and II, on tarsi and metatarsi of leg III and tarsi of leg IV; spination of leg I: Femur: 3 dorsal, 2 apicoprolateral, 1 apicoretrolateral; patella: 1 prolateral; tibia: 3 ventral pairs, 1 prolateral; metatarsus: 3 ventral pairs, 1 apicoventral.

Measurements: Male, WAM T62713 (female holotype of *L. mainae*, WAM 69/115): TL 5.92 (14.10), CL 3.24 (6.58), CW 2.12 (4.51). Eyes: AME 0.19 (0.22), ALE 0.11 (0.22), PME 0.32 (0.70), PLE 0.25 (0.48). Row of eyes: AE 0.68 (1.41), PME 0.79 (1.60), PLE 0.95 (1.83). Sternum (length/width) 1.49/1.27 (2.54/1.97). Labium (length/width) 0.36/0.44 (0.71/0.89). AL 2.26 (6.96), AW 1.97 (5.17). Legs: lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 1.41 + 1.41 +—+ 0.94 = 3.76, I 3.81 + 4.65 + 4.09 + 2.26 = 14.81, II 3.38 + 4.37 + 3.81 + 1.97 = 13.53, III 3.24 + 4.09 + 3.81 + 1.83 = 12.97, IV 4.65 + 5.50 + 5.78 + 2.26 = 18.15 (Pedipalp 2.54 + 2.63 +—+ 2.07 = 7.24, I 4.70 + 5.64 + 3.48 + 1.88 = 15.70, II 4.51 + 5.36 + 3.29 + 1.79 = 14.95, III 3.85 + 4.51 + 3.29 + 1.69 = 13.34, IV 5.08 + 6.67 + 5.92 + 3.10 = 20.77).

Variation: The dimensions of a second male, WAM T48038 (2 females, WAM 94/1940 and WAM T62730) are: TL 9.31, CL 5.08, CW 3.29 (TL 12.41, CL 6.77, CW 4.98 and TL 13.24, CL 6.49, CW 4.04).

Remarks.—The female holotype of *Anoteropsis longipes*, described from Bradley's Collection, is considered lost (Framenau 2005). However, L. Koch's (1878) description of the distinct color pattern of this species and his illustration of the female genitalia allow an accurate identification of this species. Ludwig Koch (1878) did not give any locality for his specimen, however, it is not unlikely that the spider was from Western Australia as the

Bradley Collection included other spiders collected in this state, e.g., the type material of *Tetralycosa oraria* (L. Koch 1876) from King George Sound near Albany (L. Koch 1876; see also Framenau et al. 2006).

Habitat preferences and life cycle.—*Mainosa longipes* appears to prefer open *Acacia* woodland and mallee with red clay to sandy soils (McKay 1979). Here, it constructs palisades of elongate leaves or phyllodes around the mouth of its burrow (Fig. 2). Palisades are generally constructed in heavy leaf litter below shrubs and trees, usually on the side of the tree where the afternoon sun falls (McKay 1979). A penultimate and a mature male were caught in May, a second mature male in September which suggests that this species is reproductively active in winter.

Distribution.—South Australia and Western Australia south of 25°S latitude (Fig. 11).

DISCUSSION

Mainosa longipes belongs to the subfamily Lycosinae as the male pedipalp has a transverse median apophysis with a sinuous channel on its dorsal surface (Dondale 1986). The closest relatives may be found in the genus *Dingosa* Roewer 1955, represented by *Dingosa simsoni* (Simon 1898) and the currently misplaced Australian lycosines '*Pardosa*' *serrata* (L. Koch 1877) and '*P.*' *humphreysi* McKay 1985a. Similar to *Mainosa*, *Dingosa* species construct turrets around their burrows and males have extremely elongated legs. However, genital morphology and coloration of *Dingosa* differ considerably from *Mainosa*. The male pedipalp in this genus has a large palea region with a broad, truncated (not sickle-shaped) terminal apophysis. The median apophysis of these species is not triangular, but slim and elongated apically. In addition, the coloration of the Australian *Dingosa* is very different as the abdomen displays a characteristic serrated pattern with dark chevrons but no transverse bars. A revision of this genus, that contains a further two undescribed Australian representatives, is forthcoming.

Turret-building is not only restricted to Australian wolf spiders. Some species of the Holarctic genus *Geolycosa* Montgomery 1904, such as *G. missouriensis* (Banks 1895), also construct palisades around the opening of their burrow entrance (Wallace 1942; G. Stratton pers. comm.). The New Zealand *Notocosa bellicosa* (Goyen 1888) extends the opening of its burrow with a rim of silk into which it incorporates pieces of debris (Vink 2002). The benefits of these palisades are currently unknown. In mygalomorph spiders of the genus *Aname* L. Koch 1873, burrow turrets appear to have some significance in relation to regular sheet-flood events (Main 1993). Alternative functions may include a barrier against debris that could otherwise fall into the burrow. The palisades could also play an important role in foraging. Prey may be attracted to the palisade as an elevated resting place and the turret also provides the spider with a vantage point since they can be seen sitting on the top of the turret during the day (pers. obs.). Finally, palisades may have an important thermoregulatory function such as to avoid hot surface air to penetrate the burrow.

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I am indebted to Barbara Main for sharing her immense arachnological knowledge with me every Thursday morning, and Julianne Waldock and Mark Harvey for their never-ending support at the Western Australian Museum. I thank Barbara Baehr, Robert Raven and Owen Seeman for their hospitality whilst sorting through the collection of the Queensland Museum in Brisbane, where one of the paratypes of *Lycosa mainae* is housed. I am grateful to Fred and Jean Hort from Swan View in Western Australia for permission to use their photograph of *M. longipes* (Fig. 2) in this publication. Peter Langlands provided me with the live specimen of *M. longipes* illustrated in Fig. 1. Melissa Thomas, Julianne Waldock, Mark Harvey, Torbjørn Kronestedt and Cor Vink provided helpful comments on earlier drafts of this manuscript. This study forms part of a revision of the Australian wolf spiders that is funded by the Australian Biological Resource Studies (ABRS) to Mark Harvey (Western Australian Museum) and Andy Austin (University of Adelaide).

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ECOLOGY OF *THESTYLUS AURANTIURUS* OF THE PARQUE ESTADUAL DA SERRA DA CANTAREIRA, SÃO PAULO, BRAZIL (SCORPIONES, BOTHRIURIDAE)

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ABSTRACT. Individuals of a *Thestylus aurantiurus* Yamaguti & Pinto-da-Rocha 2003 population in the Parque Estadual da Serra da Cantareira (São Paulo, SP, Brazil) show an increase of activity throughout the year. This increase is related to the reproductive season of these scorpions, from September to November. The abundance of scorpions was related to environmental factors in four different areas of the park. More scorpions were collected in the higher areas, far away from water sources of the park and not exposed to flooding. A short description of the *Thestylus aurantiurus* burrows is also presented.

Keywords: Scorpiones, *Thestylus aurantiurus*, Atlantic Rainforest, seasonality, relative abundance

Scorpions are extremely sedentary animals. According to Polis (1990a), they share the record with many spiders for the lowest arthropod metabolic rates ever recorded. Some species spend 97% of their lives inside their burrows, and they can exist one year without feeding (Polis 1990a). This is largely due to the "sit-and-wait" type of foraging activity adopted by most scorpions, which consists of being immobile and awaiting any prey that passes within reach. However, during the reproductive period, scorpions present certain behavioral changes. These changes occur mainly in surface activity, such as a reduction in female foraging activity and an increase in male surface activity in search of females (Benton 2001).

Courtship behavior is well-studied in scorpions. The behavior of 35 species of six families was described, from the about 1500 species and 16 families listed in Fet et al. (2000). The courtship behavior of many bothriurid species was studied, mainly by Peretti (1995, 1997). However, there are few works on the reproductive activity of scorpions. Peretti (1997) studied the reproductive characteristics of Argentinean scorpions, describing the reproductive period, interval between mating and litter birth behavior, and period of litter birth of some bothriurid scorpions. Matthiesen (1968) studied the courtship behavior of certain Brazilian scorpions during courtship, e.g., *Bothriurus araguayae* Vellard 1934.

The genus *Thestylus* Simon 1880 has been little studied due to its restricted geographical distribution and low abundance. The only study on the reproduction of *Thestylus* was Machado & Vasconcellos-Neto (2000). They described the courtship behavior of *T. aurantiurus* Yamaguti & Pinto-da-Rocha 2003 (mentioned as *T. glasioui* (Bertkau 1880)). According to the authors, the reproductive period is very seasonal, occurring during the hot and wet season (beginning in October), in Serra do Japi (23°17′S; 47°00′W), Jundiaí, SP, Brazil.

Abundance and its relationship to environmental factors is another well studied aspect of scorpion ecology. Evidence suggests that scorpions are selective when choosing a place to build their burrows. Polis & McCormick (1986) studied desert scorpions and noticed differences of abundance among the species related to the environment. Höfer et al. (1996) presented a study relating environmental aspects of different habitats of a Central Amazon Rainforest with the relative abundance of a certain scorpion species. Koch (1977, 1978) studied burrows in the genus *Urodacus* Peters 1861 (Urodacidae), observing a different kind of burrow for each *Urodacus* species and verifying that environmental aspects influence burrow site location.

The study presented here was conducted to assess the activity of a population of *Thestylus aurantiurus* (Figs. 1 & 2) throughout the course of one year (February 2000–January 2001), and the relationship between relative abundance and environmental aspects in Parque Estadual da Serra da Cantareira, São Paulo, SP, Brazil.

METHODS

Studied area.—Collections were made throughout one year in four areas of the Atlantic Rainforest. These areas are located in the Núcleo Pedra Grande of the Parque Estadual da Serra da Cantareira (23°22′S; 46°36′W), São Paulo, SP, Brazil, in a project conducted together with Universidade Bandeirante de São Paulo (UNIBAN).

Area 1 named Pedra Grande (23°26′30″S; 46°38′20″W at an elevation of 1050 m), possesses dense vegetation, and well-developed small and medium-sized understory strata, with lianas and bamboo groves. In area 2, named Lago das Carpas (23°25′40″S; 46°36′06″W, 700 m) possesses dense understory, with flooded areas and bamboo groves. Area 3 named Divisa (23°25′48″S; 46°38′00″W, 1050 m), is located on the boundary between the municipal districts of São Paulo and Mairiporã. It possesses dense vegetation, with numerous lianas and some exotic species, such as *Pinus* sp. Area 4, named Sede (23°27′03″S; 46°38′06″W, 650 m), is characterized by lush vegetation, with steep slopes, many lianas, a large amount of low vegetation and flooded areas.

The values of monthly median temperatures and monthly total rainfall presented in this work were supplied by the Companhia de Saneamento Básico do Estado de São Paulo (SABESP). These data were recorded at Paiva Castro's dam (23°22′11″S; 46°40′07″W), in the municipal district of Mairiporã, near to the Parque Estadual da Serra da Cantareira.

Ecological samplings.—Twelve monthly collections, of nine days each, were undertaken between February 2000 and January 2001. Scorpions were collected in drift fence pitfall traps (Fig. 3). Traps were composed of groups of four buckets of 20 L each, buried with the opening nearby ground level, arranged in a "Y" shape. Each "arm" of the "Y" was 5.0 m from the central point. One bucket was buried at each tip of the "Y" and one at the central point. Strips of canvas of 5.0 × 0.5 m, fixed with wooden stakes, connected each outlying bucket to the central one in order to steer the animals into the buckets. Ten traps were placed in each area, comprising a total of 40 buckets per area. The central point of each trap was 20 m from the next in a straight line. The bottom of each bucket was perforated to prevent the accumulation of rain water. The size of the holes prevented the animals from escaping.

Traps were checked every morning and covered on the last day to avoid captures outside the sampling period. Each trap was numbered individually, enabling the identification of scorpions according to trap, date and collection area. Since the traps were originally erected to capture small mammals alive, a preserving liquid was not used, hence animals remained alive until the moment of capture. Thus, there was a possibility of the scorpions having been devoured by toads, lizards or rodents inside the buckets. So, the number of collected scorpions may be higher than the observed. However, the results probably would not change, because the patterns of seasonality are clearcut in this work.

This kind of sampling probably produced a different result from active collection (e.g. with ultraviolet light), but with pitfall traps, the seasonality would be more evident. Pregnant females were identified according to Farley (2001), with dissections and observation of the ovariuterus, and comparison with Farley's photos. Voucher specimens were deposited in Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, SP, Brazil.

Environmental data.—The following environmental data were gathered: amount of litter, density of the canopy, perimeter of closest 10 trees measured at the breast height (PBH), soil composition and elevation. All these data were recorded on the same day, in May 2002 (subsequent to the period of collection), close to the places where traps were located. The amount of litter of an area of 0.25 m^2 was measured. Ten samples were collected randomly in each area totaling 40 samples. Each sample was placed in a stove for 48 hours and its weight was measured soon after. The density of the canopy was measured using a densiometer at 24 points in each area, totaling 96 samples. The PBH was measured at 24 points in each area, totaling 960 trees. To analyze

Figure 1, 2.—*Thestylus aurantiurus*. 1. Male. 2. Female.

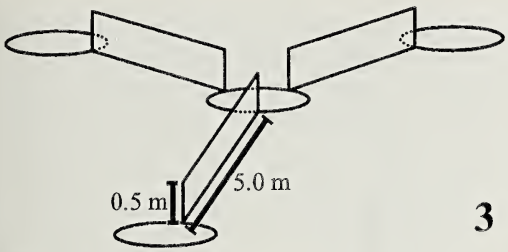


Figure 3.—Schematic representation of the drift fence pitfall traps used in sampling in P. E. Serra da Cantareira, Brazil.

soil composition, samples were collected at 8 points in each area, totaling 32 samples. The percentage of organic matter and the vegetational covering were measured.

Statistical analysis.—In the statistical analysis of the number of animals collected in each area and to verify whether environmental factors differ in the four areas, the Kruskal-Wallis test was utilized with $\alpha = 0.05$. For a comparison between the number of animals collected in the higher areas and the number of animals collected in the lower areas, a Mann-Whitney test was used with $\alpha = 0.05$. Before those statistical analysis, the normality and the homogeneity of variances were tested. The data were ranked in both cases. In order to verify whether there is a relationship between these factors and the number of collected animals in each area, the Spearman Rank Correlation was utilized with $n = 4$.

RESULTS

Burrows of *Thestylus aurantiurus*.—Individuals of *T. aurantiurus* in Parque Estadual Intervales (São Paulo, SP, Brazil) were observed foraging at the entrance of their burrows, in ravines near river margins, with pedipalps and anterior body outside (G. Machado, pers. com.), in a typical sit-and-wait foraging type. Burrowing activity of *T. aurantiurus* was observed in captivity, where all individuals constructed many burrows, apparently looking for the best place to stay. The burrows were simple, with a single vertical or oblique tunnel (1.5–3.0 cm deep), and a horizontal region at the end (about 1.5 cm long). The entrance could be circular or semicircular in shape, with 1.0–1.5 cm of maximum width.

Seasonality.—*Thestylus aurantiurus* was the only scorpion species recorded in the park. Between January (summer) and July (winter), few individuals were collected (from 0–2 scorpions/month in 40 traps). Four males were collected in August. In the three subsequent months (spring), 18, 36 and 11 scorpions were collected, respectively (about 80% of the total sampled). Twelve females were collected in October (about 70% of the total sampled females). In the remaining months of the year, one female was the maximum number captured per month (Fig. 4).

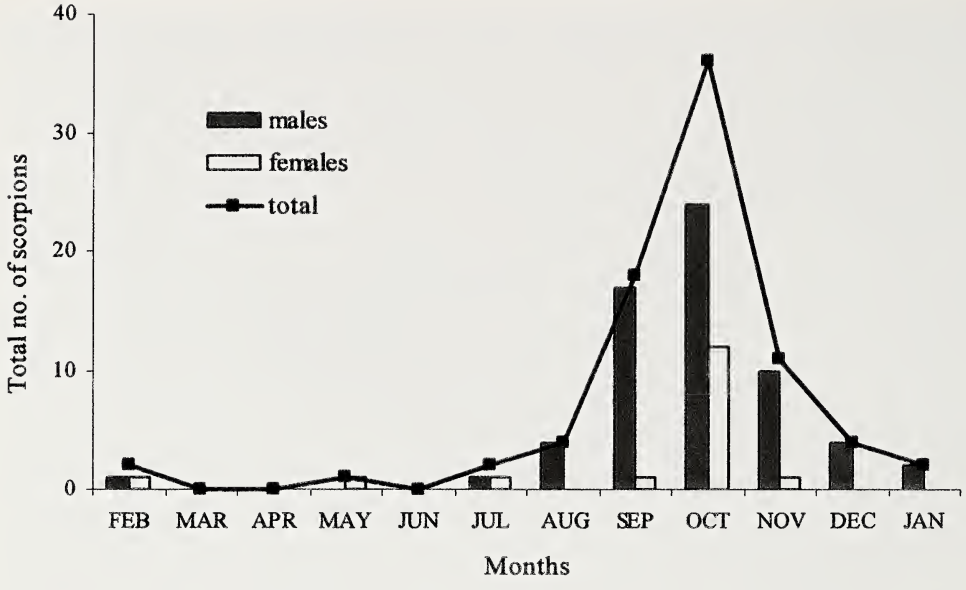
Four pregnant females were found in October and one pregnant female in November 2000. No fecund females were found in the other months.

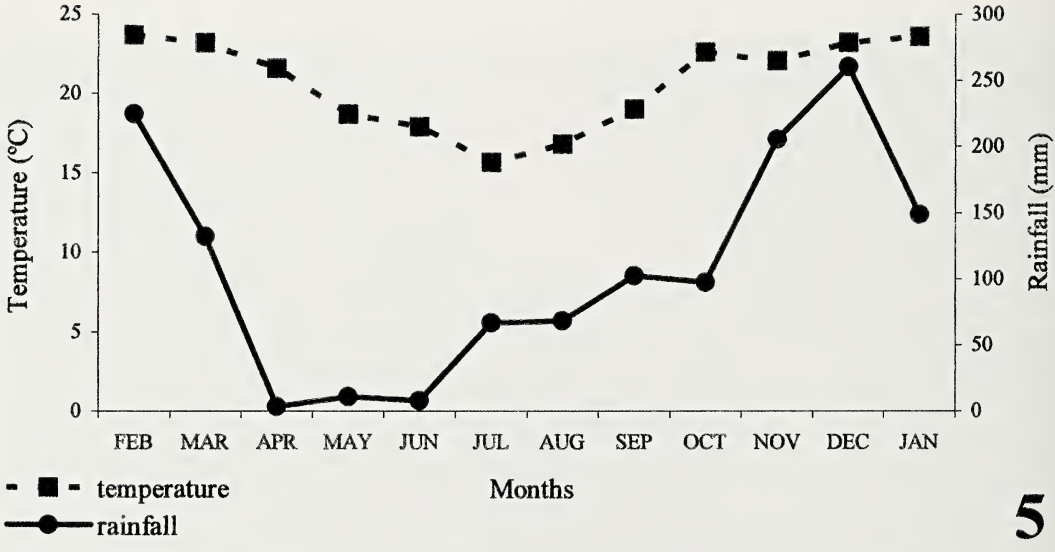
Relative abundance in four areas.—The individuals collected possessed a heterogeneous distribution in the four areas (K.W., $H = 14.966$; $P = 0.002$). The number of individuals collected in the two higher areas (1 & 3) was significantly higher than the number of individuals collected in the two lower areas (2 & 4) (Mann-Whitney test, $U = 79.500$; $P = 0.001$).

The amount of litter was different in the four areas (area 1 = 166.9 g, area 2 = 339.1 g, area 3 = 190.5 g, area 4 = 132.7 g; K.W., $H = 18.00$; $df = 3$; $P = 0.0004$; $n = 40$), but only area 2 presented a different amount of litter, the amount of the other three areas are very similar (according to the Tukey HSD test). Canopy density was different in the four areas (area 1 = 4.625, area 2 = 8.5, area 3 = 8.71, area 4 = 9.92; K.W., $H = 22.46$; $df = 3$; $P < 0.0001$) but it was not related to the number of scorpions collected ($r_s = 0.40$; $n = 4$; $P = 0.60$). The PBH was also different in the four areas (area 1 = 14.09 cm, area 2 = 18.25 cm, area 3 = 16.9 cm, area 4 = 18.86 cm; K.W., $H = 18.81$; $df = 3$; $P = 0.0003$) but not related to the number of scorpions collected ($r_s = 0.21$; $n = 4$; $P = 0.79$). Soil type was the same in the four areas. The number of scorpions collected was not significantly related to the elevation ($r_s = 0.74$; $n = 4$; $P = 0.26$). Air temperature and rainfall were not related to abundance, although the number of scorpions increased immediately after the coldest month.

DISCUSSION

Reproductive activity.—The population of *Thestylus aurantiurus* in the Parque Estadual da Serra da Cantareira presents differentiated activity throughout the year suggesting the ex-





Figures 4, 5.—4. Seasonality of the scorpion population of P. E. Serra da Cantareira, Brazil (February 2000–January 2001), with the total number of individuals collected by month. The columns represent the number of males and females collected by month. 5. Means of temperature (in °C) and total rainfall (in millimeters) by month in the P. E. Serra da Cantareira, Brazil (February 2000–January 2001).

istence of a reproductive season. The reproductive season lasts from September to November, with an activity peak in October (Fig. 4), in the beginning of the hot, wet season (Fig. 5). This can be evidenced by the fact that fertilized females were found in October and November of 2000.

Ten of the 12 females collected in October were collected together with males. These females may have fallen into traps while they

were dancing with males in search of a place to deposit the spermatophore. The sit-and-wait foraging strategy of this species consists of remaining immobile, waiting for prey. This foraging strategy type does not require the scorpion to move around (Polis 1990a), leading us to conclude that most of scorpions collected in this study were in a search of partners and not prey.

Corey & Taylor (1987) collected scorpions in pitfall traps, close to Orlando, Florida, U.S.A. during one year, sampling every two months. Only one species was collected, the buthid *Centruroides hentzi* (Banks 1900). This is an errant forager but also presenting an increase in activity throughout the year, in July and September, apparently during the reproductive period.

The reproductive period in scorpions varies according to the species. Some South-American scorpions such as *Tityus bahiensis* (Perty 1833) do not exhibit a well-defined reproductive period, instead remaining active throughout the year (Matthiesen 1968). There is information on several species of the Bothriuridae. The reproductive period of *Bothriurus bonariensis* (C.L. Koch 1841) is from November to February, *B. flavidus* Kraepelin 1911 from November to January, and *Urophonius iheringii* Pocock 1893 and *U. brachycentrus* (Thorell 1876) from May to September (Peretti 1997). However, differences in the *Thestylus aurantiurus* reproductive period may be related to climatic differences at the different localities. The beginning of the reproductive period of the Argentinean species of *Bothriurus* coincides with the beginning of the local warm, wet season (Peretti 1997). This also occurs in the *T. aurantiurus* population of the Parque Estadual da Serra da Cantareira and the Parque Estadual da Serra do Japi (Machado & Vasconcellos-Neto 2000). For these populations, the beginning of the reproductive period is September to October.

There is a great difference in activity between the sexes in the *Thestylus aurantiurus* population of the Parque Estadual da Serra da Cantareira. Many more males were captured than females (Fig. 4), probably due to the increase of male activity during the reproductive period. Females wait for males close to their shelters, which thus explain this low occurrence (Benton 2001).

The collection using pitfall traps produce a different result from active collection with ultraviolet light. Individuals standing still are also found with active collection. If ultraviolet lights were used, the expected number of captured scorpions would be higher and the expected number of females would be closer to the number of males (since the sex ratio of *Thestylus aurantiurus* is 1:1). However, seasonality of activity probably would not be as evident as in the collection with pitfall traps. We conclude that the population of *Thestylus aurantiurus* in the Parque Estadual da Serra da Cantareira possesses a reproductive season from September to November (Fig. 4).

Influence of environmental factors on abundance.—Individuals of the *Thestylus aurantiurus* population from the Parque Estadual da Serra da Cantareira apparently prefer places at a higher elevation. This can be related to the possibility of shelters in lower areas being flooded in the rainy season. The two areas with a higher number of collected scorpions (1 & 3) are located at a higher elevation and farther from water sources. On the other hand, the two areas with fewer collected scorpions (2 & 4) are located in places at a lower elevation. These areas are close to water sources, becoming flooded in the rainy season.

According to Polis (1990b), some scorpion species seek specific environmental conditions in which to build their burrows. Namibian scorpions use several places as a shelter including simple holes in the soil and under tree barks (Lamoral 1979). Harington (1978) verified that *Cheloctonus jonesii* Pocock 1892 (Liochelidae) examines a large area before beginning to dig its burrow. Additionally, in *Urodacus* there are differences among species in the choice of place, format and structure of burrows (Koch 1978).

Many researchers verified the preference of scorpions for higher elevation localities that do not flood and are far from water sources. Williams (1966) observed that burrows of *Anuroctonus phaeodactylus* (Wood 1863) (Iuridae) are located on steep slopes, their entrances being counter to surface water flow. These burrows are rarely located on the bottom of valleys, in the lower regions of drainage. Zinner & Amitai (1969) verified that two species of *Compsobuthus* Vachon 1949 (Buthidae) of Israel migrate to higher places during the rainy season. The entrances to their burrows

are also built to avoid the accumulation of rain water. Koch (1977) also observed that several species of Australian scorpions build their burrows only on slopes or where rain water does not accumulate. The individuals of *T. aurantiurus* studied in this work were more abundant in places at a higher elevation. These places are sloping, do not flood and rain water does not accumulate.

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OBSERVATIONS ON *LOXOSCELES RECLUSA* (ARANEAE, SICARIIDAE) FEEDING ON SHORT-HORNED GRASSHOPPERS

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ABSTRACT. Observations on *Loxosceles reclusa* Gertsch & Mulaik 1940, feeding on various species of short-horned grasshoppers are presented. In this paper, prey attack strategy, duration of feeding, and behaviors surrounding feeding are reported. The spiders routinely fed on prey larger than themselves. Lightly touching prey with palps prior to feeding was always observed. The first quick bites and the first attachment sites were mostly peripheral, with later attachment sites central, on the head, thorax or abdomen. Feeding times, typically 3–10 hours, ranged up to 23 hours 38 minutes. The first long attachment was usually on a peripheral location of the prey (antenna or leg), but subsequent long attachments were more often central. Overall, 39.5% of long attachments were on the main body of the prey (not antenna or leg). Long attachments were then frequently followed by web spinning, or uncommonly, bradykinesia. Rocking, tugging or pulling at prey between attachments was common. The slow feeding from multiple sites on the prey appears to be an efficient strategy for this sit-and-wait predator to extract maximum nourishment from the large prey.

Keywords: Brown recluse spider, feeding, arachnid behavior

Loxosceles reclusa Gertsch & Mulaik 1940, a species of recluse spiders found throughout the Midwestern USA, is of considerable interest medically because envenomation can cause significant cutaneous necrosis and, less commonly, severe systemic manifestations including hemolytic anemia and renal failure (Anderson 1997). Greater understanding of the details of feeding behavior of this species may have medical implications and this has motivated us to study in detail the feeding activities of *L. reclusa* on one type of prey. We studied the attack and feeding sequence of *L. reclusa* on various species of short-horned grasshoppers. We recorded latency of bites, duration of feeding, bite sites and movements of the spider during the feeding sequence.

METHODS

Fifty-six spiders (29 females, 19 males and 8 juveniles) were selected at random from a colony of 600 individually housed *L. reclusa*. All were captured from houses and outbuildings in Phelps, Dent, and Texas Counties in south central Missouri (between latitudes 37°32′ and 37°56′N, and between longitudes 91°41′ and 91°58′W) and had been in captivity from 10 days to over two years. Spiders were fed domestic crickets in captivity (one cricket per spider every 2–3 weeks) and, before our trials, prey were withheld for intervals varying from 3–98 days. The average interval between the previous feeding and the observed feeding were similar for all three groups: males: mean = 27.25 days, females: mean = 28.08 days, and immatures mean = 30.43 days. Spiders for the study were all housed individually in glass jars (5.7 cm diameter × 5.7 cm height) and were left in these jars for the feeding observations. No water source was provided, and the spiders were kept under room light with window light during the day and artificial light in the evenings, but no nocturnal light. Prey for this study consisted of short-horned grasshoppers, captured from lawns in Phelps and Dent Counties, Missouri. Total body sizes for these grasshoppers ranged from 7.9–19.1 mm.

Biting and feeding behaviors were observed after dropping one grasshopper into the spi-

Figure 1.—*Loxosceles reclusa* palpating a grasshopper, a behavior that was present in all observed predations (n = 56). Note that the prey length is greater than that of the spider predator.

der's cage at a distance of three to five centimeters from the spider. The grasshoppers were partly immobilized by severing the posterior legs at the femoral-tibial junction. This was done to allow easier capture by the spider and easier observation, but this most likely changed the number of quick bites on the posterior leg. Observations were made at a distance of 1 m to minimize disturbance to the spider. We recorded latency to first bites (time from introduction of prey to first bite), latency to long attachment (time from introduction of prey to long attachment) and duration of long attachments. Two types of bites were observed: quick bites and long attachments. We define a long attachment as an attachment lasting more than two consecutive minutes. All shorter bites are called quick bites. We recorded location of first bite, number of quick bites, actions before and after web spinning, and locations of all long attachments. Students' t-test statistics for the study, assuming normal distributions with unequal variances, were calculated using the PAST online statistics calculator (http://folk.uio.no/ohammer/past/). Voucher specimens were deposited in the Denver Museum of Nature and Science, Denver, Colorado.

RESULTS

Generally, before feeding, the spider lightly touched the prey with both palps (Fig. 1) prior to delivering a first bite. This behavior occurred in all observed predations. The latency to the initial bite averaged 5.58 ± 9.86 min after introduction of the prey, with differences between groups not significant except for females vs. immatures (males vs. females, t = 1.23, P = 0.23; males vs. immatures, t = 2.13, P = 0.05; females vs. immatures, t = 2.14, P = 0.04).

Generally, *L. reclusa* delivered one or two quick bites before a long attachment, but the total number of quick bites ranged from zero to ten (Fig. 2). Within two minutes of the first bite, the prey ceased almost all movement and the spider then began a long attachment (Table 1). The latency to the first long attachment for females was significantly longer than the corresponding times for juveniles (t = 2.548, P = 0.016) but not different for males (t = −1.650, P = 0.107). Feeding duration was longest for females (Table 1, females compared with all other spiders, males and immatures combined, t = −3.784, P = 0.002).

The quick bite sequence was extremely rapid, with the spider darting in, biting, and jumping back, normally within a fraction of a second. Data pooled from all three spider groups show that this sequence involved one or two bites in 58% of cases (Fig. 2). These bites are delivered to easily accessible peripheral parts of the prey, either legs or antennae (Figs. 3 & 4), allowing *L. reclusa* to rapidly deliver enough venom to paralyze the prey. After the first quick bite, the spider retreated quickly, as noted by Carrel (pers. comm.). Both the peripheral attack strategy and the quickness of biting and withdrawal observed in the earliest bites were observed consistently. The quick bite sequence was usually followed by a retreat and wait (holding) stage that averaged 15.55 ± 22.63 minutes. The longest holding stage noted for the 56 spiders observed was 139 minutes. For some spiders, the first bite was a "long attachment" (Fig. 2).

During feeding, spinning of silk was observed generally before a long attachment or after a long attachment (Fig. 5). Spinning was also seen when the spider was introduced to a new jar. Web production seemed to be used to immobilize the prey for a possible additional feeding, seen in 48% of the fifty-six observed predations. In 23.5% of cases, web spinning terminated the feeding sequence. A variation seen in one instance in this series and in one other observed instance is a slow stepping around the prey, a distinct pattern of bradykinesia confined to feeding. Frequently, the spiders walked around the jar spinning

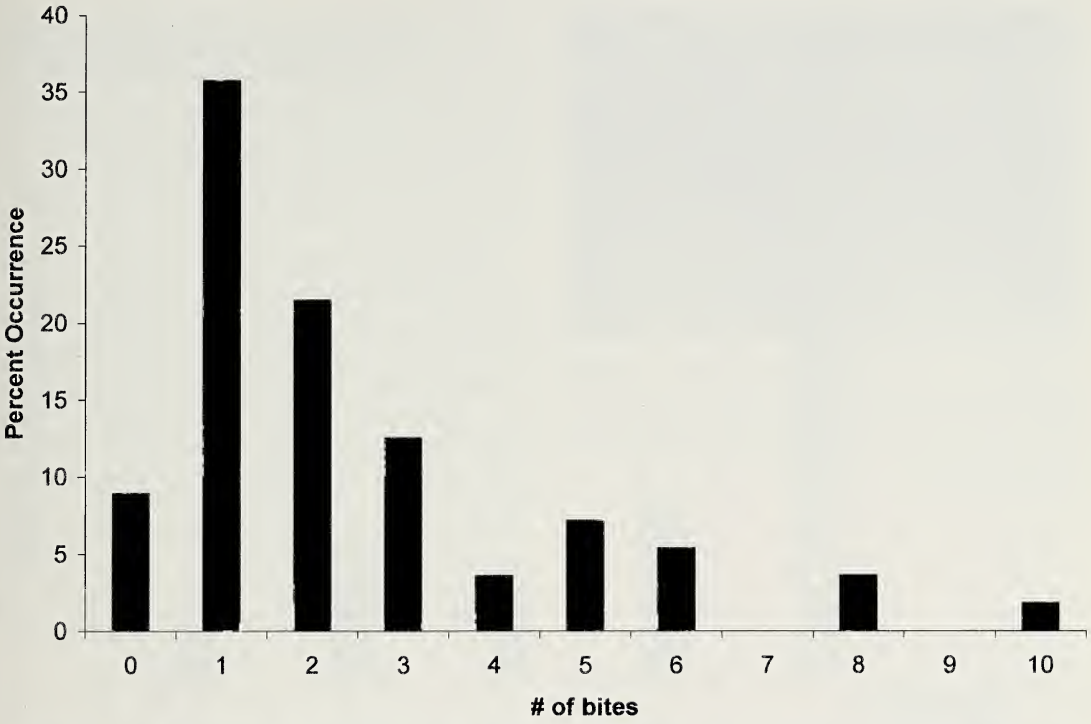

Figure 2.—The number of quick bites inflicted by *L. reclusa* on a grasshopper is typically one or two, but ranged from zero to ten. Within two minutes of these quick bites, the prey ceased almost all movement.

variable amounts of web after they had completely finished feeding on the grasshopper.

It was noted that all successful feedings (those feedings in which the spider had at least one attachment longer than two minutes) lasted at least three hours. The longest feeding reported here lasted over twenty-three hours. One other feeding lasted over 47 hours, though this was not included in this series due to the inability to observe the complete feeding. Disruptions were observed twice during feeding, and in each case the spiders resumed feeding after a brief pause, once at the previous feeding site, and the other at a different site.

DISCUSSION

The preferred initial *L. reclusa* feeding sites of legs and antenna (Fig. 4) confirm those observed by Hite (1966), who noted "when feeding on grasshoppers up to 35 mm in length, the most commonly selected part is a leg or an antenna." The preferred feeding sites cannot be generalized to all prey, as the spider appears to adapt its feeding sequence to prey morphology. As Hite noted for 1383 feedings of house flies to *L. reclusa*, head, abdomen, and thorax accounted for 39%, 26%, and 15% of feeding sites respectively, with legs accounting for only 20% of feeding sites (Hite 1966).

Table 1.—Mean latency of first quick bite and first long attachment and feeding duration, with standard deviations, for *L. reclusa* feeding on short horned grasshoppers.

Spider	Mean latency of first quick bite	Mean latency of 1st long attachment	Duration of feeding
Immature (n = 8)	2.14 ± 1.95 min	15.63 ± 16.59 min	690.25 ± 190.76 min
Female (n = 29)	8.00 ± 13.72 min	41.93 ± 45.77 min	737.62 ± 318.39 min
Male (n = 19)	4.59 ± 3.64 min	26.00 ± 19.99 min	391.63 ± 178.58 min

Figure 3.—*Loxosceles reclusa* feeding on grasshopper antenna. The antenna is chosen as a site for the first long attachment in 32.1% of feedings, but is chosen as a long attachment site in only 16.1% of cases overall.

The ability of *L. reclusa* to survive in captivity for long periods of time without prey is well known and the spiders are frequently found in areas where prey is only available sporadically. Here it was observed that *L. reclusa* can take larger and potentially hazardous prey that exceed the weight of the predator.

The behavior of *L. reclusa* indoors in a confined environment could differ from *L. reclusa* behavior in its natural environment. Greenstone (1999) noted that starvation, generally undertaken to increase the likelihood of feeding, might alter metabolic rates and therefore affect feeding behavior. This argument may be less valid for *L. reclusa* than for some other species. Hite (1966) noted that *L. reclusa* feedings appear to be less frequent than other species. Hite also observed a mature female *L. reclusa* surviving 297 days, nearly ten months, without food or water. We observed

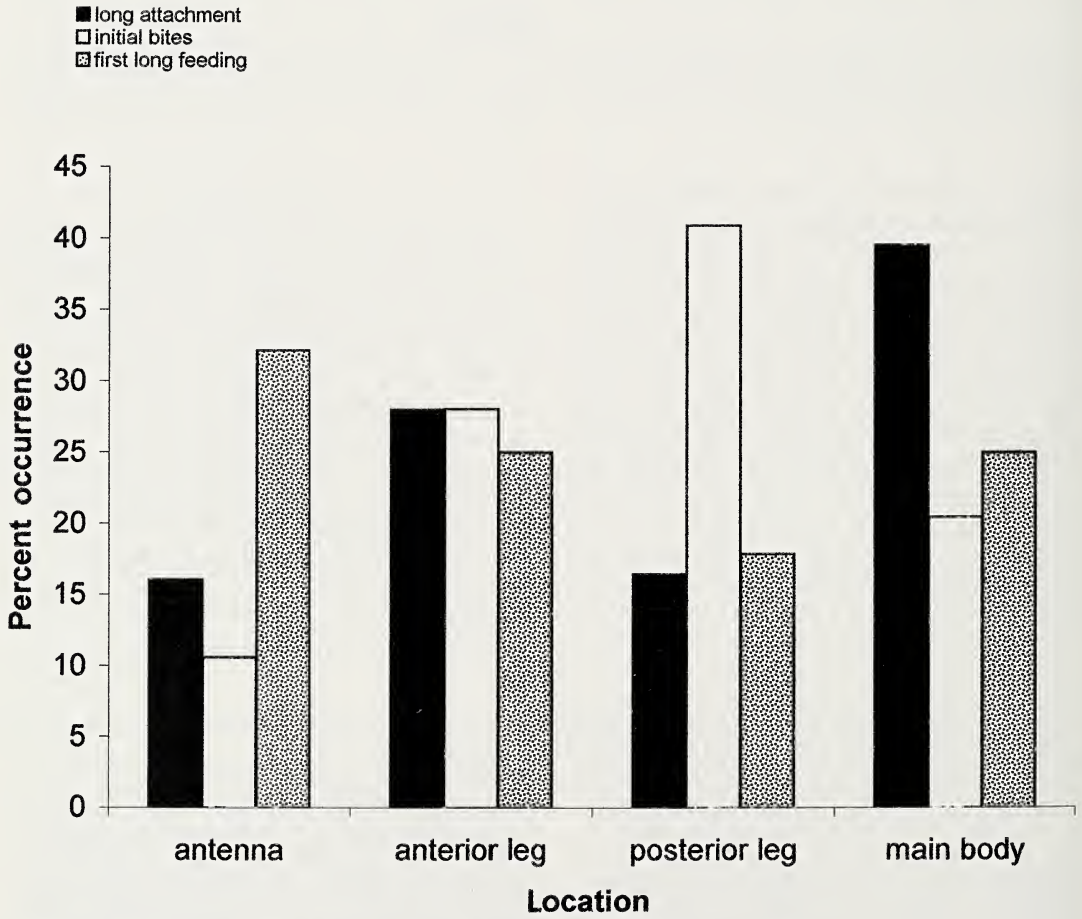

Figure 4.—Location of quick bites and long attachments of *L. reclusa* on prey.

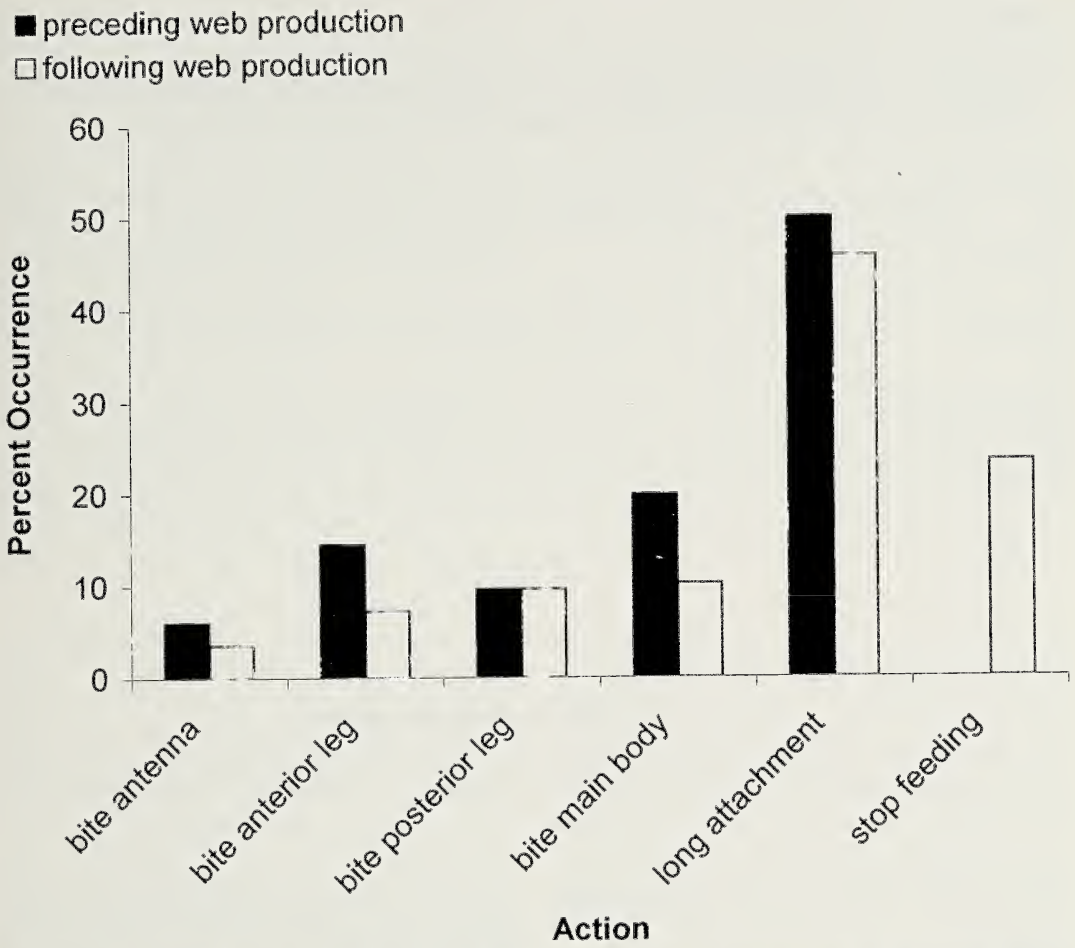

Figure 5.—Actions preceding and following web production. Long attachments are the most common actions preceding and following web production.

a mature *L. reclusa* female similarly survive 545 days. The intervals since the last feeding, 3–98 days, were well within the feeding intervals that the spider may encounter in its typical confined indoor habitat. As *L. reclusa* appears to prefer confined areas, our indoor experimental environment may not differ significantly from the situation the spider has been in when it bites humans. The behavior of the spider under these conditions is therefore of medical importance but it should be noted that most bites of humans are made under different circumstances than the predatory bites studied here.

Human encroachment on *L. reclusa* territory may have changed the natural environment for this spider and it may now be true that a significant portion of all *L. reclusa* live indoors. Hite (1966) found 430 of 626 spiders collected in indoor locations and 196 spiders in outdoor locations. Vetter & Barger (2002) trapped 2,055 *L. reclusa* in a single home in Kansas. However, we do not know what natural conditions outdoors allow high densities of *L. reclusa*. In an ongoing study, high densities of *L. deserta* in packrat dens are being investigated.

One potential problem with methodology is the variation in time since the last feeding, ranging from 3–98 days. This variation could influence spider behavior. We could find no systematic difference in behavior as a result of time since last feeding. Figure 6 shows total duration of feeding vs. time since last feeding, which appear only modestly correlated. For the 16 feedings with duration 12 days or less, the feeding duration is 598.5 ± 269.04 minutes, vs 621.75 ± 279.62 minutes for the 16

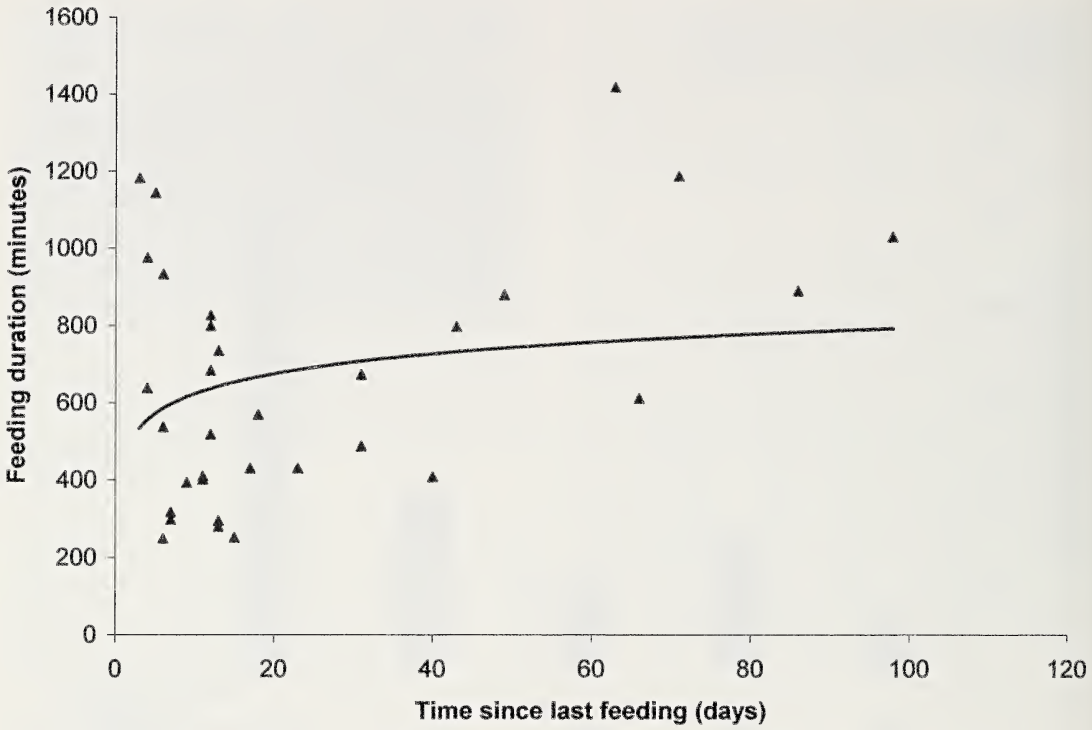

Figure 6.—Time elapsed since the last feeding vs. duration of feeding. A best-fit line shows a slow increase in feeding time with longer intervals between feedings. A minimum feeding time of about three hours was seen.

feedings with duration 13 days or more, a difference that is not significant ($t = -0.24$, $P = 0.81$).

In summary, *L. reclusa* feeding begins with quick bites and is followed with successively more central attachments. Females tended to take longer with all phases of feeding. The use of quick bites allows *L. reclusa* to take large and potentially dangerous prey. Attributes of these spiders such as the mechanics of the legs, joints, and fangs appear to be adapted for swinging in and out quickly, without physically overpowering prey. The venom appears to be effective when injected at peripheral sites. The long duration of feedings for *L. reclusa* that we report here, frequently exceeding 10 hours, are incompatible with a frequent feeding regimen. The ability to utilize large prey efficiently may be very important to the spiders in times of low prey abundance. Further explorations of the adaptive value of longer feeding times, the utilization of large meals and mode of action of the venom in insects is needed.

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THE SYSTEMATIC POSITION OF THE AMAZONIAN SPECIES OF *ALBIORIX* (PSEUDOSCORPIONES, IDEORONCIDAE)

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ABSTRACT. The new genus *Xorilbia* (Pseudoscorpiones, Ideoroncidae) is established for three species from the Amazon region previously included in the genus *Albiorix*: the type species *X. arboricola* (Mahnert), *X. gracilis* (Mahnert) and *X. lamellifer* (Mahnert). The new genus bears a peculiar structure on the arolium that is only found in a few other genera of Ideoroncidae. New locality records are presented for *X. gracilis* and *X. lamellifer*, including the first record of *X. gracilis* from Venezuela.

Keywords: Taxonomy, new genus, Neotropical, Brazil, Venezuela, *Xorilbia*

The South American ideoroncid fauna consists of 14 species in two genera. The genus *Ideoroncus* Balzan 1887 contains nine species from Brazil and Paraguay (Mahnert 1984, 2001), while five species attributed to the genus *Albiorix* Chamberlin 1930 are found in Brazil, Argentina and Chile (Mahnert 1979, 1984, 1985b). While examining the status of the various species attributed to the genus *Albiorix*, we have found that the three species from Amazonian Brazil attributed to the genus *Albiorix* differ considerably from other members of the genus, particularly in features of the arolium – the elongate, soft structure situated at the distal end of the pedal tarsus between the tarsal claws of all pseudoscorpions (Chamberlin 1931). In particular, the three Amazonian species of *Albiorix* possess a small hooked structure on the ventral surface of the arolium, first observed by Vachon (1958) for two species of *Negroroncus* Beier 1931, a feature that is lacking in species of *Albiorix*. Also, the arolium is much longer than the claws and deeply divided in all species of *Albiorix*, whereas the arolium is slightly shorter than the claws and at most only slightly divided in the Amazonian species. These features suggested to us that the Amazonian species are misplaced in *Albiorix*, and we here transfer them to a new genus *Xorilbia* which is described and compared with similar ideoroncid genera.

The specimens mentioned in this paper are lodged in the following institutions: California Academy of Sciences, San Francisco (CAS); and the University of California, Davis, California, U.S.A. (UCD). Comparative material of other ideoroncid taxa examined for this study is lodged in the Muséum d'histoire naturelle, Genéve, Switzerland (MHNG); and the Western Australian Museum, Perth, Western Australia (WAM). Morphological terminology mostly follows Chamberlin (1931) and Harvey (1992).

The specimens were studied using one of two techniques. Temporary slide mounts were prepared by immersion of specimens in concentrated lactic acid at room temperature for several days, and mounting them on microscope slides with 10 or 12 mm coverslips supported by small sections of 0.25, 0.35 or 0.50 mm diameter nylon fishing line. After study, the specimens were returned to 75% ethanol. Permanent slide mounts were prepared by removing the pedipalps, the chelicera, left leg I and left leg IV from specimens with the use of eye-scissors or small needles, and clearing overnight with 10% potassium hydroxide at room temperature. The specimens were then washed in several rinses of water and 5% acetic acid (to neutralize the potassium hydroxide), and dehydrated through a graded ethanol series. They were then transferred to Euparal essence overnight at room temperature, prior to mounting in Euparal on microscope slides using 10 or 12 mm coverslips supported by small sections of 0.25, 0.35 or 0.50 mm diameter nylon fishing line. All specimens were

studied using an Olympus BH-2 compound microscope and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study the specimens were returned to 75% ethanol with the dissected portions placed in 12 × 3 mm glass genitalia microvials (BioQuip Products, Inc.).

Family Ideoroncidae Chamberlin 1930
Genus ***Xorilbia***
NEW GENUS

Type species.—*Ideoroncus arboricola* Mahnert 1979.

Etymology.—The generic name is an anagram of *Albiorix* and is to be treated as feminine.

Diagnosis.—Members of *Xorilbia* possess a small hooked process on the ventral surface of each arolium (Fig. 1), a feature shared with *Dhanus siamensis* (With 1906) and with all species of *Typhloroncus* Muchmore 1979, *Negroroncus* Beier 1931 and *Afroroncus* Mahnert 1981. It differs from these genera as follows: *Xorilbia* and *Typhloroncus* have a chelal trichobothrial pattern of 22 on the fixed finger and 10, occasionally 11, on the movable finger (22/10 or 22/11), whereas *Dhanus siamensis*, *Negroroncus* species and *Afroroncus* species have a pattern of 20/10, with the exception of *N. jeanneli* Vachon 1958, which has a pattern of 26/12. *Xorilbia* has chelal teeth that are widely spaced whereas *Typhloroncus* has closely-spaced chelal teeth. *Xorilbia* has 5 trichobothria in the *ib* region and 6 trichobothria in the *ist* region of the fixed chelal finger, whereas species of *Typhloroncus* bear 4 trichobothria in the *ib* region and 7 trichobothria in the *ist* region. *Xorilbia* also differs from *Typhloroncus* in the presence of one pair of eyes; whereas eyes are totally absent in all species of *Typhloroncus*.

Description.—All setae long, virtually straight and acicular. Most cuticular surfaces smooth and glossy.

Pedipalps: long and slender. Fixed chelal finger with 22 trichobothria, movable chelal finger with 10 trichobothria: *eb* region with 1 trichobothrium; *est* region with 6 trichobothria; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *b* region with 2 trichobothria; and *t* region with 6 trichobothria; *st* not ventrally displaced. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near *t* region in movable finger. Chelal teeth widely spaced. Condyle on the chelal hand small and rounded.

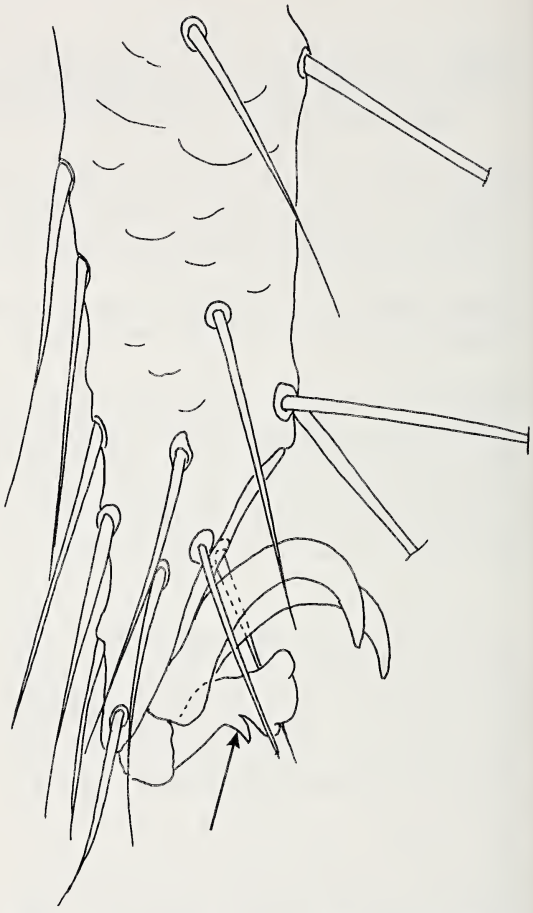

Fig. 1.—*Xorilbia lamellifer* (Mahnert): detail of tip of left tarsus IV, female from Fazenda Esteio, Brazil. The arrow indicates the ventral hooked process on the arolium.

Chelicera: with 6 long, acuminate setae on hand; movable finger with 1 long subdistal seta; flagellum of 4 thickened blades, all blades serrate; lamina exterior absent; galea long and slender.

Cephalothorax: carapace with 2 small, bulging eyes; without furrows; anterior margin with 4 setae. Manducatory process with 2 long distal setae.

Abdomen: tergites and sternites undivided. Pleural membrane longitudinally striate. Each stigmatic sclerite with 1 seta. Posterior maxillary lyrifissure present and sub-basally situated. Spiracles simple, with spiracular helix.

Legs: femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotactile seta subproximal; legs with two subterminal tarsal setae, each acuminate; arolium shorter than claws, slightly divided, with ventral hooked process; claws slender and simple.

Remarks.—The hooked process on the ventral surface of the arolium of all legs (Fig. 1) was first noted and illustrated in two species of *Negroroncus* (Vachon 1958), and we have found that it is present in *Dhanus siamensis* and in species of *Typhloroncus*, *Negroroncus*, *Afroroncus* and *Xorilbia*. It would seem likely that the hooked process is an apomorphic feature that defines this group as a monophyletic entity, but the close relationship between *Afroroncus*, which bears a ventral hook, and *Nannoroncus* Beier 1955 (Mahnert 1981), which lacks a hook, may negate the power of this feature to define a clade. The process is absent from species of *Ideoroncus*, *Dhanus* Chamberlin 1930 (excluding *D. siamensis*), *Shravana* Chamberlin 1930, *Nhatrangia* Redikorzev 1938, *Nannoroncus*, *Albiorix* and *Pseudalbiorix* Harvey, Barba, Muchmore & Perez in press. *Dhanus siamensis* bears very little resemblance to the remaining species of *Dhanus*, including the type species *D. sumatranus*, and will be placed in a new genus as part of a forthcoming review of the Asian members of the Ideoroncidae (Harvey unpub. data).

The ideoroncids with a ventral hooked process on the arolium are widely distributed around the world with *Xorilbia* occurring in the Amazon basin in northern Brazil and southern Venezuela, *Typhloroncus* species from the West Indies and Mexico (Muchmore 1979, 1982, 1986), *Negroroncus* and *Afroroncus* from eastern Africa (Mahnert 1981), and *D. siamensis* from south-east Asia (Schawaller 1994).

The removal of the Amazonian species from *Albiorix*, and the recent transfer of two species of *Albiorix* to a separate genus (Harvey et al. in press) reduces *Albiorix* to 11 species ranging from western North America to Mexico [*A. anophthalmus* Muchmore 1999, *A. edentatus* Chamberlin 1930, *A. bolivari* Beier 1963, *A. conodentatus* Hoff 1945, *A. magnus* Hoff 1945, *A. mexicanus* (Banks 1898), *A. mirabilis* Muchmore 1982, *A. parvidentatus* Chamberlin 1930, *A. retrodentatus* Hoff 1945], with isolated species in Argentina [*A. argentiniensis* (Hoff 1954)] and Chile [*A. chilensis* (Ellingsen 1905)].

Distribution.—Species of *Xorilbia* occur in the northern Brazilian states of Amazonas and Pará, and in southern Venezuela.

Xorilbia arboricola (Mahnert 1979)
NEW COMBINATION

Ideoroncus arboricola Mahnert 1979:753–755, figs. 70–74; Adis et al. 1987:488.

Albiorix arboricola (Mahnert): Mahnert 1984:672–673; Mahnert 1985a:78; Mahnert & Adis 1986: 213; Mahnert et al. 1986: fig. 10; Harvey 1991: 316; Adis & Mahnert 1993: fig. 5; Mahnert & Adis 2002:379, fig. 10; Adis et al. 2002:5.

Diagnosis.—*Xorilbia arboricola* lacks the lamelliform ridge on the fixed chelal finger that is characteristic of *X. lamellifer*, and the pedipalpal segments are more robust than in *X. gracilis*.

Description.—See Mahnert (1979, 1984).

Remarks.—*Xorilbia arboricola* occurs at several locations in Amazonas and Pará where it is occasionally sympatric with *X. gracilis* (Mahnert 1984).

Xorilbia gracilis (Mahnert 1985)
NEW COMBINATION

Albiorix aff. *arboricola* (Mahnert): Mahnert 1984: 673.

Albiorix gracilis Mahnert 1985b:223–224, figs. 27–28; Mahnert & Adis 1986:213; Harvey 1991:317.

Albiorix gracilis Mahnert: Adis & Mahnert 1990: 13, figs. 2–3; Adis & Mahnert 1993:435, figs. 2–3, 5; Mahnert & Adis 2002:379; Adis et al. 2002:5.

New material examined.—VENEZUELA: *Amazonas*: 1 ♂, 1 ♀, Alto Rio Siapa, 1°40′N, 64°35′W, 650 m, 4 February 1989, sifting leaf litter in rainforest, J. Lattke (CAS).

Diagnosis.—*Xorilbia gracilis* lacks the lamelliform ridge on the fixed chelal finger that is characteristic of *X. lamellifer*, and the pedipalpal segments are more slender than in *X. arboricola*.

Description.—See Mahnert (1985b).

Remarks.—*Xorilbia gracilis* was recorded by Mahnert (1985b) from two locations in Amazonas where it is sympatric with *X. arboricola*. The new records listed here are of two further specimens from southern Venezuela that generally fit the original description, although they are slightly larger than the type specimens; e.g., chela (with pedicel) length,

male 1.067/0.245 (= 4.36 times longer than broad) and female 1.200/0.324 (= 3.70 times longer than broad).

Xorilbia lamellifer (Mahnert 1985)
NEW COMBINATION
Fig. 1

Albiorix lamellifer Mahnert 1985b:225–226, figs. 29–31; Mahnert & Adis 1986:213; Harvey 1991: 317; Mahnert & Adis 2002:379.

New material examined.—BRAZIL: *Amazonas*: 1 ♀, Fazenda Esteio, 80 km NNE. of Manaus, 2°25′S, 59°46′W, 80 m, 15 September 1987 (UCD).

Diagnosis.—The basal teeth on the fixed chelal finger of *X. lamellifer* are modified into a lamelliform ridge, which distinguishes this species from *X. arboricola* and *X. gracilis*.

Description.—See Mahnert (1985b).

Remarks.—Mahnert (1985b) described this species based upon a single female collected 25 km NE. of Manaus. We have examined a second female from a farm situated 80 km NNE. of Manaus.

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SHORT COMMUNICATION

ADDITIONAL NOTES ON THE POST-BIRTH DEVELOPMENT OF THE SCORPION *VAEJOVIS COAHUILAE* WILLIAMS (VAEJOVIDAE)

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ABSTRACT. Fourteen specimens of *Vaejovis coahuilae* Williams 1968 were born in the laboratory and reared in an incubator at a near-constant 27 °C. A single female reached maturity at the 8th instar, as previously hypothesized, but unverified, in this species. Two other specimens reached the 7th instar, but the male died at the molt and the female was not yet mature. Data on the duration and morphometrics of observed instars are provided for all specimens.

Keywords: Life history, instars, Vaejovidae, *Vaejovis*

A study of the life history of *Vaejovis coahuilae* Williams 1968 was published earlier by Francke & Sissom (1984). In that study, three individuals were successfully reared to the sixth instar, with only one (a male) reaching adulthood. Based on comparisons with field-collected adults, the authors used an extrapolation method and a formula-based estimate to hypothesize that males of the species mature at either the sixth or seventh instar and females at either the seventh or eighth. The purpose here is to report new data that validates (at least in part) the hypothesis of Francke & Sissom (1984).

Vaejovis coahuilae is a very common scorpion found in southeastern Arizona, much of New Mexico, western Texas and northern Mexico (Sissom 2000; unpub. data). In the current study, a pregnant female specimen of *V. coahuilae* was collected along Lea County Rd. 21, 15 mi S jct. with NM 128, New Mexico on 24 May 1990 and returned to the laboratory. At the beginning of August, the female was discovered with 29 first instar offspring on her back. The molt to the second instar occurred on 5 August 1990, and the young descended from the mother's back within the next two days. After their descent, 14 offspring were transferred to individual plastic widemouth specimen jars (height, 4.45 cm; inside diameter, 4.76 cm). The specimens in their jars were placed in a tabletop incubator at a near constant temperature of 27 °C. There was no internal lighting in the incubator and the specimens kept there were in near constant darkness, experiencing light only during brief periods of maintenance.

All specimens were fed and watered on the same schedule. Food provided included wingless *Drosophila melanogaster* Meigen, field-collected termites (*Reticulutermes* Holmgren sp.), and small mealworm larvae (*Tenebrio molitor* L.), with progressively larger prey being given to later instar specimens. Two circular pieces of paper towel were placed in the bottom of each container to provide shelter and water for the scorpions. Distilled water was provided at least twice weekly by pipetting several drops directly onto the paper towel; the scorpions were frequently observed drinking from the moistened substrate. Care was taken not to oversaturate this substrate to prevent drowning of the young scorpions, and the paper towel was changed periodically. The lids of the jars were loosely replaced so as to allow the humidity inside the jars to subside to normal levels within a day or two.

Twelve of the individuals successfully completed the second instar, but one died during the molt. Only half of those ($n = 6$) survived the third instar, one more died during the fourth instar and two more died during the fifth. Two females and one male reached the seventh instar (the male dying during the molt) and, of the two females remaining, one successfully reached the eighth. The female that later died in the seventh instar was dissected and no development of the ovariuterus was observed; the eighth instar female, however, was clearly adult.

Table 1.—Growth data by instar for *Vaejovis coahuilae* Williams reared in an incubator at 27°C. Means, minima (min), and maxima (max) are given for raw measurements (in mm). Average growth factors (GF) between instars are also provided. Measurements included carapace length (CarL), pedipalp chela length (ChelaL), pedipalp chela width (ChelaW), metasomal segment V length and width (MetVL, MetVW), and metasomal segment IV length and width (MetIVL, MetIVW). Growth factors for the single specimen reaching the eight instar were calculated from its 7th instar sizes. Three specimens actually reached the seventh instar. The male died during the molt, and as a result, its cuticle was distorted and probably not expanded.

Instar	CarL	ChelaL	ChelaW	MetVL	MetVW	MetIVL	MetIVW
2nd (n = 12)							
mean	1.33	1.59	0.36	1.21	0.55	0.78	0.55
min	1.23	1.50	0.33	1.12	0.47	0.70	0.50
max	1.44	1.72	0.40	1.30	0.60	0.90	0.60
GF to 3rd	1.24	1.25	1.28	1.28	1.33	1.33	1.29
3rd (n = 6)							
mean	1.66	2.00	0.46	1.55	0.73	1.05	0.71
min	1.55	1.85	0.40	1.45	0.60	0.95	0.62
max	1.86	2.35	0.55	1.80	0.85	1.23	0.82
GF to 4th	1.12	1.13	1.15	1.21	1.15	1.17	1.18
4th (n = 5)							
mean	1.86	2.26	0.53	1.88	0.84	1.23	0.84
min	1.51	1.85	0.40	1.65	0.62	0.97	0.64
max	2.08	2.51	0.60	2.00	0.97	1.35	0.95
GF to 5th	1.27	1.31	1.36	1.28	1.35	1.46	1.35
5th (n = 3)							
mean	2.37	2.95	0.72	2.41	1.13	1.79	1.13
min	2.10	2.70	0.60	2.12	0.95	1.66	0.98
max	2.60	3.20	0.82	2.70	1.30	1.95	1.25
GF to 6th	1.25	1.26	1.29	1.28	1.26	1.17	1.24
6th (n = 3)							
mean	2.99	3.76	0.95	3.16	1.46	2.12	1.45
min	2.75	3.50	0.85	2.89	1.32	1.97	1.31
max	3.15	3.92	1.00	3.30	1.55	2.20	1.55
GF to 7th	1.18	1.21	1.29	1.20	1.25	1.21	1.26
7th (n = 2)							
min	3.42	4.67	1.25	3.80	1.81	2.60	1.79
max	3.94	4.97	1.35	4.05	1.95	2.80	1.95
GF to 8th	1.35	1.36	1.55	1.36	1.37	1.31	1.35
8th (n = 1)	4.60	6.35	1.94	5.17	2.48	3.40	2.42

That adulthood in this female was reached in eight instars corroborates the earlier hypothesis by Francke & Sissom (1984) based on the theoretical and indirect methods. Whether or not individuals can mature at the seventh instar as well was not answered in the current study, but it seems likely. In natural populations of *V. coahuilae*, there are "small" and "large" adult males and females that could belong to different instars.

Average instar duration for the incubator-reared litter is as follows: 2nd instar, 150.8 days (110.7 days, if two outliers are excluded; these individuals required 292 and 411 days to reach the 3rd instar, respectively); 3rd instar, 64.2 days; 4th instar, 95.8 days; 5th instar, 119 days; 6th instar, 422 days; and 7th instar, 835.5 days. It should be noted that in the late summer of 1992, the specimens were transported from North Carolina to Texas and placed in a similar tabletop incubator soon after arrival. Perhaps this disturbance resulted in prolonged late instars for the three surviving specimens.

Morphometric data, including measurements and growth factors for each molt are provided in Table 1. Measurements of carapace length, chela length and width, metasomal segment IV length and width, and metasomal segment V length and width were

taken as shown in Sissom et al. (1990, fig. 11.1). Growth factors were calculated by dividing the dimension of a particular structure at a given instar by its dimension at the previous instar. Growth factors were similar to those reported by Francke & Sissom (1984).

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SHORT COMMUNICATION

VARIATIONS IN WEB CONSTRUCTION IN *LEUCAUGE VENUSTA* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. The distribution of female *Leucauge venusta* (Walckenaer 1841) in a coffee plantation in southern Mexico was studied in order to determine the vertical distribution of this spider. Principal component analysis clearly identified the presence of three distinct groups of *L. venusta* webs, based on the number of spirals/web and principally on the height at which the webs were located; most *L. venusta* webs (63/100) were close to the ground. Spiders on high webs (153.8 ± 3.6 cm above ground, mean ± S.E.) were significantly larger and heavier than spiders on lower webs. Large spiders had significantly larger, better developed ovaries, than smaller conspecifics, presumably indicative of sexual maturity. Significantly more insects were captured by sticky traps placed at 50 cm height than in the traps placed at 150 cm height; the most numerous captures were Diptera. However, insects caught at 150 cm were significantly larger than those caught at 50 cm above ground. We concluded that as sexual development proceeds, the spider increases the height at which the web is constructed. This vertical migration is associated with changes in web construction and the type of prey captured. These results are discussed in terms of intraspecific competition, predation risks and sexual selection.

Keywords: Web-building, prey, predation strategy, web location

During foraging, a predator has to make several choices: where to eat, how much time to dedicate to eating, and what type of prey to select for capture and consumption. These choices depend on strategies allowing the predator to optimize its behavioral efficiency and to reduce energetic costs and time (Alcock 1993).

Orb-weaving spiders are generalist predators that do not usually compete with each other for food (Wise 1993). This absence of competition may be a result of different species using different predatory strategies. Olive (1980) asserted that the functional morphology of the predator may directly affect the type of insect predated, as a means to avoid catching the same prey. One such strategy consists of reducing competition by building webs that differ in structure and location. In this way, each spider species produces one type of web and employs it in one type of micro-habitat (Hénaut et al. 2001). Alternatively, the web can act as a general filter and trap a large diversity of insects, and if the web is constructed at different sites, it can capture different kinds of prey. For example, *Gasteracantha cancriformis* (Linnaeus 1785) builds a web in open areas whereas *Cyclosa caroli* (Hentz 1850) traps insects in the same type of habitat but only in enclosed areas (Ibarra-Núñez et al. 2001). In this case, selection of different prey items is achieved by a combination of differences in web location and spider behavior (Hénaut et al. 2001). These studies indicate that each spider species may adopt a particular strategy based on a combination of web characteristics, web location and spider behavior.

Leucauge venusta (Walckenaer 1841) is a common species in many habitats from the United States to South America (Levi 1981). In the field, *Leucauge* species generally spin inclined orb webs. The first web of the day is usually built before dawn and may be repaired or replaced during the day (Eberhard 1988). The usual sequence of orb-building is to make radii and frame lines, then hub loops followed by a temporary spiral, and finally the sticky spiral. The temporary spiral is used as a bridge when moving from one radial thread to the

next during construction of the sticky spiral (Eberhard 1987). *Leucauge venusta* is extremely abundant during the rainy season in coffee plantations in Chiapas State, Mexico (Pinkus-Rendón pers. comm.). The web of this species is constructed in semi-open sites generally between weeds or between adjacent coffee bushes (Ibarra-Núñez & Lachaud 1998).

The objective of the present study was to determine whether a relationship exists between the body size of the female spider or characteristics of the available prey, caught by sticky traps, and the structure and placement of *L. venusta* webs in a coffee plantation in the south of Mexico.

METHODS

Field observations.—The field site was a coffee plantation in the grounds of the INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias) agricultural experimental station at Rosario Izapa located at 400 m above sea level, approximately 15 km from the town of Tapachula (Chiapas, Southern Mexico) and 1 km from the border with Guatemala (14° 58′ N, 92° 09′ W). The climate is tropical; warm and humid with a typical daily temperature range of 35 °C maximum and 23 °C minimum, and a relative humidity of approximately 85%. Heavy rainfall occurs during the months of May to October (~300 mm/month) causing a marked reduction in spider activity in the field. The field collection occurred between October and November (2000), at the beginning of the dry season.

Adult female spiders were collected by walking between coffee plants (around 2 m height) in a 1000 m^2 area of the coffee plantation at intervals of six days. The characteristics of each web were recorded for each spider collected until a total of 100 spiders and webs had been sampled. Collections were performed early in the morning when the webs were still clean and undamaged. Voucher specimens of *L. venusta* collected were deposited in the entomological collection of El Colegio de la Frontera Sur (ECOSUR).

Characteristics of the web.—Web characteristics were measured directly in the field before collecting the corresponding occupant. We recorded the height (in cm) from the soil surface to the center of the orb and to the lowest and highest points of the web, the web diameter (in cm), the number of radii and the number of sticky spirals (from the centre to the bottom of the orb and from the centre to the lower point).

Spider characteristics.—The occupant of each web was collected alive in a tube and taken back to the laboratory where body length (in mm), abdomen width (in mm) were measured with binocular microscope and dry weight (in mg) of each spider was recorded. To determine the dry weight, spiders were placed in aluminium foil, killed by freezing at −6 °C them 2 min and dried for 2 h in a temperature of 60 °C in an oven. An electronic balance was used to determine the weights (Sartorius Basic model BA 110S). In November, 30 spiders were collected randomly and the abdomen and ovary width were measured to determine whether a relationship existed between abdomen size and the development of the ovary. To measure the ovary size, ovaries were dissected out and the width measured using a binocular microscope at the widest point of the dissected ovary

Prey trapping.—To determine the abundance of different types of potential prey, 12 sticky traps were hung from randomly-selected coffee plants in the experimental area for periods of 2 days. Traps were located at 50 cm or 150 cm height above the ground and consisted of a transparent plastic board (30 × 20 cm) coated with Tangle Foot ©(The Tangle Foot Company, Grand Rapids MI 49504 USA) similar to those used by Eberhard (1977) and Uetz et al. (1978). Six traps were used for each height. Trapped insects were preserved in 70% ethanol and identified to order in the laboratory. Body size (length and width in mm) of each insect was also recorded as the maximum distance between head and the posterior tip of the abdomen and the maximum width of the thorax.

Statistics.—Principle Component Analysis was applied to determine the factors (web and spiders characteristics) that may separate different groups of spiders inside the study area. Web characteristics, body weight, body length and abdomen width of the spiders of the different groups were compared by Kruskal-Wallis test. The relationship between abdomen width and web characteristics of all the spiders was analysed by a non-parametric Spearman rank order correlation. The size of insects trapped at each height was compared by Mann-Whitney U test, whereas the numbers of insects of each order trapped at each height were compared using contingency tables (χ^2 test). The relationship between abdomen and ovary width was subjected to linear regression analysis.

RESULTS

Analysis of web and spider characteristics.—Principal component analysis clearly identified the presence of three distinct groups of *L. venusta* webs (Fig. 1). The first group was numerous with 63 webs, the second group had 18 webs and the third group represented 19 webs (Table 1). The height of webs above the ground increased significantly from an average (± S.E.) of 54.5 ± 1.8 cm in group 1 to 153.8±3.6 cm in group 3 ($F = 363$, $d.f. = 2,97$, $P < 0.001$). In contrast, the number of spirals/web was negatively correlated with web height ($F = 5.6$, $d.f. = 2,97$, $P = 0.004$). Web diameter and the number of radii were statistically similar among the

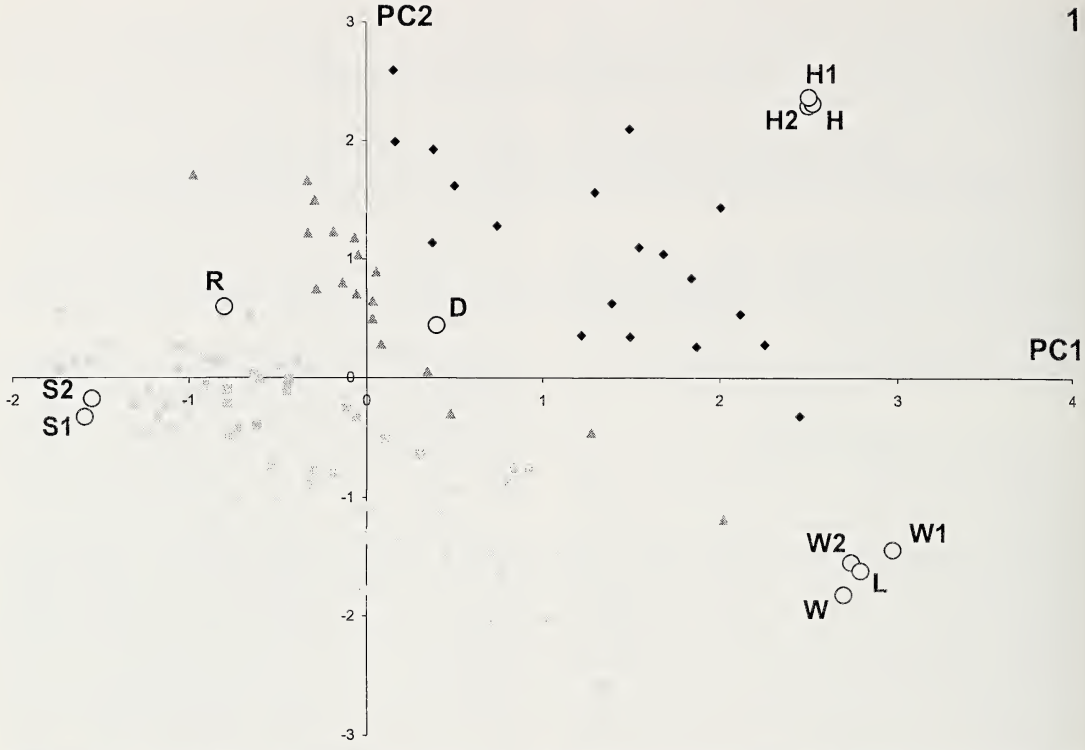

Figure 1.—Principle component analysis (n = 100) applied to the height of webs (H, H1, H2), web diameter (D), number of radii (R) per web, number of spirals (S1, S2), live weight (W1), dry weight (W2), body length (L), and abdomen width (W). We distinguished three spider groups (circles, triangles, squares). The first axis (PC1) explains 41% of the distribution and the second axis, (PC2) explains 21% of the distribution.

three groups (Table 1). The height at which the webs were located appears to be the principal factor separating the three groups; most *L venusta* webs (63/100) were close to the ground.

The characteristics of the spiders also differed between the three groups of webs (Table 2). Spiders from web groups 1 and 2 were similar in weight (13.4–13.8 mg) whereas group 3 spiders were significantly heavier with an average dry weight of 17.3 ± 1.3 mg (F = 3.45, $d.f.$ = 2, 97, P = 0.03). A similar relationship was also detected with body length (F = 3.55, $d.f.$ = 2, 97, P = 0.03) and abdomen size (F = 3.66, $d.f.$ = 2, 97, P = 0.02); group 3 spiders were larger than spiders from group 1 and group 2 webs in all respects.

Significant positive correlations were detected between *L. venusta* abdomen width and height of webs (Spearman = 0.2, $t(98)$ = 2.3, P = 0.02), and abdomen width and number of web spirals (Spearman = −0.2, $t(98)$ = −2.5, P = 0.01). The diameter of the web (Spearman = 0.07, $t(98)$ = 0.7, P = 0.5), and the number of radii (Spearman = −0.1, $t(98)$ = −1.2, P = 0.2), were not significantly correlated with abdomen width.

There was a significant positive correlation detected between abdomen size and ovary size (F =

Table 1.—Height, size and structural characteristics of three groups of *L. venusta* webs collected in Chiapas, Mexico during the rainy season of 2001. Figures represent means ± SE. *** Mann-Whitney U-test, $P < 0.001$; ns, Not significant $P > 0.05$.

	Group 1 (n = 63)	Group 2 (n = 18)	Group 3 (n = 19)	P
Height of web (cm)	54.5 ± 1.8	101 ± 2.3	153.8 ± 3.6	***
Web diameter (cm)	29.1 ± 0.6	31.8 ± 1.4	30.1 ± 1.0	ns
Number of radii	34.7 ± 0.4	35.1 ± 1.0	35.2 ± 0.9	ns
Number of spirals	52.2 ± 1.0	47.0 ± 1.9	45.7 ± 2.2	***

Table 2.—Body weight, length and abdomen width of spiders collected from the three groups. All values are means ± SE. Mann-Whitney U-test: * $P < 0.05$.

	Group 1 (n = 63)	Group 2 (n = 18)	Group 3 (n = 19)	P
Weight (mg)	13.4 ± 0.6	13.8 ± 1.2	17.3 ± 1.3	*
Body length (mm)	5.6 ± 0.7	5.58 ± 0.1	6.1 ± 0.1	*
Abdomen width (mm)	2.9 ± 0.05	2.85 ± 0.1	3.2 ± 0.09	*

22.3, $d.f.$ = 1, 12, $P < 0.001$, Pearson's correlation coefficient = 0.8); larger spiders had larger, better developed ovaries, presumably indicative of sexual maturity (Fig. 2).

Insects trapped.—Significantly more insects were captured in the traps placed at 50 cm height (n = 225) than in the traps placed at 150 cm height (n = 150) (χ^2 = 14.99, $d.f.$ = 1, $P < 0.001$). The majority of arthropods captured were Diptera (207), Hymenoptera (68) or Coleoptera (55), other arthropods found on traps included Homoptera (17), Hemiptera (2)Acari (13) and Araneae (13) (Table 3). As Diptera, Hymenoptera and Coleoptera were obviously the most common (88% of the trapped arthropods), we used these three groups for analysis.

A similar number of Hymenoptera and Coleoptera were caught on traps at 50 cm and 150 cm height (χ^2 = 2.1, $d.f.$ = 1, P = 0.1 for Hymenoptera; χ^2 = 1.4, $d.f.$ = 1, P = 0.2 for Coleoptera). In contrast, many more Diptera were caught at 50 cm than at 150 cm height (χ^2 = 5.9, $d.f.$ = 1, P = 0.01) and they were much more numerous than other insects at both 50 cm (χ^2 = 75.4, $d.f.$ = 2, $P < 0.001$) and 150 cm height (χ^2 = 53.7, $d.f.$ = 2, $P < 0.001$) (Table 3).

However, body length (U = 4165, P = 0.01) and width (U = 4210, P = 0.02) of flies trapped at 150 cm height were greater than for flies trapped at 50 cm height (Figure 3). A similar relationship was seen in hymenopterans (body length U = 373, P = 0.01; body width U = 371.5, P = 0.01). In the case of Coleoptera, body length was greater in individuals trapped at 50 cm (U = 243.5, P = 0.03) but no significant difference was detected in terms of body width (U = 350, P = 0.7) (Fig. 3).

Discussion.—The spatial distribution of the *L. venusta* population in a coffee plantation was studied in relation to different factors including web characteristics, spider maturity and prey size. It was possible to distinguish three groups of spiders in relation to the height of their webs. The majority of webs were located close to the ground (at ap-

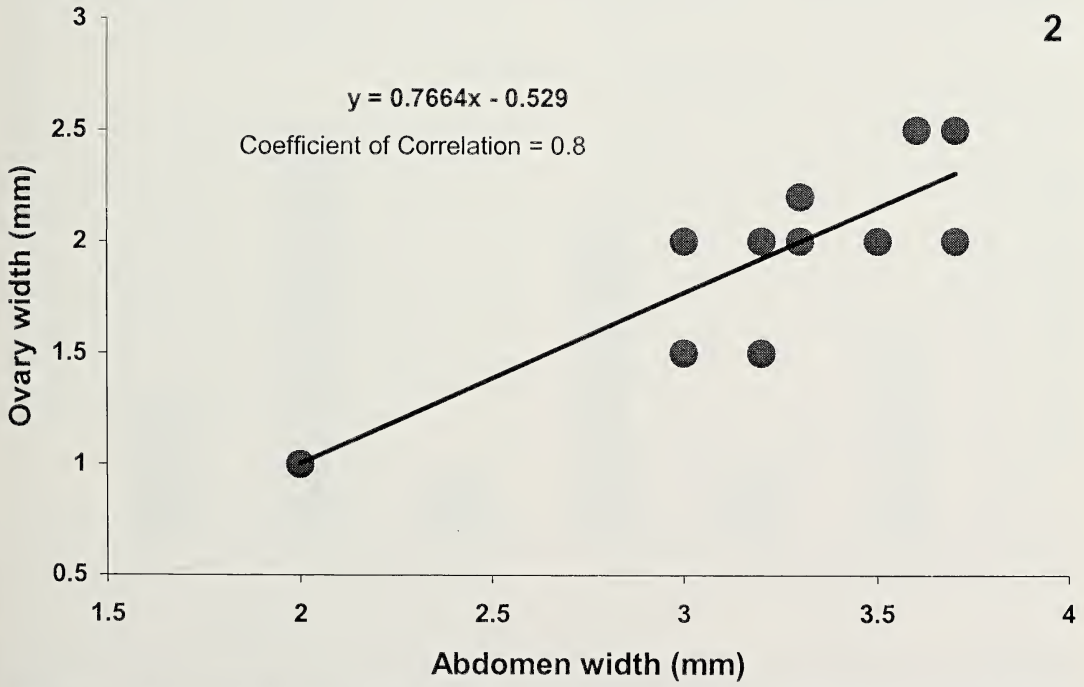

Figure 2.—Relationship between ovarian width and abdomen width ($P < 0.0001$) in *Leucauge venusta*.

Table 3.—Total number of prey trapped at two heights for the three principal groups of insects. χ^2 test: ** $P < 0.01$; *** $P < 0.001$; ns Not significant $P > 0.05$.

	50 cm height trap	150 cm height trap	*P*
Diptera	121	86	**
Hymenoptera	40	28	ns
Coleoptera	32	23	ns
Total	193	137	
P	***	***	

proximately 50 cm height), but a part of the population constructed webs at heights of ~100 cm or ~150 cm above the ground. Webs at different heights had similar diameters and number of radii but the number of spirals was reduced in webs at 150 cm height giving the webs a more open structure. Spiders occupying webs at ~150 cm were larger than conspecifics occupying lower webs. Body size was shown to be positively correlated with ovarian size in a sub-sample of these spiders.

Apparently, sexual development may influence the choice of web site. Web design may also be influenced by sexual development, or may be related to physical stresses experienced when webs are constructed high above the ground, such as air currents and movement of plant supporting structures. Traps placed at two different heights indicated that the majority of potential prey were dipterans and that more insects were captured at 50 cm than at 150 cm height. Diptera and Hymenoptera, the preferred prey of *L. venusta* (Hénaut et al. 2001), caught at 150 cm height were, however, significantly larger than those caught at 50 cm height. Chacón and Eberhard (1980) found similar results using artificial webs: smaller insects were most frequently caught in the lowest traps. Ibarra-Núñez et al. (2001) also reported that the most common insects caught in *Leucauge* spp. webs are Hymenoptera and Diptera, and that Coleoptera were not important prey items.

The web location appears related to the sexual development of the spider. Observations in the field confirmed that *L. venusta* nymphs build webs close to the ground and that immature spiders may be very abundant (Pinkus-Rendón pers.comm.). Our results suggest that young adult spiders also build webs close to the ground, but as sexual development proceeds, the spider increases the height at which the web is constructed. This vertical migration is also associated with changes in web construction and the type of prey captured, with the possible effect of reducing intraspecific competition between *L. venusta* adults and juveniles. Another possibility is that sexually maturing spiders seek the larger prey that can be caught at higher sites in and between plant canopies. In the same way, a more open web structure with a larger mesh size may be an adaptation to target the capture of larger prey, as reported in *Argiope* species (Uetz et al. 1978). Uetz and Hartsock (1987) found that webs of *Micrathena gracilis* (Walckenaer 1805) show selectiv-

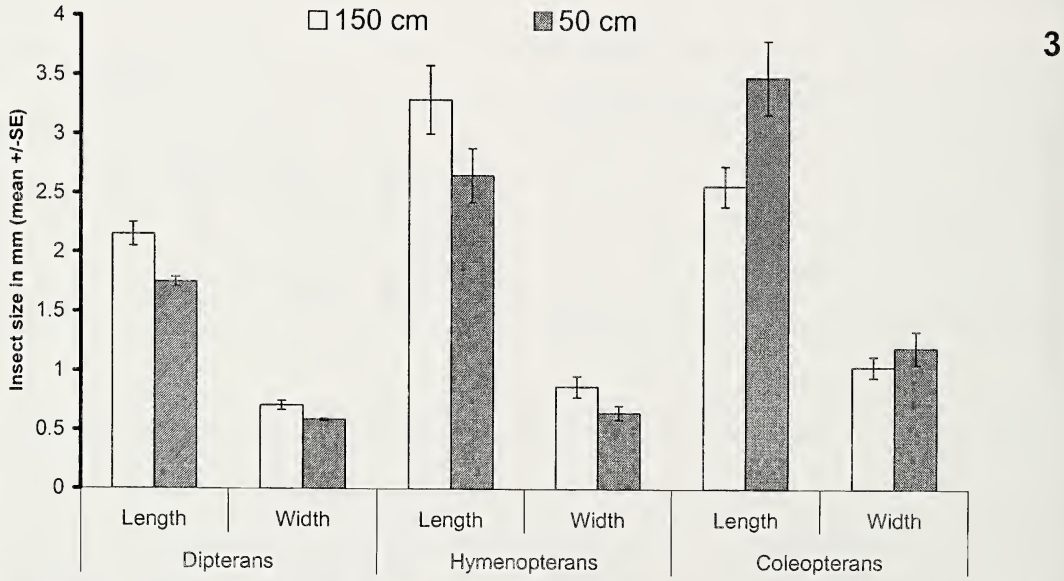

Figure 3.—Comparison of body length and width of Diptera, Hymenoptera and Coleoptera caught on sticky traps placed at 50 and 150 cm above the ground in a coffee plantation (Mean ± SE). Mann-Whitney U test: * $P < 0.05$, ** $P < 0.01$, ns Not significant $P > 0.05$.

ity for prey sized greater than 3 mm even if potential prey are smaller. The same phenomen of prey specialization may be also occur in *L. venusta* and in this case be reinforced by web relocation.

The dynamics of habitat choice in spiders are complex and difficult to analyze. Spider behavior represents a compromise between many needs during the life cycle and the choices available may often be limited (Riechert & Gillespsie 1986). Spatial distribution may be influenced by the competition for suitable web sites. Dispersal can occur on two levels, first haphazardly by ballooning on air currents followed by a controlled and active site selection (Richert 1970). This active dispersal has been described by Kronk and Riechert (1979) wherein, similar to the results of our study with *L. venusta*, the sexual maturity of females induces migration to sites in which prey are more abundant.

There are, however, alternative interpretations of these results. First, larger spiders may exclude smaller conspecifics from high locations by aggression (Danielson-François et al. 2002). Second, larger spiders that spin looser webs higher in the coffee canopy may also competitively exclude smaller spiders that construct webs with closer spirals. Third, predatory wasps may also influence the vertical distribution of spiders; larger spiders experience a significantly diminished risk of predation (Blackledge & Wenzel 2001). Finally, the vertical migration during the search for females could be a serious constraint upon male mating success in orb wearing spiders (Moya-Laraño et al. 2002). This suggests that female *L. venusta* may migrate upwards as a means of selecting especially vigorous males as mates.

In conclusion, the variability in web construction in *L. venusta* is correlated with sexual maturity and predatory opportunities perhaps dictated by the energy required for the development of eggs and reproductive activities. Constructing an open web in a site with an abundance of large prey may represent savings in terms of silk production and a reduction in intraspecific competition with immature conspecifics. These observations illustrate how web site selection may reflect physiological needs associated with spider reproduction in habitats with heterogeneous predation opportunities.

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SHORT COMMUICATION

NEST SITE FIDELITY OF *PARAPHIDIPPUS AURANTIA* (SALTICIDAE)

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ABSTRACT. We investigated the nest building behavior of *Paraphidippus aurantia* (Lucas 1833) (Salticidae) following the experimental destruction of their nests. We located 61 nests on 52 pine saplings (43 saplings with one nest, nine with two nests) and carefully displaced all spiders and destroyed their nests. On saplings with two spiders, we removed one spider. Of the 52 nests in which the resident spider was left in place, 29 new nests were constructed in the identical location as the nests we removed. Of the 9 nests in which the resident spider was removed, no new nests were constructed. There were no nests constructed in new locations. Despite other suitable nest site locations, *P. aurantia* showed extreme nest site fidelity following the disturbance.

Keywords: Nest guarding, anti-predator strategy, jumping spider, retreat

Jumping spiders (Salticidae) build small, compact nests out of silk (Richman & Jackson 1992). Adult and juvenile spiders occupy nests when they are not foraging, adult females lay eggs in nests and spiderlings may remain in nests for several days after hatching. Thus, nest sites may have a strong influence on spider success at foraging, avoiding predation and reproduction. Once constructed, nests may be destroyed by abiotic factors (e.g. rain or wind-blown vegetation) and biotic factors (e.g. grazing vertebrates or predators). While a great deal of attention has been given to spider habitat selection and site fidelity with respect to food availability (Edgar 1971; Kronk & Riechert 1979; Morse & Fritz 1982; Janetos 1986; Riechert & Gillespie 1986), relatively little is know of the responses of spiders to nest destruction.

We studied nest site fidelity of *Paraphidippus aurantia* (Lucas 1833) (Salticidae) in response to the destruction of its nest. *Paraphidippus aurantia* builds its nests at the bases of needle clusters on ponderosa pine (*Pinus ponderosa* Laws. var. *scopulorum*) sapling at the Manitou Experimental Forest (U.S.D.A. Forest Service, Rocky Mountain Experiment Station) in Woodland Park, Colorado USA (39° 06′ 02″ N, 105° 05′ 32″ W, elevation 2400 m). Voucher specimens from this work have been deposited at the Denver Museum of Nature and Science, Denver, Colorado, USA.

On 22 July 2000 and 24 July 2001 we selected 52 small ponderosa pine saplings (< 2 m) with occupied spider nests (n = 22 in 2000, n = 30 in 2001). Forty-three of these saplings had a single occupied nest, while nine saplings had two occupied nests. In the later case, the two nests were never on the same sapling branch. The 61 nests (43 saplings with one nest and nine samplings with two nests) were built on branch tips at the bases of needle clusters located at varying heights and aspects (i.e. cardinal directions) in the sapling canopies. Each sapling canopy offered many (> 20) potential nest-building sites that to our eye did not in any respects from those supporting nests. Except for occupied nests, there were no other *P. aurantia* or nests on the experimental saplings.

The weather on the days of the nest destruction was clear to partly cloudy, and it neither rained nor was it particularly windy. We coaxed the spiders from their nests using puffs of air from a rubber bulb until the spiders emerged. We waited until the spiders had traveled at least 20 cm before carefully removing all visible silk threads from the pine needles with our thumbs and forefingers. We continued to observe the displaced spiders for at least 60 seconds. The spiders typically remained motionless during nest removal and this subsequent observation period. In no instance did the spider jump from the branch or flee more than 50 cm during the time

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Table 1.—Fate of *Paraphidippus aurantia* nest sites following nest destruction.

	Spider left in place (n = 52)	Spider removed (n = 9)
No nest built	45%	100%
Nest built on original site	55%	0%
Nest built on new site	0%	0%

of our observation. For the nine saplings with two nests, we collected one of the two spiders, but removed both nests. The nest sites can thus be divided into two groups, (1) those where the occupying spider was left in place (n = 52), and (2) those where the occupying spider was collected (n = 9).

We placed flagging on the ground immediately below each nest site to mark its location. We then monitored the nest building activity on the entirety of each sapling on each of the following two days, and at three to four day intervals thereafter, for a total of 33 days in 2000 and 34 days in 2001. Because we did not mark the displaced spiders, we do not have direct evidence that the spiders observed on subsequent days were the same individuals we displaced. While we do not know the life stage or sex of the displaced spiders, we have these data on 60 spiders collected from the branches of trees surrounding the experimental saplings at the time of the experiment: 22% were adult females, 78% were juveniles, and there were no adult males (Mooney unpub. data).

Forty-two saplings had evidence of nest construction on the day following nest destruction. Thirteen of these 42 nests were abandoned by the second day, leaving 29 saplings with nest sites under active construction for two or more days. No additional nest construction began after these first two days. Furthermore, when nest construction was not initiated within these first two days, we never again observed *P. aurantia* on the saplings. In 2001 we destroyed 20 newly rebuilt nests 21 days after the first experimental destruction, and four of those nests were rebuilt a second time. Thus, in total we observed 46 instances of new nest construction following removal.

The most notable result from our study was that every new nest was constructed in precisely the same locations as destroyed nests of spiders that we had left in place (Table 1). In one particular case we observed that a nest that originally spanned several needles and a flake of bark was again constructed to incorporate the bark and needles. No nests were constructed on the nine nest sites from which we removed the spiders, and no nests were constructed elsewhere on the saplings (Table 1). While we did not mark spiders, these results provide strong, indirect evidence that the same spiders whose nests we destroyed also built the new nests; had a previously undetected spider or an immigrant spider built these new nests, some of the new nests would have been constructed on those nine sites. It is unlikely the nine nest sites of removed spiders were neglected by chance alone ($\chi^2_{(1)} = 219$, $P < 0.0001$).

Our results also show that this extreme level of nest site fidelity was not for lack of other suitable nest sites on the saplings. Nine saplings originally supported two spiders, yet the nest sites of the removed spiders were never re-used by those spiders we did not remove. In addition, to our eye there were many unused sites on each tree that were indistinguishable from those actually utilized (see above).

Paraphidippus aurantia thus showed extreme nest site fidelity, despite (1) their previous nests having been destroyed at those sites and (2) alternate, suitable nest sites apparently being available within the area the spiders would routinely travel during foraging. There are at least two possible explanations to this behavior. First, there may be some benefits to re-using a familiar nest site such as (a) more rapid nest reconstruction, (b) improved foraging surrounding the already familiar habitat of an existing nest site, or (c) improved predator avoidance in familiar habitat. Second, the benefit of switching nest sites is predicted to be lower in habitats where risk of future nest destruction is homogeneously distributed (Switzer 1993). Sources of threats from predators may be homogeneous within a sapling. For instance, birds (Gunnarrson 1993; Riechert & Hedrick 1990) and ants (Halaj et al. 1997; Eubanks 2001) are both significant predators of spiders, but there is no reason to believe their effects would vary among nest sites within a single sapling. Future work should experimentally test these hypotheses for *P. aurantia* and investigate whether similarly high nest site fidelity is exhibited by other salticids. In addition, the mechanisms by which the spider recognizes and chooses a particular site for nesting is of interest and deserves further attention.

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SHORT COMMUNICATION

A NEW *MASTOPHORA* FROM ARGENTINA AND THE MALE OF *MASTOPHORA VAQUERA* (ARANEAE, ARANEIDAE)

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ABSTRACT. A new species of the genus *Mastophora* is described from Argentina. The male of *M. vaquera* is described from Cuba.

Keywords: Taxonomy, new species, *Mastophora*

After a new revision is published, curators checking their collections often find new species belonging to the newly revised genus. Because my interest is in revisions and in adequately illustrating previously poorly described species, rather than in describing new species, I leave these to others. But the specimen of *Mastophora* Holmberg 1876, recently found from Argentina is exceptional in appearance, and I feel it should be described along with the male of *M. vaquera* Gertsch 1955, not previously known.

Mastophora adults live in trees, attached to a silken substrate, on branches or leaves sometimes on berries or leaf buds mimicking bird droppings. They have unusual predatory methods. The adults are nocturnal, and give off odors that attract specific male moths, which are caught by swinging a viscid globule on a silken thread toward the prey that has been attracted by the scent. While moths often escape from orb webs by shedding scales, the globule attaches to the moth. The animals are very difficult to find, often being located only by finding egg sacs attached to branches. Minute males are rarely found and usually have to be raised from egg sacs (Levi 2003).

The methods used are the same as those used in Levi (2003). Abbreviations: AMNH, American Museum of Natural History, New York, U.S.A.; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MNHNC, Museo Nacional de Historia Naturales, San Antonio de los Baños, Havana, Cuba; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.

TAXONOMY

Family Araneidae Simon 1895
Genus *Mastophora* Holmberg 1876
Mastophora comica new species
Figs. 1–7

Material examined.—Female holotype from Punta Indio, 35°16′S, 57°14′W, Buenos Aires Province, Argentina, 17 November 1991, M. Ramírez (MACN).

Etymology.—The specific name is an adjective referring to the clown-like appearance of the spider.

Diagnosis.—The shape, coloration (Figs. 2, 3) and the triangular plate between the slits of the posterior face of the epigynum (Fig. 6) are diagnostic and separate *M. comica* from all other species.

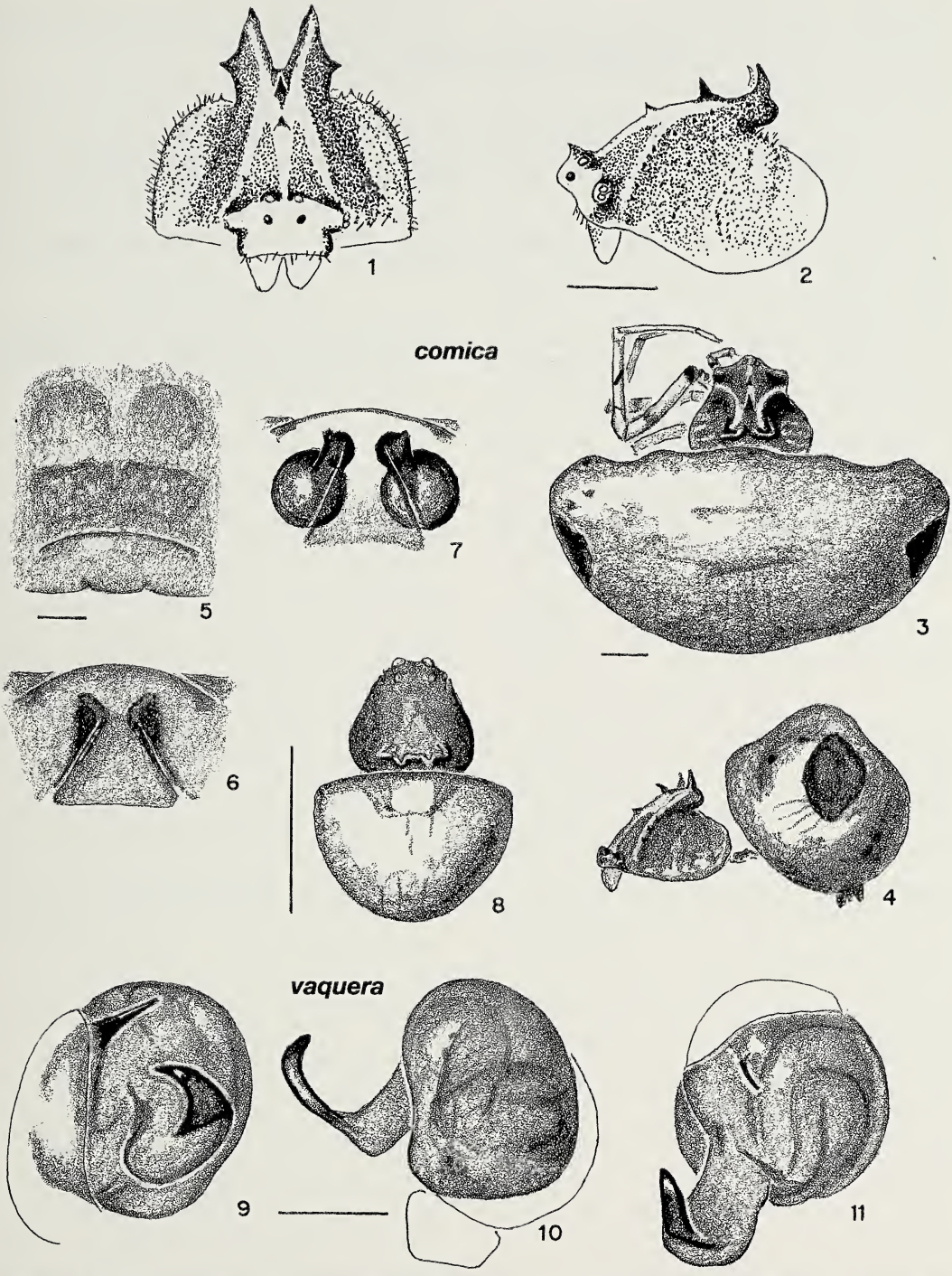
Description.—*Female holotype:* Carapace light to dark brown with three white stripes (Figs. 1–3). Chelicerae yellowish with brown mottling. Labium, endites, sternum dark brown. First coxae brown, others yellowish; legs yellowish first, second and fourth femora with proximal black ring and distal gray band; tibiae with an anterior diagonal black stripe (Fig. 3). Dorsum of abdomen with a black oval on each side and indistinct, gray patches on three anterior swellings, and some black spots (Figs. 3, 4); venter yellowish (Fig. 4). Abdomen wider than long (holotype in poor condition). Total length 7.5 mm. Carapace 3.1 mm long, 3.0 wide, 1.7 wide at constriction behind cephalic region. First femur 3.6 mm, patella and tibia 4.4, metatarsus 3.2, tarsus 0.8. Second patella and tibia 3.1mm, third 1.7, fourth 2.7.

Remarks.—The male is unknown, and no other specimens apart from the holotype have been found.

Mastophora vaquera Gertsch 1955
Figs. 8–11

Mastophora vaquera Gertsch, 1955: 240, figs. 15–18 (female holotype from Torriente, Matanzas, Cuba, in AMNH, examined); Levi, 2003: 342, figs. 142–152, 452; map 2G.

Specimens examined.—CUBA: San Antonio de los Baños, La Habana, from edge of citrus plantation, Sept. 1984, imm. ♀, adult ♂, R. Regalado (MCZ and MNHNC).



Figures 1–7.—*Mastophora comica* new species, female: 1, 2. Carapace and chelicerae: 1. Frontal; 2. Lateral; 3, 4. Carapace and abdomen: 3. Dorsal, with left legs; 4. Lateral, with chelicera; 5–7. Epigynum: 5. Ventral; 6. Posterior; 7. Posterior cleared; 8–11. *M. vaquera* Levi, male: 8. Dorsal; 9–11. Left palpus: 9. Mesal; 10. Ectal; 11. Apical. Scale bars = genitalia 0.1 mm, all others 1 mm.

Diagnosis.—As in other male *Mastophora*, the palpus shows a very large extended median apophysis (Figs. 9–11), and a small sclerotized, pointed embolus near the tip of the bulb (Figs. 9, 11). Most of the visible portion of the bulb containing the wide duct is the tegulum. *Mastophora vaquera* differs by having a heavier curl at the end of the long median apophysis than other species (Figs. 9–11).

Description.—Male (from San Antonio de los Baños, La Habana): Carapace, chelicerae, labium, endites, sternum, legs beige. Carapace with a rectangular white mark extending and covering two median tubercles and the four horns (Fig.8). Dorsum of abdomen white, anterior edge darker (Fig. 8); venter beige with two lateral gray bands that approach each other posteriorly and surround the spinnerets. Palpal patella with no macroseta. First coxa without hook. Unlike female, first femora without tubercles. Abdomen without humps. Total length 1.5 mm. Carapace 0.65 mm long, 0.61 wide, 0.41 wide behind lateral eyes. First femur 0.55 mm, patella and tibia 0.65, metatarsus 0.36, tarsus 0.23. Second patella and tibia 0.50 mm, third 0.30, fourth 0.41. Length of first patella and tibia about equal to width of carapace.

Variation: Total length of males 1.3–1.5 mm.

I thank Cristian Grismado, who found the new *Mastophora* species when sorting collections of the Museo Argentino de Ciencias Naturales and letting me describe it, Cristina Scioscia for permitting the loan of the specimen, and Giraldo Alayón for finding the male of the Cuban species. Lorna R. Levi polished the writing.

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SHORT COMMUNICATION

A REPLACEMENT NAME FOR *IRACEMA* PÉREZ-MILES 2000 (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. *Maraca* is proposed as a new name for *Iracema* Perez-Miles 2000 because it is preoccupied by *Iracema* Triques 1996 (Pisces). Two new combinations are established.

Keywords: *Iracema*, new name

The genus *Iracema* was described by Pérez-Miles (2000) for a new species of theraphosid spider from Brazil, *Iracema cabocla* Pérez-Miles 2000, unaware that the name *Iracema* had been previously used for a Neotropical freshwater fish (Triques 1996). A second species of Theraphosidae, *Paraphysa horrida* Schmidt 1994, has been attributed to *Iracema* by Bertani (2003). To remove the generic homonymy, the replacement name *Maraca* is here proposed for *Iracema* Pérez-Miles 2000 (Araneae) with two included species, *Maraca cabocla* (Pérez-Miles 2000), NEW COMBINATION, and *Maraca horrida* (Schmidt, 1994) NEW COMBINATION.

Maraca (feminine) is a noun in apposition taken from the type locality of *Maraca cabocla* ("Maracá").

I thank Cristiano Moreira, Paulo Henrique Franco Lucinda and Rogerio Bertani who advised me of this problem.

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SHORT COMMUNICATION

AN EXTREMELY LOW GENETIC DIVERGENCE ACROSS THE RANGE OF *EUSCORPIUS ITALICUS* (SCORPIONES, EUSCORPIIDAE)

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ABSTRACT. Little or no genetic divergence is detected using mitochondrial 16S rDNA sequence comparisons across the entire geographic range of the scorpion *Euscorpius italicus* (Herbst 1800) from Switzerland, Italy, Slovenia, Greece and Turkey. This is consistent with known absence of patterns of allozymes and morphological variation. *Euscorpius italicus* is found almost exclusively in human habitations. Its sister species, *E. naupliensis*, exhibits much higher genetic diversity within southern Greece. We suggest that the natural populations of the thermophilic *E. italicus* underwent a bottleneck during the glaciations, and that its modern range could be a result of dispersal with humans.

Keywords: Scorpions, genetic distance, DNA, 16S rRNA, biogeography

A large, conspicuous scorpion *Euscorpius italicus* (Herbst 1800) has been known to arachnologists for 200 years and to humankind for millennia. It is commonly found in many localities in Italy and Greece, being an especially common species in human habitations (Crucitti 1993; Braunwalder 2001). This species is found from the French Riviera to the northern and eastern shores of the Black Sea. *Euscorpius italicus* prefers a xeric microclimate (Birula 1917a, 1917b; Braunwalder 2001; Fet et al. 2001). In Italy, this species is locally very abundant and usually synanthropic. To the north of Italy it is limited by the southern Alpine valleys in Italy and Switzerland (Crucitti 1993; Braunwalder 2001); in Turkey and the Caucasus it also does not venture into high mountains (Birula 1917a, 1917b). The species' elevational preference seems to range from 0–500 m, while reported well-isolated "island" populations above 500 m could be attributed to recent human-mediated range expansion (Braunwalder & Tschudin 1997). Several subspecies were described in this species (Birula 1917a; Birula 1917b; Caporiacco 1950) but are currently not recognized (Kinzelbach 1975; Vachon 1981; Bonacina 1982; Fet & Sissom 2000)(Fig. 1). A detailed redescription and taxonomic history of *E. italicus* was recently published by Gantenbein et al. (2002), who also demonstrated the separate species status (well defined by both morphological and molecular criteria) for *E. naupliensis* (C. L. Koch 1837) from southern Greece, for many years considered a synonym of *E. italicus*.

In order to assess the species structure of *E. italicus*, we used comparative analyses of the mitochondrial 16S ribosomal RNA gene, a molecular marker that has been recently applied to resolve the species-level phylogeny of several species of *Euscorpius* (Gantenbein et al. 1999, 2000, 2001, 2002; Fet et al. 2002, 2003); for the detailed DNA analysis procedures and phylogenetic tree-building algorithms, see Gantenbein et al. (1999, 2000). Seven mtDNA sequences (ca. 400 base pairs each) were aligned using ClustalX 1.81 (Thompson et al. 1997). Two new DNA sequences, obtained for the present study, were deposited in GenBank (http://www.ncbi.nlm.nih.gov) under accession numbers: *Ei*TU1 (AY371536) Samugüney Village, Bulancak, Giresun, Turkey, 40°56′N, 38°15′E, 17 February 2003 (coll. A. Karataş), and *Ei*SM1 (AY371535) Silvi Marina, Abruzzo, Italy, 42°34′N, 14°05′E, 20 June 2000 (coll. F. Kovařík). Voucher specimens are deposited in the Unites States National Museum (USNM), Smithsonian Institution, Washington, DC, USA. Four additional DNA sequences of *E. italicus*

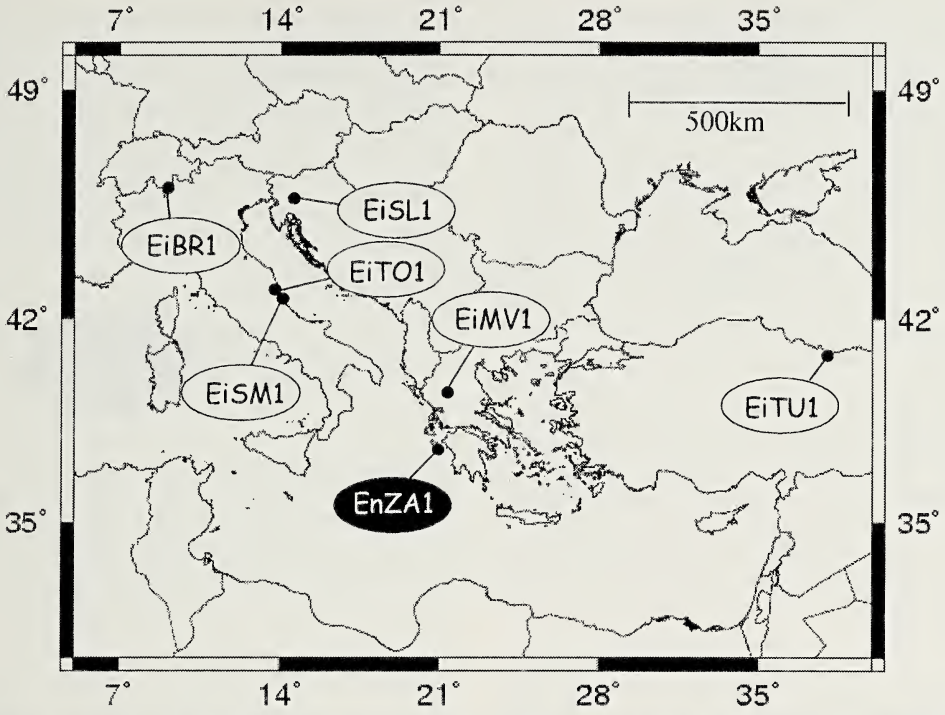

Figure 1.—Origin of population samples of *Euscorpius italicus* and *E. naupliensis* (outgroup; dark circle).

published earlier by our research group and its collaborators (Gantenbein et al. 1999, 2002) were extracted from the GenBank online database. Their abbreviations, accession numbers and geographic origin were: *Ei*BR (AJ389378), Brissago, Ticino, Switzerland, 46°07′N, 08°43′E, 25 May 1996 (coll. B. Gantenbein); *Ei*TO1 (AJ298067), Tortoreto, Abruzzo, Italy, 42°47′N, 13°55′E, 7 October 1997 (coll. M. Bellini); *Ei*MV1 (AJ506152), Metsovo, Epirus, Greece, 39°46′N, 21°10′E, 13 May 2001 (coll. V. Fet); *Ei*SL1 (AJ512752), Brje, Dobravlje, Aidovščina, Slovenia, 45°46′N, 13°50′E, 7 August 2000 (coll. B. Sket). As an outgroup, we used *E. naupliensis*: *En*ZA1 (AJ506153), Zakynthos Island, Greece, 37°46′N, 20°46′E, 20 August 1999 (coll. K. Palmer) (Gantenbein et al. 2002).

For estimation of within-species variation in species with moderate genetic variation, the application of networks and cladistic methods has been proposed to be the most efficient (Posada & Crandall 2001). Recently developed methods allow evaluation of the limits of parsimony (Templeton et al. 1992, 1995). Therefore, we calculated a statistical network that only connects haplotypes with a 95 % confidence limit using the program TCSalpha v1.01 (Clement et al. 2000). From the length of the DNA sequences we estimated the maximum number of steps that haplotypes can differ from each other for a 95% confidence limit. This statistical cladistic analysis revealed a very weak detectable geographic structure across the entire range of *E. italicus*. The statistical cladogram in Fig. 2 connects haplotypes of up to 7 mutation steps, whereas gaps are treated as the "fifth" base pair. The estimated level of divergence ranging from zero to four base pair substitutions (i.e. from 0–1.2 % uncorrected "p") is in a dramatic contrast with the elaborate, deep geographic structure detected using the same mitochondrial gene fragment in the congeneric species *E. germanus* (C.L. Koch 1837) and *E. alpha* Caporiacco 1950 (Gantenbein et al. 2000), *E. naupliensis* (C.L. Koch 1837) (Gantenbein et al. 2002), *E. tergestinus* (C.L. Koch 1837) (Fet et al. 2002), and *E. sicanus* (C.L. Koch 1837) (Fet et al. 2003); in each of the listed taxa, within-species divergences were up to 5%. The relatively poor genetic diversity of the mtDNA marker clearly supports the complete absence of nuclear variation at allozyme loci among Swiss populations of *E. italicus* (Gantenbein et al. 1998) compared with populations of other congeneric species (Gantenbein et al. 2001). The network (Fig. 2) also is consistent with the hypothesis of artificial transplantation, which is an important issue for phylogeographic studies on scorpions (Gantenbein & Largiadèr 2002). The Swiss haplotype (EiBR1) is identical with the Slovenian haplotype (EiSL1), which supports a very recent transplantation from the east into the region of

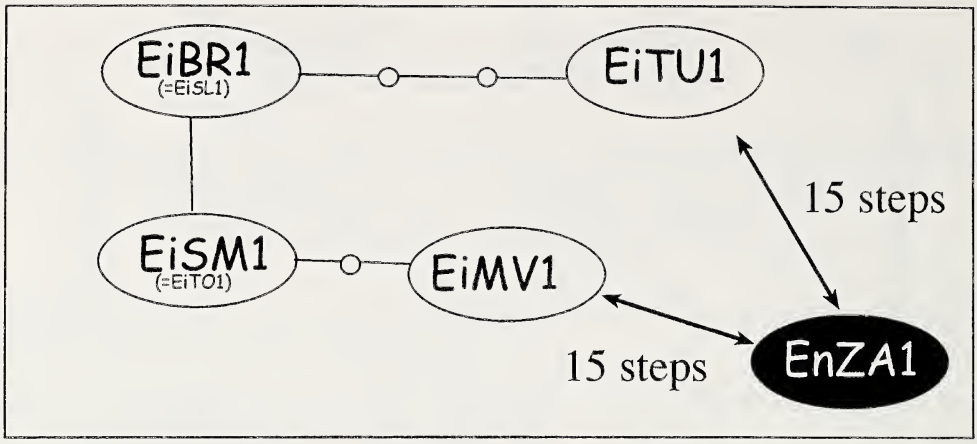

Figure 2.—Maximum Parsimony tree connecting isolated mtDNA haplotypes of a fragment of the 16S rRNA gene. Connections are exclusively drawn with a confidence limit of 95% (i.e., ≤ 7 steps) as calculated according to the method of Templeton et al. (1992). Large circles represent haplotypes; small circles represent hypothetical intermediate haplotypes that connect the haplotypes with each other. Network is not drawn proportionally to genetic distance. See text for the designation of haplotypes. Outgroup shown as a dark circle.

Northern Italy and Switzerland. On the other hand, the haplotypes from Italy (EiSM1/TO1) and from Greece (EiMV1) are each connected to each other with only a single mutational step.

Birula (1917a, 1917b) characterized in detail the geographic distribution of *E. italicus*, describing clearly two disjunct parts of the *E. italicus* range, "western" (Europe) and "eastern" (Anatolia and Caucasus). This idea still holds as the species has never been found in the eastern part of the Balkan Peninsula (Gantenbein et al. 2002). Birula (1917a, 1917b) considered the eastern part of the range (a narrow strip along the southern and eastern coasts of the Black Sea) reduced compared to the western, due either to southward increase of the Black Sea basin, or aridization of the climate in Anatolia. Morphologically, *E. italicus* from the "western" and "eastern" parts of the range are the same species (Gantenbein et al. 2002). Thus a strong case can be made for recent, even historical time, dispersal of *E. italicus* between the "western" and "eastern" portions of its range.

From the current network of sampled haplotypes one could speculate that Anatolia might have served as the refuge for *E. italicus* during the last Pleistocene glaciations. Evidence that Anatolia might have been an important refuge for plants and animals has been recently found for the gall wasp (*Andricus quercustozae*) by Rokas et al. (2003) who reported a higher within-population diversity in the Anatolian populations than in the European ones. We cannot infer any conclusions about genetic diversity of populations; for this, many more *E. italicus* populations and specimens per population need to be genotyped for the orthologous mtDNA fragment. The low genetic divergence between the haplotypes, however, supports a recent (postglacial) range expansion of this species. Similar low genetic diversity across a wide range was found in the congeneric species *E. flavicaudis*, which is not closely related to *E. italicus* (~10% sequence divergence between species; Gantenbein et al. 1999). In *E. flavicaudis*, the combined analysis of multilocus allozyme data and mtDNA sequence data also revealed a low diversity, which can be interpreted as the evidence of rapid range expansion, most likely by human transplantation (Gantenbein et al. 2001). *Euscorpius flavicaudis* is known to be an invasive species since it has been recently reported from places obviously outside its natural habitat, e.g., south of England (Benton 1991) and Uruguay (Toscano-Gadea 1998), where it manages to survive and reproduce. Hewitt (1996, 1999) lists several examples for rapid natural spreading of animals from glacial refuges into Europe, with dispersal rates of ~300 m per year and higher. Hewitt (1990) estimated that flightless grasshoppers like *Chorthippus parallelus* spread from southern Europe to England at a rate of about 300 m per year. In scorpions, however, much lower annual dispersal rates have been determined, which range between 1–30 m, males having a higher dispersal rate (Polis et al. 1985). If we assume as lower dispersal rates for scorpion species than for the flightless grasshoppers, we have to conclude that *E. italicus* and *E. flavicaudis* populations were both spread through human civilization. It is also very likely that these two species had two different glacial refuges: *E. italicus*, in Anatolia and *E. flavicaudis* probably in the south of Italy, which has been identified as a

main refuge for many other species (Taberlet et al. 1998).

Unlike other species of *Euscorpius*, *E. italicus* was never reported from any of the Aegean islands, or from any Mediterranean islands such as Baleares, Sicily, Sardinia, Corsica or Malta; it has been only recorded from the offshore islands in the Adriatic Sea (Dalmatian coast of Croatia) and Ionian Sea (Corfu, Greece) (Gantenbein et al. 2002). At the present time, this species appears to be successfully dispersing with human assistance, since in parts of its range it is almost or exclusively synanthropic, being found only in human habitations or ruins but not in the wild (Crucitti 1993). Braunwalder (2001) documented that in only 33 records out of 1,031 records in southern Switzerland, *E. italicus* has been found in decidedly natural habitats. Another sign of its probable dispersal with humans is the fact that this species, like *E. flavicaudis*, establishes new reproducing populations, often remotely disjunct from its continuous range. As examples we can mention established populations in lower Don, Russia (Zykoff 1912); in Sion, Valais, Switzerland (Braunwalder 2001); in Ljubljana, Slovenia (Fet et al. 2001); and even in Yemen (Birula 1937) and Iraq (Fet & Kovařík 2003). Records from southwestern Romania (Mehadija, Oravitza; Birula 1917a, 1917b; confirmed by Vachon 1981) probably also refer to introduced populations. Single specimens of *E. italicus* have been found in many localities well outside the main range (Fet & Gruodis 1987; Fet & Sissom 2000; Gantenbein et al. 2002). Moreover, at least within Europe, the active transplantation of *Euscorpius* with the human peddlers of "scorpion oil" (an infusion of olive oil with live scorpions, allegedly of medicinal value) has been possible until recently (Komposch et al. 2001). This frequent anthropochory and synanthropy, absence from most islands, and high morphological and genetic similarity of the studied populations from Switzerland, Italy, Slovenia, Greece and Turkey, all suggest that the dispersal of *E. italicus* (likely from glacial refugia) might not be an ancient event. Further investigation of multiple populations could determine an exact refugial origin and possible ways of dispersal of *E. italicus*.

We thank Michael E. Soleglad for his valuable insights, help, and enthusiasm in the study of *Euscorpius*. We thank Marco Bellini, František Kovařík, Kevan Palmer, and Boris Sket for providing specimens. We are grateful to Elizabeth V. Fet and W. Ian Towler for their skilled assistance in the lab. B.G. was supported with an SNF-IHP grant 83EU065528.

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SHORT COMMUNICATION

DISPERSAL BY *UMMIDIA* SPIDERLINGS (ARANEAE, CTENIZIDAE): ANCIENT ROOTS OF AERIAL WEBS AND ORIENTATION?

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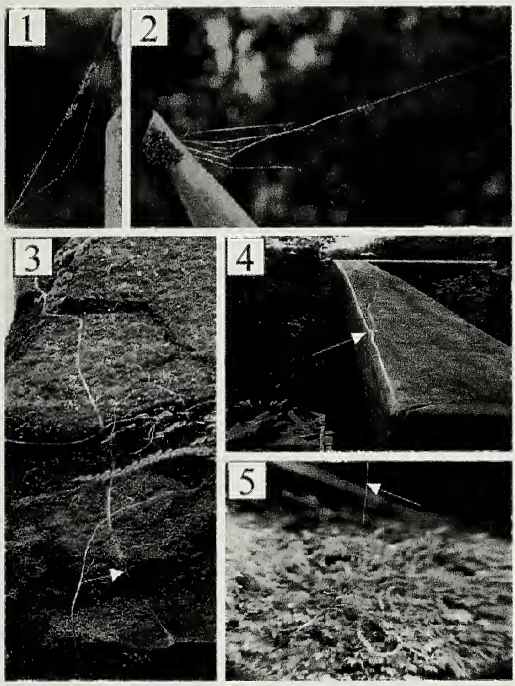
Keywords: Mygalomorph ballooning behavior, orientation

It is well known that many araneomorph spiders disperse by ballooning (e.g. Decae 1987; Suter 1999), but similar dispersal abilities of mygalomorph spiders are much less well established. Previous publications are easily summarized. The most complete observations are those of Coyle (1983, 1985) of spiderlings of *Sphodros* sp. (prob. *S. atlanticus* Gertsch & Platnick 1980) (Atypidae), and *Ummidia* sp. (Ctenizidae). Spiderlings of both species moved along bands of silk lines, and launched themselves into the air after dangling at the ends of draglines. Other descriptions of mygalomorph ballooning did not provide details on how spiders took to the air. Baerg (1928) carefully observed movements of *Ummidia carabivora* (Atkinson 1886) (originally described in the genus *Pachylomerus*) spiderlings from their mother's burrow along wide silk trails to elevated sites, but did not witness the spiders taking off. Enock (1885) saw that *Atypus piceus* (Sulzer 1776) spiderlings followed ascending silken cords to upwardly projecting objects, from which they were "blown off into midair . . . until they became attached to other sticks" (p. 394). Muma & Muma (1945) also observed silk bands produced by the spiderlings of *Sphodros rufipes* (Latrielle 1829) (= *Atypus bicolor* Lucas); they stated that the spiderlings dispersed by ballooning, but gave no details. Cutler & Guarisco (1995) observed a group of spiderlings of *S. fitchi* Gertsch & Platnick 1980 and apparent ballooning attempts at the top of a small tree. Main (1957) suggested that *Conothele malayana* (Doleschall 1859) (Ctenizidae) spiderlings balloon, but only on the basis of observing large numbers of fine threads of silk produced by spiderlings held in collecting tubes. This note reports an observation of dispersal and ballooning by spiderlings of the another ctenizid, an undetermined species of *Ummidia*.

Observations were made in San Antonio de Escazu, San José Province, Costa Rica (el. 1325 m; approximately 9° 51′ N, 84° 10′ W). Observations with the naked eye were complemented using a 2x headband magnifier. Some individual silk lines were extremely fine and difficult to see; checks for unseen lines were made by moving an object where a line might have been, and noting whether this movement produced tugs on the spider or nearby silk lines. A voucher (mature female) specimen will be deposited in the Museum of Comparative Zoology, Cambridge, MA 02138, USA.

At about 09:00 on the cool rainy season morning of 17 Oct. 2002 with only intermittent sunshine and weak, erratic wind (a very fine, weak, intermittent drizzle fell briefly at 12:30, but it did not rain until after 15:00), I noted a small ball of spiderlings at the tip of a long thin leaf growing at the edge of the deck of my house (Figs. 1, 2). A file of spiderlings toiled slowly up the edge of the leaf toward the ball. Below the ball of spiders, I traced a more or less straight trail of shiny silk downward along the edge of the leaf, across an open space of about 10 cm to the rock wall supporting the deck, and then across this irregular surface (Fig. 3) for about 70 cm to its end, the edge of the extremely well-camouflaged ctenizid burrow lid covered with green moss (Fig. 5). In places the trail ran along the surface of the wall as a wide band, about the width of a spiderling's body. In others, where it bridged cracks and spaces of up to 7 cm between rocks, it narrowed to a single thick, aerial line (Fig. 3). Spiderlings were scattered along this trail. The burrow entrance was about 10 cm above the ground, in detritus in a shallow indentation in the wall. Spiderlings were emerging one by one from under the lid, which was hinged at the top and slightly open, and climbing up along the trail. Judging by their rates of movement, they must have been emerging for at least 30 min previously. My tentative attempt to lift the lid was answered by a sharp tug that closed and held it tight, showing that the female resident was evidently holding the inner side of the lid (see Bond & Coyle 1995).

The silk trail also continued in the other direction beyond the ball. A few flimsy lines radiated from



Figures 1–5.—Dispersal by *Ummidia* sp. spiderlings. 1. aerial lines to post of railing; 2. spiderling (right) leaves a ball of spiderlings to walk along an aerial portion of the trail; 3. relatively straight silk trail followed by spiderlings across uneven rock face; where the trail was aerial, the band narrowed to a single, thick thread (arrow); 4. horizontal portion of the trail of silk along the top of the railing (arrow indicates fork where some spiders went to the right, others to the left); 5. the trail (single vertical line, arrow) ends on an adult female's burrow lid, which is camouflaged with green moss.

the tip of the leaf, forming aerial bridges to other leaves 10–20 cm away, and a longer and stronger, approximately horizontal line about 30 cm long connected the leaf tip to the post of the railing of the deck (Figs. 1, 2). From here it ran horizontally along the railing for about 6 m (Fig. 4) until it went straight up the corner of the house for about 4 m to the underside of the roof, where several thin lines bridged to the underside of the eaves. Several lines that streamed downwind from the eaves waved about in the light breeze as if their tips (which I was not sure I could see) were free; the nearest object in that direction was some 10 m away. It is possible that these were lines which had broken when the spider was several m from this takeoff site. An estimated 50–100 spiderlings were seen at different points along the trail during the next two hours, nearly all moving away from the burrow.

The spiderlings dispersed aerially, both from near the ball and from under the eaves. Most of the spiderlings in the ball dispersed in the space of 10–15 min around 10:45. No obvious change in wind strength or intensity was noted at this time, but the wind was so light that a subtle change could have gone unnoticed. The last spiderling was seen at about 11:30. In each of five cases in which I observed take-off behavior from the beginning, the spiderling first descended on a dragline that was attached to a horizontal aerial line, and then glided smoothly upward and laterally, moving in the same direction as the wind. The longest glide I was able to follow took the spider just over 5–10 m until the line it was on became entangled in a bush. Another glide, in which I lost sight of the spider when it was about 5 m above the ground, probably took the spider at least 10 m, judging by the direction in which it was moving and the closest objects in that direction.

Much of the spiderlings' behavior near the ball was apparently tentative. Spiders moved back and forth on the more or less horizontal lines, and ascended and descended vertical draglines. Most descents were followed by ascents of the same line rather than by glides. The draglines were too thin to be easily observed directly, and only occasionally, when lighting and background conditions were appropriate, did I succeed in seeing the silk as the spider descended. Nevertheless, the spider's movements (slow descent straight downward with the spider facing downward, with its legs more or less spread and moving little if at all; legs never moving as if walking along a line), left no doubt that they were descending at the tips of lines they were producing. The spinnerets were spread, at least in some cases, as the spider descended.

Spiders produced drag lines as they walked along horizontal lines. Some spiders kept their spinnerets spread as they walked, and in these cases it was clear that the spider produced at least two lines, and probably more. When the spinnerets were directed rearward, these lines apparently merged into a single thread. Coyle (1985) reported that each spiderling of *Ummidia* sp. produced a band of numerous fibers as it moved. In no case did I see a spider break and reel up a line as it walked along it (as is typical of araneoid spiders—Eberhard 1982, 1990; Griswold et al. 1998). Nor did a spiderling ever slide tarsus IV along the dragline as it emerged, or break and reel up aerial lines as it moved along them, other traits that are common in araneomorph spiders as they ascend draglines and produce spanning lines (Eberhard 1986, 1987).

I was not able to decipher with certainty how spiders initiated the horizontal aerial lines along which they walked, or the lines with which they ballooned. As in *Sphodros* and *Ummidia* (Coyle 1983, 1985), ballooning was preceded by descent on a dragline. But in no case did the spider give any sign that this dragline broke as it glided up and

away, as described in these other species (Coyle 1983, 1985). The spider's upward and lateral gliding movement was observed carefully: it was very smooth, and was not interrupted by any perceptible jerk that would be produced when a line broke. Nor did the spider move its legs as if reeling in lines, as occurs in some araneomorphs (Eberhard 1987). These details suggest that no lines were broken. It was as if the spider smoothly lengthened its dragline while being pulled by another airborne length of silk.

One long (>1 m) horizontal line was established by a ballooning spider and then used by several other spiders, supporting the idea that at least these early stages of flight during ballooning did not involve breaking the drag line. The new horizontal line ran in just the direction in which the first spider glided away several minutes previously. This line was not present before this spider glided away, because I had walked past this spot several minutes earlier and would have broken any lines there.

In a second case, a line was apparently formed by one spider during the time it hung more or less motionless at the tip of a vertical line. The spider was first observed dangling at the end of a dragline. I passed my hands through the air at its sides and between the spider and my own body without having any effect on its position, thus confirming that there were no unseen lines running from the spider or its dragline in these directions. Nevertheless, in the following minute, during which the spider remained at the tip of its dragline, a line was formed that connected the spider or the dragline near it to my body (perhaps 30 cm away): each time I moved, the spider was displaced. A minute or so later, this spider then glided smoothly away out of sight in a slightly different direction.

These observations of *Ummidia* sp. ballooning are compatible with two different hypotheses regarding the initiation of ballooning lines: the spinneret spreading idea of Blackwell (fig. 1C in Eberhard 1987); and the "second line" method (fig. 2 in Eberhard 1987). It is not clear whether my inability to confirm the third "dragline breaking" technique for initiating ballooning lines, which was proposed by Coyle (1983, 1985) for other mygalomorphs, was due to limitations in the resolution of my observations imposed by my general inability to see the lines the spiderlings were producing, to my inability to follow spiders for longer distances (perhaps they break their draglines after having moved several meters through the air), to differences between species in the process of ballooning, or to imprecisions in previous descriptions. If, as in the observations reported here, the extra ballooning lines (in addition to the dragline) were difficult to see in the *Sphodros* and *Ummidia* species observed by Coyle, his observations are consistent with both the spinneret-spreading and the second line hypotheses, as well as the dragline breaking hypothesis (F. Coyle pers. comm.). Resolution of this uncertainty will unfortunately have to await further lucky occasions when ballooning behavior by mygalomorph spiders can be observed again. Perhaps the most useful technique to employ in such a situation would be to lightly dust the lines with cornstarch or talcum powder, to make additional fine lines visible.

Several details of pre-ballooning dispersal by mygalomorphs merit comment. In both genera that have been observed, the spiderlings migrate as a group from their mother's burrow to the ballooning site, forming a strong band of silk (Baerg 1928, Fig. 3). Spiderlings of the theraphosid *Brachypelma vagans* (Ausserer 1875) also migrate in single file on the ground, perhaps also following a band of silk (Reichling 2000). Such mass movement, and the resulting formation of compact aerial silk highways, is very unusual in araneomorph spiders. I know of only one other case; the highways produced when colonies of the social theridiid *Achaearanea wau* Levi 1982 migrate (Lubin & Robinson 1982). The general pattern for dispersing araneomorphs seems to be for each spiderling to strike out on its own. Spiderlings may benefit from moving as groups; following lines established by nest mates may facilitate rapid movement to ballooning sites.

The ability (and readiness) of *Ummidia* sp. spiderlings to walk upside down along aerial cables (Figs. 1, 2) was surprising. Such dexterity in walking under aerial lines may thus be a very ancient trait, and it could have been important in facilitating the evolution of aerial webs in other groups.

How did these mygalomorph spiderlings orient? Perhaps a partial answer is related to a further remarkable detail of the highways: the trails are quite extraordinarily straight (Figs. 3, 4). Baerg (1928), who observed about 30 different trails of *U. carabivorus* ranging from 10–68 feet long, also noted that trails were "a straight line to the nearest tree of considerable size. A tree less than 6 inches in diameter is usually ignored, even if it is much nearer than some larger tree." Coyle (pers. comm.) has also seen a straight 4 m trail of *Ummidia* across a grassy lawn to the base of a small holly tree. The trail of the theraphosid *B. vagans* may also be relatively straight; the text description says it "snaked its way" along a road, but the accompanying photo shows a straight line of spiderlings (Reichling 2000). If one makes the apparently reasonable assumption that the path of a trail reflects the path followed by the first spiderlings to emerge from the maternal burrow, it seems likely that these animals must have used some sort of landmark orientation or a sun compass to maintain such straight trajectories when crossing irregular terrain, an ability documented in some araneomorphs (Görner 1973, 1986; Tongiorgi 1959). Such an ability is surprising

in spiders that probably seldom venture from their burrows once they are established, and that are generally thought to depend largely on substrate vibrations rather than visual stimuli to orient in other contexts (Coyle 1986). One possibility is that this possibly ancient orientation ability may have evolved to enable males to search more effectively for females, instead of simply wandering randomly (Bell 1991). Male *S. abboti* Walckenaer search for females during the day, and may orient visually toward tree trunks (Coyle & Shear 1981). The searching behavior of mature male mygalomorphs (and for that matter, of mature male spiders in general) seems to be little known, and would repay further study.

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SHORT COMMUNICATION

REGURGITATION AMONG PENULTIMATE JUVENILES IN THE SUBSOCIAL SPIDER *ANELOSIMUS* CF. *STUDIOSUS* (THERIDIIDAE): ARE MALES FAVORED?

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ABSTRACT. Regurgitation from adult females towards juveniles is a well known phenomenon in social spiders. However, occasional observations in *Anelosimus* cf. *studiosus* from Uruguay showed the occurrence of food transfer also between large juveniles. We experimentally tested if well fed penultimate females were capable of regurgitating fluids to starved males, and if well fed penultimate males were capable of regurgitating fluids to starved females. Other isolated and starved penultimate males and females were used as controls. Starved males and females of the experimental groups significantly increased their body weight, whereas body weight decreased in controls. Males increased their weight more than females. We conclude that both well fed penultimate males and females can feed other starved subadults, but when given access to members of the opposite sex, males benefit than females. This bias in the regurgitation exchange among subadults could contribute to accelerate the maturation of males.

Keywords: Social spider, inter-juvenile regurgitation, *Anelosimus* cf. *studiosus*, Uruguay

Although some solitary species feed their spiderlings by regurgitation, this maternal behavior is considered the first step in the subsocial pathway to social life in spiders (Foelix 1996). Sociality evolved in a few families of spiders in which the juveniles depend on maternal regurgitation feeding (Kullmann 1972; Brach 1977; Buskirk 1981; Darchen & Delage-Darchen 1986; Foelix 1996). This phenomenon has been frequently described in the theridiid genus *Anelosimus* (Brach 1977; Christenson 1984; Vasconcellos-Neto et al. 1995), which contains both "non-territorial, permanent-social" species such as *A. eximius* Keyserling 1884, and "non-territorial, periodic-social" species such as *A. studiosus* (Hentz 1850), following Avilés (1997). However, inter-juvenile regurgitation in spiders has yet to be described. In laboratory conditions, we observed regurgitation from penultimate females to soliciting penultimate males in the subsocial *Anelosimus* cf. *studiosus* (reported in an abstract, Viera et al. 2001). In this paper, we indirectly tested the food transfer and sexual bias among penultimate juveniles by weighing individuals before and after they had access to well fed individuals. This analysis demonstrates an additional means of cooperation among spiders.

Anelosimus cf. *studiosus*, taxonomically close to *Anelosimus studiosus* (Agnarsson pers. comm.) were collected as subadults in Montevideo, Uruguay (34°53′15″S, 56°08′33″W) during June 2001, from several nests located in low branches of a single tree. In the laboratory, they were reared in social groups (mixed from different nests) in large petri dishes (8.7 cm diameter and 1.4 cm height), until they reached the penultimate stage. They were fed various fly species (*Musca* sp. and *Drosophila* spp.) ad libitum.

Penultimate individuals were recognized by size and secondary sexual characters. For the experiment, spiders were confined in small petri dishes 3 cm diameter and 1 cm height, without water, and were weighed before the experiment and 24 h later at the end of the experiment. A scale of 0.1 mg of accuracy was used. For the experiments, one spider per dish was deprived of food for 6 days (starved spider). Four experimental groups were carried out simultaneously. In group A (n = 80), a starved penultimate male was maintained with four satiated penultimate females. In group B (n = 40), a starved penultimate female was maintained with four satiated penultimate males. In group C (n = 20), a single starved penultimate male was maintained isolated, as a control for group A. In group D (n = 20), a single starved penultimate female was maintained isolated, as a control for group B. When one or more individuals molted or died during the ex-

Table 1.—Spider weights in the four experimental groups (in mg) after a 24 hour period. Only starved individuals from groups A and B were weighed. Mean weight changes were calculated from the individual differences for each group; relative weight changes were calculated in relation to the initial weight.

Experimental groups	N	Initial weight Mean ± SD	Final weight Mean ± SD	Weight changes Mean ± SD	Relative weight changes (%) Mean ± SD
Group A	63	2.314 ± 0.439	2.451 ± 0.438	0.135 ± 0.118	6.164 ± 5.314
Group B	34	2.597 ± 0.521	2.682 ± 0.527	0.085 ± 0.110	3.505 ± 4.865
Group C	20	2.585 ± 0.574	2.540 ± 0.529	−0.045 ± 0.110	−1.392 ± 4.357
Group D	20	2.720 ± 0.884	2.690 ± 0.895	−0.030 ± 0.130	−1.198 ± 5.484

periment, that trial was discarded. Room temperature during the period of study averaged 18.7 °C (± 2.5 SD; range 13.5–23.0). The non-paired Student *t*-test was used to compare difference in weight gain between groups. Voucher specimens were deposited in the Arachnological collection of the Faculty of Sciences, Montevideo, Uruguay.

Starved individuals of groups A and B increased their weight, whereas the weight decreased in the control groups C and D (Table 1). Mean weights changes showed statistically significant differences between males from groups A and C ($t = 6.39$, $P < 0.001$); between females from groups B and D ($t = 3.32$, $P < 0.01$); and between males from group A and females from group B ($t = 2.49$, $P < 0.02$); but not between the control groups ($t = 0.39$, $P > 0.60$). We estimated the mean weight of these regurgitations by adding the daily mean loss of weight per spider (caused by metabolic expenditure, defecation, water loss, silk generation) of the groups C and D plus the mean increment in weight observed in the starved spiders in A and B. Then, we estimated the weight of the regurgitations received by penultimate males of group A as 0.180 mg, which represents the 7.73 % of their initial weight, whereas females from group B gained 0.115 mg, representing 4.42 % of their initial weight.

The increment of body weight in starved penultimate males and females can only be attributed to the transfer of food from well fed conspecifics, because no other significant source of weight gain, food or water, was available in the experimental petri dishes. These gains in weight seem to be important, taking into account that they occur in only a 24 h period. The increment in group A, where one male was with 4 well fed females, was greater compared to B, where one female was with 4 well fed males in agreement with previous observations. Penultimate females could be better "donors" of regurgitations than penultimate males, or that males could be better "beggars" than the females.

We conclude that immature *A.* cf. *studiosus*, at least in the penultimate stage, share food among juveniles helping the starving individuals of both sexes, and equalizing the food distribution in the colony. Regurgitation among juveniles could have an important role in the colony, because generally, the mother dies when juveniles are at the fourth or fifth stage (Viera et al. 2002; Viera et al. submitted). Food transfer in the field could be especially significant for males, considering that they received more food than females in this experiment and in the field, there are two females per male in this species (Viera et al. 2001; Viera et al. submitted). Regurgitation from subadult females could have an important role in determining the early maturation of males observed in this and other *Anelosimus* species, possibly reducing inbreeding (Viera et al. 2001; Bukowski & Avilés 2002). Furthermore, it could also provide competitive advantages for mating, as was pointed out by Henschel et al. (1995) and Schneider & Lubin (1997) for *Stegodyphus* spp. (Eresidae).

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SHORT COMMUNICATION

ACTIVITY OF JUVENILE TARANTULAS IN AND AROUND THE MATERNAL BURROW

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ABSTRACT. Despite their notoriety, little is known about tarantulas in their natural environment. Here we describe activity of juvenile tarantulas (*Brachypelma vagans*) in and around the maternal burrow as well as emergence and dispersal behavior. Juveniles remain within the natal burrow for several weeks and undergo at least one molt after emerging from the egg sac. Small numbers of juveniles are active at night and emerge along with the adult female where they remain close to the entrance of the burrow. Most juvenile activity outside the burrowed occurred in the early morning shortly after sunrise when the female was no longer active or visible at the burrow entrance. We also observed juveniles dispersing en masse from the maternal burrow. Spiderlings moved away from the burrow in lines, following one behind each other.

Keywords: Juvenile dispersal, natal burrow, tarantulas

Cooperation and coordinated movement and activities are common behaviors among social spiders (see reviews in D'Andrea 1987; Avilés 1997; Uetz & Hieber 1997). However, these types of behaviors have also been observed in solitary spiders which, during early developmental stages, often undergo a brief gregarious phase (Gundermann et al. 1986; Horel et al., 1996; Reichling 2000, 2003; Jeanson et al. 2004). Here we report on activities and behaviors of juvenile tarantulas, *Brachypelma vagans* (Ausserer 1875) still living in the maternal burrow and also describe their unique aggregative dispersal (see also Reichling 2000, 2003).

Study site.—Our field site was located on a private dairy ranch in Puebla, Mexico, 0.8 miles west the town Venustiano Carranza. At this site in May 2003, we monitored 117 tarantula burrows in the mowed lawn (approximately 0.5 hectares) immediately surrounding the family ranch house. We conducted field observations as part of an ongoing study of the life history of tarantulas. Females with egg sacs were observed in mid-April (pers. Comm.), and on 16 May 2003, we found juveniles still within the natal burrows along with the female (n = 6). These burrows were closely monitored for a two week period. All observations were made from approximately 50 cm from the burrow entrance and substrate vibrations caused by our movements were kept at a minimum to avoid disturbing the animals. If tarantulas were startled they quickly retreated into their burrows but typically reappeared within 5–10 minutes if there were no further disturbances. The majority of observations were performed using a red flashlight but white light was sometimes used briefly for greater clarity.

Females were visible within their burrows soon after sunset (~ 8:02pm). As sit-and-wait predators, they remained around the burrow entrance for most of the night and were often motionless for more than an hour at a time. In a typical "waiting posture" females positioned themselves halfway out of the burrow with their legs on the 1–2 cm silk collar around the entrance (Fig. 1) (see also Minch 1978). Juveniles appeared at the burrow entrance at least 30 minutes after the female's nightly emergence. During nocturnal observations, the maximum number of juveniles visible was 15. They always emerged from the burrow on the side that was not occupied by the female (Fig. 1). Although they actively moved around and often climbed over each other, there was little physical contact with the female. Juveniles were active throughout the night and constantly changed positions on the silk collar and/or moved in and out of the burrow. They were approximately 6 mm in length (including legs) and, unless they were moving, were sometimes difficult to see in the vegetation surrounding the burrow. Because of the constant movement in and out of the burrow, we could not determine if the same individuals were active throughout the night. In addition, because of their small size and the low light conditions, it was not possible to determine if they

Figure 3.—Exoskeletons from juveniles around the entrance of the natal burrow. White arrows indicate some of the individual exoskeletons.

were actively involved in prey capture although we assumed this was the purpose of their emergence from the burrow.

Females often remained at the burrow entrance throughout the night and retreated into their burrows around sunrise (7:05 am) and were not visible during daylight hours. The end of the nocturnal foraging period was signaled when the female started laying a thin silk covering over the burrow entrance. Surprisingly, juveniles often remained active and visible for up to one hour after the female had retreated. They were able to move easily through the web covering laid by the female over the burrow entrance and during these times we observed as many as 64 individuals around the burrow entrance (Fig. 2). We suggest that the presence of the female may limit juvenile activity at night. The silk network around the burrow provides an important chemotactic cue for orientation (Minch 1978) and juveniles probably remain in contact with this network at all times. When the female forages at night, she occupies a substantial portion of the silk collar so less area is available for juvenile activity.

Dispersal of juveniles.—Dispersal of juveniles was observed from only one of the six burrows. On 24 May 2004, the female emerged shortly after sunset and removed the silk covering from the burrow entrance. She remained inside the burrow with her first pair of legs and pedipalps at the burrow lip. However, at approximately 8:30 pm she disappeared into the burrow and many juveniles suddenly started to emerge. Although we were unable to count individuals because of the large numbers we estimated that there were > 100 juveniles. Although clutch sizes for *B. vagans* have not been reported, it is not unusual for tarantulas to produce more than 100 offspring in a single egg sac (see summary in Punzo & Henderson 1999). Because of the large number of individuals, many juveniles moved off the web collar lining the burrow but they remained around the burrow entrance. Within a few minutes of this mass emergence, individuals started to move

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Figure 1.—Female and juvenile tarantulas at the burrow entrance. The double-headed arrow indicates the silk collar and the three single-headed arrows point to three of the spiderlings around the burrow.

Figure 2.—Juveniles around the natal burrow after sunrise. Note the thin silk strands across the burrow entrance.

Figure 4.—Female burrow with egg sac at entrance. The egg sac was discarded from the burrow after all juveniles had dispersed.

away from the burrow, starting with the individuals at the outer edge. Instead of dispersing randomly in all directions, juveniles left the burrow in three lines, following one behind each other. Similar lines of juvenile *B. vagans* have been observed in Belize (Reichling 2000, 2003). We followed the longest line which initially had 52 individuals in a single column. There was no discernable silk trail but juveniles closely followed the path of the individuals ahead of them. At a distance of over 3 meters from the burrow, the line suddenly forked. This started when a single individual left the main column and headed in a different direction. At random intervals, other individuals also left the main column and instead followed the new path. At this point, we continued to follow the longest column of individuals and used flags to indicate the path that they traveled. Over a 2.5 hour period, several additional "forks" occurred and the number of individuals in the observed column was eventually reduced to three. Because of their small size, these individuals were quickly lost in the grass. The distance traveled by these three individuals while we were following them was 14.3m, however; the maximum distance from the maternal burrow was 9m. Over the 2.5 hour period, the path curved around and seldom followed a straight-line direction away from the natal burrow. There did not appear to be any specific directionality to the movement nor was it influenced by the slope of the terrain. Instead "leaders" appeared to choose the easiest path through the vegetation.

The next morning (25 May 2003) we observed many juvenile exoskeletons around the natal burrow (Fig. 3). Presumably, the female had discarded them from the burrow although we did not observe this behavior. The small exoskeletons were only visible around the burrow entrance for approximately one day. Because of their light weight, we assumed they were dispersed by air currents or crushed by the female's movements around the entrance within a very short period of time. Later that same evening, we observed seven additional juveniles emerging from the burrow soon after sunset. Their behavior was similar to that of their siblings the night before. They sat around the lip of the burrow for only a few minutes and then started to move away. Interestingly, they started along the same path as the column we had followed the previous night which suggests they were able to detect a chemical or tactile cue laid down by their siblings.

Finally, on the morning of 26 May 2003, we observed the egg sac at the entrance to the female's burrow (Fig. 4). After removing the egg sac from the burrow, we did not see any other juveniles in or around the burrow although juveniles were still present at the other five burrows. Unfortunately we did not observe emergence and dispersal of juve-

niles from the other burrows although by the end of May 2003, juveniles had disappeared from two additional burrows.

The emergence and dispersal from the natal burrow occurs very suddenly and from our observations we were unable to predict when these behaviors would occur. More information is needed to better understand and explain the gregarious phase in these typically solitary animals and to identify the mechanisms underlying this type of collective dispersal. As suggested by Reichling (2000) these behaviors may explain aggregations of tarantula burrows in their natural environment and may allow spiderlings to cluster in a more favorable environment (Jeanson et al. 2004).

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SHORT COMMUNICATION

TYPES OF SHELTER SITES USED BY THE GIANT WHIPSCORPION *MASTIGOPROCTUS GIGANTEUS* (ARACHNIDA, UROPYGI) IN A HABITAT CHARACTERIZED BY HARD ADOBE SOILS

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ABSTRACT. Shelter site selection by *Mastigoproctus giganteus* in an atypical microhabitat in the northern Chihuahuan Desert characterized by hard adobe soils is described for the first time. The majority of the 321 whipscorpions (70.4%) were found within rock crevices during periods of highest daytime ambient temperatures, as compared to those found under plant debris (4.4%) or inside small mammal holes (25.2%). The percentage of available crevices, holes or plant debris that were occupied by whipscorpions was 41.5, 3.8 and 7.3%, respectively. Most occupied crevices (66.7%) were in the shade. Depths of occupied crevices ranged from 6.4–36.7 cm. Crevice widths ranged from 0.7–2.9 cm. Whipscorpions used crevices whose height above the surface of the ground ranged from 6.5 cm–1.1 m. No whipscorpions were observed at the ground surface, even in shaded areas, between 0645 and 1910 hr (CST).

Keywords: Retreat, rock crevices

Whipscorpions (Arachnida, Uropygi) are found worldwide, from southeastern Asia, Indonesia, Australia, New Zealand, India, the whole of Africa and Europe, as well as North and South America (Pocock 1895; Haupt 2000). The posterior 3 pairs of legs are used for walking whereas the anterior pair are modified as sensory organs which allow then to detect and respond to chemical and tactile stimuli (Geethabali & Moro 1988). Thelyphonids possess an attenuated, multi-segmented tail, and typically have median and lateral eyes (Shultz 1990).

The genus *Mastigoproctus* (Arachnida, Uropygi, Thelyphonidae), with 14 species, occurs in Cuba, the Antilles, Mexico, southern regions of the United States, and South America (Haupt 2000). Depending on the species, these arachnids typically inhabit mesic habitats and can be found beneath logs, leaf litter, and within burrows (Cloudsley-Thompson 1991). Some species have adapted to xeric conditions and can be found in more arid woodlands and forests in Columbia, Brazil, and desert regions in Mexico and North America (Rowland & Cooke 1973). These arachnids are well known for their ability to spray defensive, vinegar-like secretions from their pygidial glands (Schmidt et al. 2000).

The giant whipscorpion *Mastigoproctus giganteus* (Lucas 1835) is a common representative of the arachnid fauna of the northern Chihuahuan Desert (Punzo 2001). It is a nocturnal predator that feeds on a wide variety of arthropod prey (Punzo 2000a). It typically seeks shelter during daylight hours beneath surface plant debris, in shallow burrows, or within rock crevices (Punzo 2000b). In Big Bend National Park (BBNP), located in the Big Bend region of far west Texas (Brewster County; northern region of the Chihuahuan Desert), *M. giganteus* is most commonly found in microhabitats associated with sand-loam soils characterized by soil hardness values ranging from 7.2–8.3 kg/cm^2, and least likely to be found in areas where hard, adobe soils predominate (penetrometer readings: 37–41 kg/cm^2; Punzo 2000a, 2001).

Burro Mesa (31°47′N, 103°18′W; elevation: 870–917 m) is located in the west-central region of the Park (Maxwell et al. 1967). Although this site is characterized by hard, adobe soils (38–40 kg/cm^2) and an abundance of rocks and small boulders, *M. giganteus* does occur at this location (Punzo 2001). Because plant surface debris is sparse at this site, nymphs and adults of *M. giganteus* typically seek shelter from harsh summer daytime temperatures within rock crevices. The purpose of this study was to identify types of shelter sites and analyze specific physical features of rock crevices used by *M. giganteus*.

The study sites consisted of three 30 m transects chosen at random within a 1.0 km radius of Burro Mesa. Whipscorpions were hand-collected (between the hours of 1200 and 1500 hr) during June and July of 2002 by walking slowly through the

area during daylight hours. This time period is characterized by the highest ambient temperatures at this site (36.9–41.2 °C). For each animal collected I recorded total body length, the air temperature (held 1 cm above substrate where animal was initially observed), and type of shelter site where it was found.

Rock crevices were inspected using a high-intensity fiber optic illuminator (Model ER-59–2242, Wards, Rochester, NY). This provided adequate illumination of the deepest crevices. When an animal was observed within a crevice, a 1m wooden ruler was slowly inserted into the crevice until its tip touched the animal in question, and the distance from the crevice opening to the animal was recorded. In order to determine the species encountered the animal was then gently prodded to the surface using a plastic rod, 75 cm in length.

I also recorded the following measurements associated with rock crevices occupied by *M. giganteus*: (1) depth of the crevice; (2) width of the crevice; (3) height of the crevice from the ground and (4) whether the occupied crevice was found in the shade, open sun or sun-shade mosaic. Additionally, I counted the number of crevices and other potential shelter sites (plant debris, occupied and abandoned mammal burrows) within the transects, and searched under plant debris and within burrows for the presence of whipscorpions. Burrows ranged in depth from 12–48 cm. Voucher specimens (SR-67815–67821) have been deposited in the Invertebrate Collections at Sul Ross State University (Alpine, TX), and at the University of Tampa.

Mean monthly air temperatures (1200 CST) at study sites were 37.8 °C ± 0.14 SE (June) and 38.7 °C ± 0.08 (July). A total of 456 whipscorpions were found. Thirty-nine of these were tritonymphs (8.5%) ranging in body length from 35–40 mm; 231 (50.7%) were adult males (44–52 mm); and 186 (40.8%) were females (48–57 mm). No proto- or deutonymphs were found.

The majority of whipscorpions were found within rock crevices (n = 321; 70.4%; 26 nymphs, 152 males, 143 females) as compared with those found under surface plant debris (n = 20; 4.4%; 3 nymphs, 12 males, 5 females) and within holes in the ground (n = 115; 25.2%; 29 nymphs, 39 males, 47 females) (Chi square: X^2 = 46.73, $P < 0.05$). Along transects there were 773 crevices, 1564 holes and 516 clumps of plant debris. The percentage of available crevices, holes or plant debris that were occupied by whipscorpions was 41.5, 3.8 and 7.3%, respectively. The most common plant debris sheltering whipscorpions were fallen leaves or stems of lechuguilla (*Agave lechuguilla*), sotol (*Dasylirion leiophyllum*), blind prickly pear (*Opuntia rufida*), and rat-tail cactus (*Coryphantha pottsii*). Holes ranged from 8–37 cm in depth.

All whipscorpions found within crevices, burrows or under plant debris were alone and those found in rock crevices had their entire bodies within the crevice. Most of the crevices with animals were in the shade (66.7% or 201 out of 301), as compared to crevices with animals in sun-shade mozaic (20.9% or 63 out of 301) and open sun (12.2% or 37 out of 301).

Depths of crevices occupied by whipscorpions ranged from 6.4–36.7 cm (mean: 18.23 ± 5.41 SE). Width of crevices ranged from 0.7–2.9 cm (mean: 1.64 ± 0.44 SE). Whipscorpions used cracks in surface rocks whose height above the surface of the ground ranged from 6.5 cm–1.1 m (mean: 11.32cm ± 2.58 SE).

These results show that individuals of *M. giganteus* prefer to use rock crevices at these study sites, where hard adobe soils predominate, even though there are over twice the number of holes present. Out of 1564 holes that were located, only 115 (3.8%) contained a whipscorpion. Most of the holes examined were occupied by rodents (n = 863; 55.1%) or shrews (n = 121; 7.7%) which indicates that small mammals are capable of excavating burrows, even in the presence of hard soils. *Mastigoproctus giganteus*, in contrast, may not only lack this ability, but may avoid burrows occupied by small mammals such as grasshopper mice, deer mice and shrews, animals known to include arthropods in their diets (Schmidly 1977; Punzo 2003).

Previous studies on the efficacy of different types of shelter sites to protect desert arthropods from high daytime summer temperatures have indicated that ambient temperatures immediately below plant debris are typically higher than those associated with crevices and burrows (Cloudsley-Thompson 1975; Crawford 1981). Thus, during periods of highest ambient temperature, seeking refuge under plant debris may not allow ectotherms to adjust body temperatures within the preferred range (Punzo 2000b). This may explain why only a small percentage of whipscorpions (4.4%) were found under plant debris at Burro Mesa. This appears to apply to other large arthropods as well. Out of 516 clumps of plant debris, only 11 (2.1%) were occupied by scorpions (Vaejovidae), 8 (1.5%) by solifugids (Eremobatidae), 7 (1.3%) by wolf spiders (Lycosidae), 6 (1.1%) by male tarantulas (Theraphosidae), and 9 (1.7%) by centipedes (Scolopendromorpha).

No whipscorpions were found at the ground surface, even in shaded areas, between 0645 and 1910 hr (CST). This is in agreement with the nocturnal activity patterns reported for *M. giganteus* at other sites within BBNP (Punzo 2000a) as well as other desert areas (Cloudsley-Thompson 1991). The only arthropods regularly observed actively moving over the ground surface between 1200 and 1500 hr were harvester ants (Formicidae: *Pogonomyrmex* spp.), velvet ants (Mutillidae: *Dasymutilla* spp.), and the desert millipede (*Orthoporous ornatus*).

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SHORT COMMUNICATION

FIRST CASE OF MATERNAL CARE IN THE FAMILY CRANAIDAE (OPILIONES, LANIATORES)

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ABSTRACT. In this paper, we provide the first observations of maternal care for the harvestman family Cranaidae. Adult females of two species, *Santinezia serratobialis* Roewer 1932, which belongs to the group curvipes, and *Santinezia* sp., which is probably a new species of the group gigantea, were found in association with egg clutches. Since the microhabitats used for oviposition by these species are very similar, we believe that maternal care may be a synapomorphic trait of the genus *Santinezia*.

Keywords: Evolution, Gonyleptoidea, *Santinezia*, subsocial behavior

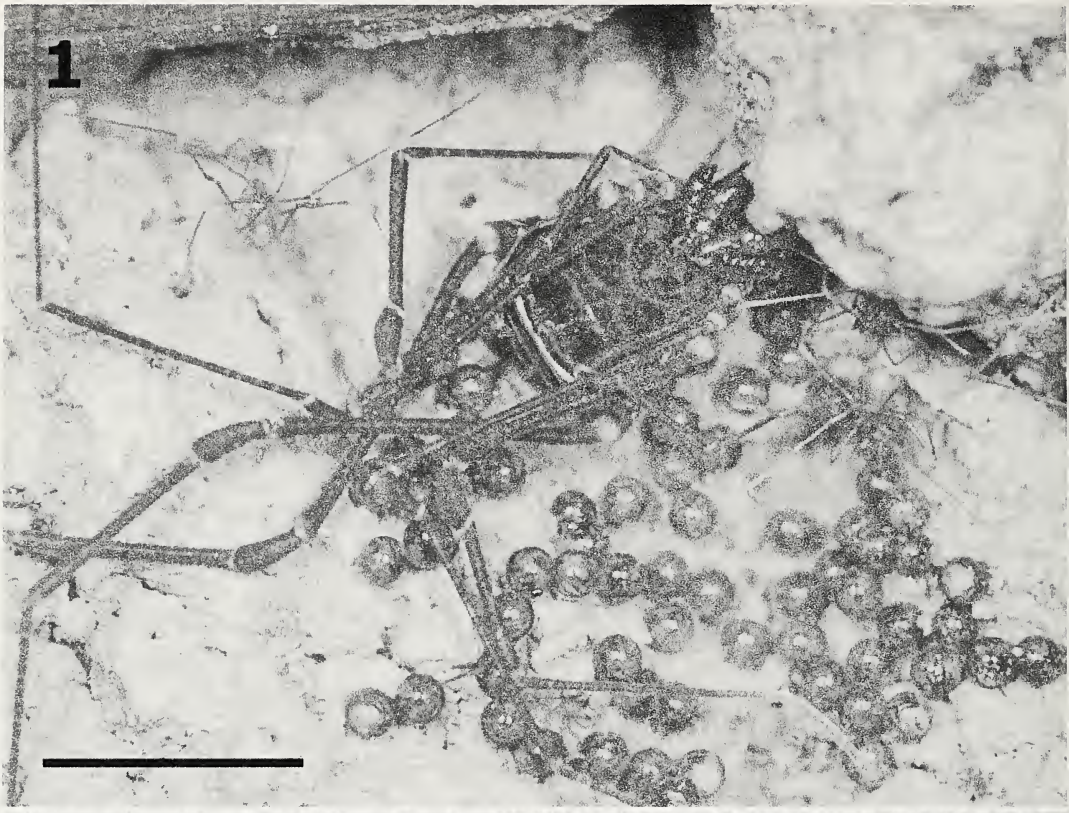
The Cranaidae comprises 75 genera and 143 species of large-bodied harvestmen (Kury 2003). The family is distributed in the northern region of South America, along the Andes and Amazon Basin up to Panama and Venezuela (Pinto-da-Rocha & Kury 2003). So far, there is no information on the biology of the cranaids, perhaps because they occur in a biome where few studies on harvestmen have been done (but see Friebe & Adis 1983). In this paper, we provide the first behavioral data for the family, describing maternal care in two species, namely *Santinezia serratobialis* Roewer 1932 and *Santinezia* sp., which probably is a new species.

Two females of *S. serratobialis* were found caring for offspring during a field trip to Trinidad, conducted in July 1999 by the second author. Observations were made at two sites, Mount St. Benedict (10°39′N; 61°14′W) and Paria Springs (10°46′N; 61°14′W). The Mount St. Benedict site is located 10 km northeast of the capital Port of Spain, and field observations were done in a small forest fragment. The Paria Springs site is located near the village of Brasso Seco, in the northern coastal mountains of Trinidad, and field observations were made along an isolated road cut. The batches were photographed in the field so that it was possible to count the number of eggs in the laboratory and also to identify the harvestmen.

Only two cranaids are known to occur in Trinidad and Tobago (cf. Kury 2003): *Santinezia serratotibialis*, which is one of the most common harvestmen species on the island (R. Pinto-da-Rocha pers. comm.), and *Phareicranaus calcariferus* (Simon 1879), which was described from Colombia but was also recorded for the Tucker Valley, nearly 15 km south of Port of Spain (Goodnight & Goodnight 1974). Comparisons between our photos and individuals of the former species collected in Trinidad and deposited in the Museu de Zoologia da Universidade de São Paulo, Brazil, allowed us to identify the guarding females as *S. serratotibialis*. However, since the individuals were not collected, there are no voucher specimens.

Individuals of *S. serratotibialis* at Mount St. Benedict site were found at the bottom of a small ravine, a short distance off a trail inside the forest. One female was observed resting on 38 white, recently laid eggs within a small sheltered damp pocket, high up on a steep overhanging embankment. These eggs were very large compared to the guarding female, with diameters ranging from 23–26% of the dorsal scutum length of the female. At Paria Springs, another guarding female was found near the bottom of a small creek bed within a small damp pocket among tree roots exposed on the steep slope (Fig. 1). There were 70 dark eggs and three early-hatched nymphs (Fig. 1). Both females were found in a stereotyped position, similar to that described for guarding females in other harvestman species (e.g., Gnaspini 1995; Machado & Oliveira 1998, 2003). Although they were not seen grooming or protecting the offspring against predators, we assume that the behavior described here corresponds to a case of maternal care.

An analysis of the harvestmen collection of the Museum of Comparative Zoology (MCZ), Harvard, USA, revealed another case of maternal care in a cranaid species. One female of *Santinezia* sp. was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collected in Valle del Cava (ca. 1800 m), above Felidia, western Cali, Colombia. The individual was collected in January 1977, and the collecting label stated that the female was "guarding the eggs". The female was found on the eggs in a typical resting position and the eggs were attached to the roof of a small natural cavity in a ravine along a road cut bordering the forest (W.G. Eberhard pers. comm.). According to the collecting label, the eggs numbered 103 and there was a sample of 21 large eggs in the vial containing the female. Unfortunately, the eggs were not well preserved, thus it was not possible to measure their diameter accurately.

Recently, Pinto-da-Rocha & Kury (2003) published a phylogenetic hypothesis for the genus *Santinezia*, dividing it into three monophyletic groups: group curvipes (11 spp.), group festae (2 spp.), and group gigantea (8 spp.). The species studied here are representatives of two of these groups: *S. serratobialis* belongs to the group curvipes and *Santinezia* sp. belongs to the group gigantea (Pinto-da-Rocha & Kury 2003; A.B. Kury pers. comm.). Until more information on the other species of the genus become available it is not possible to know if the maternal behavior in these two species is homologous. Since the microhabitats used for oviposition by these species are very similar, we hypothesize that subsocial behavior is a synapomorphic trait of the genus *Santinezia* and predict that study of congeneric species will reveal further cases of maternal care.

The genus *Santinezia* shows several morphological convergences with the genus *Goniosoma* (Gonyleptidae), which is endemic of the Atlantic Forest (Kury 2003). According to Pinto-da-Rocha & Kury (2004), only details of leg armature and the male genitalia betray their far remote common ancestry. Species of both genera are large-bodied harvestmen, with glossy teguments, stout and long legs bearing few spines, robust and heavily armed pedipalps, and area II projecting into I until it touches the scutal groove (Fig. 2). In this study we add other convergent traits relating to behavior: females in the two genera lay large eggs and care for the offspring until the nymphs hatch (Figs. 1–2). Moreover, some species of *Goniosoma* may also lay eggs on damp pockets in ravines and on rocks along river banks (Machado 2002; Fig. 2).

As studies on harvestmen behavior have advanced, several cases of parental care have been described (review in Machado & Raimundo 2001). Maternal care is present in at least five families of the suborder Laniatores, including representatives of the infra-orders Grassatores (Cosmetidae, Cranaidae, Gonyleptidae and Stygnopsidae) and Insidiatores (Triaenonychidae). The cranaids belong to the superfamily Gonyleptoidea, which embraces the great majority of cases of maternal care in the order (nearly 80% of the total). All families comprising the Gonyleptoidea have an almost exclusively pantropical distribution, being most common in wet, warm environments, such as forests and caves (Shear 1982). Therefore it is possible that maternal care in harvestmen is a convergent behavioral trait adopted by some lineages in response to similar ecological pressures (Machado & Raimundo 2001).

One important question to be investigated in the future is why this behavior has evolved in some species, and not in others. The hypothesis first put forth by Wilson (1971) postulates that intense predation on eggs by conspecifics and ants, as well as the high risk of fungal attack in tropical rain forests may have been the major forces favoring the evolution of parental care in arthropods. Although this hypothesis may explain why maternal care is so frequent among the tropical Gonyleptoidea, it does not provide an answer to question raised above. More recently, Tallamy & Wood (1986) proposed that the answer to this question involves many interacting factors, such as morphological and physiological characteristics of the species, the presence of some behavioral pre-adaptations and phylogenetic constraints. Accordingly, maternal care in arthropods is expected to evolve when females (1) live long enough to benefit the offspring after oviposition, (2) are able to defend the offspring against predators, and (3) are constrained to semelparity (sensu Tallamy & Brown 1999). The morphological and behavioral convergence between goniosomatines and cranaids may provide phylogenetically independent data to test these predictions and thus may constitute appropriate starting point for studies on the evolution of maternal care in harvestmen.

We thank Bill Eberhard for additional information on *Santinezia* sp., Adriano B. Kury and Ricardo Pinto da Rocha for identifying the species and for comments on the manuscript, Paula Cushing for helping us during the fieldwork and for providing the coordinates for the Trinidad sites, Bruno A. Buzatto for the photo of the *Goniosoma* female, Jim

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Figures 1–2.—1. Female of the cranaid havestman *Santinezia serratotibialis* caring for prior hatching eggs and some early hatched nymphs on a small damp pocket among tree roots in Trinidad (photo by J. Warfel); 2. Female of the gonyleptid havestman *Goniosoma* sp. caring for recently laid eggs on a quite similar microhabitat in Parque Estadual Intervales, São Paulo state, southeastern Brazil (photo by B.A. Buzatto). Note that, despite phylogenetic distance, these species are morphologically very similar. Scale bars = 1 cm.

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SHORT COMMUNICATION

FIRST UNEQUIVOCAL MERMITHID–LINYPHIID (ARANEAE) PARASITE–HOST ASSOCIATION

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ABSTRACT. The first description of a Mermithidae–Linyphiidae parasite–host association is presented. The nematode is preserved exiting the abdomen of the host, which is a juvenile *Tenuiphantes* species (Araneae, Linyphiidae), collected from the Isle of Mull, UK. An updated taxonomic list of known mermithid spider hosts is provided. The ecology of known spider hosts with regard to the direct and indirect life cycles of mermithid worms suggests that both occur in spiders.

Keywords: *Aranimermis*, Isle of Mull, Linyphiidae, Mermithidae, Nematoda

Nematode parasites of spiders are restricted to the family Mermithidae but are not uncommon (Poinar 1985, 1987) and were first reported almost two and a half centuries ago (Roesel 1761). However, given the difficulty of identifying and rearing post-parasitic juvenile mermithids, they have received inadequate systematic treatment (Poinar 1985). In addition, the complete life history is known for only one species of these spider parasites (Poinar & Early 1990). Poinar & Welch (1981) supported the use of the genus *Agamomermis* Stiles, 1903 for previously described mermithids that could not be placed in existing taxa and that were considered *species inquirendae*. This is the case for all spider mermithids described prior to 1986 (Poinar 1987). Currently three extant species of spider mermithid parasites are recognized: *Aranimermis aptispicula* Poinar & Benton 1986, *A. actereki* Gufarov & An 1987 (spider host species unknown) and *A. giganteus* Poinar & Early 1990. In addition, the fossil species *Heydenius araneus* Poinar 2000 (a genus restricted to Tertiary fossil nematodes [Poinar 2003]) has been described from a crab spider (Thomisidae) in Baltic amber.

Poinar (1985, 1987) provided lists of spider species with records of mermithid nematode parasitism. However, many of these taxa have now received taxonomic revisions and or transfers. In addition, a number of subsequent reports of parasitism have been published (Gafurov & An 1987; Poinar & Early 1990; Camino & de-Villalobos 1998; Matsuda 1999; Poinar 2000; Allard & Robertson 2003; Iida & Hasegawa 2003; Vandergast & Roderick 2003; Ahtiainen et al. 2004). We provide an updated and taxonomically correct list in Table 1. Here we describe the first Mermithidae–Linyphiidae parasite–host association and discuss the ecology of known spider hosts with regard to the life cycles of mermithid worms.

This paper concerns three spider specimens, one with a worm in situ and two that are presumed to have been parasitized, but from which the worms have emerged and are lost. The specimens were collected during May 2004, in pitfall traps containing 50 ml of 70% alcohol, from a hazel forest in the Tireragan Estate on the Isle of Mull, UK. The spiders belong to the linyphiid genus *Tenuiphantes* but the female with the worm in situ cannot be identified to species because it is a juvenile. In the specimen with the mermithid, the anterior and posterior regions of the worm have exited the abdominal cavity just anterior to the epigastric furrow and close to the pedicel (Fig. 1), but at least one coil can be observed interiorly, as a distortion beneath the abdominal integument, which is devoid of white guanine pigmentation. The worm is pale white/cream with a diameter of 0.13 mm and an approximate length (assuming only one coil exists in the spider) of 15.6 mm. The body length of the spider is 2.14 mm. The two other specimens are both female *Tenuiphantes tenebricola* (Wider 1834) but no worms are visible, although the abdomens of both are severely damaged at the same point at which the worm is emerging in the other specimen. We consider it probable that both of these specimens were parasitized as well. One of the specimens has an emaciated, disk-shaped abdomen (similar to that of the specimen with the worm in situ), which gives

Table 1.—Spider hosts of mermithid worms: * *A. aptispicula*, ** *A. giganteus*, remainder *species inquirendae*.

Family	Species	Reference	Comments
Agelenidae	*Agelenopsis oregonensis* Chamberlin & Ivie 1935	in Poinar (1987)	
Amaurobiidae	*Eurocoelotes inermis* (L. Koch 1855)	in Poinar (1987)	as *Coelotes i.*
Antrodiaetidae	*Atypoides riversi* O.P.-Cambridge 1833	in Poinar (1987)	
Anyphaenidae	*Wulfila albens* (Hentz, 1847)*	in Poinar (1987)	as *W. alba*
Araneidae	*Aculepeira ceropegia* (Walckenaer 1802)	in Poinar (1987)	as *Araneus ceropegius*
Araneidae	*Araneus diadematus* Clerck 1757	in Poinar (1987)	
Araneidae	*Verrucosa arenata* (Walckenaer 1842)*	in Poinar (1987)	
Ctenidae	*Leptoctenus byrrhus* Simon 1888	Poinar (2000)	as *Ctenus bryrrbus*
Cybaeidae	*Argyroneta aquatica* (Clerck 1757)	in Poinar (1987)	
Gnaphosidae	*Cesonia bilineata* (Hentz 1847)*	in Poinar (1987)	
Gnaphosidae	*Gnaphosa lucifuga* (Walckenaer 1802)	in Poinar (1987)	
Hexathelidae	*Porrhothele antipodiana* (Walckenaer 1837)**	Poinar & Early (1990)	as *P. a.* (Dipluridae)
Idiopidae	*Misgolas borealis* (Forster 1968)**	Poinar & Early (1990)	as *Cantuaria b.* (Ctenizidae)
Linyphiidae?	*Micryphantes bicuspidatus* C.L. Koch 1838	in Poinar (1987)	*nomen dubium* (Platnick 2004)
Lycosidae	*Alopecosa inquilina* (Clerck 1757)	in Poinar (1987)	as *Tarentula i.*
Lycosidae	*Alopecosa trabalis* (Clerck 1757)	in Poinar (1987)	as *Lycosa vorax*
Lycosidae	*Arctosa alpigena* (Doleschall 1852)	Poinar (2000)	possible mermithid
Lycosidae	*Geolycosa patellonigra* Wallace 1942	in Poinar (1987)	
Lycosidae	*Hygrolycosa rubrofasciata* (Ohlert 1865)	Ahtiainen et al. (2004)	
Lycosidae	*Pardosa agrestis* (Westring 1861)	in Poinar (1987)	
Lycosidae	*Pardosa amentata* (Clerck 1757)	in Poinar (1987)	as *Lycosa saccata*
Lycosidae	*Pardosa furcifera* (Thorell 1875)	in Poinar (1987)	
Lycosidae	*Pardosa glacialis* (Thorell 1872)	in Poinar (1987)	
Lycosidae	*Pardosa hortensis* (Thorell 1872)	in Poinar (1987)	
Lycosidae	*Pardosa lugubris* (Walckenaer 1802)	in Poinar (1987)	
Lycosidae	*Pardosa milvina* (Hentz 1844)	in Poinar (1987)	as *P. nigropalpis* and *P. scita*
Lycosidae	*Pardosa palustris* (Linneaus 1758)	in Poinar (1987)	as *Lycosa tarsalis*
Lycosidae	*Pardosa pseudoannulata* (Boesenberg & Strand 1906)	Iida & Hasegawa (2003)	
Lycosidae	*Pardosa riparia* (C.L. Koch 1833)	in Poinar (1987)	
Lycosidae	*Pardosa sphagnicola* (Dahl 1908)	in Poinar (1987)	as *Lycosa riparia s.*
Lycosidae	*Pardosa suwai* Tanaka 1985	Matsuda (1999)	
Lycosidae	*Pardosa vancouveri* Emerton 1917	in Poinar (1987)	
Lycosidae	*Rabidosa rabida* (Walckenaer 1837)	in Poinar (1987)	as *Lycosa scutulata*
Lycosidae	*Schizocosa saltatrix* (Hentz 1844)	in Poinar (1987)	as *Lycosa versimilis*
Lycosidae	*Sosippus floridanus* Simon 1898	in Poinar (1987)	
Nemesiidae	*Stanwellia kaituna* (Forster 1968)**	Poinar & Early (1990)	as *Aparua k.* (Dipluridae)

Table 1.—Continued.

Family	Species	Reference	Comments
Oxyopidae	*Oxyopes sertatus* L. Koch 1877	Okochi (1969)	
Oxyopidae	*Peucetia viridans* (Hentz 1832)	in Poinar (1987)	
Philodromidae	*Tibellus oblongus* (Walckenaer 1802)	in Poinar (1987)	
Salticidae	*Habronattus signatus* (Banks 1900)	Vandergast & Roderick (2003)	
Salticidae	*Myrmarachne formicaria* (De Geer 1778)	in Poinar (1987)	as *Salticus formicarius*
Salticidae	*Phidippus borealis* Banks 1895	in Poinar (1987)	
Salticidae	*Phidippus clarus* Keyserling 1885	in Poinar (1987)	
Salticidae	*Phidippus johnsoni* (Peckham & Peckham 1883)	in Poinar (1987)	
Salticidae	*Phidippus putnami* (Peckham & Peckham 1883)	in Poinar (1987)	
Salticidae	*Sitticus floricola palustris* (Peckham & Peckham 1883)	in Poinar (1987)	as *Sitticus p.*
Stiphidiidae	*Cambridgea foliata* (L. Koch 1872)	in Poinar (1987)	
Tetragnathidae	*Tetragnatha anuenue* Gillespie 2002	Vandergast & Roderick (2003)	
Tetragnathidae	*Tetragnatha brevignatha* Gillespie 1991	Vandergast & Roderick (2003)	
Tetragnathidae	*Tetragnatha praedonia* L. Koch 1878	Okochi (1969)	
Tetragnathidae	*Tetragnatha quasimodo* Gillespie 1991	Vandergast & Roderick (2003)	
Theridiidae	*Enoplognatha ovata* (Clerck 1757)	in Poinar (1987)	as *Theridion ovatum* and *T. redimitum*
Thomisidae	*Diaea dorsata* (Fabricius 1777)	in Poinar (1987)	
Thomisidae	*Misumenops tricuspidatus* (Fabricius 1775)	Okochi (1969)	
Thomisidae	*Xysticus deichmanni* Soerensen 1898	in Poinar (1987)	
Thomisidae	*Xysticus durus* (Soerensen 1898)	in Poinar (1987)	
Thomisidae	*Xysticus funestus* Keyserling 1880	in Poinar (1987)	
Zoridae	*Zora maculosa* Roewer 1951	in Poinar (1987)	as *Z. maculata* O.P.-C; *nomen dubium* (Platnick 2005)

the impression of having been host to a worm. It has a normal degree of guanine pigmentation. The second specimen is not emaciated and has almost no guanine pigmentation. It cannot be ruled out that the specimens were damaged upon sorting the pitfall trap contents, but as no other spiders (including many smaller species) were damaged, we consider this unlikely. Alternatively, they may have been hosts to non-mermithid parasites, such as acrocerids or phorids. Unfortunately, the pitfall contents are no longer available to check for emerged worms. It is probable that the specimen with the worm also belongs to *T. tenebricola*, given that six other individuals (three males and three females) were also collected at the same time from the same locality, whereas only one female of each of the following species was collected: *T. alacris* (Blackwall 1853), *T. cristatus* (Menge 1866) and *T. mengei* (Kulczynski 1882).

Poinar (1985, 1987) cited von Siebold (1848) as having identified an unknown mermithid worm in the spider *Micryphantes bicuspidatus* (listed in Table 1 under Linyphiidae?). At the time of von Siebold's paper (his description consisted of only five lines and no figures), only six spider families had been established, Linyphiidae was not erected until 1859. The genus *Micryphantes* C.L. Koch 1833 and *M. bicuspidatus* are both *nomina dubia* (Platnick 2005). Therefore, the new specimen described here represents the first described record of a mermithid–

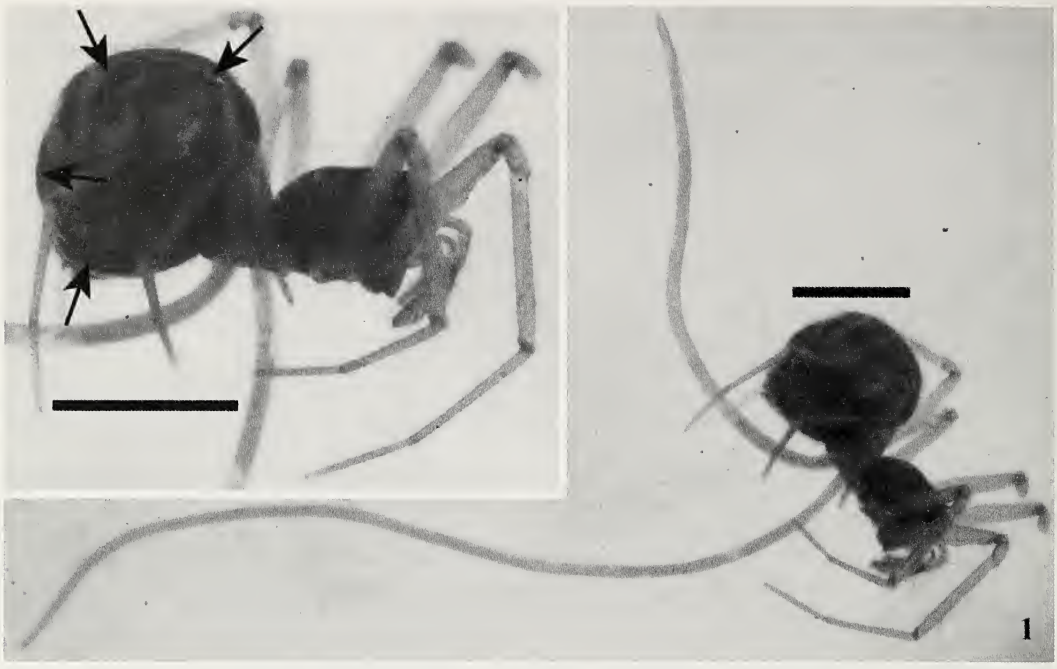

Figure 1.—The mermithid-carrying spider. Note the absence of abdominal guanine pigmentation, arrows point to the internal coil of the worm visible as a distortion in the integument. Scale lines = 1.0 mm.

linyphiid parasite–host association. Furthermore, the claims of Allard & Robertson (2003) of having identified mermithids in *Pardosa milvina* (Hentz) (Lycosidae) for the first time are unjustified, because they were previously reported by Montgomery (1903) under the junior synonyms *Pardosa nigropalpis* Emerton 1885 and *Pardosa scita* Montgomery 1902.

Being host to the worm carries a physiological cost for the spider in addition to its ultimate demise upon the emergence of the parasite. Infection signs generally start with a reduction or absence of digestive structures, and other organs may also be reduced in extreme cases (Poinar 1985). It is interesting to note the reduced amount of guanine deposition in two of the above specimens, and indeed the total absence of it in the specimen with the worm. Guanine is a crystalline purine excretory product, which accumulates in specialized, peripheral cells of the digestive diverticula lying directly beneath the hypodermis (Oxford & Gillespie 1998) and has a white, blocky appearance. Although patterns of guanine deposition can vary intraspecifically and throughout an individuals' development (Oxford 1998), there is usually a distinct pattern of guanine pigmentation present in *Tenuiphantes* Saaristo & Tanasevitch 1996 specimens (DP pers. obs). In the case of mermithid-carrying individuals however, the worm may be compromising the spider to such an extent, that the spider is receiving insufficient nourishment to produce enough of these metabolic waste products for pigmentation purposes. Further research would be required to confirm this hypothesis.

At the time of emergence from the spider host, mermithid worms are mature third stage postparasitic juveniles. Thus, the individual described above cannot be identified to species because diagnosis is based on adult characters. Mermithid life cycles are either direct or indirect. Direct life cycles are characterized by direct penetration of the spider host through the integument by the infective stage larva following emergence from the egg. Indirect life cycles involve a paratenic host (or a host in which significant development does not occur) in addition to the developmental (spider) host, which is infected by ingesting the infective stage of the parasite (Poinar 1985). The direct cycle is by far the most common among mermithids studied to date, however, it has been suggested that spider mermithids first undergo an indirect life cycle involving an aquatic paratenic host (Poinar 1987). Reasoning for this was based on observations of the life cycle of the spider mermithid *Aranimermis aptispicula* as follows: "adults were found in an aquatic habitat, whereas parasitized spiders were found in a variety of foraging habitats. Parasitized spiders were observed to enter the water and the nematodes were seen to emerge from the hosts' bodies. These observations support an indirect type of cycle, but further studies are required to substantiate this" (Poinar 1987). Poinar (1987) did not rule

out that some spider mermithid species may also have a direct life cycle. The life cycle of *A. actereki* presumably has an indirect life cycle because all worms studied (12 males, two females and four post-parasitic larvae) were collected from the bottom of a freshwater spring (Gufarov & An 1987). *A. giganteus* from New Zealand does have an indirect life cycle involving aquatic invertebrates (Poinar & Early 1990).

Given that most aquatic insect larvae have winged adults, the ecology of the spider hosts may provide insights that support or refute Poinar's idea regarding the indirect life cycle of *A. aptispicula*. For example, winged, flying insects are more likely to be consumed by web spinning or foliage/flower hunting spiders than they are by non-web spinning, ground hunters or burrowing, sit and wait predators, which can be expected to feed primarily on non-flying, mainly fully terrestrial prey and are thus, more likely to be hosts to mermithids with a direct life cycle. Interestingly, the ecology of all but one of the spiders reported by Poinar & Benton (1986) as hosts of *A. aptispicula* (Gnaphosidae, *Cesonia bilineata*; Thomisidae, *Misumenops* sp. and *Tmarus* sp.; Salticidae, *Phidippus* sp.; Araneidae, *Verrucosa arenata*; Amaurobiidae, *Wadotes* sp. and Anyphaenidae, *Wulfila albens*), supports the idea of an indirect life cycle for this parasitic worm. The potential problem species of those listed is *C. bilineata* (Gnaphosidae). These are fast moving, agile hunters usually found under loose leaf litter at ground level and males are often found in pitfall traps. However, they have been collected by sweeping low vegetation and have also been collected from malaise traps (Platnick & Shadab 1980), which are primarily designed for catching flying insects.

The large number of non-web spinning, cursorial Lycosidae (Table 1; 38% of all species, excluding *nomina dubia*) with undescribed mermithids, suggests that a direct life cycle may be involved in some instances. Admittedly, some lycosids are common by freshwater, such as *Hygrolycosa rubrofasciata* and *Pardosa pseudoannulata* (known to be mermithid hosts, see Table 1) and may be hosts to worms with indirect life cycles. However, lycosid genera such as *Pirata* and the pisaurid genus *Dolomedes*, which are encountered almost exclusively near freshwater are unknown as mermithid hosts. The mermithid life cycle type in relation to the spider host *Argyroneta aquatica* also poses interesting questions, as this spider spends its entire life under water. Clearly, much work needs to be done before we can fully understand these interesting host–parasite relationships, but a knowledge of the ecology of the host spiders can provide helpful clues in resolving these.

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SHORT COMMUNICATION

THREE HOMONYMOUS GENERIC NAMES IN ARANEAE AND OPILIONES

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ABSTRACT. Three junior homonyms were detected among the Arachnida and the following replacement names are proposed: *Neoarminda* for *Arminda* Roewer 1949 (Opiliones); *Alpazia* for *Lapazia* Roewer 1949 (Opiliones); and *Araneotanna* for *Tanna* Berland 1938 (Araneae). Accordingly, three new combinations are herein proposed for the respective type species. All three genera are monotypic.

Keywords: Araneae, Opiliones, homonymy, replacement names, Bolivia, Brazil, New Hebrides

While recently researching the "Nomenclator Zoologicus" (Neave 1939–1950) three homonymous arachnid generic names were found. As far as it could be ascertained from our sources (Kury 2003 for the Opiliones and Platnick 2004 for the Araneae), all these homonymies have been hitherto undetected. The opportunity is here taken to provide replacement names for them in accordance with the International Code of Zoological Nomenclature (1999).

Order Opiliones
Family Gonyleptidae
Genus *Neoarminda* NEW NAME

Remarks.—The name *Arminda* Roewer 1949 was proposed as a monotypic genus of Opiliones in the Phalangodidae, Tricommatinae (Roewer 1949b: 144) for the species *Phalangodella colatinae* Soares & Soares 1946 from Brazil. The generic name *Arminda* is preoccupied by *Arminda* Krauss 1892 (Orthoptera, Caelifera, Catantopidae) (Krauss 1892: 168). Therefore, *Neoarminda* NEW NAME is here proposed as a replacement name. The following new combination is established: *Neoarminda colatinae* (Soares & Soares 1946), NEW COMBINATION.

Gonyleptoidea incertae sedis
Genus *Alpazia* NEW NAME

Remarks.—The genus *Lapazia* Roewer 1949 was proposed as another monotypic genus of Opiliones in the Phalangodidae Phalangodinae (Roewer 1949a:14) for the species *Lapazia minima* Roewer 1949 from Bolivia. Kury (2003:25) removed this genus from the Phalangodidae and left it as incertae sedis. The generic name *Lapazia* is preoccupied by *Lapazia* Ferris 1937 (Insecta, Homoptera, Diaspididae) (Ferris 1937:68). Consequently, *Alpazia* NEW NAME is here proposed as a replacement name. The following new combination is established: *Alpazia minima* (Roewer 1949), NEW COMBINATION.

Order Araneae
Family Salticidae
Genus *Araneotanna* NEW NAME

Remarks.—The genus *Tanna* Berland 1938 was proposed as a monotypic genus of Araneae in the Salticidae for the species *Tanna ornatipes* Berland 1938 from the New Hebrides (Berland 1938:141). The generic name is preoccupied by *Tanna* Distant 1905 (Insecta, Homoptera, Cicadidae) (Distant 1905:61). Therefore, *Araneotanna* NEW NAME is here proposed as a replacement name. The following new combination is established: *Araneotanna ornatipes* (Berland 1938), NEW COMBINATION.

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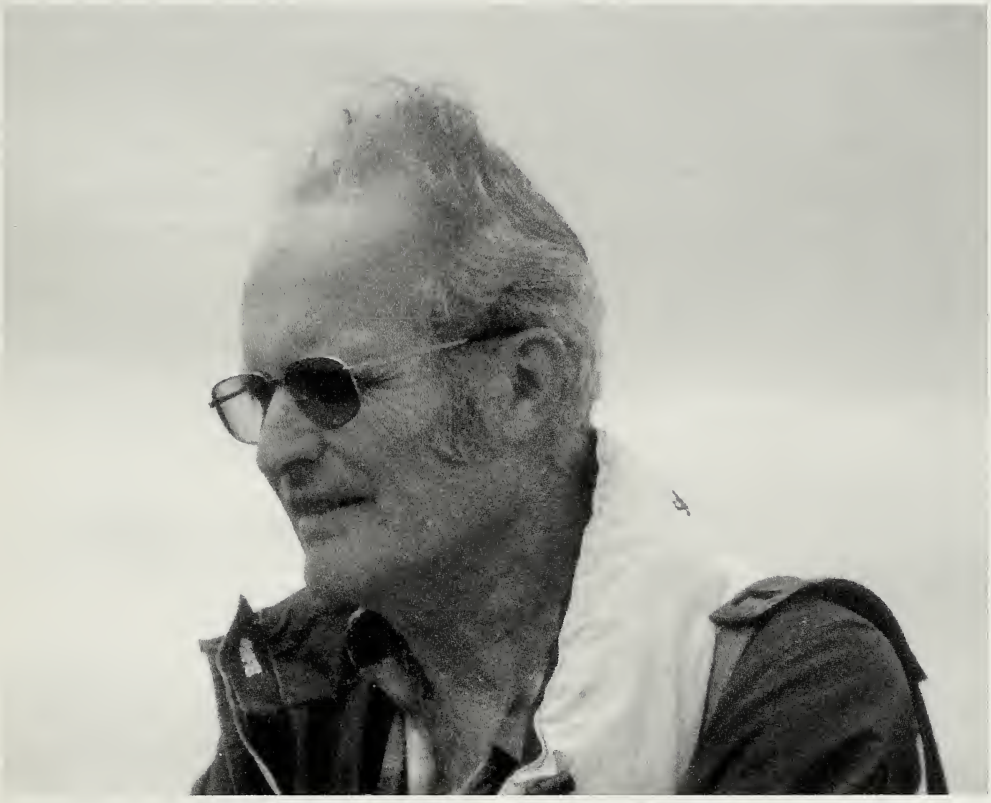
OBITUARY



LE TEMPS MARCHE SI VITE—IN MEMORY OF KONRAD THALER

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It is hard in the moment of sorrow to measure the degree of loss, but European arachnologists must come to terms with the passing of one of their most influential figures. On the 11th June, 2005, Konrad Thaler died suddenly and unexpectedly at the age of 64 during a student excursion in the Stubaier Alps. With him we have lost someone who has left his mark on a whole generation of zoogeographers, taxonomists, mountain ecologists and entomologists and who was described at his funeral by a long-time friend as a scientist of "enthusiastic heart and rational words".

Konrad Thaler was born on December 19th, 1940 in Innsbruck, Austria and stayed true to his Tyrolean mountains throughout his life.

After attending school in Innsbruck, he received his leaving certificate in 1958, spent two years in military service and began his studies in zoology and botany at the University of Innsbruck in 1959/60. His professors, H. Janetschek, O. Steinböck, H. Gams and W. Larcher, were important figures in the study of Alpine biogeography. His 1967 dissertation was (in translation): "On the spider fauna of Northern Tyrol (excluding Linyphiidae and Micryphantidae. Prelude to a catalog of the large spiders of North Tyrol)". Subsequently, linyphiids would become one of his favorite groups. Field-experience and much material for future revisions was gathered in the six years he spent at the Alpine Research Station in Obergurgl, before taking on an assistant post at the University of Innsbruck in 1970. He submitted his 1978 'Habilitation' thesis on "The taxonomy and zoogeography of Alpine spiders" and since 1983 led the department of Terrestrial Ecology and Taxonomy at the Institute of Zoology and Limnology of Innsbruck University. He was a council member of the "Centre International de Documentation Arachnologique" (CIDA) from 1986–1989, CIDA (later ISA) correspondent for Austria, and President of the Austrian Entomological Society from 2002–2005.

Konrad Thaler died at the peak of his productivity. Until the very end he worked tirelessly each day, almost as if he knew how little time he had left. The bare facts are clear: between 1963 and 2005 he authored or coauthored more than 220 journal articles. There was a continual increase in his yearly output: on average one a year during his time in Obergurgl (1964–1970), three as a university Assistant (1970–1978), and seven a year since his 'Habilitation' in 1978. Since 2002 alone he published 40 papers! Additionally, there were popular science articles, often in the journal of the Austrian Alpine Society, plus abstracts and book reviews. From 1973–2005 he supervised 41 diploma theses and 10 PhDs; mostly faunistic and ecological, or taxonomic and morphological projects. As well as arachnids, he supervised numerous studies of myriapods and beetles. Thanks to his careful record-keeping, we know he gave exactly 100 presentations at Austrian and international meetings; the last four days before his death on "Areal forms of invertebrates in the eastern Alps".

It is hard to pick out individual research highlights. His work on the arachnids near Lunz in Austria (Thaler 1963), published when he was only 23, remains of great value as the first, and until recently, the only record of males of the parthenogenetic harvestman *Megabunus lesserti*. Characteristic would be the serial publications "Über wenig bekannte Zwergspinnen aus den Alpen", which was published over nine issues; as well as "Fragmenta Faunistica Tirolensia". Here, Konrad attempted, as part of partial inventory of the North-Tyrol fauna, to make what little was known about the less-familiar invertebrate groups successively accessible; thus impressively demonstrating the breadth of his knowledge. The reprints of part 17 (Thaler 2005) were posted on the day of his death. In his last years he was particularly keen to produce summary works, such as the faunistic synopsis of North-Tyrol spiders (Thaler 1998) and a review of the ecology of high-Alpine species (Thaler 2003). Also important was his editorial work on the "Diversity and biology of spiders, scorpions and other arachnids" which included papers from long-term collaborators and showed Austria as a working environment for arachnologists (Thaler 2004). For a full measure of the merit of his life's work one should compare our state of knowledge at the end of his studies in the "Contributions to the spider fauna of North-Tyrol" (Thaler 1992, 1994, 1995, 1997a,b, 1999) with how things were before he started, when the spiders were ". . . an unhappy picture of insufficient faunistic research." (translated from Holdhaus 1954). A full inventory of Austrian spiders (begun by Thaler & Knoflach 2002, 2003, 2004) was sadly not to be completed in his lifetime.

Konrad's taxonomic work included the authorship of two genera (*Carniella*, *Mysmeniola*), 77 species and one subspecies of spider, and one harvestman species. Of these, 48 he collected himself, and none have so far proved to be synonyms. His new taxa spanned 17 families, predominantly Linyphiidae (42 species) and Amaurobiidae (12 species), with a geographical concentration in the Alps and the Mediterranean. Twenty-six species from various animal groups bear his name, including twelve spiders, four flies, a tardigrade and an oligochaete worm.

It's obvious that such productivity could

only be achieved through great personal and passionate commitment to research. For Konrad, science was his life-work (*labor vincit omnia*). Insiders knew one could invariably meet Konrad in the institute seven days a week, so long as he wasn't on excursion. He had the good fortune with his second wife Barbara to find an equally enthusiastic and talented comrade-in-arms. Their years together were a particularly productive phase of cooperative activity, during which the Mediterranean arachnids became a further focus of research.

Although he enjoyed considerable international recognition, his achievements were not always recognized by his own institute. Here, he was often accused of failing to keep up with the latest trends or buzz-words. It is not that he rejected, for example, molecular methods, but simply felt that ". . . the state of knowledge achievable by 'conventional' means was far from being reached. . . ". Indeed it was through conventional methods that Konrad became a leading figure of 20th century arachnology. His death means, regrettably, a further substantial loss of taxonomic expertise among the German-language universities. It can only be hoped that those in authority recognize the consequences of this before it is too late.

Everyone who visited Konrad in his office was impressed by the concentration of literature, in particular the many originals of standard works and a rich collection of comparative material. They were also astounded by their host's memory. Konrad could recognize almost every Central European spider, without the use of literature, and when he said "I haven't seen anything like that before." you knew you had found something special. But most of all, people remember his courtesy and helpfulness, his stimulating inquisitiveness, constant ability to enthuse and his many words of encouragement. As an example, between two stressful meetings he was asked to check the identification of a *Troglohyphantes* male and got up from the microscope with the words "Thanks for the nice view". No one left his room without a better understanding, a constructive thought, or feeling more motivated. He always had an open door for his students and it is no accident that shortly after his death many of them offered thanks on the university homepage for his remarkable personal contact and the enthusiasm and devotion he brought to his teaching.

Administrative duties meant that despite his discipline and industry, time for research became increasingly scarce. He often wrote of a "Mountain of paper in front of the microscope." and the "Lure of the mountains for arachnological collecting". At the 8th meeting of the German-speaking arachnologists in Salzburg, he mused about whether we should go into the Alps, simply to enjoy the distinctive fauna or the landscape *per se*. For Konrad, life without the mountains was impossible to imagine. He felt happiest at 3,000 m; where the motto might have been: concentrate on that which is most important. Longer collecting trips were made to the Caucuses, Pyrenees and Atlas mountains, where the local guides were said to have whispered "he marches like an Arab". His student trips into the Alps were legendary, and up to the very end he would be walking way ahead of the younger participants, especially on critical passes. The excursions took place in all weathers, often with the résumé that this enabled one to better understand the requirements of Alpine animals. It seems fate that Konrad died during his final regular student excursion, only a few months before he was due to retire, when he would have had more time for fieldwork and his own projects. His friends, colleagues and students must now take over his legacy and try to ". . . write at least one new line each day".

For advice and information we are very grateful to Barbara Knoflach. A German version of this obituary has been published in the Arachnologische Mitteilungen 30 (2005), which also includes a complete bibliography of Konrad Thaler's publications by this date. We thank the editors for permission to offer this translation.

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(revised July 2006)

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Figures 1-4.— *A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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