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HOW SPIDERS INITIATE AIRBORNE LINES

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ABSTRACT

Airborne line initiation was observed in spiders of at least 46 genera in 16 araneomorph families. At least three different methods of initiation were observed, two of which have apparently not been described previously. Two other methods of airborne line initiation described in the literature may not occur. In one araneid it was determined that the anterior spinnerets are apparently not involved in producing airborne lines.

INTRODUCTION

It has long been known that many spiders produce airborne silk lines that are pulled from the spider by air currents and are used either as "spanning lines" that serve as bridges to distant objects (e.g. McCook 1889) or as "balloon lines" that allow the spider itself to become airborne (e.g. Bristowe 1939). It seems not to have been generally appreciated, however, that the initiation of such silk lines cannot be explained by the accepted notion that a silk line emerges from a spider's spinnerets only as a result of being pulled. Also, spiders are thought to be incapable of emitting silk lines unless the lines are drawn from their bodies by tension on silk that has already been emitted (e.g. Witt et al. 1968). Although it is reasonable to suppose that friction with moving air can pull out additional line once an airborne line has been initiated, it is not clear how production of the line is started when there is nothing on which the air can pull.

Literature accounts on this point are unclear and contradictory. Several authors have commented on the initiation of airborne lines (see Fig. 1), but few have addressed this particular problem, and some have made what are probably erroneous descriptions of the process. Bristowe (1939) stated that the spider "squeezes out a little silk" in order to start an airborne line (Fig. 1A), but as noted, this is unlikely to be true. Both Savory (1952) and Witt, Reed, and Peakall (1968) saw that spiders sometimes produce multiple lines as they descend and only hold one with a hind leg, allowing the other to blow free in the wind. Savory reported that this second line is cut at the spinnerets and flies free from an attachment above to the drag-line (Fig. 1B), and thought that the airborne line can thus only be as long as the spider's descent. As will be shown below, this description is probably incorrect. Richter (1970) stated that the lycosid *Pardosa* breaks its drag-line prior to initiating a balloon line, but did not describe initiation itself.
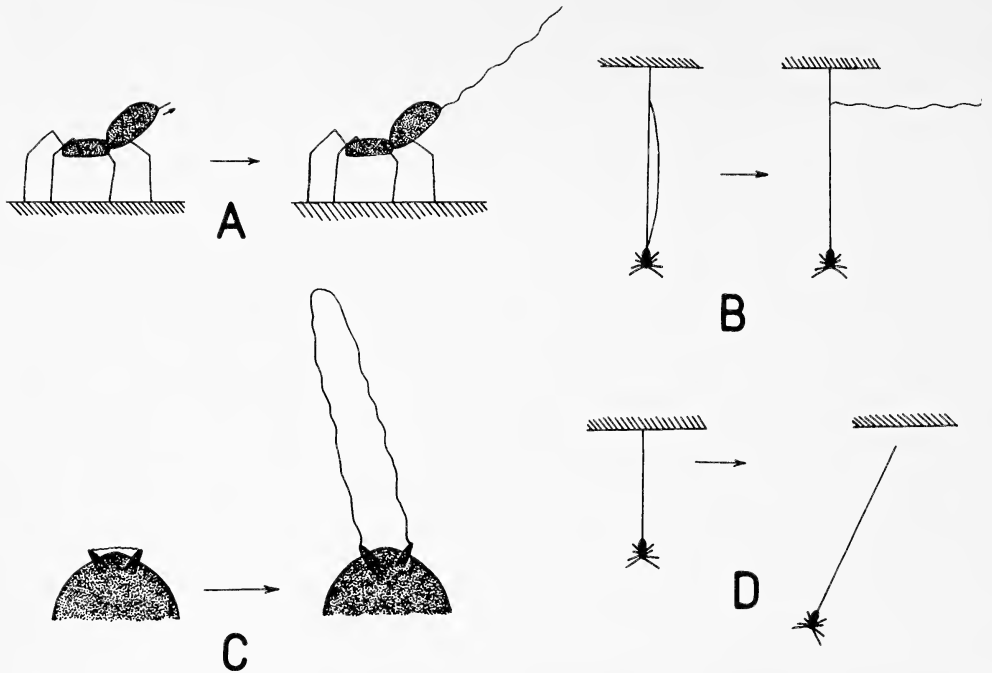
Fig. 1.—Diagramatic representation of previous descriptions of mechanisms of initiation of airborne line production. A, Bristowe (1939) thought that the spider "squeezed out" the first bit of line (small arrow) and the rest was then pulled out by the wind; B, Savory (1952) thought the spider produced two different lines as it descended, then broke one at the spinnerets so that it drifted free in the breeze; C, Blackwell (in McCook 1889) thought the original line was produced by moving the spinnerets apart, and additional line was then pulled out by the wind; D, Coyle (1983,1985) and Braendegaard (1938) saw spiders descend on trail lines in a strong breeze, and after the lines lengthened substantially, they broke near where they were attached.

Both Blackwall (in McCook 1889) and Nielson (1931) thought that the spinnerets are first brought together and then spread apart, thus drawing out a short span of silk, and that this short line then catches the breeze and is pulled from the spider (Fig. 1C). Recently Coyle (1983, 1985) reported field observations of the mygalomorphs *Sphodros* and *Ummidia* using their drag-lines as balloon lines; in this case the line is pulled and lengthened by the weight of the spider as it falls and is pushed by a breeze, and a free end is produced when the line breaks, apparently near the point where it was attatched to the substrate (Fig. 1D). Braendegaard (1938) had earlier made similar observations of *Dictyna borealis* O. P.-Cambridge placed in somewhat unnatural conditions (the tip of his finger).

Hingston (1920) noted that in *Argiope* " . . . the tip of the line that it gives to the wind is not a single filament but a complex structure. It is divided into a sheaf of the very finest fibrils. . . These float freely in the air and serve to support the more compact and single thread that follows them from the spinnerets." Hingston (1922) also saw that *Nephila maculata* Fabricius makes a similar set of fine lines merging to a single filament near the spider. McCook (1889) and Richter (1970) also noted multiple lines, but none of these authors clarified how these fine fibrils were originally drawn from the spider.

There are thus several contradictory and partial explanations of how airborne lines are initiated. I report here observations of at least 65 spider species, and show that different spiders use at least four different methods of initiating such lines.

METHODS

Observations were made indoors on mature females, with a bright light and a dark background placed behind the spider so as to make lines most easily visible as they were produced. Other objects were kept at a distance so that airborne lines did not usually become tangled with them. Doors and windows were kept closed so that there was little air movement in the room. In some cases the spiders were stimulated to produce airborne lines by blowing on them gently.

Specimens of all species have been deposited in the Museum of Comparative Zoology in Cambridge, Massachusetts 02138, USA. Some specimens could not be identified to species, and are referred to by the numbers that are on labels in the vials containing the spiders.

Detailed observations of *Leucauge mariana* (Keyserling) were made using an "Emskop®" 5x magnifier mounted on a Zeiss headband magnifier, giving, in effect, a completely portable low power dissecting microscope.

RESULTS

Initiation using a second line.—In some species (Table 1) spiders produced airborne lines as they descended drag-lines (Fig. 2). They attached a second line to the drag-line as they descended so that both lines were pulled from the spinnerets by the spider's weight (Fig. 2A). As the spider descended, the second line (which, judging by the amount of light it reflected, was smaller in diameter) was apparently pulled by air currents and sagged away from the straight drag-line that was sustaining the spider's weight (Fig. 2B). In some species more than one thin line emerged (footnote c in Table 1. Often the spider then stopped descending, and hung motionless while more and more thin line (up to several meters) was pulled by air currents (Fig. 2C). In some species one leg IV held the drag-line but not the thin line as the spider descended (see Eberhard 1986), but in others neither line was touched by any leg (Fig. 2). Finally, spiders often turned and climbed part way back up the drag-line before reeling in the airborne line (Fig. 2D). If the line had snagged on an object, the spider pulled it taut and attempted to walk along it to the object.

Thus, in these cases, the airborne line was initiated during descent by being drawn from the spider by gravity, and air currents then pulled it out further.

Initiation by wrapping.—In two species of pholcid (Table 1), the spider hung at the end of a drag-line, and pulled a line with alternate movements of its legs IV similar to those used to wrap prey (e.g. Eberhard and Briceño 1983), and the line it produced floated upward in the gentle updraft. This line may have been an extension of the drag-line, as it did not have a free end.

"Spontaneous" Initiation.—In some species (Table 1) the spider did not employ either of the techniques just described, but instead simply elevated its abdomen while hanging on a line or lines, or while standing on some surface (Fig. 1A),

Table 1.—Types of airborne line initiation observed. Unless noted otherwise, all spiders were mature females. Numbers and letters after genus names indicated identification numbers included in the vials housing the spiders in the Museum of Comparative Zoology. The methods of initiation refer to descriptions in the text.

Spider	Method of Initiation		
	Second Line	Wrap	Spontaneous
ARANEIDAE			
Alpaida TL13-6, TL31-6			?
Araneus marmoreus Clerck	+		
Azilia TL25-1	?[c]		
Chrysometa TL33-5, TL40-3, TL45-1	+		
Cyclosa turbinata (Walckenaer)	+		?[a]
Enacrosomma TL12-4, TL32-5	+		?
Eriophora edax (Blackwall)	+[c,d]		
Leucauge mariana (Keyserling)			+
Metazygia TL9-2,TL15-7, TL18-3,TL43-5	+		+?[b]
Metepeira TL45-5	+[c]		
Micrathena fidelis (Banks)	+		
M. gracilis (Walckenaer)	+		
M. quadriserrata F.O.P.Cambridge	+		
M. schreibersi (Perty)			+
Nephila clavipes (Linneaus)	+		
Nephilengys cruentata Simon	+		
Tetragnatha TL3-2, TL9-1	+		
Verrucosa arenata (Walckenaer)	+[c]		
Wagneriana tauricornis (O. P. Cambridge)			?
THERIDIIDAE			
Achaearanea tepidariorum (C. L. Koch)			+
Argyrodes caudatus (Taczanowski)	+6		+
Chrosiothes			?
Dipoena nigra Emerton	+		
Theridion TL10-4, TL14-3, TL31-2	+		?
Tidarren TL25-2	+		+
MIMETIDAE			
undet. genus TL60-2	+		
NESTICIDAE			
undet. genus TL10-2, TL40-3	+		?
THERIDIOSOMATIDAE			
Epeirotypus FN3-7H, TL38-1	+		+
Ogulnius TL12-2			?
Theridiosoma TL4-2			+[e]
Wendilgarda galapagensis Archer			+(?)
LINYPHIIDAE			
Erigone			?[g]
"*Frontinella*" *linguatula* (F.O.P.Cambridge)TL38-3			+[f]
Linyphia TL5-1	+		
undet. genus TL54-6	+		
ULOBORIDAE			
Miagrammopes sp., prob. *intempus* Chickering			?
M. simus Chamberlin and Ivie			?[h]
Philoponella sp. TL22-1	+		
Uloborus campestratus Simon			?[h]
U. glomosus (Walckenaer)	+		
U. sp.	+		+
DICTYNIDAE			
Dictyna TL9-7	+		
D. TL44-5			+[i]

Table 1.—Continued

HERSILIIDAE			
undet. genus TL44-2			+[b,h]
SALTICIDAE			
Beata sp.			+[h]
Myrmarachne TL53-3	+		
Paraphidippus aurantius (Lucas) (a)			+[h]
P. marmoratus F.O.P.Cambridge			+[h]
P. sp. "ii" TL22-3, TL23-1	+[c]		+[h]
Titanattus TL17-1	+(?)		
undet. genus TL44-1	+		
OXYOPIDAE			
Hemataliwa helia (Chamberlin)			?[h]
H. puta (O. P. Cambridge)	+[c]		
H. sp. TL42-5	+(?)		
undet. genus TL55-3	+		
ANYPHAENIDAE			
Anyphaena			?[h]
undet. genus TL51-1, TL14-2	+		
undet. genus TL53-2			+[h]
CTENIDAE			
undet. genus (a)			?[h]
AGELENIDAE			
Agelenopsis	+[c]		
THOMISIDAE			
Misumenops sp. TL24-1	+[c]		?[h]
PHOLCIDAE			
prob. *Modissimus*		+[j]	
undet. genus		+	

[a]Initiate airborne line with very little movement along drag-line.
[b]Spider stimulated to emit airborne line when blown on.
[c]Swath of fine threads produced in addition to drag-line.
[d]Fine lines sag very little even in wind, so function as spanning or balloon line uncertain.
[e]Some with two threads in airborne line.
[f]Tip of airborne line free as spider descends.
[g]"D" form (indicative of second line method) not seen.
[h]Spread spinnerets wide as produced airborne line.
[i]Spread spinnerets, close them with a clap, and then reopen them as or just before producing airborne line.
[j]Behavior seen in field at night.

and, apparently without making any attachment of any kind, simply emitted a line. This technique appeared not to be as reliable as the others, as in some cases the spider assumed the typical posture and waited, but did not produce an airborne line. In *Leucauge mariana* such "failures" were induced by blowing gently on the spider until it assumed a typical ballooning position, then ceasing to blow.

The free ends of at least some of the spontaneously produced airborne lines were extraordinarily thin. For instance, when I observed adult *Uloborus diversus* Marx in an ideal viewing situation with very strong light from all sides and a pitch black background, I was unable to convince myself that I had found the free end of any of the many airborne lines they emitted. When I slowly reeled in the lines, the visible end moved in the gentle updraft in a way that suggested that there was an additional invisible length of line beyond the line's tip that was pulling on it. The most distal portions of airborne lines of *Leucauge mariana*
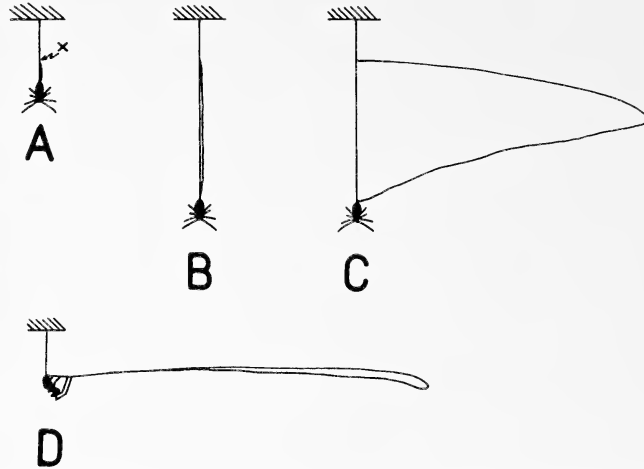
Fig. 2.—"Second line" method of airborne line initiation. A, A thin line (or swath of thin lines) is attached (at x) to the drag-line as the spider descends; B, As the spider descends further, this line is pulled from the spinnerets (along with the drag-line) by the weight of the spider's body; C, Eventually the second line becomes long enough that friction with air movements causes more line to be pulled from the spinnerets; D, Finally the spider reels in the airborne line, often having reascended the drag-line to near the point where the airborne line was initiated.

were also thin, and were not visible except when coated with talc (Fig. 3). There was usually an abrupt transition where the line suddenly became visible when these spiders produced airborne lines, presumably marking the site where thicker lines were added to or replaced thinner ones. In one case at least 20-30 cm of thin line was produced before such a transition occurred.

I was thus not able to confidently determine the exact moment of the initiation of any single airborne line. In some species, however, it was clear that the spinnerets were spread very wide (e.g. Fig. 1C) when the line was initiated (footnote h in Table 1), suggesting that the initial events were those described by Blackwall, with a short line being drawn by the movements of the spinnerets themselves, and then the pull of the breeze on this line resulting in its being drawn from the spider.

Mature *Leucauge mariana* females that were initiating airborne lines spontaneously were observed under about 7X magnification. The anterior spinnerets were held apparently immobile in their normal appressed positions before and during initiation, but the posterior lateral spinnerets were flexed to spread both laterally and posteriorly, and were occasionally clapped together and then spread again. Contrary to expectations under the Blackwell hypothesis (Fig. 1C), however, double lines were not seen emerging from these spinerets. Instead, the lines emerged from the depression between the bases of the posterior lateral spinnerets. These spinnerets were kept spread even after the emerging line had thickened and the tip was tens of centimeters away. It is possible that the line came from the short posterior median spinnerets, which were completely hidden from view. Hingston (1922) noted that the airborne line of *Nephila maculata* comes from the posterior spinnerets, but did not specify which ones.
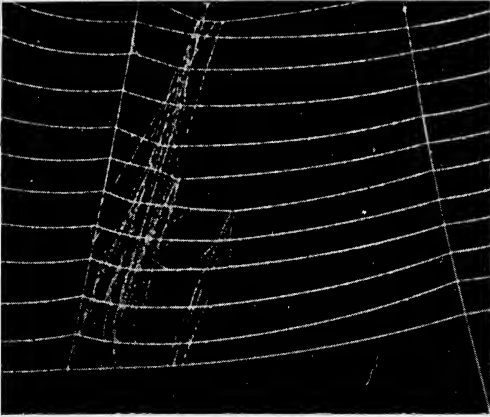
Fig. 3.—A portion of the distal portion of the multistranded airborne line produced by a mature female *Leucauge mariana*. The swath of lines was trapped on a partially completed orb web and coated with talc. Despite good viewing conditions I was not able to see this line as it emerged from the spider.

DISCUSSION

It should be kept in mind that airborne lines have two different functions—to establish spanning lines the spider can use to walk along to reach distant objects, and to produce balloon lines that carry the spider through the air, out of contact with any other object. It is possible that different behaviors are employed to acheive these different ends. The nearly windless conditions under which my observations were made are not those in which balloon line production is elicited in some spiders (Richter 1970, Greenstone 1982). The relatively large sizes of most of the spiders I observed also suggests that the behaviors observed in this study were in general designed to establish spanning rather than balloon lines. Certainly a number of spiders did walk along their new lines when these snagged on nearby objects. The possible lack of true balloon lines may explain some differences with previous observations (e.g. the lack of the obvious differentiation of the tip of the balloon line that was noted by Hingston (1920, 1922) in *Arigiope*, and the failure to observe the apparent rupture of the drag-line seen by Richter (1970) in *Pardosa*).

Initiation of airborne lines by wrapping was seen only in pholcids, and probably represents an independent origin of airborne line production. Other related species observed under captive conditions (at least nine species of pholcids, nine species of scytodids) failed to produce any airborne lines. None of the more than 60 araneomorph species observed performed behavior similar to that reported for the mygalomorphs *Sphodros* and *Ummidia* (Coyle 1983, 1985), and the araneomorph *Dictyna* (Braendegaard 1938), but since my observations occurred under less windy conditions, it is premature to conclude that these spiders do not balloon in this manner.

The other two types of behavior are widely distributed among araneomorph spiders, and several species (uloborids, salticids, theridiids, araneids, and theridiosomatids—see Table 1) performed both types. It is possible that in those cases in which I verified that the airborne line was not attached to the drag-line (see footnote f in Table 1), it nevertheless had been attached there when it was initiated and subsequently broke free at or near the attachment. This sequence of events occurred in some but not all descents of *Micrathena gracilis* (Walckenaer) (Araneidae). This explanation requires that airborne lines break preferentially near the attachment point. Spiders apparently modulate the diameters of airborne

lines (Hingston 1920, 1922, also descriptions above) as well as those of other lines (Witt et al. 1968, Wilson 1969, Work 1976), and could also possibly produce weakened attachments, so selective breakage of lines or attachments is not unreasonable. Coyle's (1983) and Braendegaard's (1938) observations of mygalomorphs and *Dictyna* suggest that selective breakage occurs in these groups.

In a number of species it seemed clear that "spontaneous" airborne line production could not have resulted from any of the other types of behavior (either the spider's spinneret area and the lines it produced were especially easy to see, or I moved objects near the drag-line and saw by the lack of tugs on the drag-line that no other lines were attached there). Thus it is clear that some species possess two alternative methods of producing airborne lines. Although other selective factors may also be involved, spontaneous initiation would be advantageous in producing given lengths of airborne line with less silk since the line is not doubled. The clear tendency for some spiders to spread their spinnerets wide as they initiated spontaneous lines accords well with Blackwell's idea that initiation involves opposite spinnerets pulling short lines from each other, but direct observations of these lines are still lacking, and Blackwell's account may have been a good guess rather than a report of actual observations. The failure to observe double lines in *Leucauge mariana* does not completely rule out the Blackwell mechanism in this species, as the original double lines might have been too thin to see. But it is puzzling that at least the thicker portion of the airborne line seemed not to emerge from the widespread posterior lateral spinnerets. No species performed the behavior described by Savory (1952—see Fig. 1B), and it seems likely that he actually observed the second line method (Fig. 2) but failed to notice the bottom portion of the airborne line.

ACKNOWLEDGEMENTS

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THE GENUS *CENTRUROIDES* IN SOUTH AMERICA (SCORPIONES, BUTHIDAE)

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ABSTRACT

The systematics of the genus *Centruroides* Marx, 1889, in South America is reviewed. Three taxa are retained as valid: *C. gracilis* (Latreille), *C. margaritatus* (Gervais), and *C. exsul* (Meise). Of these, *C. margaritatus* is redescribed, based on the rediscovery of the holotype female from Isla Puná, Ecuador. Three new synonymies are proposed: *Centruroides dasypus* Mello-Leitão, 1948 = *Centruroides vittatus* (Say, 1821); *Centruroides argentinus* Werner, 1939 = *Centruroides margaritatus* (Gervais, 1841); and *Centruroides danieli* (Prado and Rios-Patiño, 1939) = *Centruroides margaritatus* (Gervais, 1841).

RESUME

La systématique du genre *Centruroides* Marx, 1889, est révisée pour l'Amérique du Sud. Trois taxa sont retenus comme valables: *C. gracilis, C. margaritatus* et *C. exsul. Centruroides margaritatus* est redécrit en se fondant sur l'holotype femelle de l'île de la Puná, en Equateur. Trois nouvelles synonymies sont proposées: *Centruroides dasypus* Mello-Leitão, 1948 = *Centruroides vittatus* (Say, 1821); *Centruroides argentinus* Werner, 1939 = *Centruroides margaritatus* (Gervais, 1841); et *Centruroides danieli* (Prado et Rios-Patiño, 1939) = *Centruroides margaritatus* (Gervais, 1841).

INTRODUCTION

The buthid genus *Centruroides* Marx, 1889, is one of the most complex scorpion genera in the New World, and is widely distributed in North America, the Antilles, and Central America. Six species are recognized from South

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America and associated islands. Although a generic revision of *Centruroides* is badly needed, the South American taxa, in particular, have not been collectively studied since Mello-Leitão's (1945) monograph. In the present study we reevaluate the taxonomic status of the six species of *Centruroides* and their synonyms in South America, based on the examination of type material for most of the nominal taxa.

Among the specimens of the Gervais collection is an adult female from Isla Puná, Ecuador which almost certainly is the original type specimen of *Scorpio margaritatus*. The rediscovery of this specimen is of considerable taxonomic importance, as *C. margaritatus* is a highly variable, widespread, and poorly understood species, occurring from Mexico to South America and the Antilles. A complete redescription of *C. margaritatus* is given here based on this adult female.

<center>

Centruroides gracilis (Latreille, 1804)
Figs. 1-10
</center>

Scorpio australis, DeGeer 1778:248.
Scorpio gracilis Latreille 1804:127.
Scorpio biaculeatus, Gervais 1843:130 (nomen nudum).
Scorpio (Atreus) biaculeatus Gervais 1844a:54; 1844b:218; 1857:43.
Centrurus biaculeatus, Thorell 1877:166.
Centrurus gracilis, Karsch 1879a:18; Kraepelin 1891:131; 1894:95; 1899:92; 1905:339, Pocock 1893:385; Penther 1913:243.
Centruroides gracilis, Pocock 1902:32; Hoffman 1939:323; Werner 1934:274; Mello-Leitão 1945:257; Caporiacco 1951:3; Scorza 1954a:165; 1954b:160; 1954c:200; Bücherl 1959:267; 1971:327; Stahnke and Calos 1977:112; Wagner 1977:45; Francke and Wagner 1978:159; González-Sponqa 1984:66.
Rhopalurus gracilis Meise 1934:30 (part).
Note: The above synonymy reflects usage of names as applied to South American specimens and other relevant citations.

Type data.—Latreille (1804) created the name "*Scorpio gracilis*" for specimens that DeGeer (1778) had referred to *Scorpio australis* Linnaeus. Apparently, he never examined these specimens and did not designate a holotype; however, DeGeer's specimens must be regarded as the types of *S. gracilis*. T. Kronestedt (pers. comm., Mar. 1986) indicates that two pinned specimens of *Scorpio australis* from DeGeer's collection are currently housed in the Naturhistoriska Riksmuseet.

The types of *Scorpio (Atreus) biaculeatus*, presumably deposited in the MNHN (Paris) were not located in that collection and are almost certainly lost.

In conjunction with this study of *C. gracilis*, we have also attempted to locate and examine other synonyms previously referred to this species. The types of *Androctonus biaculeatus* Lucas (MNHN), *Tityus mulatinus* Koch (ZMB), *Tityus congener* Koch (ZMB), and *Tityus nebulosus* Koch (ZMB) are no longer in their respective depositories and are almost certainly lost. The types of *Centrurus heterurus* Karsch and *Tityus macrurus* Koch, both deposited in the Zoologisches Museum (Berlin), were examined and are referable to *C. gracilis* (see also Francke and Wagner 1978).

Distribution.—*Centruroides gracilis* is widely distributed in the Neotropical Region, known from the U.S.A. (southern Florida), much of Mexico, Central America, Cuba, and northern South America. It is also a commonly introduced species in other tropical areas. In South America, the species occurs in Venezuela
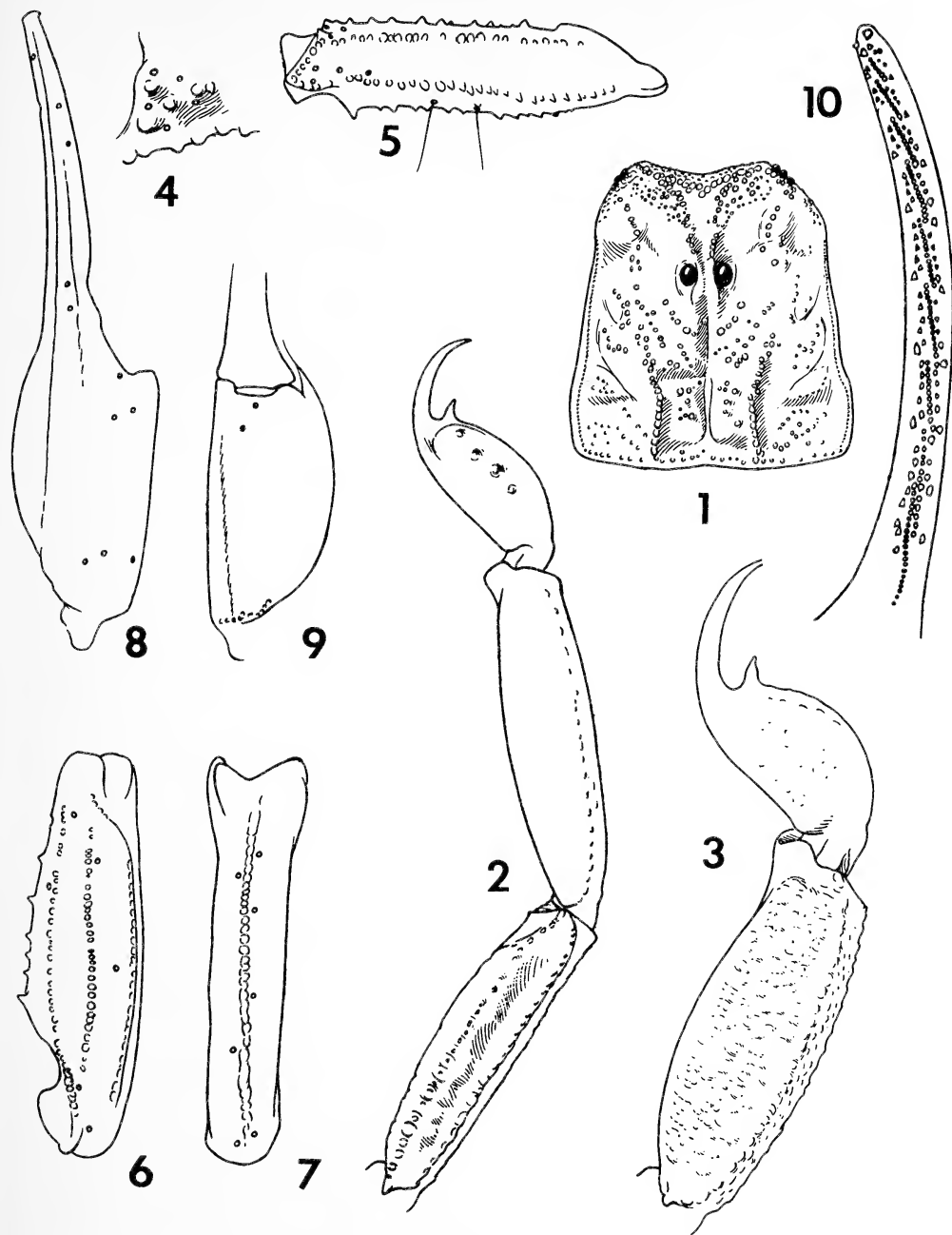
Figs. 1-10.—Morphology of *Centruroides gracilis* (Latreille): 1, carapace of male; 2, distal end of metasoma and telson of male; 3, metasomal segment V and telson of female; 4-9, trichobothrial pattern of pedipalp; 4, proximal end of internal face of femur; 5, dorsal view of femur; 6, dorsal view of tibia; 7, external view of tibia; 8, external view of chela; 9, ventral view of chela; 10, movable finger of pedipalp chela, showing dentition.

(González-Sponga 1984); we have seen a few specimens labeled "Columbia" and "Ecuador", but these represent old and, possibly, unreliable records.

Description.—Large species of *Centruroides*, adults up to 110 mm in length. Color of carapace, tergites, and metasoma dark reddish brown to dark brown; legs yellow brown; pedipalp femur and tibia yellow brown, chela manus reddish

brown with fingers slightly darker. Carapace (Fig. 1) with dense, coarse (but rounded) granulation. Mesosoma: median keel on I vestigial; on II weak, granular; on III-VI moderate to strong, granular. Tergite VII with median keel weak to moderate, granular; lateral keels moderate to strong, crenulate. Sternite VII tetracarinate, with submedian pair of carinae weak, smooth; lateral pair moderate, finely granular. Pectinal tooth counts 29-35 in males, mode 31-32; 27-30 in females, mode 29.

Metasomal segments I-IV: Carinae in males moderate, finely crenulate to crenulate, except as follows: Ventrolaterals granular on I-II; ventral submedians weak on I-IV, smooth to finely granular on I-II, finely crenulate on III-IV. Metasomal carinae of female as in male, except crenulations, where present, typically more coarse. Segment V (Figs. 2, 3): Male with dorsolateral and lateromedian carinae obsolete; ventrolateral and ventromedian carinae weak, smooth to finely granular. Female with dorsolateral carinae weak, finely granular; lateromedian carinae obsolete; ventrolateral and ventromedian carinae weak, finely crenulate.

Telson with subaculear tooth strong, spinoid, directed away from aculeus (Fig. 2, 3).

Pedipalps: Orthobothriotaxia A (Figs. 4-9), femur with α configuration (Figs. 4, 5). Chela (Figs. 8-10) with digital carina vestigial on palm, weak and smooth on fixed finger; ventroexternal carina weak; finely granular in males, smooth in females; dorsointernal carina weak, finely granular; all other chela carinae obsolete. Fixed finger with nine oblique rows of denticles (or eight when basal rows fused); movable finger (Fig. 10) with nine oblique rows of denticles (eight when basal rows fused) plus a short apical row of four granules; supernumerary granules present in later instars. Inner margins of chela fingers subtly scalloped. Chelicerae: fixed finger ventrally with one nodule.

Variation.—The most notable variation occurs in pectinal tooth counts (Table 2) and pedipalp chela finger dentition (Table 3). *Centruroides gracilis* typically has nine oblique rows of granules on the chela fixed finger, but many South American specimens have the two basalmost rows fused. Fusion of the basalmost rows on the movable finger also occurs. In such cases, it appears that only eight rows are present.

Coloration, which is quite variable in other parts of the range of this species, is rather consistent among South American specimens. The specimens we have examined are dark reddish brown with yellow brown legs and lighter reddish brown pedipalps. The chela manus is considerably lighter than the fingers. This color scheme is quite similar to that found in Central American specimens. In Mexico and Florida (USA), however, there is considerable variation, with specimens tending to be blackish with gray-brown legs (Hoffman 1932; pers. obs.). The taxonomic importance of this color variation in *C. gracilis* is poorly understood, and any future analysis of it must necessarily incorporate the close relatives of *C. gracilis* in Central America.

Specimens examined.—VENEZUELA: no specific locality, 25 Feb. 1892 (Meinert), 4 females (ZMR); Caracas, 8 June 1891 (Meinert), 1 male (ZMR); no specific locality, 1 male, 1 female RS-1065 (MNHN); San Fernando de Apure, 5 Oct. 1897 (L. Leglaise), 1 male, 3 females, RS-1053 (MNHN); no specific locality, 1899 (M. Maindron), 1 male, RS-1067 (MNHN); El Vigia, Depto, Vargas (A. R. Lancini, det.), 1 male (IB-Sc-896).

Table 1.—Measurements in mm of *Centruroides* spp. from South America, including the type specimens of *C. argentinus* Werner and *C. danieli* Prado and Rios-Patiño.

	C. gracilis		C. margaritatus		C. danieli	C. argentinus	C. exsul	
	Male Colom.	Female Colom.	Male Colom.	Female holotype	Male holotype	Female holotype	Male paratype	Female holotype
Total length	108.2	86.5	99.7	79.1	92.8	53.9	?	?
Carapace length	9.1	8.6	8.5	9.0	8.3	5.8	?	5.4
Anterior width	5.9	5.5	5.7	5.9	5.5	4.2	?	3.7
posterior width	8.7	8.8	8.9	9.8	8.8	6.4	?	5.9
Mesosoma length	27.7	27.8	23.4	20.3	21.7	15.5	?	15.7
Metasoma length	71.4	50.1	67.8	49.8	62.8	32.6	26.0	?
I length	9.0	6.7	9.4	6.7	9.1	4.2	3.3	3.9
I width	4.1	4.4	4.4	5.5	4.5	3.3	2.7	2.9
II length	11.8	8.0	11.7	7.7	10.6	5.2	4.0	4.5
II width	4.0	4.3	4.3	5.4	4.4	3.2	2.5	2.7
III length	13.0	8.7	12.5	8.6	11.2	5.5	4.2	4.7
III width	4.0	4.2	4.3	5.3	4.3	3.2	2.5	2.7
IV length	12.9	8.5	12.2	8.4	10.8	5.5	4.2	4.7
IV width	3.8	4.2	4.3	5.2	4.2	3.2	2.5	2.7
V length	14.0	9.5	12.8	9.7	12.0	6.2	5.0	5.5
V width	4.0	4.1	4.3	5.0	4.1	3.2	2.3	2.5
V depth	3.8	3.7	4.0	4.4	3.7	2.8	2.2	2.3
Telson length	10.7	8.7	9.2	8.7	9.1	6.0	5.3	?
Vesicle length	7.8	5.7	6.5	5.4	6.4	3.5	3.3	?
Vesicle width	3.7	3.1	3.8	3.4	3.6	2.3	1.9	2.0
Vesicle depth	3.4	2.9	2.6	2.9	2.7	2.0	2.0	2.0
Aculeus length	2.9	3.0	2.7	3.3	2.7	2.5	2.0	?
Pedipalp length	38.4	32.2	35.9	32.9	35.3	23.2	20.1	22.3
Femur length	10.4	8.5	9.7	8.5	9.5	5.7	5.0	5.5
Femur width	2.3	2.2	2.3	2.3	2.3	1.9	1.5	1.6
Tibia length	10.6	8.8	10.0	9.1	9.7	6.4	5.5	6.2
Tibia width	3.0	2.9	2.9	3.2	2.9	2.6	2.0	2.2
Chela length	17.4	14.9	16.2	15.3	16.1	11.1	9.6	10.6
Chela width	3.7	3.2	4.0	3.7	3.4	2.9	2.2	2.5
Chela depth	3.5	3.1	4.8	4.3	4.0	2.6	2.1	2.4
Mov. Fing. length	10.6	9.7	9.7	9.5	10.1	7.3	6.3	6.8

Centruroides margaritatus (Gervais, 1841)
Figs. 11-31

Scorpio margaritatus Gervais 1841:281; 1844a:55.
Scorpio (Atreus) margaritatus, Gervais 1843:130; 1844b:224.
Scorpio (Atreus) edwardsii, Gervais 1843:130; 1844b:216; 1857:41; Thorell 1877:167.
Scorpio edwardsii, Gervais 1844a:53.
(?) *Scorpio degeeri* Gervais 1843:130; 1844a:54.
(?) *Scorpio (Atreus) degeeri*, Gervais 1844b:217.
Centrurus degeeri, Thorell 1877:167; Kraepelin 1891:133.
Centrurus (Atreus) degeeri, Karsch 1879b:124.
Centrurus (Atreus) edwardsii, Karsch 1879b:124.
Centrurus margaritatus, Pocock 1893:386; Kraepelin 1899:93; 1984:95; 1905:339; Borelli 1899:11; Penther 1913:240.
Centruroides margaritatus, Pocock 1902:30; Kraepelin 1914:22; Werner 1934:274; Mello-Leitão 1940:51; 1945:260; Scorza 1954b:160; 1954c:201; Bücherl 1959:268; 1971:327; Aguilar & Meneses 1970:3; Stahnke & Calos 1977:112.
Rhopalurus margaritatus, Meise 1934: 40 (part).

Table 2.—Variation in the number of pectinal teeth among species of *Centruroides* in South America. Only adults are used in the analysis.

No. Teeth:	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
MALES:																	
C. exsul			2			2	2	3	1								
C. gracilis											1	4	5	5	3	1	1
C. margaritatus							7	11	21	17	14	5	8	3	2		
FEMALES:																	
C. exsul	6	5	3	1	6	3											
C. gracilis										2	5	10	7				
C. margaritatus					3	13	33	51	12	16	2						

Rhopalurus danieli Prado & Rios-Patiño 1939:42; Prado 1939:28. **NEW SYNONYMY.**

Centruroides danieli, Mello-Leitão 1940:51; 1945:253; Bücherl 1959:268; 1971:327; Stahnke & Calos 1977:112. **NEW SYNONYMY.**

Centruroides argentinus Werner 1939:357; Mello-Leitão 1945:252; Weidner 1959:99; Abalos 1963:111; Maury 1979:705; Stahnke and Calos 1977:112. **NEW SYNONYMY.**

Type data.—Holotype female of *Scorpio margaritatus* Gervais, 1841, from Isla Puná, Ecuador (Eydoux and Souleyet). Deposited in the Muséum National d'Histoire Naturelle, Paris; examined.

The types of *Scorpio edwardsii* Gervais were not positively identified among the collection of the MNHN. We have examined some material labeled "*Centrurus edwardsii* Gervais" which may be part of the old Gervais collection. Because the identity of these specimens is questionable, we will not designate a lectotype.

Likewise, the types of *S. degeeri* Gervais were not identified among MNHN material, although they are presumably deposited there. Specimens used in the original description reportedly originated from Colombia and Chile (Gervais 1844a,b). All Colombian *Centruroides* we have seen are referable to *C. margaritatus*, but no reliable records of that genus from Chile have been obtained in the nearly 150 years since the original description. We have chosen, therefore, to follow earlier workers and retain *Scorpio degeeri* as a probable synonym of *C. margaritatus*.

The types of *Tityus carinatus* Koch and *Tityus ducalis* Koch, long considered synonyms of *C. margaritatus*, are lost from the Zoologisches Museum, Berlin (M. Moritz, pers. comm.); these synonymies cannot be confirmed.

The types of *Rhopalurus danieli* Prado & Rios-Patiño (male holotype and three male paratypes, IB-Sc-54-57) from Colombia, Andes Colombianos, 26.VI.1936 (H. Daniel) were examined and determined to be conspecific with *C. margaritatus* (see Comments). They are permanently deposited in the Instituto Butantan, São Paulo.

The type female of *Centruroides argentinus* Werner from Campo Santo (Prov. Salta), Argentina, 20.XII.1908 (J. Schmidt), deposited in the Zoologisches Museum, Hamburg, was examined and determined to be a subadult female of *C. margaritatus* (see Comments).

Distribution.—*Centruroides margaritatus* is widely distributed in the Neotropical Region, being recorded from parts of México, Central America, several Antillean Islands (Cuba, Jamaica, and Hispañola), and northern South America. In South America, *C. margaritatus* occurs in Colombia, Ecuador, Venezuela, and
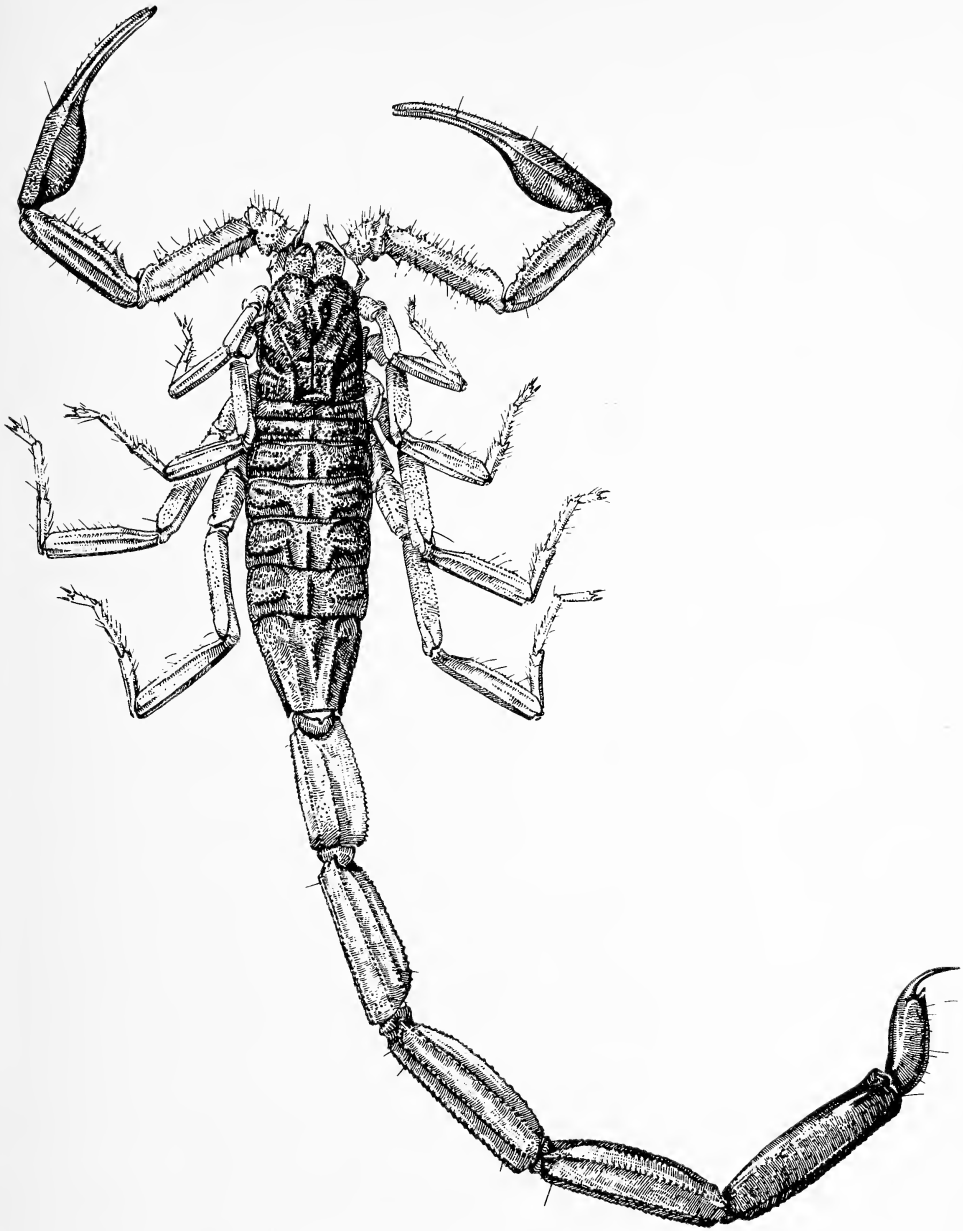
Fig. 11.—Dorsal view of male *Centruroides margaritatus* (Gervais) from Colombia.

possibly Peru. We have also seen a few labeled specimens from Bolivia, Brazil, Chile, and Paraguay, but it is unlikely that the species occurs there.

Redescription.—The following is a complete redescription of the holotype female from Isla Puná, Ecuador. Morphology of an adult male and female from Colombia is illustrated, and figure references in the description refer to those specimens. Male characters are discussed separately (see Variation). Measurements of the holotype and an adult male are given in Table 1.

Prosoma. Carapace (Fig. 12) dark yellow-brown with variable underlying dusky markings; granulation dark brown; ocular tubercle black. Anterior median,
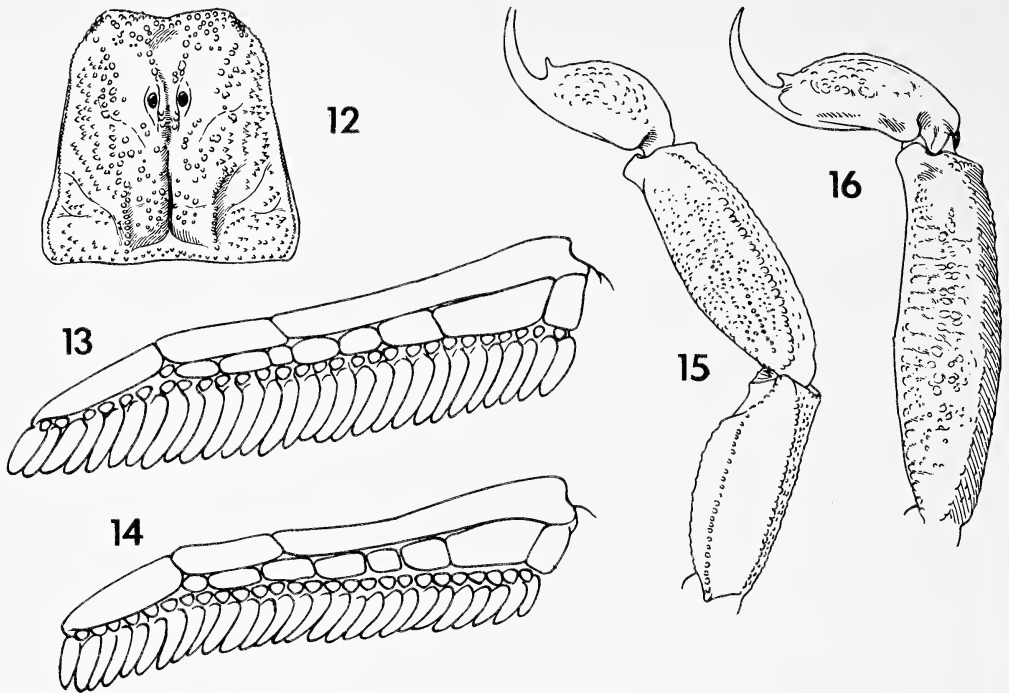
Figs. 12-16.—Morphology of *Centruroides margaritatus* (Gervais): 12, carapace of male; 13, right pectine of male; 14, right pectine of female; 15, distal segments of metasoma and telson of female; 16, metasomal segment V and telson of male.

superciliary, and posterior median keels moderate, composed of large, rounded granules; remainder of carapace with moderately dense, rounded granules. Anterior median furrow moderately deep, ovate; posterior median furrow narrow, shallow anteriorly, deep posteriorly; posterior marginal furrows narrow, deep; posterior lateral furrow shallow, wide, curved. Venter yellow-brown with dark brown tinging; coxal gnathobases orange-brown. Sternum subtriangular, median longitudinal furrow Y-shaped, shallow anteriorly, deep and narrow posteriorly.

Mesosoma. Tergites dark yellow-brown with underlying fuscous pattern; VII lighter than preceding segments; granulation dark brown. Tergites I-VI: pretergites shagreened; post-tergites with moderately dense, coarse, rounded granules. Median keel on I weak, composed of several small granules; on II weak, composed of distinct rounded granules; on III-VI moderate with larger rounded granules. Tergites III-VI with pair of indistinct lateral keels. Tergite VII: granulation as in I-VI; pentacarinate, all keels strong, crenulate. Venter: Genital operculum completely divided longitudinally; genital papillae absent. Pectines (Figs. 13-14): basal piece subrectangular with distinct anteromedian notch; pectinal tooth count 28-29. Sternites yellow-brown with dark brown tinging; III-VI smooth, with elongate stigmata; VII with four moderate keels, median pair smooth, lateral pair finely crenulate.

Metasoma. Segments I-III yellow-brown; IV yellow-brown proximally, dark brown distally; V dark reddish brown. Ventral aspect of all segments darker than dorsal aspect; metasomal carinae dark brown. Segments I-IV: dorsolateral and lateral supramedian keels strong, crenulate. Lateral inframedian keels on I complete, strong, crenulate; on II-III represented by only two to three distal

granules; on IV absent. Ventrolateral keels strong, crenulate. Ventral submedian keels on I moderate, finely crenulate; on II-IV strong, crenulate. Intercarinal spaces with scattered fine granules. Segment V (Figs. 15-16): dorsolateral keels moderate, granular; lateromedian keels obsolete; ventrolateral and ventromedian keels strong, crenulate. Lateral intercarinal spaces coarsely granular, dorsal and ventral spaces finely granular.

Telson (Figs. 15-16). Dark reddish brown. Moderately globose, with strongly curved aculeus. Dorsal surface rounded, smooth; ventral surface coarsely granular. Subaculear tooth moderate, spinoid, directed more towards base of aculeus.

Chelicerae. Yellowish with dark brown mottling on dorsal surface of manus; fingers and teeth dark brown. Dentition as in other *Centruroides*. Fixed finger ventrally with one nodule. Ventral aspect of both fingers and manus with dense, long setae.

Pedipalps. Femur (Figs. 17-18, 23-24) medium brown, lighter than body; carinae dark brown. Tetracarinate: dorsointernal and ventrointernal carinae strong, crenulate; dorsoexternal carina strong, serrate. External carina vestigial, with strong, sharp granules distally. Internal face with about 15 moderate conical granules; other faces shagreened. Orthobothriotaxia A, configuration α.

Tibia (Figs. 19-20, 25-26): Medium brown, lighter than body; carinae dark brown. Hexacarinate: dorsointernal carina moderate, finely serrate. Dorsomedian, dorsoexternal, and external carinae moderate, granular. Ventroexternal carina moderate, granular. Ventrointernal carina moderate, with irregularly spaced large granules. Internal face with moderate basal tubercle; with about 10 moderate conical granules; other faces shagreened. Orthobothriotaxia A.

Chela (Figs. 21-22, 27-30): Palm reddish brown on outer surface, yellowish on inner surface; carinae dark brown. Fingers reddish brown basally, yellowish distally; dentate margins dark brown. Dorsal marginal carina weak, smooth. Dorsal secondary carina moderate, smooth. Digital and ventroexternal carinae strong, granular. External secondary carina incomplete, moderate, granular. Ventromedian carina strong, smooth. Ventrointernal and dorsointernal carinae weak, finely granular. External face with short, granular, basal accessory carina. Fixed finger typically with eight oblique rows of granules; movable finger (Figs. 29-30) typically with eight oblique rows plus a short apical row of 4 granules. Supernumerary granules present. Orthobothriotaxia A.

Legs. Yellowish with variable underlying dusky markings. Tarsus ventrally with numerous short fine setae (Fig. 31).

Variation.—Variation in pectinal tooth counts is given in Table 2. Male pectinal tooth counts range from 25-33 (mode = 27); female counts range from 23-29 (mode = 26). Variation in pedipalp chela finger dentition is given in Table 3.

Males differ from females in the following characters: carapace and tergites with moderately dense, coarse, subconical granules, rather than rounded granules; anterior median, superciliary, and posterior median carapacial carinae strong, not moderate. Genital papillae present. Metasoma: carinae of I-IV moderate, crenulate, with granules widely spaced; all segments elongate, slender. Telson elongate oval with flattened dorsal surface.

There is considerable variability in cuticular granulation and pectinal tooth counts among populations in South America. Specimens in Ecuador and Peru have moderately dense granulation on the carapace and tergites and pectinal
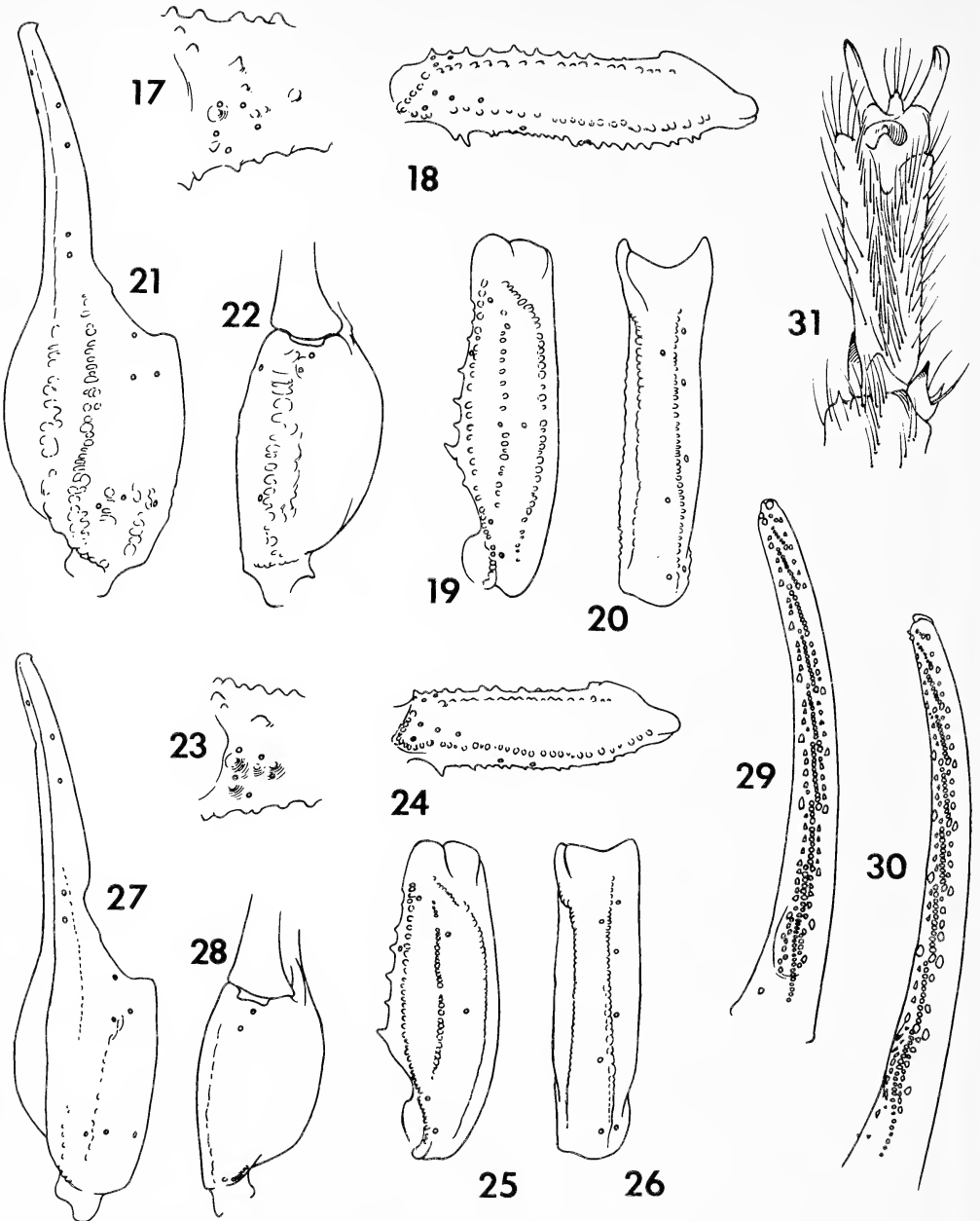
Figs. 17-31.—Morphology of *Centruroides margaritatus* (Gervais): 17-22, pedipalps of males, showing trichobothrial pattern (see legend of *C. gracilis* for explanation); 23-28, pedipalps of females, showing trichobothrial pattern; 29, movable finger of male, showing dentition; 30, movable finger of female; 31, ventral aspect of tarsus of leg IV (female specimen).

tooth counts usually between 24-28. Specimens from Colombia (including specimens of the Gervais collection labeled as "*Centrurus edwardsii*") have more dense granulation and pectinal tooth counts above 27.

   Comments.—*Centruroides margaritatus* is a widespread species, occurring from Mexico to northern South America and in the Antilles. There is a marked tendency for local populations to differ considerably from one another, leading

Table 3.—Variation in the number of oblique rows of granules on the inner margins of the pedipalp chela fingers. Movable finger counts do not include the short apical row.

	No. Rows Fixed Finger				
	6	7	8	9	
C. exsul	—	9	11	—	
C. gracilis	—	—	43	3	
C. margaritatus	2	113	18	—	
	No. Rows Movable Finger				
	5	6	7	8	9
C. exsul	—	—	13	7	—
C. gracilis	—	—	—	18	28
C. margaritatus	2	—	10	110	

some authors to recognize subspecies (e.g., Hoffmann 1932, Mello-Leitão 1945). Unfortunately, records of the species throughout the range are rather patchy and specimens generally few in number, yielding a very poor understanding of the nature of the great variation exhibited. Until variation in this species is better known, the recognition of subspecies seems premature at best.

In South America, the problem is intensified. There are few specimens in museum collections, and what specimens exist often have poor locality data. Many of our specimens are from old collections and give only the country of origin. Preliminary evidence indicates that *C. margaritatus* varies considerably in cuticular granulation, morphometrics, and pectinal tooth counts. These differences do not appear great enough in light of the current understanding of *C. margaritatus* to warrant specific or subspecific status for the different populations.

Specimens of the old Gervais collection labeled "*Centrurus edwardsii*" (but not positively identified as his type material) and the types of *C. danieli* (Prado & Rios-Patiño) exhibit no significant differences from other Colombian material referable to *C. margaritatus*. "*Centrurus edwardsii*" has long been considered a synonym of *C. margaritatus* and it seems appropriate to regard *C. danieli* as a synonym of that species as well. Mello-Leitão (1945) separates *C. danieli* from *C. margaritatus* on the basis of the size of the subacular tubercle and the color of the carinae of the tergites and metasoma. Both of these characteristics exhibit considerable variability in *C. margaritatus* throughout its range, and the characters exhibited by *C. danieli* fall within the normal range of variation of *C. margaritatus*.

Our examination of the holotype of *Centruroides argentinus* has revealed it to be a subadult female of *C. margaritatus*. Since Werner's original description of *C. argentinus*, a considerable amount of work has been done on the scorpion fauna of Argentina (Maury 1979 and included references); however, the type remains the only known specimen from that country. Two characteristics of the type specimen are noteworthy: (1) the movable finger of the pedipalp chela bears eight oblique rows of granules plus a short apical row of four granules, and (2) the size, shape, and angle of the subacular tubercle are identical to those of *C. margaritatus*. Werner (1939) and Mello-Leitão (1945) reported that there are nine rows of granules on the chela movable finger, providing the main characteristic used to separate *C. argentinus* from *C. margaritatus*. By convention established

by earlier workers, however, the ninth (= apical) row is not counted (see Wagner 1977 for a discussion). Obviously, Werner was unaware of this convention; Mello-Leitão apparently based his key on Werner's description, rather than on examination of the type.

Specimens examined.—COLOMBIA: Antioquia, Medellin Valley (1700-1900 m), 1973 (A. B. Schneble), 1 imm. (MCZ); Bogota, 1924 (F. Apollinaire), 5 males, 3 females, RS-1072 (MNHN); no date (Linding), 1 female, RS-1131 (MNHN); Cali, 19-21 June 1948 (P. Nielsen), 1 male (ZMK); Cordoba, Cundinamarca, June 1952, 1 female (IB-Sc-513); Coyaima, Sept. 1944 (R. A. Stirton), 1 female (CAS); Tolima, Coyaima (450 m), Dec. 1944 (R. A. Stirton), 2 females (CAS); Magdalena (Prov. El Banco), no date (W. Cannon), 1 female (AMNH); Popayan, no date (Joannis), 1 male, 2 females, RS-1148 (MNHN); Villavieja, Mar. 1945, 1 imm. male (CAS); no specific locality, date, or collector, 4 males, 2 females RS-1075 (MNHN); 1 female, 1 imm. (AMNH); no specific locality, 28 Sept. 1900 (M. Andre), 1 female RS-1104 (MNHN); Dec. 1973 (A. Negett), 1 female (MNHN). ECUADOR: Balzapamba, June 1938, 1 female (CAS); Guayaquil, 4 males, 1 female (RS-1122); vic. Guayaquil, 1 female (CAS); Guayaquil, no date (Reiss), 2 males, 3 females, 1 imm. female (ZMB); Guayaquil, 10 males, 18 females, 7 imm. (ZMB); Guayaquil, 4 Mar. 1964 (R. O. Schuster), 1 male, 1 female, 26 neonates (CAS); vic. Guayaquil, Feb. 1959, 1 female (CAS); Isla Puná, no date (M. Souleyet), 1 female holotype, RS-1051 (MNHN); Isla Puná, 9 Nov. 1950 (E. S. Ross, A. E. Michelbacher), 1 male, 1 female, 1 imm. female (CAS); Quito, ?1907 (Vorbeck), 1 male (ZMK); Riobamba, ?1901 (Rivet), 1 female, RS-1146 (MNHN); Vallee de Tabacundo (Prov. Quito), May 1884, 1 male, RS-1150 (MNHN). PERU: no specific locality, date, or collector, 2 males, 5 females, RS-1124 (MNHN); ?1901 (Baer), 1 male, 1 female, RS-3336 (MNHN). VENEZUELA: Ciudad Bolivar, ?1901 (Baer), 4 females, RS-3375 (MNHN); Guanoco (Depto. Sucre) (Beebe), 1 female, 70 neonates (AMNH).

Centruroides exsul (Meise, 1934)
Figs. 32-39

Centruroides luctifer Marx 1890:211. **NOMEN NUDUM.**
Isometroides aequatorialis Marx (?): label name in the U.S.N.M., **NOMEN NUDUM.**
? *Androctonus americanus*, Butler 1877:75.
Centrurus princeps, Banks 1902:68; Kraepelin 1899:95.
Rhopalurus testaceus exsul Meise 1934:25.
Centruroides exsul, Mello-Leitão 1945:255; Roth & Craig 1970:119; Kinzelbach 1973:2; Sissom & Francke 1983:1.

Type data.—Holotype female and four paratypes (1 male, 1 female, and 2 immatures) from Isla Floreana, Post Office Bay, Gálapagos Islands (A. Wollebaek, coll.), Sept.-Oct. 1925. Deposited in the Zoologisk Museum, Oslo; examined.

Distribution.—Known from the following islands in the Galápagos Archipelago: Abingdon (= Isla Pinta); Bindloe (= Isla Marchona); Charles (= Isla Santa María, Isla Floreana); Chatham (= Isla San Cristobal); Hood (?) (= Isla Española); and Indefatigable (= Isla Santa Cruz, Isla Chavez). We have also seen specimens from Peru, but the species probably does not occur there naturally.

Description.—Smaller species of *Centruroides*, adults 40-55 mm in length. Color uniformly reddish yellow to reddish brown, lacking dorsal stripes on the mesosomal tergites. Carapace, post-tergites, and intercarinal spaces of metasoma and pedipalps densely, coarsely granular. Median carina of tergites I-VI strong, granular; tergite VII pentacarinate, all five keels strong, crenulate to serrate. Sternite VII tetracarinate, all keels moderate, granular. Pectinal tooth count 21-32 (mode = 26) in males, 19-24 (mode = 23) in females; female basal pectinal piece with small central depression. Metasomal segments of adult males more or less
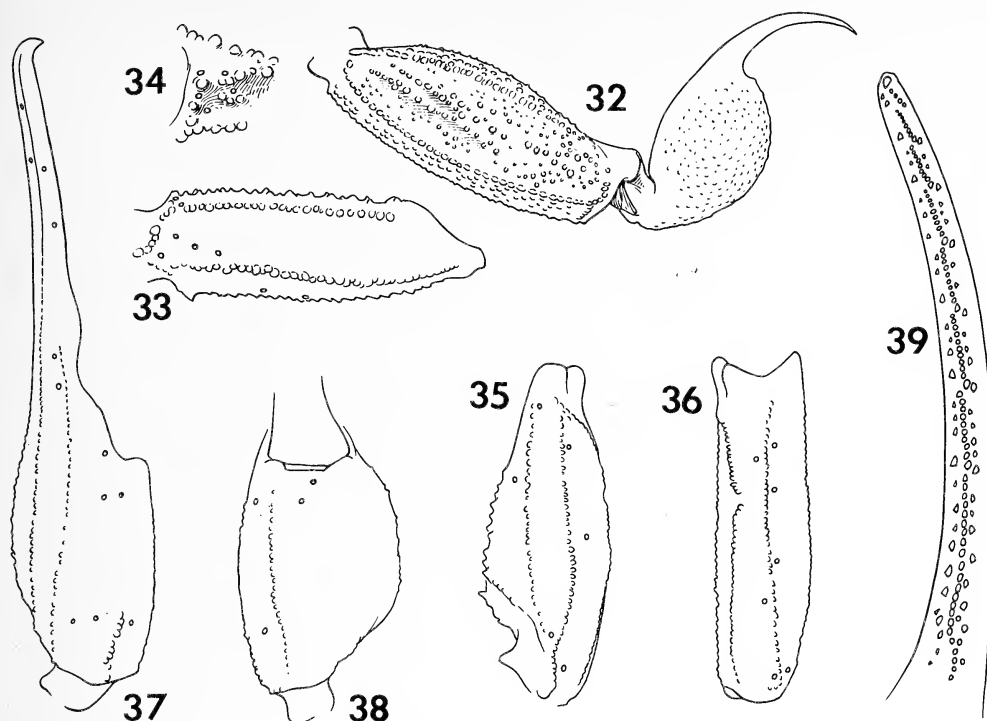
Figs. 32-39.—Morphology of male paratype of *Centruroides exsul* (Meise): 32, metasomal segment V and telson; 33-38, trichobothrial pattern of pedipalp (see legend of *C. gracilis* for explanation); 39, movable finger of pedipalp chela showing dentition.

equal in length to those of female. Metasomal carinae on I-IV moderate to strong, crenulate to serrate; metasomal segment V (Fig. 32) pentacarinate. Telson vesicle irregularly granular; subaculear tooth obsolete to vestigial (Fig. 32). Dorsal marginal, dorsal secondary, ditigal, ventroexternal, and dorsointernal carinae of pedipalp chela strong, granulose; external secondary carina vestigial, granulose distally. Fixed finger with 7-8 oblique rows of granules; movable finger (Fig. 39) with 7-8 such rows plus a short apical row of 3-4 granules; supernumerary granules present in older instars. Orthobothriotaxia A, with α configuration (Figs. 33-38) (Vachon 1973, 1975). Cheliceral fixed finger with one ventral nodule.

Variability.—Variation in pectinal tooth counts and pedipalp chela finger dentition are summarized in Tables 2 and 3, respectively. Kinzelbach (1973) reported a variability of 7-12 rows of granules on the chela fingers for this species, with the high counts occurring on Abingdon, Chatham, and Charles Islands. We have seen only 7-8 rows on the fixed finger and 7-8 rows on the movable finger on all specimens we have examined, including those from Charles and Abingdon Islands. Further, the possession of 12 rows is unknown in *Centruroides*; therefore, Kinzelbach's report is apparently in error.

Comments.—The type material is in good condition, although coloration is somewhat faded in alcohol. The pectines of the male paratype are destroyed. Measurements of the holotype female and the paratype male are given in Table 1.

Specimens examined.—GALÁPAGOS ISLANDS; *Isla Floreana*, Post Office Bay, Sept.-Oct. 1925 (A. Wollebaek), holotype female, 1 male, 2 females and 2 juv. paratypes (ZMO); 19 Aug. 1975 (C.

Ribera), 1 male, 1 juv. (UB); *Indefatigable Is.*, Academy Bay, Dec. 1968 (A. and J. DeRoy), 1 juv. (CAS); *Isla Marchona*, Cabo Espijo Camp (10 m, dry *Bursera* litter, under box in camp), 27 Jan. 1978 (W. G. Reeder), 1 juv. (UT); *Isla Pinta*, South coast, 25 May 1964 (D. Q. Cavagnaro), 4 males, 1 female, 11 juvs. (CAS); South slope (400 m, under small lava rocks and decaying wood), 19 July 1977 (W. G. Reeder), 1 juv. (UT); (400 m, night collection on *Xanthoxylum* and basal rock outcrop), 20 July 1977, 1 male (UT); (250 m, under rock, *Pisonia* coppice), 20 Jan. 1977, 1 male (UT); (at night, rocky outcrop), 1 female (UT); South Playa (5 m, under driftwood on lava shell beach), 21 Jan. 1977 (W. G. Reeder), 1 juv. (UT); 16 July 1977, 1 male (UT); *Isla Santa Cruz*, Academy Bay (under stones), 23 Aug. 1968 (A. and J. DeRoy), 1 female (CAS); Academy Bay, Darwin Research Station, 8 Feb. 1964 (Schuster), 1 juv. (CAS); no date (Cavagnaro and Schuster), 1 female (CAS); Table Mountain (440 m), 16 Apr. 1964 (D. Q. Cavagnaro), 5 females, 1 juv. (CAS). PERU: no specific locality, no date (M. Eydoux), 1 male, 1 female, RS-1111 (MNHN).

Centruroides dasypus Mello-Leitão, 1948

Centruroides dasypus Mello-Leitão *in* Mello-Leitão & Araújo-Feio 1948:316; Aquilar & Meneses 1970:3; Stahnke & Calos 1977:112; Francke 1977:75.

Type data.—One male holotype, 1 female allotype, and 3 female paratypes from Andahuaylas, Perú (3000 m), W. Weyrauch, coll. Deposited in the Museu Nacional, Rio de Janeiro; examined.

Comments.—Since its original description (Mello-Leitão 1948), *Centruroides dasypus* has been considered a rather unique species in South America, known only from the type locality. Examination of this material has led to the clarification of the identity of *C. dasypus*. The following evidence will clearly establish that *C. dasypus* is a junior synonym of *Centruroides vittatus* (Say) from south-central USA and northern Mexico.

Color pattern.—Although the color pattern is somewhat faded in alcohol, specimens of *C. dasypus* possess the same distinctive pattern as *C. vittatus*. The mesosoma bears a pair of darkened, longitudinal, submedian stripes, which extend into the posterolateral regions of the carapace. The interocular triangle of the carapace is conspicuously darkened and offset from the surrounding areas on the carapace, as in *C. vittatus*. Finally, the ventral aspect of the metasoma has a dark median stripe, and the pedipalp chela fingers are the same color as the chela manus. Although color variation in *C. vittatus* is great, this particular combination of color characteristics (particularly the offset interocular triangle) is definitely the most common pattern observed.

Pedipalp chela finger dentition.—Mello-Leitão (1948) reported seven rows of granules on the chela fingers of *C. dasypus*, a characteristic which has made *C. dasypus* distinct among *Centruroides* spp. (see, for example, the key of Stahnke & Calos 1977). However, in *Centruroides*, the two basal rows of granules are frequently fused (Wagner 1978, Francke & Sissom 1980). Therefore, a species which normally has eight rows of granules would appear to have only seven, and this is precisely the case for *C. dasypus*. The female allotype of *C. dasypus* has "seven" rows on the left chela; however, it clearly has eight rows on the right chela, a fact apparently missed by Mello-Leitão (1948). The holotype male has eight rows on both chelae. The possession of eight rows on the chela fingers is widespread in *Centruroides* and occurs in *C. vittatus*.

Legs.—Mello-Leitão (1948) reported that the tarsi of *C. dasypus* are very pilose, and that this distinguishes the species from others in the genus. This statement is not true, and the pilosity of the tarsi of *C. dasypus* is not different from that of *C. vittatus* or many other species in the genus.

We have also found *C. dasypus* to be virtually identical to *C. vittatus* in trichobothrial pattern, size and shape of the subaculear tubercle, and in carinal development of the pedipalps, metasoma, tergites, and sternite VII. The specimens of *C. dasypus* exhibit slightly lower pectinal tooth counts than the average value observed in *C. vittatus*, but this can be attributed to sampling error. The types of *C. dasypus* also exhibit smaller body size than the typical *C. vittatus*, but the latter exhibits a wide range of adult body size throughout its range and even within populations (W. D. Sissom, pers. obs.). The differences in these last two features cannot be considered important as species characters. An additional point to consider is that the striped forms of *Centruroides* possessing eight subrows on the pedipalp chela fingers are restricted to the United States, México, and the Caribbean (with the exception of *C. thorelli*, which occurs as far south as Costa Rica).

Conclusions.—The evaluation of the above taxonomic characters has demonstrated that *C. dasypus* is not a valid species. We hereby propose the following synonymy: *Centruroides vittatus* (Say, 1821) = *Centruroides dasypus* Mello-Leitão, 1948.

The occurrence of *C. vittatus* at Andahuaylas, Perú is very difficult to explain, as this locality is deep in the Andes in the province of Apurimac. Although we have seen North and Central American specimens of *Centruroides* which apparently were introduced to South America (most are from port cities), it seems doubtful that the Andahuaylas record is an introduction. We suspect, instead, that the record is the result of a labeling error.

Specimens examined.—PERU: Andahuaylas (3000 m), (W. Weyrauch), 1 male holotype, 1 female allotype, 3 females paratypes of *C. dasypus* (MNRJ).

ACKNOWLEDGMENTS

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EL GENERO *NEOCTENIZA* POCOCK, 1895 (ARANEAE, MYGALOMORPHAE, IDIOPIDAE) EN. LA ARGENTINA Y PARAGUAY

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ABSTRACT

Five new species of *Neocteniza* are described: *N. spinosa*, *N. minima*, *N. toba* and *N. australis* from Argentina, and *N. platnicki* from Paraguay. *N. toba* and *N. australis* together are proposed as the sister group of all other species of *Neocteniza*. Some biological data of these trapdoor spiders are given.

EXTRACTO

Se describen cinco especies nuevas de *Neocteniza*: *N. spinosa*, *N. minima*, *N. toba* y *N. australis* de Argentina, y *N. platnicki* de Paraguay. *N. toba* y *N. australis* juntas son propuestas como grupo hermano de todas las demás especies de *Neocteniza*. Se dan algunos datos biológicos de estas arañas albañiles.

INTRODUCCION

Las arañas albañiles, muy abundantes en ciertos lugares, son, por sus costumbres, raramente encontradas por los colectores no especializados. En viajes realizados por el autor a distintos puntos de la Argentina se puso mayor atención en las arañas de este grupo; el resultado ha sido muy satisfactorio, siendo de destacar el hallazgo de varios ejemplares de *Neocteniza* Pocock 1895 (Idiopidae) (Fig. 1), casi siempre junto con especies de *Idiops* Perty 1833 (Idiopidae) y *Actinopus* Perty 1833 (Actinopodidae), dos géneros más comunes. En la colección del Museo Argentino de Ciencias Naturales se ubicaron tres ejemplares más del género. Además, el Dr. Norman I. Platnick, del American Museum of Natural History, tuvo la gentileza de enviar material de Paraguay colectado por el Sr. John A. Kochalka, voluntario del Cuerpo de Paz de ese país. Todo este material de estudio (que sobrepasa el medio centenar de ejemplares) ha sido separado en cinco especies, cuatro de Argentina (*N. minima* sp. n. de Salta y Jujuy, *N. spinosa* sp. n. de Santiago del Estero, *N. toba* sp. n. de Salta, Jujuy y Tucumán y *N. australis* sp. n. de Córdoba y Buenos Aires) y una de Paraguay (*N. platnicki* sp. n. de Chaco).

MATERIALES Y METODOS

Excepto las medidas de las cuevas, todas las demás están dadas en milímetros; fueron tomadas con ocular micrométrico, según Coyle (1974), excepto el ancho y largo del área de los ojos medios (medido por el centro de los ojos), y largo del área ocular (medido desde extremo posterior de ojos laterales posteriores hasta extremo anterior de ojos laterales anteriores).

Las descripciones son hechas utilizando un solo ejemplar. Las cifras separadas por una barra que se mencionan al citar las espinas de las patas (por ejemplo, fémur IV de *N. spinosa* 46/49 D ant.) se refieren a ambos lados de un mismo ejemplar. Las variaciones observadas en otros ejemplares que se consideran importantes, son puntualizadas aparte.

Las abreviaturas utilizadas para la notación de la quetotaxia son las siguientes: P, prolateral; R, retrolateral; D, dorsal; V, ventral; inf., inferior; sup., superior; ant., anterior; post., posterior; ap., apical; b., basal. Las abreviaturas (1:2 ap.) o (1:3 ap.), colocadas a continuación de una cifra, indican que esas espinas se encuentran en la mitad apical o en el tercio apical del artejo, respectivamente.

Los ejemplares estudiados están depositados en el American Museum of Natural History (A.M.N.H.) y en la Colección de Arácnidos del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (M.A.C.N.).

BIOLOGIA

Al igual que otras Mygalomorphae de Argentina (como muchas Nemesiidae, Dipluridae, Idiopidae y Actinopodidae), las *Neocteniza* se encuentran principalmente en lugares con vegetación natural, cerca de ríos o arroyos, en sitios inclinados o de barrancas. Este no es el caso para las Theraphosidae de gran tamaño, que no parecen restringidas a este tipo de hábitat. La distribución de las Mygalomorphae pequeñas parece estar sumamente relacionada con la cubierta vegetal y, sobre todo, con la naturaleza del suelo; es posible que los factores más importantes sean la temperatura y la distribución del agua.

Las únicas especies del género de las que hay datos biológicos son *N. minima*, *N. toba*, *N. australis* y *N. platnicki*. Esta última fue encontrada por J. Kochalka "cavando a un pie de profundidad, aproximadamente, en suelo blando, húmedo, donde había un pedazo de madera podrida enterrado. La araña apareció allí, entre la tierra, mientras se cavaba, y no se vio cueva, opérculo ni nada". Las otras tres especies mencionadas hacen una cueva poco profunda, con un opérculo fino, sin bordes biselados y no muy rígido, que apoya en los bordes (Fig. 2). La cueva forma un ángulo de unos cuarenta y cinco grados (o menos) con la horizontal, con la cámara de reposo no ensanchada y con la misma inclinación. Las paredes están relativamente poco rastrilladas, y tapizadas con abundante seda, muy blanca, que se separa en hebras (es posible que la araña aplique nuevas capas periódicamente). La cueva, en *N. australis* y *N. toba*, tiene un diámetro de 1.5 cm y una profundidad de hasta 15 o 20 cm aproximadamente; en *N. minima* es más pequeña, de 1 cm de diámetro y unos 10 cm de profundidad. Los machos jóvenes construyen una cueva similar a la de las hembras, pero más pequeña, de 0.5 cm de diámetro, cuya tapa clausuran antes de mudar.

Las cuevas de *Actinopus* e *Idiops* son facilmente diferenciables de las de *Neocteniza*. Las primeras construyen un opérculo grueso, biselado, con cueva más
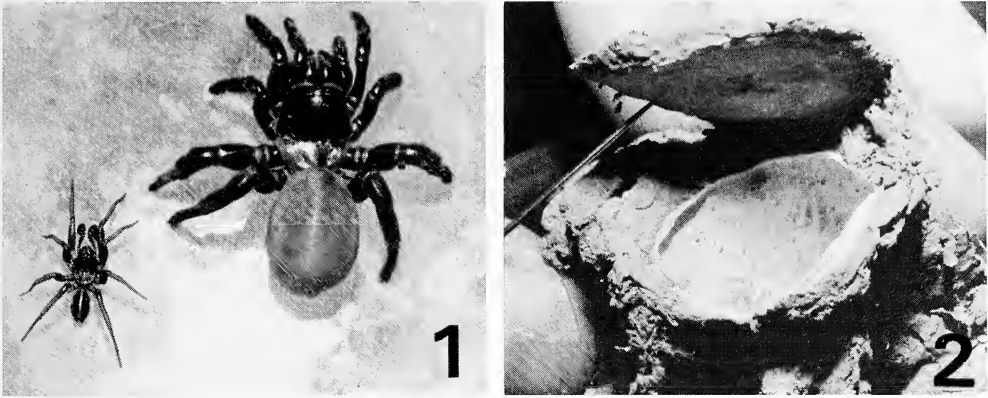
Figs. 1-2.—*N. australis*: 1, macho y hembra; 2, entrada a la cueva.

profunda y vertical (a veces inclinada); paredes muy rastrilladas, con o sin capa de seda (cuando la hay, acartonada e incorporada a las paredes). Las cuevas de *Idiops* son un poco más parecidas a las de *Neocteniza* puesto que son cortas, de opérculo fino y tapizadas con mucha seda; pero son bastante verticales, con cámara ensanchada, y si bien la seda es abundante, no se separa en hebras, sino que es compacta y rígida, desprendiéndose de las paredes como un tubo.

Los machos subadultos de *N. minima* y *N. australis* mantenidos en cautiverio efectuaron su última muda a principios de la primavera (cuatro machos, en setiembre-octubre) o, más raramente, a principios del otoño (un macho, a fines de marzo).

En el mes de mayo, en la provincia de Salta (Argentina), pudo observarse la ooteca de *N. minima*: muy parecida a la de *Actinopus*, plano convexa, cuadrada, de 7 u 8 mm de lado, con una capa superior de tela y otra inferior que cuelga conteniendo los huevos. La ooteca estaba sostenida por los cuatro ángulos de las paredes de la cueva, en posición horizontal. Una ooteca contenía 54 huevos de 1.64 mm de diámetro. Hembras con cría fueron observadas en enero, en la provincia de Córdoba, y en marzo, en la provincia de Buenos Aires, en Argentina; las crías permanecían aún en la cueva materna, y se deslizaban rápidamente hacia abajo al abrir la tapa.

En casi todas las localidades mencionadas en este trabajo se encontraron pupas de avispa en cuevas de *Neocteniza* (o más raramente, sus larvas sobre el abdomen de arañas vivas, sin paralizar). Las avispas pertenecían a la familia Pompilidae, pero no se pudo identificar la especie. En la foseta torácica de dos ejemplares de *N. minima* se encontró una especie no identificada de ácaro.

En las cuevas se han encontrado a menudo restos de presas, sobre todo de coleópteros.

LA GENITALIA DE *NEOCTENIZA*

La genitalia de *Neocteniza* está sumamente modificada. Esta parece ser la sinapomorfía más importante del género, como claramente lo sugiere la comparación con géneros relacionados (ver Raven 1985).

El bulbo del macho es particularmente curioso. Mientras que en las demás Mygalomorphae es generalmente rígido y prácticamente inmóvil, en *Neocteniza*
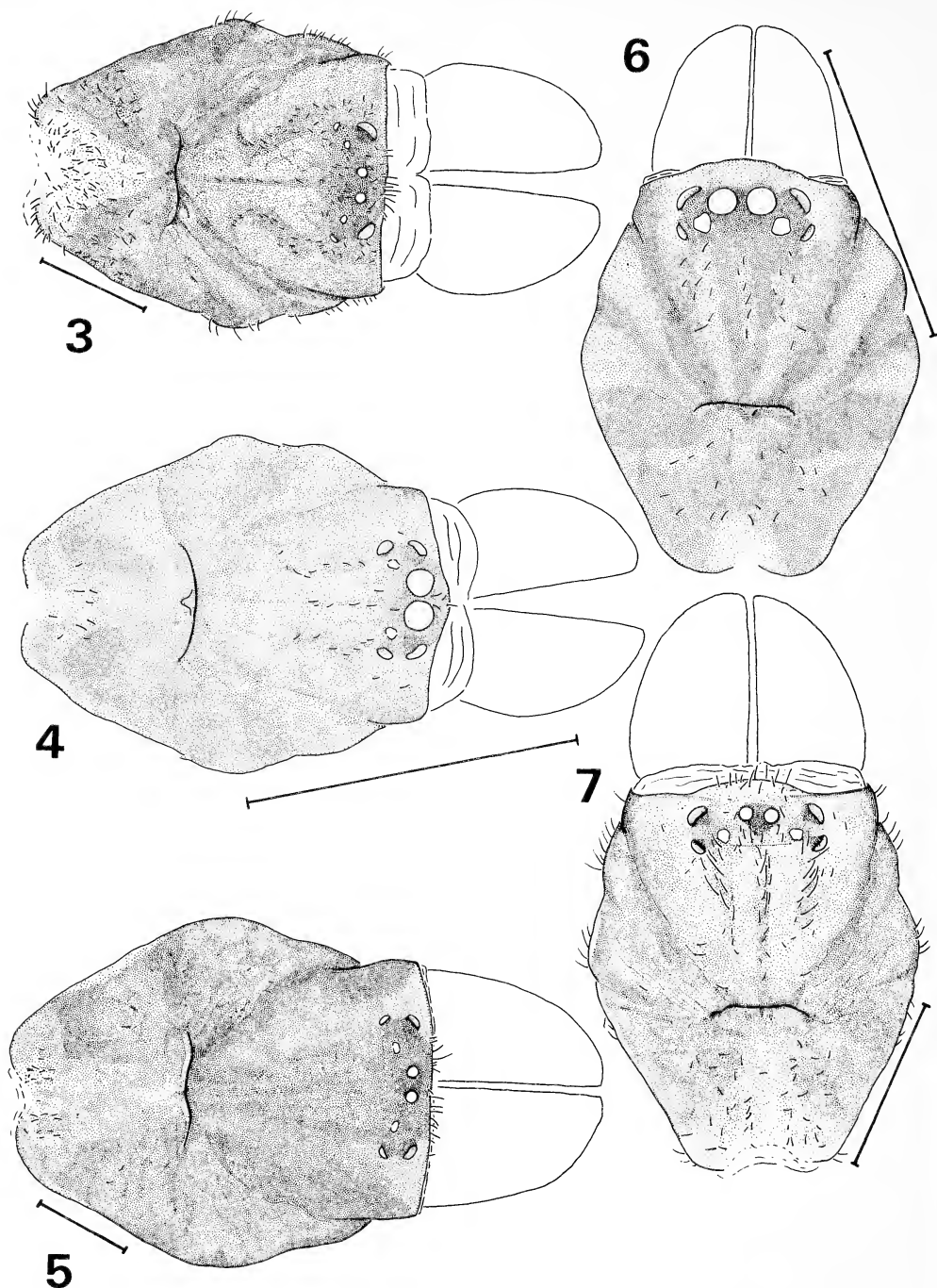
Figs. 3-7.—Cefalotórax. 3-4, *N. australis*: 3, hembra; 4, macho. 5, *N. spinosa*, hembra. 6-7, *N. minima*: 6, macho; 7, hembra. (Escala = 3 mm)

tiene partes membranosas que lo hacen de forma variable. En los machos vivos el bulbo permanece expandido; pero en algunos machos el bulbo se contrae con la fijación, descargándose, y rompiéndose las membranas en torno al émbolo, quedando éste sostenido sólo por su base (Figs. 36, 40). Probablemente una contracción similar ocurra durante la cópula—a diferencia de las Araneomor-

phae, en las que ocurre una expansión—con la que el émbolo pueda desprenderse y quedar retenido en las espermatecas de la hembra (Figs. 10, 14, 44, 45).

La genitalia femenina se encuentra adaptada para la retención del émbolo. Los ductos de las espermatecas tienen dos porciones bien diferenciadas: la parte distal (más próxima a las espermatecas, con abundantes glándulas) y la parte inicial. En el grupo *sclateri*, de genitalia más modificada, la porción inicial de los ductos está fuertemente esclerosada (formando las bolsas copulatrices *sensu* Platnick y Shadab 1976), mientras que en el grupo *australis* es membranosa.

En *N. minima* (grupo *sclateri*) la fijación del émbolo se produce aparentemente en la porción inicial del ducto.

En *N. australis* (grupo *australis*) la fijación del émbolo se realiza por el enganche de las carenas de su extremo en la porción distal del ducto, quedando la parte basal retenida entre las membranas de la porción inicial, con la cara externa (plana) ubicada hacia arriba y la parte interna hacia abajo. El émbolo derecho se introduce en la espermateca izquierda, y viceversa (ver Figs. 10 y 37,38). Uno de los ejemplares estudiados de esta especie, encontrado con las crías en la cueva, tiene émbolo solamente en una de sus espermatecas; puede deberse a que el bulbo no se haya roto durante la cópula o a una rotura previa de éste. Otro ejemplar tiene, en una de sus espermatecas, dos émbolos; es evidente que las cópulas adicionales de las hembras pueden ser raras pero no imposibles.

Género *Neocteniza* Pocock

Neocteniza Pocock 1895:190; Platnick y Shadab 1976:1.

Diagnosis.—Se distingue por la presencia simultánea de ojos en dos filas, rastrillo, foseta torácica recurva (en forma de T), bulbo del macho con escleritos apicales separados y haematodocha media enormemente desarrollada.

Especie tipo.—Por monotipia, *N. sclateri* Pocock 1895.

Lista de especies.—*N. australis* sp. n., *N. fantastica* Platnick y Shadab 1976, *N. malkini* Platnick y Shadab 1981, *N. mexicana* Cambridge 1897, *N. minima* sp. n., *N. occulta* Platnick y Shadab 1981, *N. osa* Platnick y Shadab 1976, *N. paucispina* Platnick y Shadab 1976, *N. platnicki* sp. n., *N. pococki* Platnick y Shadab 1976, *N. sclateri* Pocock 1895, *N. spinosa* sp. n., *N. subirana* Platnick y Shadab 1976, *N. toba* sp. n.

CONSIDERACIONES SISTEMATICAS

El género *Neocteniza* ha sido incluído por la mayoría de los autores en la familia Actinopodidae; sin embargo, Raven (1985), encuentra evidencia en la estructura del bulbo de los machos como para incluirlo en Idiopidae.

En cuanto a su monofiletismo, está evidenciado no sólo por la gran similitud morfológica general, sino también por la presencia común de un carácter indiscutiblemente derivado, puesto que hasta ahora no se ha encontrado en ninguna Mygalomorphae fuera de *Neocteniza*: el acondicionamiento del aparato copulador para la rotura del émbolo durante la cópula y su fijación en los ductos de las espermatecas. Dicho acondicionamiento implica, obviamente, modificaciones morfológicas de esas estructuras. En los machos los escleritos apicales del

bulbo están muy separados, el subtegulum es de gran tamaño, y las haematodochae están muy desarrolladas, en especial la haematodocha media, globosa y replegable. Es posible que la prolongación membranosa de los labios de la abertura genital de las hembras (que podría ser llamada con propiedad bolsa copulatriz), también esté relacionada, dado que forma una cámara mucho mayor que en otros géneros (Figs. 8-10).

En varias especies de *Neocteniza*, las modificaciones son más pronunciadas. En las hembras la porción inicial del ducto está engrosada y fuertemente esclerosada, con su entrada sobre la abertura genital; el área epigástrica también está muy esclerosada (presentando a menudo elevaciones). En los machos el émbolo es muy largo y delgado, el bulbo tiene un esclerito apical con una apófisis y la haematodocha apical está tan desarrollada como la media. Estas parecen ser sinapomorfías de dichas especies, mientras que en las restantes los mismos caracteres se encuentran en un estado que sería plesiomórfico: la porción inicial del ducto es membranosa, aplanada, con su entrada alejada de la abertura genital, comunicada a una suerte de atrio; el émbolo del bulbo es más grueso, no existe esclerito apical con apófisis, y la haematodocha apical es pequeña. Estos sentidos de transformación podrían determinarse aún sin conocer con seguridad el grupo hermano de *Neocteniza*, ya que los caracteres considerados aquí como derivados, son únicos entre las Mygalomorphae.

El primer grupo de especies es llamado grupo *sclateri*, y contiene a *N. fantastica*, *N. malkini*, *N. mexicana*, *N. minima*, *N. occulta*, *N. osa*, *N. paucispina*, *N. platnicki* , *N. pococki*, *N. sclateri*, *N. spinosa* y *N. subirana*. Se caracteriza por las sinapomorfías mencionadas. En cuanto al segundo grupo, los caracteres que lo diferencian del anterior estarían en estado plesiomórfico. De todas maneras, aún ante la falta de sinapomorfías conocidas, dada la gran similitud de sus dos únicas especies se lo puede considerar un grupo con posibilidades ciertas de ser monofilético, al que se llama grupo *australis*, y contiene a *N. australis* y *N. toba*.

CLAVE DE LAS ESPECIES DE *NEOCTENIZA* DE ARGENTINA Y PARAGUAY

1. Machos...2
   Hembras..3

2. Tibia del palpo muy corta y gruesa, con espinas agrupadas. Embolo muy delgado (Figs. 32-36). Protarso I con una espina apical larga (Fig. 24) ....*N. minima* sp. n.
   Tibia del palpo más alargada, espinas separadas. Embolo más grueso (Figs. 37-40). Protarso I sin espina apical larga (Fig. 31)................*N. australis* sp. n.

3. Area epigástrica fuertemente esclerosada, con elevaciones (Fig. 15). Porción distal de los ductos larga, porción inicial fuertemente esclerosada..............4
   Area epigástrica poco esclerosada, sin elevaciones. Porción distal de los ductos corta, porción inicial membranosa...6

4. Porción inicial de los ductos recta (Fig. 11). Ojos bastante separados entre sí (Fig. 5). Palpo sin espina larga....................................*N. spinosa* sp. n.

Porción inicial de los ductos curvada (Figs. 14, 45). Ojos más próximos entre sí (Fig. 7). Tibia del palpo con una espina prolateral muy larga (Fig. 20)......5

5. Espinas de las patas anteriores muy cortas. Tarsos I con 15 espinas prolaterales (Figs. 42, 43). Entrada a los ductos más ancha que alta (Fig. 44) ....*N. platnicki* sp. n.
Espinas de las patas anteriores más largas. Tarsos I con no más de 10 espinas en cada cara (Figs. 22,23). Entrada a los ductos ancha como alta (Fig. 16)...... ....*N. minima* sp. n.

6. Ductos rectos (porción distal e inicial en la misma dirección). Espermatecas convergiendo hacia el ápice (Fig. 9). Tarsos I y II con espinas más numerosas en la cara retrolateral que en la prolateral (Figs. 27, 28) ......*N. australis* sp. n.
Ductos curvados hacia afuera (porción distal formando con la inicial un ángulo de cuarenta y cinco grados). Espermatecas más o menos paralelas (Fig. 8). Tarsos I y II con espinas más numerosas en la cara prolateral que en la retrolateral (Figs. 25, 26) ....*N. toba* sp. n.

DESCRIPCION DE LAS NUEVAS ESPECIES

Neocteniza spinosa, especie nueva
Figs. 5, 11, 12, 17, 18

Etimología.—Así denominada por ser la especie del género que más espinas tiene en las patas.

Diagnosis.—Se distingue de todas las demás especies del género por el gran número de espinas de las patas y por su genitalia. De las otras especies argentinas se distingue además por sus ojos más separados, la región cefálica más baja, las dos espinas (en lugar de cerdas) en la corona del protarso I y las uñas tarsales sin dentículos.

Descripción del Holotypus hembra.—Cefalotórax (Fig. 5) de largo 12.17, ancho 10.64, alto 9.31. El ancho es el 87% del largo. Región cefálica menos elevada que en las otras especies argentinas, menos convexa, de largo igual al 91% del ancho; el largo es el 59% del largo del cefalotórax, y el ancho es el 74% del ancho de la región torácica. La fóvea ocupa el 34% del ancho de la región torácica.

Ojos ocupando el 52% del ancho de la región cefálica; área ocular de ancho 332% del largo; área de los ojos medios de ancho 441% del largo. Por delante de los ojos hay 35 cerdas; por detrás, 15, y 3 filas, la media de 33 y las laterales de 10 o 12 (muchas cerdas están caídas, pero se advierten sus puntos de inserción).

Labio de largo igual al 83% del ancho. Coxas de los palpos con 1 o 2 espínulas. El ancho del esternón es el 85% del largo, con la depresión anterior del mismo largo que el labio.

Margen interna de los quelíceros con 6 o 7 dientes grandes y 3 pequeños, margen externa con 10 de la mitad (o menos) del tamaño de los dientes de la margen interna; entre ambas márgenes, unos 30 dentículos de las 2/3 partes del tamaño de los dientes de la margen externa. Rastrillo formado por cúspides romas, más cortas que en las otras especies, en número aproximado de 20.
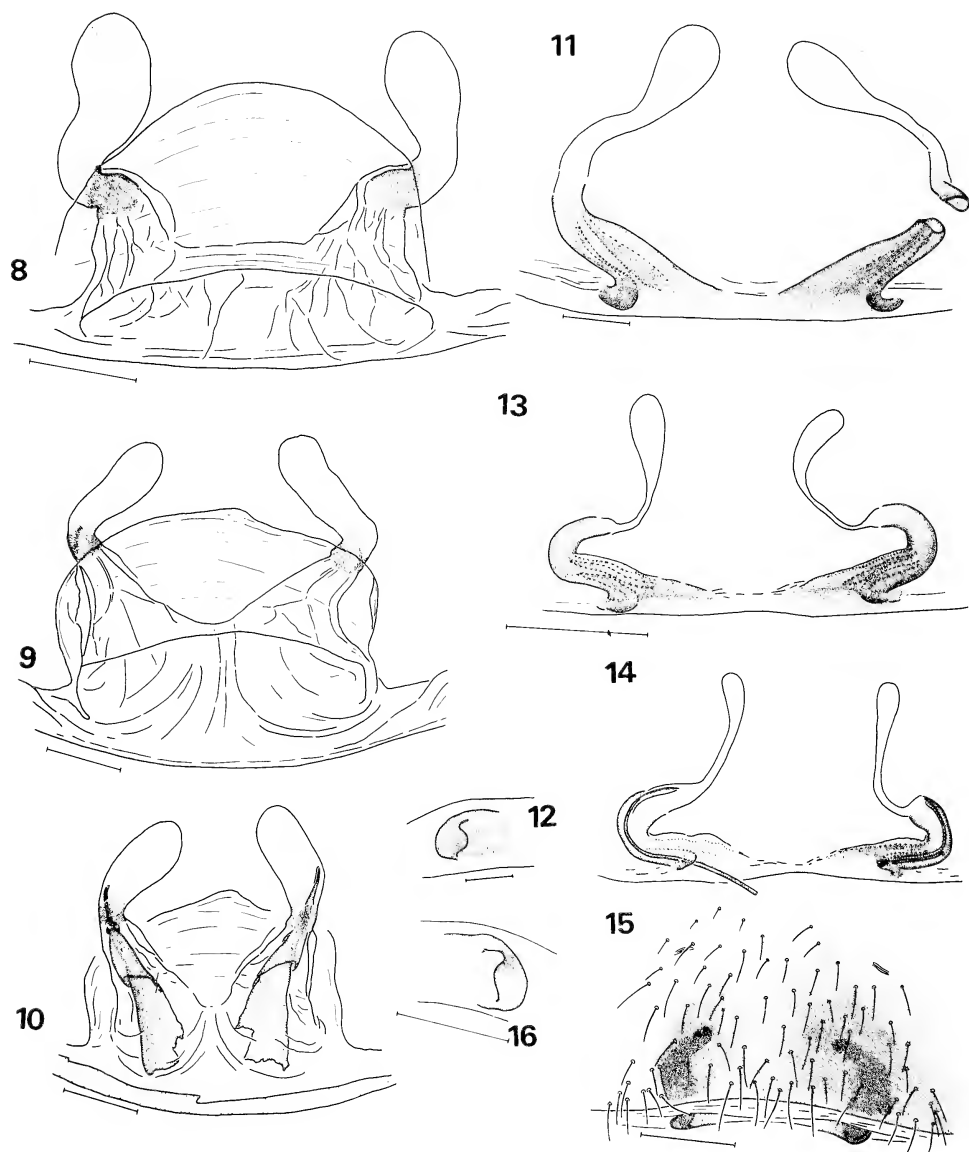
Figs. 8-16.—Genitalia femenina. 8, *N. toba*, espermatecas, vista dorsal. 9-10, *N. australis*: 9, espermatecas, vista dorsal; 10, espermatecas con émbolos, vista ventral. 11-12, *N. spinosa*: 11, espermatecas, vista ventral; 12, entrada al ducto izquierdo, vista desde atrás. 13-16. *N. minima*: 13, espermatecas, vista ventral; 14, espermatecas con émbolos, vista ventral. 15, área espigástrica; 16, entrada al ducto derecho, vista desde atrás. (Escala = 0.5 mm)

Patas IV, III = I, II.

	Fémur	Patella + Tibia	Protarso	Tarso
I	6.65	8.11	3.39	1.66
II	6.38	7.51	3.32	1.66
III	5.98	7.05	4.26	2.66
IV	8.45	9.38	6.38	2.13
P	5.32	5.85	-	3.59

Tricobotrias: Tibias: I, fila anterior 8, posterior 7; II, fila anterior 8, posterior 9; III, fila anterior 7, posterior 8; IV, fila anterior 8, posterior 13; palpo, fila anterior 7, posterior 5. Protarsos: I, 24; II, 21; III, 16; IV, 15. Tarsos: I, 21; II, 23; III, 22; IV, 19; palpo, 18.

Quetotaxia: Fémur IV, 46/49 D ant. ap.; I, II, III y palpo, inermes. Patella III, 39/40 P, peine P ap. de 13/15, 3/4 R ap.; IV, aproximadamente 20 cúspides D ant. b. que se adelgazan hacia el ápice; I, II, inermes; palpo 1/1-1 P. Tibia I (Fig. 19), 20/21 P, 55 R inf.; II, 13 P, 34/35 R inf.; III, 52/55 P, 30 D, 16/20 R; IV, inerme; palpo, 22/25 P, 29/30 R. Protarso I (Fig. 17), 39/43 P, 45/49 R; II, 39/43 P, 34/40 R; III, 25/26 D ant., 21/26 D post., 1 V ap.; IV, 8/12 P, 1/1-1 P inf., 1-1 R sup. (1:3 ap.), peine P inf. ap. de 5/6, 1 V ap. Tarso I (Figs. 17-18), 17 P, 12/17 R; II, 16/18 P, 9 R; IV, 2/3 P; III, inerme; palpo, 34/38 P, 32/35 R, 2 V ap.

Protarso I con 2 pequeñas espinas (Fig. 18) en lugar de la corona de cerdas de las demás especies; protarso II con 2 cerdas gruesas; protarso III con 2 coronas, ambas de 3 o 4 cerdas, con la espina ventral apical entre ambas; protarso IV con 2 coronas, la anterior de 3 o 4 y la posterior de 6 o 7, con la espina ventral apical entre ambas.

Uñas tarsales cortas y gruesas, con un solo diente y sin dentículos.

Area epigástrica fuertemente esclerosada, con elevaciones que han sido parcialmente destruídas (posiblemente al hacer la disección de las espermatecas). Genitalia: Figs. 11-12.

Hileras cortas, con fúsulas numerosas, de tamaño más o menos uniforme. Las anteriores tienen unas 50 fúsulas; el artejo basal de las posteriores tiene unas 110 o 120 (10 de ellas agrupadas en el ápice), el artejo medio unas 90 (unas 20 agrupadas) y el artejo apical unas 35 (unas 10 o 12 agrupadas).

Colorido: cefalotórax marrón oliváceo uniforme; abdomen oscuro, con el vientre más claro; esternón y coxas de las patas amarillentos, labio y coxas de los palpos más oscuros, rojizos.

Macho.—Desconocido.

Observaciones.—Se ha colectado en una sola localidad, llana y semidesértica; el suelo es seco, con un monte bajo, xerófilo. El lugar fue visitado por el autor; se encontraron seis especies de Mygalomorphae (*Actinopus* sp. *Idiops hirsutipedis* Mello-Leitão 1941, *Ischnothele cranwelli* Gerschman de Pikelin y Schiapelli, 1948, *Oligoxistre argentinensis* (Mello-Leitão 1941), *Androthelopsis modestus* (Schiapelli y Gerschman 1942) y *Chaco* sp.), pero no se pudo hallar ninguna *N. spinosa*.

Material examinado.—Solamente el tipo, de Argentina, provincia de Santiago del Estero; Colonia Dora (7945 M.A.C.N.).

Neocteniza minima, especie nueva
Figs. 6, 7, 13-16, 20-24, 32-36

Etimología.—Así denominada por ser una de las especies más pequeñas dentro del género.

Diagnosis.—Se reconoce por su genitalia. Las hembras se diferencian de las hembras de las demás especies argentinas también por la espina larga en la cara prolateral de la tibia del palpo, las fúsulas de las hileras de tamaño no uniforme, y la disposición de las cerdas postoculares. Los machos se distinguen de los de *N.*

australis por los caracteres de la clave y porque el fémur I no es fusiforme, los quelíceros no tienen granulaciones entre ambas márgenes y la región cefálica es más baja.

Descripción del Holotypus hembra.—Cefalotórax (Fig. 7) de largo 6.56, ancho 5.25. El ancho es el 80% del largo. Región cefálica elevada, de largo igual al 98% del ancho; el largo es el 60% del largo del cefalotórax y el ancho es el 76% del ancho del cefalotórax. La fóvea ocupa el 31% del ancho del cefalotórax.

Ojos ocupando el 54% del ancho de la región cefálica; área ocular de ancho 250% del largo; área de los ojos medios de ancho 383% del largo. Por delante de los ojos, 19 cerdas, 3 o 4 de ellas más largas; por detrás, unas 20, y 3 filas longitudinales (formadas por cerdas más largas y gruesas que en *N. australis* y *N. toba*), la media de 17 y las laterales de 16.

Labio de largo igual al 76% del ancho. Coxas de los palpos con 1 o 2 espínulas. El ancho del esternón es el 78% del largo, con las sigillas posteriores bien visibles.

Margen interna de los quelíceros con 6 dientes, la externa con 7 de la mitad de tamaño; entre ambas márgenes hay 14 granulaciones, de entre la mitad y la tercera parte del tamaño de los dientes de la margen externa. Rastrillo formado por cúspides romas en la prolongación, más largas que en *N. spinosa*, en número aproximado de 10, y además 2 espinas gruesas más afuera.

Patas IV, III = I, II.

	Fémur	Patella + Tibia	Protarso	Tarso
I	3.44	4.10	1.65	0.93
II	3.28	3.84	1.72	0.93
III	3.04	3.57	2.05	1.52
IV	4.57	5.16	3.31	1.26
P	2.58	2.96	-	1.72

Tricobotrias: Tibias: I, ambas filas 5; II, fila anterior 5, posterior 6; III, ambas filas 5; IV, fila anterior 8, posterior 10; palpo, fila anterior 5, posterior 4. Protarsos: I, 14; II, 11; III, 10; IV, 11. Tarsos: I, II, III, IV y palpo, 12.

Quetotaxia: Fémur IV, 21/24 D ant. ap.; I, II, III y palpo, inermes. Patella III, 19/20 P, peine P ap. de 8/9, 1 R; IV, aproximadamente 10/12 D ant. b. que se adelgazan hacia el ápice; I, II y palpo, inermes. Tibia I (Fig. 21), 1-1 P (1:3 ap.), 6/7 R inf.; III, 1-1-3/2-1-2-1 D, 16/20 D ant., 9/10 R sup. (1:2 ap.); IV, solamente con algunas cerdas gruesas ventrales; II, inerme; palpo, 11 P (la segunda larguísima, de casi las 3/4 partes del largo del artejo - Fig. 20), 4 R (1:3 ap.). Protarso I (Fig. 22), 13/15 P, 17 R; II, 10/13 P, 8/13 R; III, 15 D ant., 8/9 D post., 1 V ap.; IV, 1-1 P, 1-1 R sup., peine P inf. ap. de 5, 1 V ap. Tarso I (Figs. 22, 23), 6 P, 7/9 R; II, 7 P, 5 R; III, 0/1 P sup.; IV, inerme; palpo, 16/18 P, 9/12 R, 2 V ap.

Coronas de cerdas: protarsos I (Fig. 23) y II, formada por 2 cerdas; protarso III con 2 coronas, la anterior de 4 cerdas y la posterior de 3; protarso IV con 2 coronas, la anterior de 1 o 2 cerdas y la posterior de 4.

Uñas tarsales superiores de todas las patas con un diente y un dentículo basal. Uña del palpo con un diente, un dentículo en la base y dos dentículos más hacia el ápice.

Area epigástrica (Fig. 15) con 2 elevaciones pequeñas, más esclerosadas. Genitalia: Figs. 13-16.
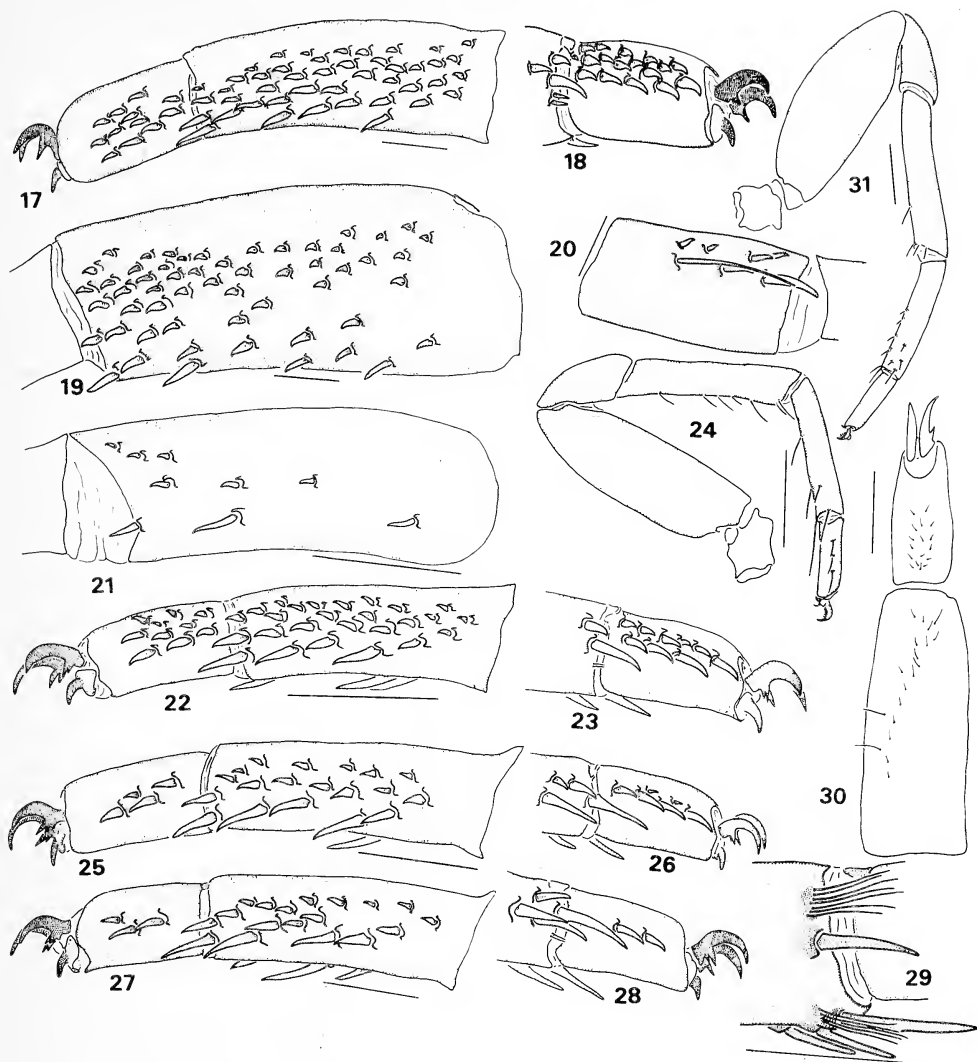
Figs. 17-31.—Quetotaxia. 17-23, 25-30, hembras. 24, 31, machos. 17-19, *N. spinosa*: 17, tarso y protarso I, retrolateral; 18, tarso I, prolateral; 19, tibia I, retrolateral; 20-24, *N. minima*: 20, tibia del palpo, prolateral; 21, tibia I, retrolateral; 22, tarso y protarso I, retrolateral; 23, tarso I, prolateral; 24, pata I, prolateral; 25-26, *N. toba*: 25, tarso y protarso, I retrolateral; 26, tarso I, prolateral. 27-31, *N. australis*: 27, tarso y protarso I, retrolateral; 28, tarso I, prolateral; 29, coronas de cerdas del protarso IV; 30, tricobotriotaxia de tarso y protarso I; 31, pata I, prolateral. (Escala: para la Fig. 20, 0.5 mm; para todas las demás, 1 mm)

Hileras con fúsulas numerosas, de tamaño desigual, siendo mayores las agrupadas en el ápice de cada artejo de las hileras posteriores; el artejo basal tiene agrupadas unas 8 de estas fúsulas más grandes, el artejo medio 6 y el apical 14.

Colorido: cefalotórax marrón oliváceo claro, patas del mismo color. Abdomen con el dorso oscuro, con reflejos iridiscentes desde ciertos ángulos; vientre más claro. Area epigástrica amarillenta, con las elevaciones más oscuras. Esternón y coxas de las patas amarillentos, labio y coxas de los palpos más oscuros, rojizos.

Descripción del Paratypus macho (7947 M.A.C.N.).—Cefalotórax (Fig. 6) de largo 2.93, ancho 2.28, alto 1.92. El ancho es el 78% del largo. Región cefálica de alto igual al 109% del alto de la región torácica. El largo de la región cefálica es el 109% del ancho de la misma; el largo es el 57% del largo del cefalotórax; el ancho es el 67% del ancho de la región torácica. La fóvea ocupa el 33% del ancho del cefalotórax.

Ojos ocupando el 62% del ancho de la región cefálica; área ocular de ancho 238% del largo; ancho del área de los ojos medios, 300% del largo. Por delante de los ojos unas pocas cerdas cortas, por detrás 3 filas de cerdas cortas.

Labio de largo igual al 57% del ancho. Coxas de los palpos inermes. El ancho del esternón es igual al 80% del largo; las sigillas con disposición similar a las de la hembra pero menos nítidas.

Margen interna de los quelíceros con 6 dientes, la externa con 8 o 10 más pequeños, sin granulaciones entre ambas márgenes. Rastrillo formado por 3 espinas largas y romas en la prolongación, 1 un poco más arriba y más adentro,y otras 2 más afuera.

Patas IV, III, I, II.

	Fémur	Patella + Tibia	Protarso	Tarso
I	2.08	2.05	1.26	0.76
II	1.85	2.05	1.20	0.73
III	1.59	2.78	1.36	0.96
IV	2.22	1.59	2.15	0.96
P	1.06	1.09	-	0.64

Tricobotrias: Tibias: I, fila anterior 4, posterior 3; II, fila anterior 3, posterior 4; III, fila anterior 4, posterior 3; IV, fila anterior 5, posterior 6; palpo, fila anterior 3, posterior 1. Protarsos: I, 7; II,8; III, 5; IV, 5. Tarsos: I, II, III y IV, 7; palpo, 4.

Quetotaxia: Fémur IV,10/12 D ant. ap.; I, II, III y palpo, inermes. Patella III, 8/9 P, peine P ap. de 6/8; I, II, IV y palpo, inermes. Tibia I, 1-1 P (1:3 ap.), 1 R inf. ap.; II, 1-1 P (1:3 ap.), 1 R inf.; III, 11/13 (1-2-2-3-2/2-2 D ant., 1-1/2-2-1 D, 1/1-1 R sup. ap.); IV, 1-1-1/1-1-2 V; palpo, con cuatro hileras de espinas, la basal de 5, la segunda de 6, la tercera de 7 y la apical de 5, todas muy cortas y gruesas. Protarso I, 1-2 P (1:4 ap.), 1-1-1-1-2 R (las 2 ap. muy largas, alcanzando la mitad del tarso); II, 1-2 P (1:4 ap.), 1-1-1-2 R (las 2 ap. muy largas); III, 7 D ant., 4 D post., 1 V ap.; IV, 2/3 P inf., 1-1 R sup. (1:2 ap.), peine P inf. ap. de 3, 1 V ap. Tarso I, 1-1 P, 2-1-2 R; II, 1-2-1 P, 1-1 R; III, IV y palpo, inermes.

Coronas de cerdas: en los protarsos I y II, formada por 2 cerdas; protarsos III y IV con 2 coronas, la anterior de 2 cerdas y la posterior de 3, con la espina ventral apical entre ambas.

Uñas tarsales superiores pectinadas en una sola fila. Dientes: pata I, uñas anterior y posterior, 7; patas II y III, anterior 6, posterior 7; pata IV, anterior 8, posterior 7. Tercer uña inerme.

Area epigástrica con 18 glándulas epiándricas. Hileras con fúsulas numerosas, siendo las de los grupos apicales de mayor tamaño que el resto.

Palpo: tibia muy corta y ancha, con las espinas sobre una elevación común. El bulbo tiene en el ápice una placa esclerosada que porta una apófisis que, al descargarse el bulbo, apoya en las espinas tibiales; émbolo muy largo y delgado (Figs. 32-36). Pata I: Fig. 24.

Colorido: cefalotórax marrón oliváceo claro, área ocular y clípeo más oscuros. Patas del mismo color que el cefalotórax, con las patellas y tarsos de color más claro. Abdomen con el dorso oscuro, sin reflejos iridiscentes como en la hembra, vientre claro. Esternón y coxas de las patas amarillo pálido, labio y coxas de los palpos un poco más oscuros.

Variaciones.—El largo del cefalotórax (medido en 14 hembras) varía entre 6.88 y 4.17 ($\bar{x}$ = 5.22, SD = ± 0.83), el ancho entre 5.96 y 3.44 ($\bar{x}$ = 4.27, SD = ± 0.78). Se observan también variaciones en las proporciones de largos y anchos relativos, superponiéndose los valores de las especies aquí descritas para varias proporciones. El ancho del área ocular como porciento del ancho de la región cefálica podría ser de cierta utilidad: en esta especie varía entre 56% y 43% ($\bar{x}$ = 51.0%, SD = ± 2.8%), bastante distinto del rango de *N. australis*. Las variaciones observadas en la quetotaxia son mínimas.

Observaciones.—Es propia de la selva húmeda de Salta y Jujuy. Fue colectada junto con especies de *Idiops* y *Actinopus*; en distintos lugares suele ser una de estas dos últimas (o ambas) la dominante; en cambio, solamente en dos sitios se vio más abundancia de *N. minima*: a 3 km de Campamento Vespucio (Sierra de Tartagal, Salta) y en Yuto (Jujuy). Los ejemplares restantes fueron encontrados aislados.

Se la ha hallado en los cañadones de los cerros más que en las barrancas de los arroyos; los ejemplares colectados cerca de Campamento Vespucio estaban en una bajada de agua, que daba a un arroyito muy pequeño de 20 o 30 cm de ancho, habiendo allí un microhábitat muy húmedo. Aquí no se vieron *Idiops* ni *Actinopus*, muy abundantes a sólo unos metros. En Yuto (donde también existe *N. toba*) se la halló en un ambiente distinto, en terreno llano, en la selva marginal del río San Francisco. Construye la tapa de su cueva bajo la capa de hojas caídas, y puede ponerle encima hojas secas en lugar de tierra. Las *Actinopus* eran aquí escasas, y no se vieron *Idiops*.

Otras mygalomorphae que se han colectado junto con *N. minima*, además de las mencionadas, son *Oligoxistre argentinensis* (Mello-Leitão 1941) (en Yuto), *Dryptopelma crassifemur* (Gerschman de Pikelin y Schiapelli 1959) (en Campamento Vespucio), *Diplura argentina* (Canals 1931) y otra especie de Dipluridae.

Material examinado.—ARGENTINA: provincia de Jujuy; Yuto, 17 V 1983 (M. Viñas—P. Goloboff), 1 hembra (Holotypus, 7947 M.A.C.N.), 3 hembras, 2 juveniles (Paratypi, 7951 M.A.C.N.); El Bananal, 16 V 1983 (M. Viñas—P. Goloboff), 1 hembra, 2 juveniles (Paratypi, 7950 M.A.C.N.). Provincia de Salta; Campamento Vespucio, 9-12 V 1983 (M. Viñas—P. Goloboff), 1 hembra, 1 juvenil (Paratypi, 7948 M.A.C.N.); 3 km O. Campamento Vespucio, 13 V 1983 (M. Viñas—P. Goloboff), 1 macho (Paratypus, 7946 M.A.C.N.), 1 macho, 9 hembras, 4 juveniles (Paratypi, 7949 M.A.C.N.).

Neocteniza toba, especie nueva
Figs. 8, 25, 26

Etimología.—Se conocía con el nombre de tobas a los indios de varias tribus que habitaban la región chaqueña.

Diagnosis.—Se distingue de *N. australis* (muy próxima) por la desviación hacia afuera de los ductos de las espermatecas y las espinas de los tarsos anteriores; de todas las demás especies porque la porción inicial de los ductos es membranosa. Las hembras se diferencian también de las de *N. minima* y *N. spinosa* por tener

los ojos en un grupo un poco más compacto, la disposición de las cerdas postoculares (similar a la de *N. australis*), y la espina prolateral apical larga en los protarsos anteriores.

Descripción del Holotypus hembra.—Cefalotórax largo 8.71, ancho 7.98. El ancho es el 92% del largo. Región cefálica muy elevada y convexa, de largo igual al 86% del ancho; el largo es el 57% del largo del cefalotórax y el ancho es el 72% del ancho del cefalotórax. La fóvea ocupa el 31% del ancho del cefalotórax.

Los ojos ocupan el 49% del ancho de la región cefálica; área ocular de ancho igual al 286% del largo; área de los ojos medios de ancho igual al 303% del largo. Delante de los ojos, 43 cerdas desiguales; detrás, 25, y 3 filas (similares a las de *N. australis*), la media de 20 y las laterales, sinuosas, de 15.

Labio de largo igual al 80% del ancho. Coxas de los palpos con 1 espínula o inermes. El ancho del esternón es igual al 77% del largo, con la depresión anterior más corta que el labio (de las 2/3 partes aproximadamente).

Margen interna de los quelíceros con 7 u 8 dientes grandes, la externa con 10 de la mitad de tamaño; entre ambas márgenes unas 20 granulaciones. Rastrillo formado por unas 28 cúspides en la prolongación y 3 espinas gruesas más afuera.

Patas IV, I, II = III.

	Fémur	Patella + Tibia	Protarso	Tarso
I	5.30	6.42	2.58	1.32
II	5.00	5.96	2.65	1.39
III	4.57	5.39	3.44	1.82
IV	6.29	7.52	4.77	1.65
P	4.10	4.77	-	2.52

Tricobotrias: Tibias: I, fila anterior 7, posterior 8; II, ambas filas, 7; III, fila anterior 7, posterior 8; IV, fila anterior 7, posterior 10; palpo, fila anterior 9, posterior 5. Protarsos: I, 16; II, 20; III, 14; IV, 19. Tarsos: I, 12; II, 13; III, 15; IV, 14; palpo, 15.

Quetotaxia: Fémur IV, 24/28 D ant. ap.; I, II, III y palpo, inermes. Patella III, 12/13 P, peine P ap. de 6, 1 R; IV, cerdas muy gruesas D ant. b. que se adelgazan hacia el ápice; I y II, inermes; palpo, 1 P. Tibia I, 1-1-1/1-1-1-1 P sup. (1:2 ap.), 1-2-2-2/1-3-2 R; II, 1-1/1-1-1 P sup., 1/1-1-1 R; III, 1-3-3-2/1-1-2-3 P, 1-1 D post, 2-1/1-3 R (1:3 ap.); IV, 1 V ant. ap.; palpo, 9/11 P, 3/5 R. Protarso I (Fig.25), 15/16 P, 19/21 R; II, 18 P, 10 R; III, 16/17 D ant., 15/17 D post., 1 V ap.; IV, 1-0-2-1 P, 1-1 R sup. (1:3 ap.), peine P inf. ap. de 2, 1V ap. Tarso I (Figs. 25, 26), 5/6 P, 3/4 R; II, 4/5 P, 2 R; III y IV, inermes; palpo, 16/17 P, 9/10 R, 2 V ap.

Protarso I con sólo una cerda gruesa en lugar de la corona; II con corona de 2 cerdas; III con 2 coronas, la anterior de 3 y la posterior de 2 o 3, con la espina ventral apical entre ambas; IV, con 2 coronas, la anterior muy reducida, de 1 o 2 cerdas, la posterior de 5 o 6, con la espina ventral apical entre ambas coronas.

Las uñas superiores de todas las patas con un diente y un dentículo.

Area epigástrica poco esclerosada, sin elevaciones. Genitalia: Fig. 8.

Hileras con sus fúsulas de tamaño uniforme.

Colorido: cefalotórax marrón oliváceo claro, patas del mismo color que el cefalotórax. Abdomen gris claro, con el vientre amarillento; la región epigástrica más oscura. Esternón y coxas de las patas amarillo pálido; labio y coxas de los palpos más oscuros, rojizos.

Macho.—Desconocido.
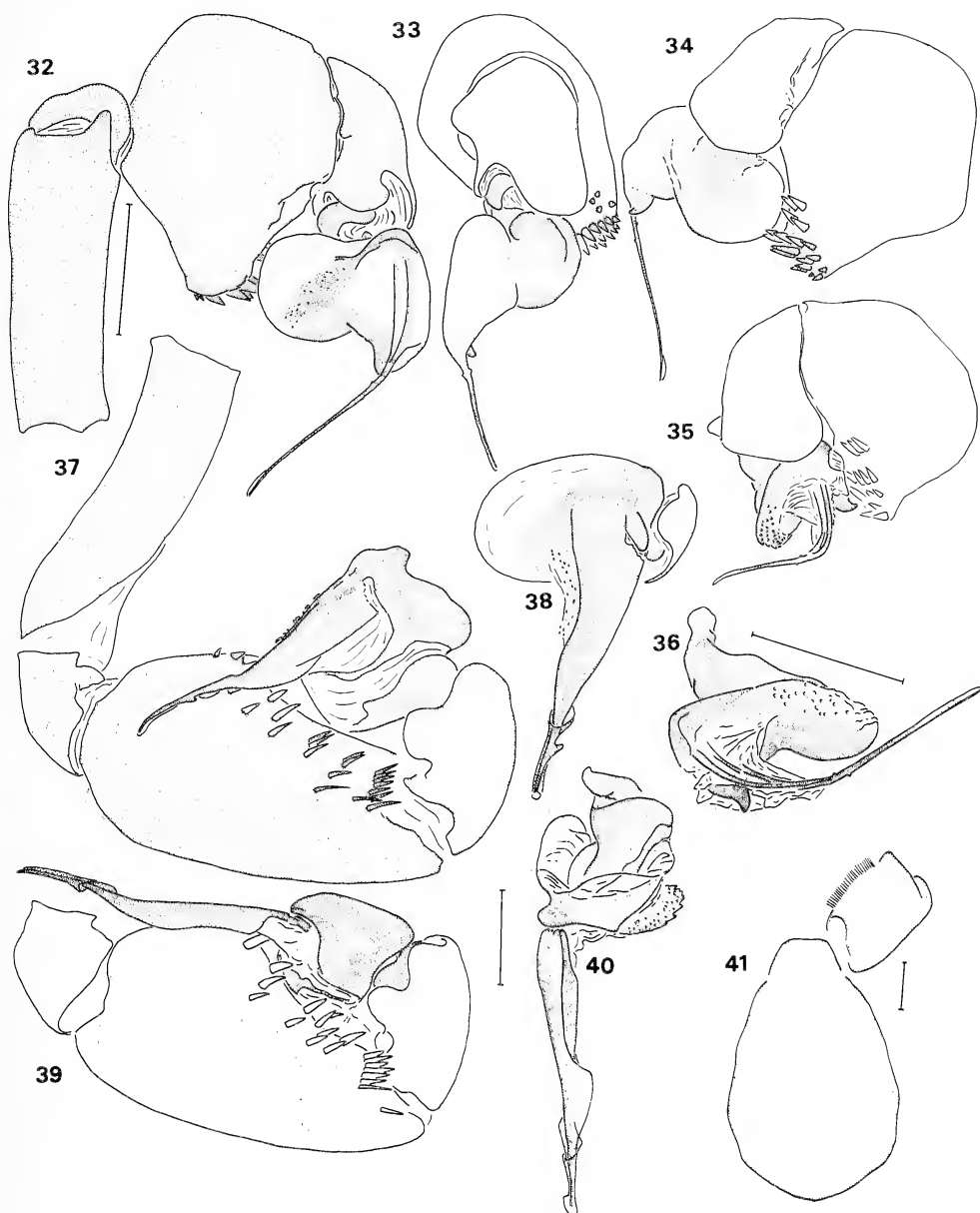
Figs. 32-41.—Machos. 32-36, *N. minima*: 32-35, palpo izquierdo: 32, prolateral; 33, ventral; 34, retrolateral; 35, retrolateral, con el bulbo descargado; 36, bulbo derecho descargado. 37-41. *N. australis*; 37-39, palpo izquierdo: 37, retrolateral; 38, ventral; 39, retrolateral, bulbo descargado; 40, bulbo derecho descargado; 41, esternón y piezas bucales. (Escala = 0.5 mm)

Variaciones.—Se han estudiado sólo cuatro ejemplares adultos de esta especie; la relación ancho/largo del cefalotórax es, como en las otras especies, variable según los individuos; el ancho del grupo ocular como porciento del ancho de la región cefálica ($\overline{x}$ = 48.4%), es menos variable. En cuanto a la quetotaxia, aparece bastante constante, permitiendo diferenciar incluso a los ejemplares muy jóvenes de los de *N. australis*.

Observaciones.—Parece ser de lugares un poco más secos que *N. minima*. En Tucumán se la halló en una zona de selva más empobrecida que las localidades

anteriores, donde convive con especies como *Chaco* sp., *Oligoxistre argentinensis* (Mello-Leitão 1941), *Actinopus* sp., *Idiops hirsutipedis* Mello-Leitão 1941; cerca de allí se colectó también *Diplothelopsis ornatus* Tullgren 1905. En Yuto se la colectó en la pequeña barranca del río San Francisco, y en La Quena se la colectó en la barranca del río Bermejo, donde existe un monte espinoso, apareciendo, además de *Actinopus* spp., *Idiops clarus* (Mello-Leitão 1946), *Chaco obscura* Tullgren 1905, especies sumamente típicas como *Ischnothele cranwelli* Gerschman de Pikelin y Schiapelli 1948 y *Sicarius* sp.

Material examinado.—ARGENTINA: provincia de Salta; La Quena, 15-16 V 1983 (M. Viñas—P. Goloboff), 1 hembra (Holotypus, 7952 M.A.C.N.), 1 macho joven (Paratypus, 7953 M.A.C.N.), 4-5 II 1985 (C. Szumik—P. Goloboff), 1 hembra (8242 M.A.C.N.). Provincia de Jujuy; Yuto, 17 V 1983 (M. Viñas—P. Goloboff), 1 hembra (Paratypus, 7954 M.A.C.N.); El Bananal, 16 V 1983 (M. Viñas—P. Goloboff), 1 juvenil (Paratypus, 8031 M.A.C.N.). Provincia de Tucumán; Arroyo Saladillo, 23 V 1983 (M. Viñas—P. Goloboff), 1 hembra, 12 juveniles (Paratypi, 7955 M.A.C.N.).

Neocteniza australis, especie nueva
Figs. 1-4, 9-10, 27-31, 37-41

Etimología.—Así denominada por ser la especie más austral de todo el género.

Diagnosis.—Se diferencia de *N. toba* (muy próxima) por su genitalia y por las espinas de los tarsos anteriores; de todas las demás especies del género por los ductos de las espermatecas membranosos y el émbolo del bulbo del macho grueso. Las hembras se diferencian fácilmente de las de *N. spinosa* y *N. minima* por la espina apical prolateral larga en los protarsos anteriores, por la disposición de las filas de cerdas postoculares y por los ojos más próximos. Los machos se distinguen de los de *N. minima* (además de por los caracteres mencionados en la clave) por tener la región cefálica más elevada, los quelíceros con granulaciones entre ambas márgenes y el fémur I ligeramente fusiforme.

Descripción del Holotypus hembra.—Cefalotórax (Fig. 3) de largo 9.04, ancho 7.45. El ancho es el 82% del largo. Región cefálica elevada, convexa, de largo igual al 94% del ancho; el largo es el 61% del largo del cefalotórax; el ancho es el 79% del ancho del cefalotórax. La fóvea ocupa el 32% del ancho del cefalotórax.

Ojos ocupando el 46% del ancho de la región cefálica; área ocular de ancho igual al 300% del largo; área de los ojos medios de ancho igual al 389% del largo. Por delante de los ojos, unas 30 cerdas; por detrás, 24, y 3 filas, la media de 10 y las laterales, sinuosas, de 15 cerdas cortas y delgadas.

Labio de largo igual al 98% del ancho. Coxas de los palpos con 1 espínula. El ancho del esternón es el 87% del largo, con las sigillas en la disposición típica, bien nítidas.

Margen interna de los quelíceros con 6 dientes grandes, margen externa con 9 dientes de la mitad de tamaño, entre ambas márgenes 18 o 20 granulaciones. Rastrillo formado por cúspides romas, que gradualmente pasan a cerdas yendo hacia la base, en número de 25 aproximadamente; 2 espinas más largas un poco más afuera.

Patas IV, III = I, II.

	Fémur	Patella + Tibia	Protarso	Tarso
I	4.93	5.96	2.53	1.33
II	4.53	5.32	2.46	1.27
III	4.00	4.83	2.96	1.83
IV	5.79	6.83	4.53	1.63
P	4.13	4.33	-	2.60

Tricobotrias: Tibias: I, ambas filas 7; II, fila anterior 6, posterior 8; III, fila anterior 5, posterior 8; IV, fila anterior 8, posterior 11; palpo, fila anterior 7, posterior 5. Protarsos: I, 7; II, 20; III, 12; IV, 18. Tarsos: I, 14; II, 16; III, 20; IV, 14; palpo, 15.

Quetotaxia: Fémur IV, 35 cerdas muy gruesas D ant. ap.; I, II, III y palpo, inermes. Patella III, 2-1-2/2-1-1-2 P, peine P ap. de 6/7, 1 R; IV, cerdas espiniformes D b. que se adelgazan hacia el ápice; I, II y palpo, inermes. Tibia I, 1-1 R inf., 1 P ap.; II, 1-1/1-1-1 R inf.; III, 1-3/1-1-2 P sup., 1-1 D post., 1 R ap.; IV, inerme; palpo, 6/7 P, 1 R ap. Protarso I (Fig. 27), 12/13 P, 12 R; II, 15 P, 6 R; III, 10/11 D ant., 11/12 D post., 0/1 V ap.; IV, 3/4 P, peine P inf. ap. de 2/3, 1-1 R (1:3 ap), 1 V ap. Tarso I (Figs. 27, 28), 0/1 P, 2 R; II, 1 R; III y IV, inermes; palpo, 10/11 P, 8 R, 2 V ap.

Protarso I con una corona formada por 2 cerdas (Fig. 28); protarso II, con 3 cerdas; III con 2 coronas, la anterior de 5 y la posterior de 4, con la espina ventral apical entre ambas coronas; IV, también con 2 coronas, la anterior de 4 y la posterior de 8 (Fig. 29), con la espina apical ventral entre ambas.

Uñas tarsales superiores de todas patas con un diente y un dentículo basal.

Area epigástrica poco esclerosada, sin elevaciones. Genitalia: Figs. 9, 10.

Hileras con fúsulas muy numerosas, de tamaño uniforme. En el artejo basal de las hileras posteriores están más o menos uniformemente distribuídas; en el artejo apical hay unas 6 o 7 fúsulas agrupadas, y en el artejo medio unas 15.

Colorido: cefalotórax marrón oliváceo, con el abdomen grisáceo claro, vientre amarillento. Esternón y coxas de las patas amarillentas, labio y coxas de los palpos más oscuros.

Descripción del Paratypus macho (7959 M.A.C.N.).—Cefalotórax (Fig. 4) de largo 3.38, ancho 2.78, alto 2.52. El ancho es el 82% del largo. Región cefálica de alto igual al 127% del alto de la región torácica. El largo de la región cefálica es el 104% del ancho; el largo es el 58% del largo del cefalotórax y el ancho es el 68% del ancho del cefalotórax. La fóvea ocupa el 34% del ancho del cefalotórax.

Los ojos ocupan el 50% del ancho de la región cefálica; área ocular de ancho igual al 228% del largo; área de los ojos medios de ancho igual al 287% del largo. Por delante de los ojos, 8 cerdas, por detrás 6, y 3 filas, la media de 3 o 4, y las laterales, sinuosas, de 6. Todas las cerdas son cortas y gruesas.

Labio de largo igual al 78% del ancho. Coxas de los palpos inermes. Esternón de ancho igual al 75% del largo; las sigillas posteriores poco visibles (Fig. 41), con disposición similar a las de la hembra.

Margen interna de los quelíceros con 6 dientes, margen externa con 7 dientes muy pequeños; entre ambas márgenes, 9 granulaciones más pequeñas aún, ocupando la parte basal del canal. Rastrillo formado por 3 espinas gruesas, 3 más delgadas hacia arriba y 2 más largas hacia afuera.

Patas IV, I, II, III.

	Fémur	Patella + Tibia	Protarso	Tarso
I	2.81	2.98	1.92	0.86
II	2.38	2.58	1.46	0.79
III	1.79	2.05	1.69	1.06
IV	2.68	3.38	2.65	1.22
P	1.59	2.15	-	1.00

Tricobotrias: Tibias: I y II, ambas filas 5; III, fila anterior 3, posterior 4; IV, fila anterior 6, posterior 7; palpo, fila anterior 4, posterior 3. Protarsos: I, 8; II, 11; III, 5; IV, 9. Tarsos: I, 7; II, 9; III, 7; IV, 6; palpo, 5.

Quetotaxia: Fémur IV, 15/17 D ant. ap.; I, II, III y palpo, inermes. Patella III, 1-1/1-1-2 P, peine P ap. de 5; I, II, IV y palpo, inermes. Tibia I, 1-1/1-0-1-1 V post., 1 V ant. ap. (todas muy delgadas); II, 1-0-1-1 V post., 1 V ant. ap. (muy delgadas también); III, 1/1-1 D ant., 1-1 D post., 1 R, (más gruesas), 3 V ap. (muy delgadas); IV, 3 cerdas gruesas V ap.; palpo, 22 R (15 y peine apical de 7). Protarso I, 1-1 P inf. (1:4 ap.), 1-2 R inf. (1:3 ap.); II, 1 P inf. ap., 1-1-1 R; III, 1-1-1 V muy delgadas, 1-1-1 D ant., 1 D mesial, 1-1-1-1/1-1-1-1-1 D post.; IV, 5/6 R inf. (1:4 ap.), sin peine. Tarso I, 1/1-1 R; II, 1 R; III, IV y palpo, inermes.

Coronas de cerdas: protarso I, 2 cerdas; protarso II, 3 cerdas; protarso III con 2 coronas, la anterior de 4 y la posterior de 3, con la espina ventral apical entre ambas; protarso IV también con 2 coronas, la anterior de 4 y la posterior de 6, con la espina ventral apical entre ambas.

Uñas tarsales superiores de todas las patas con una sola fila de dientes, curva, estando los basales del lado de afuera de la uña y los apicales del lado interno. Dientes: I, anterior 8, posterior 7; II, anterior 7, posterior 6; III y IV, anterior y posterior, 6. Tercer uña inerme.

Area epigástrica con 35 glándulas epiándricas. Hileras con fúsulas numerosas, de tamaño uniforme.

Palpo: tibia fusiforme, con las espinas distribuídas en la cara retrolateral del artejo (4-2-2-3-4-7). El émbolo es una placa esclerosada que se separa del bulbo. El bulbo carece de placa esclerosada apical y apófisis (Figs. 37-40). Pata I con el fémur ligeramente fusiforme (Fig. 31).

Colorido: cefalotórax oliváceo, con áreas más oscuras. Patas uniformes, del mismo color que el cefalotórax. Abdomen grisáceo oscuro; vientre claro. Esternón y coxas de las patas de color claro, labio y coxas de los palpos más oscuros.

Variaciones.—El largo del cefalotórax (medido en 17 hembras) varía entre 12.63 y 6.51 ($\bar{x}$ = 8.85, SD = ± 1.57). El ancho del cefalotórax varía entre el 99.1 y el 75.9% del largo ($\bar{x}$ = 88.5%, SD = ± 5.9%). Los ojos ocupan entre 48.4 y 33.8% del ancho de la región cefálica ($\bar{x}$ = 42.1%, SD=± 3.9%). Las espinas de la tibia I y tibia II de las hembras son variables, pudiendo ser solo 2 largas y delgadas, hasta 4 o 5 más cortas y gruesas, en la cara retrolateral. En la cara prolateral de tarsos I y II, generalmente hay 1 o 2 espinas, a veces ninguna; las espinas de la cara retrolateral (normalmente 2 a 4) siempre son más numerosas que las de la prolateral.

Observaciones.—Fue hallada en dos ambientes distintos: las sierras de Córdoba y la costa del río Paraná.

En las sierras de Córdoba se la ha encontrado en los cerros, a una altura en que la vegetación (más abundante al pie de los cerros) es escasa. Las cuevas se encuentran en la tierra que se junta entre las rocas más grandes. Otras especies de arañas, en su mayoría terrícolas o lapidícolas, colectadas en el lugar, son: *Actinopus* sp., *Idiops hirsutipedis* Mello-Leitão 1941 (al igual que *N. australis*, poco abundantes), *Acanthogonatus* sp., *Oligoxistre argentinensis* (Mello-Leitão 1941), *Grammostola doeringi* (Holmberg 1881b), *Diplothelopsis ornatus* Tullgren 1905, *Ischnothele cranwelli* Gerschman de Pikelin y Schiapelli 1948, *Ctenus birabeni* Mello-Leitão 1941, *Sicarius terrosus* (Nicolet 1849).

En la costa del Paraná fue encontrada en solo dos localidades, en la barranca del río, donde todavía se conserva un poco del monte típico de la zona, cerca de Puerto Obligado. Las cuevas fueron encontradas en sitios sombríos, donde la

vegetación es más abundante, sobre todo en la mitad superior de la barranca. Cuando se encuentran varias cuevas próximas, se distribuyen sobre todo una encima de la otra, es decir, a lo alto de la barranca, no a una altura determinada. Esto podría deberse a caídas accidentales de los juveniles. En varios lugares se encontraron dos o más cuevas a muy poco distancia, una sobre otra; en el lugar de mayor densidad había, a lo largo de una franja de un metro de alto y unos veinte centímetros de ancho, seis ejemplares adultos, y otros tres hacia un costado, a menos de medio metro. En las proximidades de las cuevas de los adultos se encuentran, además, abundantes juveniles. *Actinopus insignis* (Holmberg 1881a) es muy común en la zona, pero en estas dos localidades se encontraron pocos ejemplares, siendo mucho más numerosos los de *N. australis*. Otras Mygalomorphae colectadas en esta zona son *Rechosticha weijenberghi* (Thorell 1894), *Homoeomma uruguayensis* (Mello-Leitão 1946) y *Stenoterommata* sp.

Material examinado.—ARGENTINA: provincia de Buenos Aires; 10 km N puerto Obligado, 20 III 1983 (A. Roig Alsina—M. Viñas—P. Goloboff), 1 hembra (Holotypus, 7957 M.A.C.N.), 1 macho (Paratypus, 7959 M.A.C.N.), 1 macho, 13 hembras, 2 juveniles (Paratypi, 7968 M.A.C.N.), 2 IV 1983 (E. Maury—P. Goloboff), 1 macho, 1 juvenil (Paratypi, 7956 M.A.C.N.); 1.5 km N Puerto Obligado, 15 II 1986 (N. Platnick —P. Goloboff), 1 hembra, 1 juvenil (8287 M.A.C.N.); Provincia de Córdoba; Bosque Alegre, 15.I.1981 (A. Zanetic—P. Goloboff), 1 hembra, 1 juvenil (Paratypi, 7960 M.A.C.N.), 27 IX-2 X 1981 (P. Goloboff), 2 hembras, 1 juvenil (Paratypi, 7961 M.A.C.N.); Bajo Grande (Maldonado), 1 juvenil (Paratypus, 7962 M.A.C.N.); Cabana, VII 1950 (M. Birabén), 1 hembra (Paratypus, 7963 M.A.C.N.).

Neocteniza platnicki, especie nueva
Figs. 42-47

Etimología.—Así denominada en reconocimiento a los importantes trabajos sobre *Neocteniza* y otras Mygalomorphae realizados por el Dr. Norman I. Platnick.

Diagnosis.—Especie muy próxima a *N. minima*, de la que se diferencia por su mayor tamaño, por las espinas de las patas más numerosas, y la entrada a los ductos más ancha que alta.

Descripción del Holotypus hembra.—Cefalotórax de largo 10.68, ancho 9.18. El ancho es el 86% del largo. Región cefálica de largo igual al 87% del ancho; el largo es el 56% del largo del cefalotórax y el ancho es el 75% del ancho del cefalotórax. La fóvea ocupa el 36% del ancho del cefalotórax.

Los ojos ocupan el 57% del ancho de la región cefálica; área ocular de ancho igual al 317% del largo; área de los ojos medios de ancho igual al 429% del largo. Delante de los ojos, 50 cerdas desiguales; detrás 25 y 3 filas, la media de 20 y las laterales de 15.

Labio de largo igual al 93% del ancho. Coxas de los palpos inermes. El ancho del esternón es igual al 79% del largo, con la depresión anterior más larga que el labio.

Margen interna de los quelíceros con 6 dientes grandes, la externa con 9; entre ambas márgenes, aproximadamente 12 granulaciones. Rastrillo formado por unas 18 cúspides en la prolongación y 2 o 3 espinas gruesas más afuera.
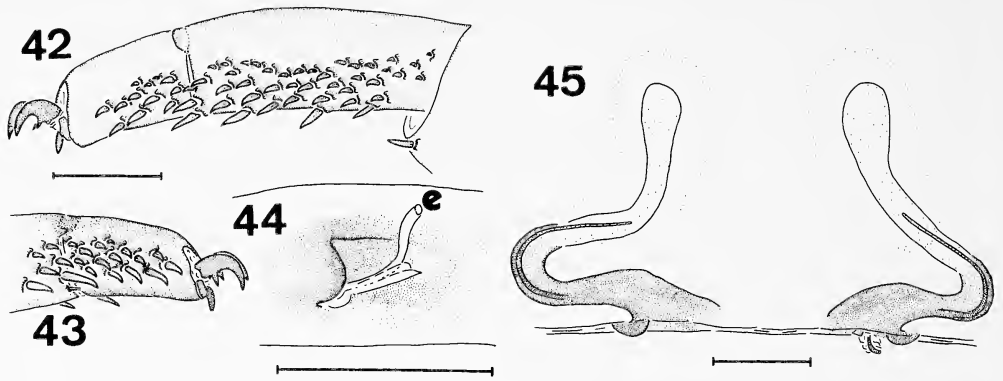
Figs. 42-45.—*N. platnicki*, hembra: 42, tarso y protarso I, retrolateral; 43, tarso I, prolateral; 44, entrada al ducto derecho, vista desde atrás (e: émbolo); 45, espermatecas, vista dorsal. (Escala: 42-43, 1 mm; 44-45, 0.5 mm)

Patas IV, III, I = II.

	Fémur	Patella + Tibia	Protarso	Tarso
I	5.23	6.18	2.71	1.32
II	5.10	6.07	2.78	1.36
III	4.97	5.36	3.54	2.05
IV	6.31	7.78	4.96	1.65
P	4.59	4.46	-	2.91

Tricobotrias: Tibias: I, fila anterior 6, posterior 7; II y III, ambas filas 7; IV, fila anterior 6, posterior 7; palpo, fila anterior 7, posterior 5. Protarsos: I, 15; II, 12; III, 11; IV, 14. Tarsos: I, II y III, 18; IV, 17; palpo, 17.

Quetotaxia: Fémur IV, 21/24 D ant. ap.; I, II, III y palpo, inermes. Patella III, 17/19 P, peine P ap. de 7/9, 1 R sup.; IV, 15 a 20 cúspides romas D ant. b. que se transforman en cerdas hacia el ápice; I, II y palpo, inermes. Tibia I, 7/9 P, 21/23 R inf.; II, 2 P ap., 1-0-1-1/1-0-2-1 R inf.; III, 27/28 P sup., 10 D, 11/12 R sup; IV, inerme; palpo, 17 P (en el tercio mesial una espina muy larga -similar a la del palpo de *N. minima*-), 12/13 R. Protarso I (Fig. 42), 31/32 P, 40 R; II, 26/27 P, 26 R; III, 16 D ant., 11/17 D post., 1 V post. ap.; IV, 5/7 P, peine P inf. ap. de 3/4, 1 R ap., 1 V ap. Tarso I (Figs. 42, 43), 15/17 P, 12/13 R; II, 16/17 P, 7/10 R; III y IV, inermes; palpo, 24/25 P, 31/34 R, 2 V ap.

Coronas de cerdas: protarso I, 2 cerdas; II, 2 cerdas; III, con 2 coronas, la anterior de 4 cerdas y la posterior de 3, con la espina ventral apical entre ambas coronas; IV, también con 2 coronas, la anterior muy reducida, de 1 o 2 cerdas, la posterior de 3, con la espina ventral apical entre ambas coronas.

Las uñas superiores externas de todas las patas con 1 diente y sin dentículos; las uñas internas de patas I y II con 1 dentículo, 1 diente, y 2 dentículos; las uñas internas de patas III y IV con 1 dentículo y 1 diente.

Area epigástrica con elevaciones bastante similares a las de *N. minima*, pero más pronunciadas. Genitalia: Figs. 44, 45. La entrada a los ductos, vista desde atrás, es claramente más ancha que alta.

Hileras con fúsulas numerosas, de tamaño desigual, siendo mayores las agrupadas en el ápice de cada artejo de las hileras posteriores: el artejo basal tiene agrupadas unas 8 o 10 de éstas fúsulas más grandes, el artejo medio 18 y el apical 13.

Colorido: cefalotórax marrón oliváceo claro, patas del mismo color. Abdomen con el dorso oscuro, con reflejos iridiscentes desde ciertos ángulos; vientre más claro. Area epigástrica amarillenta, con las elevaciones más oscuras. Esternón y coxas de las patas amarillentos, labio y coxas de los palpos más oscuros, rojizos.

Macho.—Desconocido.

Observaciones.—Se ha estudiado solo un ejemplar de esta especie. Fue encontrado "al borde de un monte empobrecido, en suelo arcilloso gris poco drenado, que estacionalmente se inunda. Este suelo, según reportes, tiene un alto contenido de sal". A poca distancia de allí J. Kochalka encontró un macho de *Neocteniza* que "estaba caminando en el suelo, por la noche, a la luz de una linterna, en un monte alto, sombrío, en suelo barroso-arenoso que nunca se inunda. En este lugar, una severa falta de sal parece ser el principal factor limitante de todas las formas de vida del área". La comparación del émbolo (retenido en las espermatecas del Holotypus) de *N. platnicki* con el bulbo de este macho permite asegurar que no son coespecíficos. El macho pertenece aparentemente al grupo *australis*. Como no existe certeza de su asignación a *N. toba* (de la cual se conocen solo hembras), se aguardará para su publicación a tener la posibilidad de ver más material que permita fundamentar una decisión.

Material examinado.—PARAGUAY: Departmento de Chaco; Parque Nacional Defensores del Chaco, Madrejón, 17 XII 1981 (J. Kochalka), 1 hembra (Holotypus, A.M.N.H.).

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DEVELOPMENT AND EGG SAC PRODUCTION OF *ACHAEARANEA TEPIDARIORUM* (C. L. KOCH) (ARANEAE, THERIDIIDAE) UNDER LONG AND SHORT PHOTOPERIODS

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ABSTRACT

The development and egg sac production of *Achaearanea tepidariorum* were investigated at 25°C and long (16L-8D) or short (10L-14D) photoperiod. The development of nymphs was completed in 30-80 days in 4-6 molts in the male and in 40-100 days in 5-7 molts in the female. Under the long photoperiod, the development of males was accelerated by the omission of one or two molts when food conditions were favorable, but under the short photoperiod such an acceleration tended to be cancelled by prolongation of either the last instar or the last and penultimate instars. This tendency was also observed in the female, but not so clearly as in the male. The development proceeded more speedily in complete darkness than under light. Adult females produced a mean of 9.7 egg sacs at intervals of 8.1 days. The mean egg number per sac showed a gradual decrease with time. The mean total egg number produced per female was 1812.7, and the mean longevity was 116.5 days in the female and 33.9 days in the male.

INTRODUCTION

The house spider, *Achaearanea tepidariorum* (C. L. Koch) is a cosmopolitan species, and quite abundant in many areas. However, studies on the biology and ecology of the spider are unexpectedly few. Although the life history of the spider must have a close connection to the seasonal change of environmental conditions in different localities, there are no detailed analyses on developmental characteristics in relation to the seasonal change in temperature and photoperiod.

In the present paper, I report the results from investigations on the development and egg sac production of the spider under laboratory conditions, with long and short photoperiods.

MATERIALS AND METHODS

The place where all experimental animals were collected was Abiko City (140°02′E—35°52′N), Chiba Prefecture, Japan.

First-instar spiderlings collected in June, 1984, were reared separately in vials 1.4cm in diameter by 3.0 cm in height. The vial size was increased as the development of each spider proceeded, adults being contained in vials 3.8cm by 10.5cm. In each vial, a strip of thick paper was placed as a substrate.

Spiders were reared at 25°C and long (16L-8D) or short (10L-14D) photoperiod. Light source was a 6w fluorescent tube, which gave 250-300 lux. Relative humidity fluctuated from 55% to 85%.

Rearings were divided into two experiments, A and B, according to the difference in food conditions. In the former, feeding intervals were 3-4 days, but in the latter 2-3 days for first and second instars only. Additionally, two groups were kept at 23°C, one in complete dark except for feeding and vial change, the other under 14L-10D in order to investigate the development under darkness.

Spiders were fed collembolans, mainly *Sinella cuspidatus*, during first and second instars and *Drosophila melanogaster* from third instar to adult. An excess unmber of collembolans was provided at each feeding. The number of fruit flies provided was changed from one to six following the process of the spiders' development.

The number of individuals used in each experiment varied from 12 to 30. The mortality ranged from 30% to 40% in first and second instars. After this period deaths occurred sporadically due to ecdysis failure.

Wild adult and last-instar females were collected in May 1984, and reared at 25°C and long photoperiod to investigate egg production. Each female was fed a single well-grown larva of *Phaenicia sericata* at the intervals of 3-4 days. Virgin females, except three, were mated with males in the laboratory. The egg sacs produced were removed together with first-instar spiderlings when they had emerged, and the number of spiderlings was counted as an indicator for total eggs since healthy egg sacs rarely contained dead eggs.

RESULTS

Effects of photoperiod on development.—Fig. 1 shows the difference in development of the males reared at 25°C and long or short photoperiod. In experiment A, the development was not significantly affected by photoperiod. The number of days required for the development from first instar to adult was 50-60 days, and the number of molts was five or six.

In experiment B, in which the food regimes during first and second instars were improved, the development was quite accelerated only under the long photoperiod. The development was concluded in 30-40 days, and the number of molts was five, except one individual which molted only four times. Under the short photoperiod, the development required 60-80 days and five or six molts. This difference was mainly due to the prolongation of either the last instar or both the last and penultimate instars. In other words, under the long photoperiod the developmental period becomes short by the omission of one or two molts, if food conditions are favorable. Under the short photoperiod, however, there occurs a tendency to prolong the last instar or both the last and penultimate instars, irrespective of difference in food conditions.

Fig. 2 shows the result for females. The result was essentially the same as the males show in Fig. 1. Developmental acceleration was also observed under the long photoperiod in experiment B. The prolongation of the last instar or both the last and penultimate instars was not clearly observed under the short photoperiod, although one female in experiment B molted seven times and spent more than 40 days in the last instar.
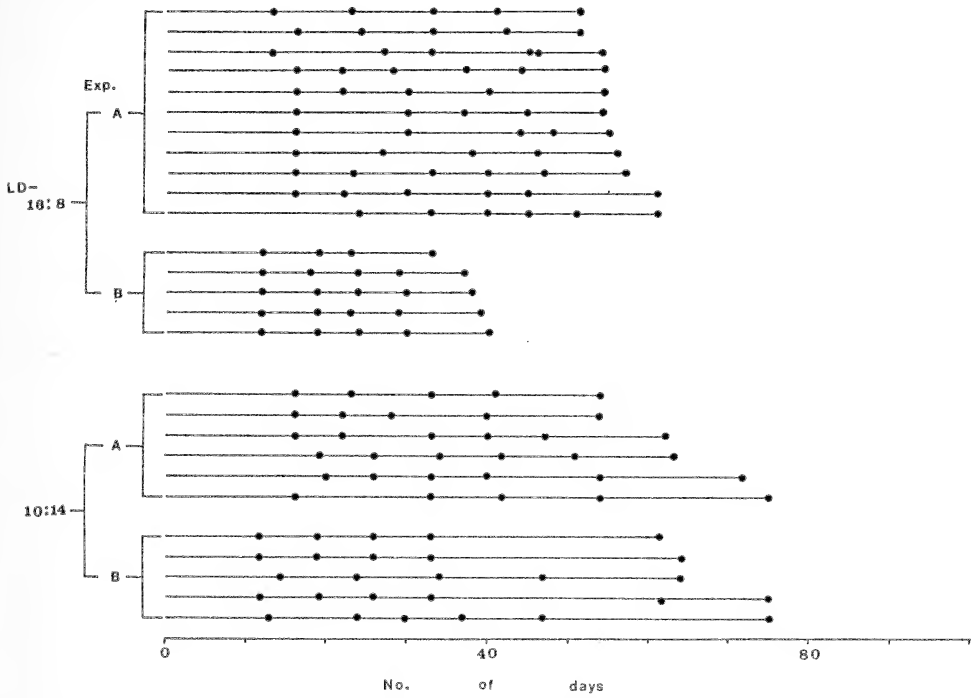
Fig. 1—Development of males reared at 25°C and 16L-8D or 10L-14D. The length of horizontal line indicates the number of days required for development in each individual. Solid circle shows molt. In experiment A feeding intervals were 3-4 days, in experiment B 2-3 days for first and second instars.
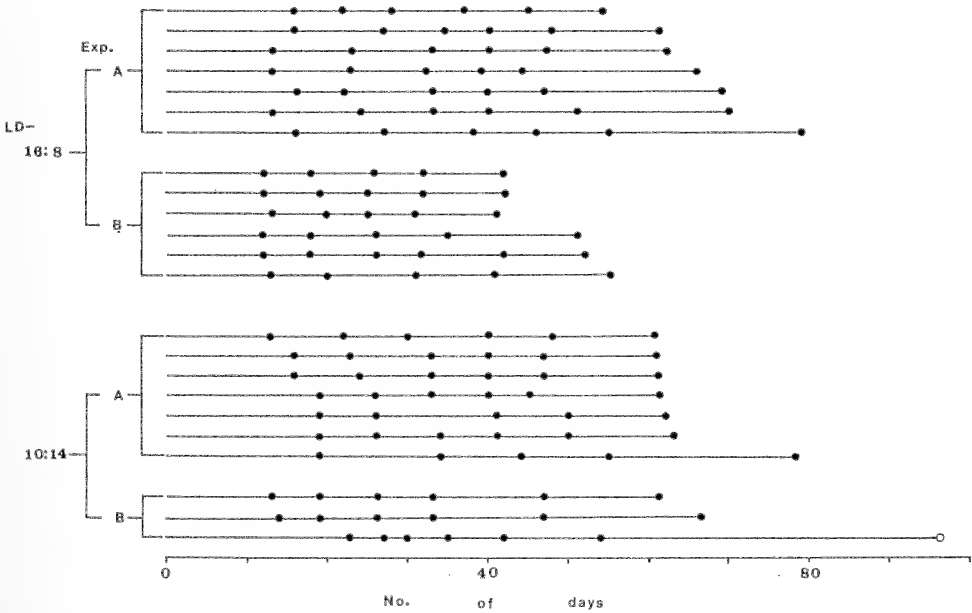
Fig. 2.—Development of females reared at 23°C and 16L-8D or 10L-14D. Symbols and experimental conditions are the same as in Figure 1. The bottom horizontal line with a hollow circle on the tail indicates the individual that passed the longest last instar and molted seven times.

Table 1—Carapace widths of adult *A. tepidariorum* obtained from laboratory rearings *vs* those collected from the field. The former were the individuals obtained from the experiments shown in Figs. 1, 2, and 3, and the latter those used for the experiment in Fig. 4.

Source	Sex	No. of molts	No. of indiv.	Mean (mm)	Range (mm)
Laboratory	Males	4	1	1.31 —	—
		5	20	1.50 ± 0.14†	1.31 − 1.75
		6	6	1.52 ± 0.08	1.38 − 1.63
		Total	27	1.49 ± 0.21	1.31 − 1.75
Laboratory	Females	5	3	1.71 ± 0.03	1.69 − 1.75
		6	12	1.83 ± 0.13	1.63 − 2.06
		7	1	2.25 —	—
		Total	16	1.95 ± 0.22	1.63 − 2.25
Field	Females	Unknown	16	2.16 ± 0.19*	1.94 − 2.41

† SD, * Significant in *t-test*(5%).

It should be noted that the body size of the females reared in the laboratory was significantly smaller than that of the individuals collected from the field (Table 1). Schaefer (1977) also noted that the body size of the reared *Clubiona phragmitis* C. L. Koch was smaller than that of individuals collected from the field. The cause(s) are unknown, but it could be due to a simplified menu in the laboratory rearing.

Development under complete darkness.—Fig. 3 shows the development under complete darkness as compared with that under 14L-10D. The graph shows that development under complete darkness proceeded more speedily than under 14L-10D. In four of the five females, the number of molts was also reduced. It can be said from these results that this spider is able to perform prey capture and feeding normally without visual sense. However, the reason why the development is accelerated under complete darkness is not understood.

Effects of photoperiod on egg sac production.—Fig. 4 shows the egg sac production of 15 females reared under either long or short photoperiod. The females which mated successfully either in the field or in the laboratory produced egg sacs during 2/3 or more of life span, irrespective of the difference in photoperiod. When mating was delayed, egg sac production was also delayed. When mating was prohibited, no egg sac was produced, except for one female which produced a sterile egg sac. It seems that the female receives enough spermatozoa to fertilize almost all the öocytes in her body by a single mating.

The number of egg sacs produced per female differed from individual to individual. In addition, sterile egg sacs were occasionally produced in a series of otherwise healthy egg sacs. The total healthy egg sacs per female varied from 5 to 15. The mean was 9.7 ± 2.9 when three females which were prohibited to mate were excepted. Similarly, the mean egg sac production interval was 8.1 days when the sterile egg sacs were included. The mean egg sac production intervals for each individual are shown by the figures attached on the tails of each horizontal line in Fig. 4. The mean longevity was 116.5 ± 10.3 days. The mean egg period from egg sac production to the emergence of spiderlings was 11.0 ± 1.5 days.

In males reared under the same conditions, the mean longevity was 33.9 ± 4.4 days.
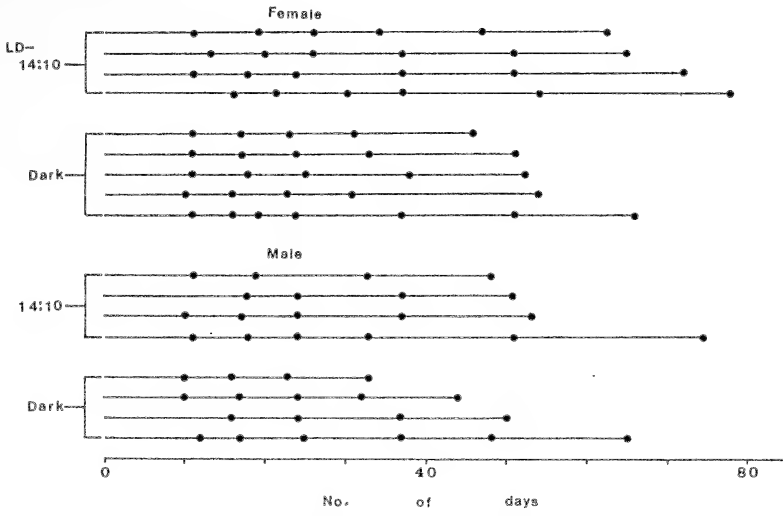
Fig. 3.—Development in both sexes reared at 23°C in complete darkness or 14L-10D. Symbols are the same as in Figure 1. Feeding intervals were 3-4 days.

Egg number per sac in relation to egg sac sequence.—Fig. 5 shows the relationship between the number of eggs per sac and egg sac sequence. In the graph, the sterile eggs were included in counts of the egg sac sequence but omitted in the calculation of the egg number per sac.

As shown by vertical lines, the range of variation in the egg number per sac was large irrespective of the egg sac sequence. However, the mean number of eggs per sac shows a gradual decrease with time. This tendency somewhat differs from that reported by Valerio (1976). He investigated egg sac productions at natural
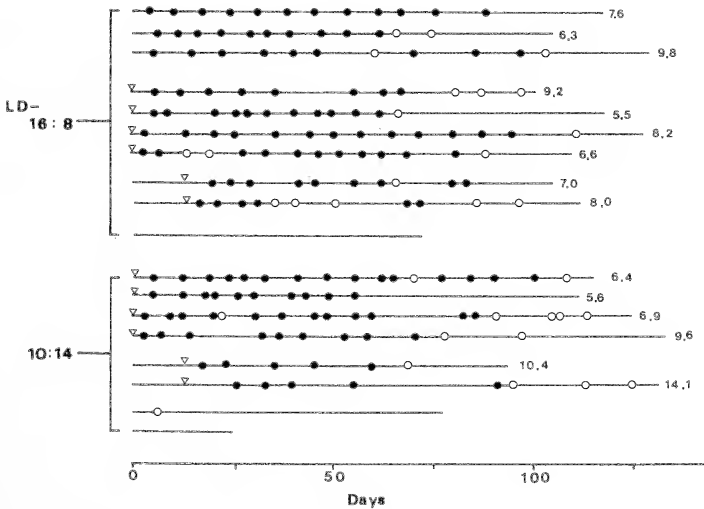
Fig. 4—Egg sac production at 25°C and 16L-8D or 10L-14D. Feeding intervals were 3-4 days. The lengths of horizontal lines indicate longevities in days for each female. Solid or hollow circles show healthy or sterile egg sacs, respectively. The upper three individuals were females mated in the field, and triangles indicate matings in the laboratory. Figures attached on the tails of each line indicate the mean interval between egg sacs.

Fig. 5—The relationship between egg number per sac and egg sac sequence. Vertical lines and solid circles indicate the ranges and means of egg number per sac in relation to position in the sequence.

room temperature in the tropics, Costa Rica, and presented the result which indicated a downward curve with two peaks related to the females' ages.
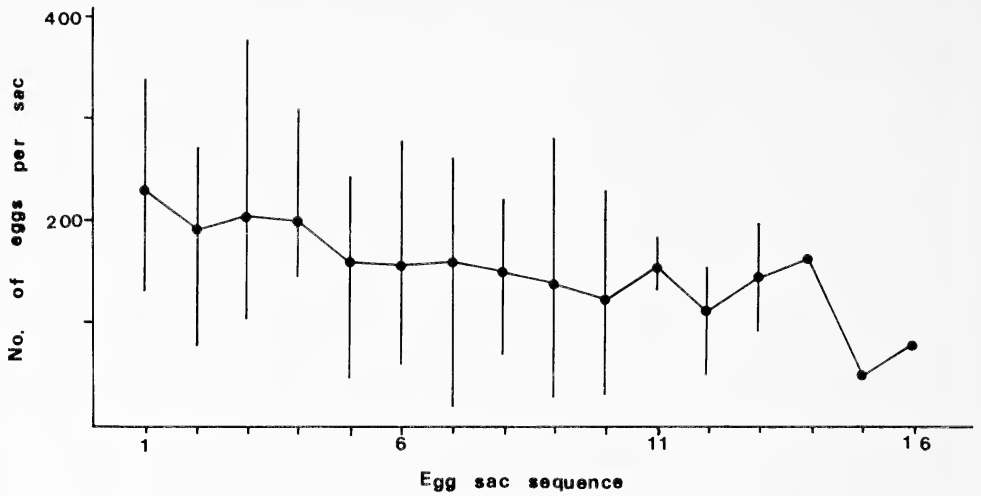
The mean total egg number produced per female was 1812.7. This figure was quite small as compared with Valerio's 3211.9 in the tropics. As shown in Fig. 4, the female continued to produce egg sacs through 2/3 of her life, but the frequency of sterile egg sacs was somewhat increased in the latter half of adult life. In addition, several females began to construct incomplete, thin egg sacs from which eggs often dropped out when touched.

DISCUSSION

The development of the house spider seems to be very flexible. As shown in Figs. 1 and 2, when food conditions were favorable, the development at 25°C and long photoperiod was accelerated by omission of one or two molts. According to Kaston (1970), even under careful rearing at 25°C, the number of molts varied from three to six in the male and five to eight in the female of *Latrodectus hesperus* Chamb. and Ivie, and three to seven in the male and five to eight in the female of *L. mactans* Fabr. The same fact was also reported by Schaefer (1977) in *Clubiona phragmitis* C. L. Koch, *Tetragnatha montana* Simon, and *Alopecosa accentuata* (Latreille), and by Mansour et al. (1980) in *Chiracanthium mildei* L.Koch. Deevey (1949) reported that the developmental period and the number of molts in *L. mactans* were strongly affected by the available food amount. Miyashita (1968) also reported the same fact in *Lycosa t-insignita* Boes. and Str. It can be said, therefore, that the developmental flexibility of the house spider is connected closely to such a variability in number of molts. In addition, this flexibility will be reinforced further by a strong resistance to fasting. As shown in Table 2, the spiderlings emerging from the egg sac could survive for 16-30 days without food and water. It is of interest that the mean longevity was significantly shorter when they were kept in solitary than when kept in a group. The reason for this is unknown.

Table 2.—Mean longevities in days of spiderlings in solitary and group under fasting at 23°C and 4L-10D.

| Condition | No. of indiv. | Longevity | |
		Mean	Range
Solitary	33	15.5 ± 1.5†	12-23
Group	38	30.4 ± 1.8**	14-36

† SD, ** Significant in *t-test* (1%).

According to Schaefer (1977), there are two different groups among spiders in reaction to photoperiods, one retains normal development irrespective of the difference in photoperiod, and the other retards development under short photoperiod. If we follow this classification, the house spider seems to belong to the latter group. Hamamura (1982) reported that in *Philodromus subaureolus* Boes. and Str., the development in early life was accelerated by a short photoperiod but retarded by a long one, although this characteristic was reversed in overwintered nymphs developed up to middle stage.

In the house spider, a developmental acceleration occurred under the long photoperiod when food conditions were favorable, but a prolongation of the last instar or both the last and penultimate instars occurred under the short photoperiod (Fig. 1). This characteristic seems to have a close connection with the overwintering of this species. In the field, overwintering populations generally consisted of nymphs at different instars and of adults, but mainly nymphs, in the last instar or the penultimate one. Such a structure of the overwintering population will reasonably be explained by the above-mentioned characteristics in reaction to the short photoperiod, since egg sac production in the field mainly occurs during June and July.

When the overwintering nymphs were collected from the field at different dates during winter and early spring, and incubated at 23°C and 14L-10D, the length of period from the commencement of incubation to the resumption of molting became gradually shorter from winter to early spring as shown in Table 3. The same phenomenon was already reported by Miyashita (1969) in *L. t-insignita*, but in the house spider, the shortening degree in that length was rather small. Among overwintering adult females, both mated and virgin individuals were included, and the former collected in December of the previous year and January began to

Table 3.—Change in the period from the commencement of incubation to molt occurrence in the overwintering nymphs collected on four different dates. Incubation was made at 23°C and 14L-10D.

| Condition | No. of indiv. | | Longevity | |
			Mean	Range
25 Dec. 1983	Female	4		
	Male	1	15.2 ± 3.5†	10-21
15 Jan. 1984	Female	3		
	Male	2	14.4 ± 2.8†	11-20
16 Feb. 1984	Female	4		
	Male	2	11.2 ± 1.3†	3-13
24 Mar. 1984	Female	2		
	Male	3	8.0 ± 0.9†	7-10

† SD

produce egg sacs after 20-30 days from the commencement of incubation. When the females which had developed to the adult stage during incubation were mated with the males obtained under the same condition, they began to poduce egg sacs only 10 days from that mating. In addition, as shown in Fig. 4, egg sac production in the female was scarcely affected by photoperiod. It appears that the overwintering individuals are in a status similar to dormancy or diapause among certain insects and mites, but the degree of the spider's dormancy is not so strong, because every individual resumes feeding soon after the commencement of incubation. Bonnet (1935) inferred that this spider originated in the tropics. If this is true, an acquisition of the above-mentioned characteristics will probably have had an adaptive significance for expanding their habitat into the temperate regions of the world.

ACKNOWLEDGEMENTS

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THE NEW SPECIES *PHILOPONELLA HEREDIAE* AND ITS MODIFIED ORB-WEB (ARANEAE, ULOBORIDAE)

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ABSTRACT

The new Costa Rican species *Philoponella herediae* and its web are described and illustrated. The web consists of a horizontal orb-web beneath which converging, vertical threads are spun.

INTRODUCTION

Most members of the family Uloboridae spin horizontal orb-webs. However, a number of modified webs have been described. These include the reduced webs of *Polenecia* Lehtinen (Wiehle 1931), *Hyptiotes* Walckenaer (Opell 1982, Peters 1938), and *Miagrammopes* O. Pickard-Cambridge (Lubin et al. 1978). Other modified webs are first spun as orb-webs and subsequently altered. Lubin et al. (1982) describe orb-plus-cone-webs constructed by one species of *Conifaber* Opell and five species of *Uloborus* Latreille. This web form is produced when a spider spins a horizontal orb-web, pulls the hub of this web downward to form a cone and then spins a second orb-web over the cone's aperture. Some *Philoponella* Mello-Leitão and *Uloborus* species spin a tangle of non-sticky threads above their webs and occasionally add what appears to be stabilimentum silk to some of these threads (Eberhard 1972, Lubin 1986, Peters 1953). *Lubinella morobensis* Opell and some *Philoponella tingena* (Chamberlin & Ivie) spin orb-webs that have a vacant sector through which a signal line runs (Lubin 1986, Opell 1979). These spiders use the signal line to monitor the web from adjoining vegetation, rather than from the typical hub position. The modified web spun by the new species described below also represents a simple alteration of an orb-web. Here, the orb itself is not altered, but converging vertical threads are spun beneath it.

Philoponella herediae, new species
Figs. 1-5

Types.—Female holotype from the Organization for Tropical Studies' La Selva research station near Puerto Viejo de Sarapiqui, Heredia Province, Costa Rica. Collected 30 June 1985 by B. D. Opell. Three female paratypes from the same locality, collected 14 Jan. 1984 by W. G. Eberhard. Holotype and two paratypes deposited in the Museum of Comparative Zoology; one paratype in the American

Museum of Natural History. The specific epithet is a noun of the genitive case derived from the Costa Rican province where the type specimen was collected.

Diagnosis.—This small species is distinguished from all other known American *Philoponella* species by its anteriorly rather than ventrally directed epigynal crypt (Fig. 4). It is the only species that lacks a precipitous posterior plate and has a centrally rather than posteriorly located "posterior rim." It is also the only known American species to lack an anterior epigynal rim, although in *P. vittata* (Keyserling) this rim is rounded and not as prominent as in most species.

Description.—Males of this species are unknown. Female carapace length 1.02-1.06 mm, sternum length 0.62-0.68 mm, first femur length 1.40-1.54 mm, abdomen length 1.82-2.08 mm. Holotype calamistrum composed of 23 setae, ventral comb of fourth leg composed of four metatarsal and 14 tarsal macrosetae. Clypeus height equal to one anterior median eye diameter. Carapace black with a central, irregular white guanine patch and light posterior lateral margins (Fig. 1). Sternum black, legs light tan with prominent black rings (Figs. 2, 3). Abdomen's dorsum with prominent black and white (guanine) spots (Fig. 1), lower sides black, venter black, without the light paraxial stripes typical of most *Philoponella* species (cf. Opell 1979, figs. 249, 256). Spinnerets and anal tubercle black.

In ventral view, the black epigynum looks like a pocket with its opening agape (Fig. 4). Unlike other new world *Philoponella* species (cf. Opell 1979 figs. 220-222, 287-288), this species lacks a precipitous posterior plate and has an anteriorly rather than a ventrally directed epigynal crypt. The region corresponding to the posterior plate of other species slopes gradually anteriorly and ventrally from the epigastric furrow to a narrow, rounded posterior rim of the crypt located near the center of the epigynum. An anterior epigynal rim is absent (cf. Opell 1979, figs. 250, 266) and the large, round epigynal openings (bursae) are located at the extreme anterior lateral margins of the epigynal crypt. In ventral view (Fig. 4) the ellipsed crypt is four times as wide as deep and in anterior view almost twice as wide as deep. Each long epigynal duct loops thrice before connecting to a round spermatheca located at the posterior of the epigynum (Fig. 5).

The clypeus height, extreme lateral position of epigynal openings, and looped epigynal ducts place this species in the *Philoponella semiplumosa* species group (Opell 1979). Within this group, it is very distinct, but most similar to *P. vittata* by virtue of the latter's broad, rounded anterior epigynal rim (Opell 1979, fig. 266).

When first observed and photographed, the holotype female was resting beneath the web's dense circular stabilimentum in the tucked posture (posture D, Opell and Eberhard 1984) typical of the genus. However, later photographs, such as Fig. 7, show her first legs extended, probably in response to vibrations produced while I was photographing the web.

Distribution.—Known only from the type locality. The La Selva field station is located in a tropical lowland wet forest (Hartshorn 1983, Holdridge 1967). The holotype was collected from low vegetation along a trail near the laboratory clearing (elevation, ca. 40 m).

WEB STRUCTURE

The female holotype was collected from an orb-web suspended at an angle of 35⁰ from horizontal with its dense, 9 mm diameter, circular hub stabilimentum
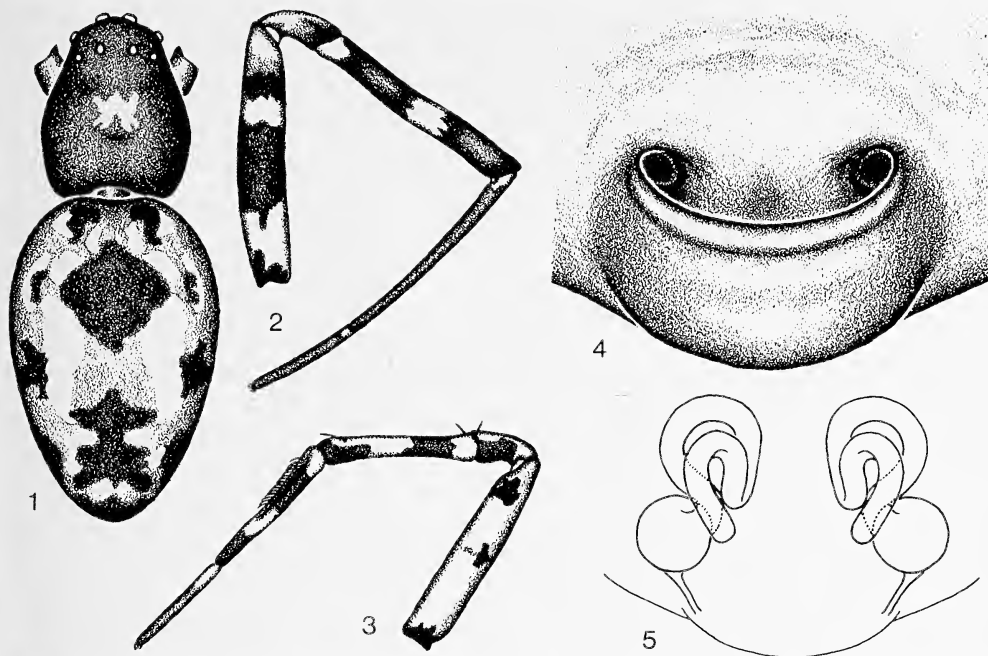
Figs. 1-5.—*Philoponella herediae* n. sp.: 1, dorsal view of female; 2, retrolateral view of right first leg; 3, prolateral view of right fourth leg; 4, ventral view of epigynum; 5, dorsal view of cleared epigynum.

about 30 cm from the forest floor. This orb had a length of 19 cm and width of 10 cm and contained 39 radii (Fig. 6). Extending from the more elevated half of the web's perimeter were six thick threads, each wider than the orb's spiral capture elements (Fig. 7). The width and looped appearance of these vertical threads (Fig. 8) suggest that they were framework threads to which stabilimentum silk was added. Eberhard (1973) reports that *Uloborus diversus* Marx (in Banks) occasionally lay stabilimentum silk on lines at the edge of and below their webs. He has also observed *P. herediae* webs similar to the one described here and believes these thicker, vertical threads likewise include stabilimentum silk (personal communication).

All but one of the vertical elements were anchored at two points to the orb's periphery. One was attached to a single radius, two to two radii, two to a radius and framework thread, and one to a radius and adjacent leaf. These vertical elements were under low tension and did not significantly deform the orb (Fig. 7). Stabilimentum silk extended from near their attachment to the orb to their final convergence 20 cm below the orb. The lengths of these vertical elements ranged from 9.2 to 18.4 cm, averaged 12.8 cm, and totaled 76.5 cm. They converged in pairs (Figs. 7, 8) and a single, 6 cm long framework thread connected the point of their final convergence to a grass blade beneath the web.

The vertical elements of this web did not noticeably deform the orb and their varied attachment points indicate that they were added after the orb was completed. These two features indicate that any resemblance of this web to a uloborid cone-web (Lubin et al. 1982) is only superficial. The function of these vertical elements is unclear. They do not seem broad enough to camouflage the spider should it run onto them after being disturbed; although they might serve to distract a searching predator. Stabilimentum silk distinguishes these vertical
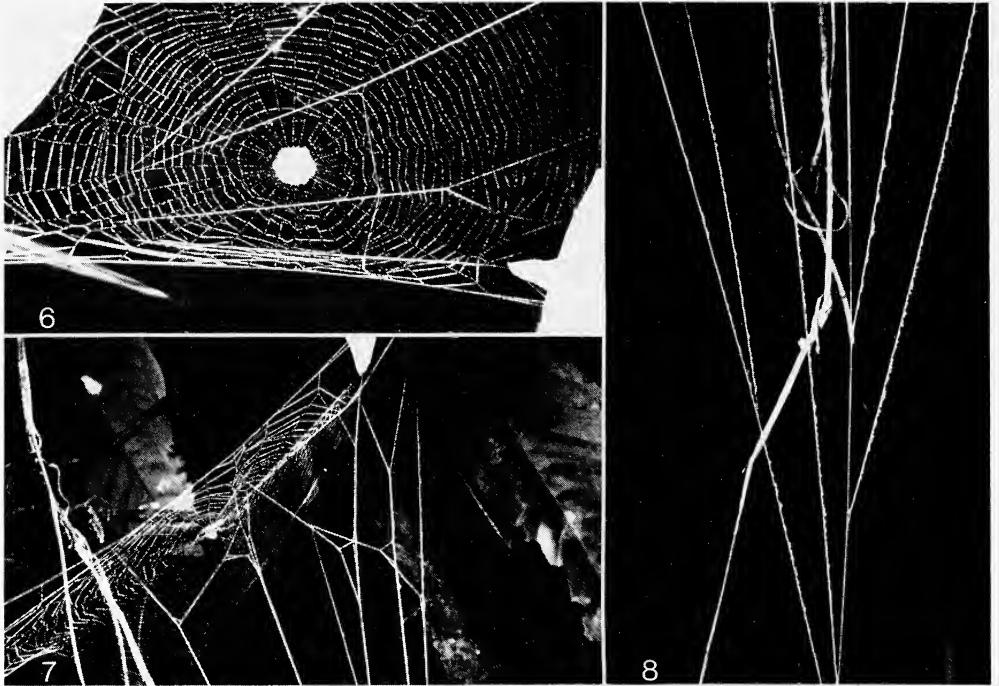
Figs. 6-8.—Web of *Philoponella herediae* n. sp.: 6, top view; 7, side view; 8, side view showing vertical elements converging beneath the web.

threads from the many silk strands in understory vegetation and may, thereby, permit a male *P. herediae* to identify and locate a female's web. Until more observations on this species are made, the variability and function of this web form will remain uncertain.

ACKNOWLEDGEMENTS

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THE AMINO ACID COMPOSITIONS OF MAJOR AND MINOR AMPULLATE SILKS OF CERTAIN ORB-WEB-BUILDING SPIDERS (ARANEAE, ARANEIDAE)

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ABSTRACT

Amino acid compositions are given for forcibly secured major ampullate silk ($n = 59$ from 4 subfamilies, 8 genera, 11 species) and minor ampullate silk ($n = 11$, 3 subfamilies, 6 genera, 8 species) of mature, female, orb-web-building, spiders. The compositions of major ampullate silk samples are neither uniform within species nor when taken from an individual spider, or even when taken from an individual spider during a single forcible silking. Chemical compositions of the two types of silk are correlated to a limited degree with their physico-chemical properties and with the taxonomic position of the spiders.

INTRODUCTION

The objectives were (1) to determine the amino acids in major and minor ampullate silk fibers (MaAS and MiAS, singular and plural) of orb-web-building spiders, and (2) to look for correlations between their chemical compositions and physical properties and the taxonomic position of the spiders (see Work 1977 and 1981b). During the study, it was discovered that these chemical compositions vary in samples from within each species and even from within an individual spider and the study was expanded to investigate these aspects.

Only eleven papers have reported original chemical analyses of the amino acid compositions of spider silks or progenitive silk polypeptides from the major or minor ampullate gland systems. The possibility of variability of the chemical composition within species or among samples taken from a single spider has been ignored. E. Fischer (1907) made the first analysis of spider silk on samples from *Nephila madagascariensis* (Vinson). Braunitzer and Wolff (1955) analyzed the contents of silk glands and silk from the same species and reported that the forcible silk samples sometimes consisted of four fibers, two about 6μm and two of smaller diameters. These samples thereby contained both MaAS and MiAS. Lucas et al. (1960) semi-quantitatively analyzed the silks of 70 species of Insecta

and six arachnid silks through paper chromatography while quantitative analyses included "reeled" silks of *N. madagascariensis* and cocoon (egg) silk of *Nephila senegalensis* (Walckenaer). Lucas (1964) later analyzed the dragline and cocoon of *Araneus diadematus* (Clerck), but supplied no information on conditions of sample procurement or duplicability of analyses. Fischer and Brander (1960) reported the amino acid analyses of frame fibers, dragline, cocoon, and entire web of *A. diadematus, Nuctenea sclopetaria* (Clerck) (= *Araneus undatus* (Oliv.)), and *Araniella cucurbitana* (Clerck) (= *Araneus cucurbitanus* (Clerck)). Their Table 1 gives two sets of data on frame fibers and three on dragline from *A. diadematus*, the data in each set being based on means from three separate analyses. Peakall (1964) pooled three to five samples from the same spider (*A. diadematus*) for each analysis and made six to eight duplicate runs, and indicated that the variability for major components was ± 5%. He recognized each of the fibroins might be composed of "a group of proteins rather than a single protein" but upon electrophoresis of the material from the ampullate "only a single, although somewhat diffuse, peak was found". He further noted that Warwicker (private communication) "considers that each gland produces a single protein". Zemlin (1968) analyzed silks from *Nephila clavipes* (Linnaeus), *Nephilengys cruentata* (Fabricius) (= *Nephila cruentata* (Fabricius)), and an unidentified spider from Paneiras, Brazil. He discussed sources of variability, as functions of sample size, in some detail (loc. cit., p. 63) and reported upon two conditions of hydrolysis for one sample. Andersen (1970) analyzed the contents of the silk producing glands, including the major ampullate secured from an unstated number of *A. diadematus* spiders. Tillinghast (1984) determined the amino acid compositions of the contents of six different glands, including major ampullate, taken by dissection from female *Argiope aurantia* Lucas. Tillinghast and Christenson (1984) made similar analyses on the major ampullate gland contents of female *N. clavipes*. The number of specimens used was not stated in either case.

In a study of the morphology and ultrastructure of the duct of the major ampullate gland of *A. diadematus* (Kovoor and Zylberberg, 1972) it was not suggested that its contents may be bicomponent and the same is the general case for observations made in a comprehensive review of arachnid silks (Koovor, 1977). However, Hans M. Peters illustrated (see Work 1981a, figs. 25 and 26) that two fibers may emerge from single major ampullate spigots. Duality of the lumenal contents of ducts and skin-core structures of fibers from these same gland systems have been described (Work 1984). But physical differences in fibers do not imply that these are based on chemical dissimilarity, as is well known among man-made fibers. Nylon and polyester 'stretch garments' depend upon fibers which are physically non-uniform in cross section. Viscose rayon fibers based on a single polymer may have a skin-core morphology, as has been described and illustrated by Morehead and Sisson (1945), Horio and Kondo (1953), Sisson and Morehead (1953), and Sisson (1960). Kovoor and Zylberberg (1980) reported a dual composition in pyriform silk while Palmer, et al. (1982) described chemically differentiable skin-core in the contents of the four silk ducts of *Antrodiaetus unicolor* (Hentz) and (1985) in the silk from spiders of the genus *Euagrus*. Gosline et al. (1984) have carried duality to a molecular level by suggesting that wetted, supercontracted, major ampullate fibers consist of crystallites (x-ray diffraction definition) in a matrix of amorphous polypeptide

rubber. Where pertinent to this paper, chemical analyses recorded in the above-mentioned papers have been compiled in Table 1. In some cases these data will be found to differ from corresponding data in Kovoor's Table 2 (loc. cit., 1977), because the latter were not converted from the original g/100g results to residues/1000 residues, as is captioned for that table. The results given in Table 1 will be discussed later in this paper.

MATERIALS AND METHODS

Sampling.—Forcible silking is limited to those spiders which are large enough to be adequately manipulated, but some resist and make sampling impossible. Responses for an individual spider appear to be essentially fortuitous, even with spiders which have been successfully silked. The operation may last from a few seconds to as long as about fifteen minutes and MaAS or MiAS, or both may be obtained and, as a practical matter, it is impossible to obtain balanced sets of samples with which to make symmetrical measurements.

Mature female spiders provided samples under constant microscopic (mag. = 10-70X) observation as described by Work and Emerson (1982). This made possible separation of MaAS and MiAS whenever the spider produced them simultaneously. Each sample was examined at higher magnification (250-430X) for freedom from contaminants and subsamples were tested for supercontractability to further confirm the glandular source.

Set 1 samples were taken when it had been mistakenly assumed that the MaAS composition was uniform within species and from individual spiders. Set 2 samples were secured to expand the study and better quantify the early indication. Set 3 samples produced time-progressive subsamples for examination of variability during continuous silkings. Samples of MiAS were obtained whenever they were produced.

Species.—Samples were obtained from the following araneid species: *Araneus diadematus* Clerck, *Araneus marmoreus* Clerck, *Eriophora fuliginea* (C. L. Koch), *Eriophora ravilla* (C. L. Koch), *Neoscona hentzii* (Keyserling), *Metazygia wittfeldae* (McCook), all subfamily Araneinae; *Argiope argentata* (Fabricius), *Argiope aurantia* Lucas, both subfamily Argiopinae; *Nephila clavipes* (Linnaeus), *Nephilengys cruentata* (Fabricius), both subfamily Nephilinae; *Leucauge argentea* (Keyserling), subfamiy Metinae (Classification according to H. W. Levi, per. comm., 1980-81).

Instrumentation.—The first group (Set 1) of samples was analyzed using a Beckman 118 amino acid analyzer. This device was incapable of determining amino acids present in very small amounts, but it is estimated that the total amount of these non-measurable components in any single analysis was not greater than two in a total of 100 residues actually present. A Durrum D-500 instrument, capable of analyzing smaller samples, became available for the second group of samples (Set 2). For the third period of the investigation, analyses (Set 3 samples) were divided between the Durrum and a Waters HPLC analyzer. Unfortunately, neither author was aware when the operation was planned that the latter device is incapable of determining proline. Thus for statistical analysis, the proline values secured by means of the Durrum analyzer on the adjacent sample or bracketing samples, were inserted into the Waters data. In the single case

Table 1.—Published literature on the amino acid composition of spider silk: Amino acid residues/100 total residues, i.e., mole % (converted thereto if otherwise reported by the author). Column 1, Author: 1 = Fischer & Brander 1960; 2 = Lucas et al. 1960; 3 = Lucas 1964; 4 = Peakall 1964; 5 = Zemlin 1968; 6 = Andersen 1970; 7 = Tillinghast 1984; 8 = Tillinghast & Christenson 1984. Column 2, Source of Silk: 1 = Frame; 2 = Dragline; 3 = Pulled; 4 = Scaffold; 5 = Major Ampullate Gland; 6 = Reeled; 7 = Foundation; 8 = Minor Ampullate Gland. Column 3, Taxa: 1 = *Araneus diadematus*; 2 = *Nephila clavipes*; 3 = *Nephilengy cruentata*; 4 = *Nephila madagascariensis*; 5 = *Nuctenea sclopetaria* (= *Araneus undatus* Oliv.); 6 = *Araniella cucurbitana* (= *Araneus cucurbitanus* Clerck); 7 = *Argiope aurantia*. ND = Not determined. TR = Trace. **ILE + LEU.

1	2	3	ASP	THR	SER	GLU	PRO	GLY	ALA	CYS	VAL	ILE	LEU	TYR	PHE	HIS	LYS	ARG	MET
1	1	1	1.68	1.45	5.57	10.28	14.46	27.83	28.26	0.23	1.49	1.66	2.08	2.51	<.11	ND	1.22	1.17	ND
1	1	1	1.70	1.65	7.67	9.82	14.39	29.75	24.95	0.20	1.27	1.74	2.22	2.43	ND	ND	1.43	1.27	ND
1	2	1	0.69	1.14	8.41	12.46	15.55	30.36	21.05	0.13	2.04	0.79	1.27	3.72	ND	ND	1.30	0.90	ND
1	2	1	2.35	2.07	7.99	11.76	13.46	33.05	19.61	<.06	<1.64	0.62	0.62	3.58	ND	ND	1.63	1.44	ND
1	2	1	1.84	1.50	7.72	13.01	14.00	31.56	20.79	<.06	0.97	0.84	0.84	3.66	ND	ND	1.79	1.30	ND
3	2	1	1.4	1.2	6.3	9.4	10.6	37.2	22.6	0.6	1.2	0.6	1.4	4.6	0.40	0.00	0.9	0.9	0.50
4	1	1	1.0	1.5	5.5	12.0	2.7	31.3	36.8	ND	1.0	1.6	1.4	1.3	ND	ND	1.5	2.4	ND
4	3	1	1.0	1.8	5.9	12.0	2.7	31.7	36.4	ND	1.7	1.3	1.6	1.0	ND	ND	1.3	1.8	ND
4	4	1	1.0	1.4	6.0	12.0	2.0	31.7	37.2	ND	1.1	1.8	1.1	1.1	ND	ND	1.3	2.1	ND
6	5	1	1.04	0.91	7.41	11.49	15.77	37.24	17.60	ND	1.15	0.63	1.27	3.92	0.45	ND	0.54	0.57	ND
5	2	2	2.5	1.2	6.9	9.0	1.1	41.5	27.0	0.0	1.2	0.6	2.0	2.7	0.5	TR	0.8	2.0	TR
8	5	2	1.9	1.0	3.0	10.1	1.7	40.3	28.4	—	1.5	0.6	4.5	3.1	0.5	0.02	0.8	2.0	0.3
5	2	3	1.3	0.7	3.0	10.0	2.6	43.3	30.4	0.0	0.1	0.5	1.8	4.0	0.04	<.03	0.3	1.1	0.01
2	6	4	0.9	0.6	4.2	11.6	ND	40.6	32.1	ND	0.9	**	2.90 **	3.2	0.6	ND	ND	2.4	ND
1	7	5	3.1	1.2	9.3	10.2	8.5	30.5	13.1	<.1	5.4	3.3	6.4	2.0	3.9	ND	1.3	1.8	ND
1	7	6	2.8	1.7	9.1	10.6	11.1	35.1	14.4	<.1	2.6	1.6	5.5	1.7	0.8	ND	1.6	1.3	ND
8	5	7	1.1	0.6	4.6	12.3	10.3	37.8	22.8	—	1.4	0.5	1.8	3.4	1.2	0.2	0.5	1.4	0.6
6	8	1	1.91	1.35	5.08	1.59	TR	42.77	36.75	ND	1.73	0.67	0.96	4.71	0.41	TR	0.39	1.69	ND
7	8	7	2.8	2.0	5.2	2.2	0.9	41.2	31.3	—	2.3	1.0	1.8	4.8	0.9	0.3	1.0	2.2	0.4

Table 2.—Analyses on each of two halves of a single primary sample of MaAS: ND = Not determined. Column headings and code numbering are explained in the Results section of the text.

OBS	SF	GP	SPIDER	SAMPLE	SPAN	ANAL	ASP	THR	SER	GLU	PRO	GLY	ALA	CYS	VAL	ILE	LEU	TYR	PHE	HIS	LYS	ARG	TRY	MET
1	2	2	4	7929	243	B	0.87	0.31	3.47	11.99	9.22	40.10	24.92	0.12	0.76	0.48	1.82	3.04	1.07	0.06	0.41	1.37	ND	ND
2	2	2	4	7929	243	B	0.79	0.31	3.58	12.14	8.93	40.04	24.88	0.11	0.76	0.48	1.83	3.27	1.07	0.06	0.39	1.35	ND	ND

where this was not possible, a mean value of all proline determinations for that species was used. Values of all other amino acids were adjusted to 100 total residues. Data are reported in amino acid residues per 100 total residues (mole %).

Analytical procedures and variances.—The procedures used for the analyses were those commonly associated with the three instruments. Because of the high percentage of glycine and alanine, when the Beckman and Waters instruments were used, it was necessary to dilute aliquots from the hydrolysate solutions for their analyses.

The potential sources of analytical variances in the procedures are 'machine (instrument)-operator errors'. The three instrument-operator combinations used in the present study have been used on a daily basis for a variety of protein analyses and have been subjected to normal quality maintenance tests to establish precision, accuracy and duplicability of analyses. Although the instrument-operator error is a function of the amount of amino acid present, it is reasonable to report all results to two decimal places (Tables 2, 3 and 5) for the statistical analyses made by the authors and for readers who may wish to extend them.

As an additional check on MaAS, a toroidal bundle from the sampling mandrel was cut on a diameter and the two halves were separately analyzed (Table 2). Duplicate analyses were made at appropriate intervals in the continuing study when hydrolysate quantities permitted.

RESULTS

The results obtained in the present study are found in Tables 2 and 3 for MaAS and Table 5 for MiAS. In the first column of these, OBS (OBS = observation) refers to an analysis of a single sample of forcibly taken MaAS or MiAS, with the following exceptions. Table 2 provides the analytical results on the two toroidal bundle samples as mentioned before. Mean values from these appear in OBS #32 of Table 3. In Table 3, OBS #44 was comprised of three primary samples and in Table 5, both OBS #7 and #8, were comprised of two primary samples. In all these cases the primary samples were too small to be analyzed alone.

The classification (by H. W. Levi) of the spiders producing the samples is found in the second to fourth columns: SF = subfamily, G = genus, and SP = species. Subfamilies: 1 = Araneinae; 2 = Argiopinae; 3 = Metinae; 4 = Nephilinae. Genera: 1 = *Araneus*; 2 = *Argiope*; 3 = *Eriophora*; 4 = *Leucauge*; 5 = *Nephila*; 6 = *Nephilengys*; 7 = *Metazygia*; 8 = *Neoscona*. Species: 1 = *diadematus*; 2 = *marmoreus*; 3 = *argentata*; 4 = *aurantia*; 5 = *fuliginea*; 6 = *argentea*; 7 = *clavipes*; 8 = *cruentata*; 9 = *wittfeldae*; 10 = *ravilla*; 11 = *hentzii*.

"Spider" and "sample" indicate the source and numbered identity of the samples in the log book (R.W.W.).

"Group" refers only to Set 3 samples. Each numbered group was secured from a single, continuous, forcible silking, and the alphabetical letters indicate the chronological order in which the individual samples were produced.

Analytical instruments ("ANAL") are identified by manufacturer: B = Beckman (Set 1), D = Durrum (Sets 2 and 3), and W = Waters (Set 3).

The remaining columns present the results of the analyses of major (Table 3) and minor (Table 5) ampullate silk samples, expressed in amino acid residues per 100 total residues (mole %).

DISCUSSION

It has been mentioned that the simple demonstration of skin-core morphology in organic fibers does not alone connote that the two phases differ in chemical composition. But the very limited study of physical behavior of the skin-core structure in MaAS (Work 1984) indicates that its basis is other than the physical factors of segmental orientation, molecular conformations, or crystallite-amorphous domains (x-ray diffraction defined). A chemical difference is suggested by the ease of fracture between skin and core when the primary fiber is allowed to supercontract and is then wet extended. This possibility is vastly reinforced by the results obtained from amino acid analyses. It must be kept in mind that for an individual sample so analyzed, it was not known whether it was single phase or skin-core, and if the latter, what the ratio of these two phases might be.

Chemical compositions reported in the literature.—It is seen in Table 1 that items 1-9 of presumed MaAS and the one analysis (item 10) of its progenitive polypeptide from *A. diadematus* are far from uniform. Although the techniques and equipment used at least 25 years ago could be expected to produce variances larger than those found today, the wide differences seen among the analyses suggest something more fundamental than instrument-operator errors. As already noted, the presumed samples of MaAS (but not the progenitive polypeptide) might have been contaminated with MiAS. To the degree that this might have occurred, both glutamic acid and proline would be expected to be reduced while both glycine and alanine would increase. Examination of the data from samples taken from *A. diadematus* show no uniform trends. It is our conclusion that the variability among items 1-10 was not entirely caused by analytical inconsistencies, contamination by MiAS, or a combination of both. It is suggested that they demonstrate real differences in the chemical compositions of MaAS from *A. diadematus* spiders.

Variability of chemical composition.—*Set 1 samples.* Set 1 provided nine samples from four species (Table 3, "ANAL" = B and Group is blank). Of these, there were four samples from *A. aurantia*, and three from *N. clavipes*, and in these two subsets, three samples came from spiders 7917 and two from 7915, respectively. When considerably greater variability was found within species (see next section), than from the two halves of a single sample (Table 2), experimental procedures were examined without finding any source of gross error. All spiders maintained in captivity were fed house flies (*Musca domestica*) raised under controlled conditions in the North Carolina State University Department of Entomology. Statistical analyses were made on results on silk samples from left, right, and both major ampullate spigots, without providing any useful information. It was concluded that the variability of chemical composition was not due to instrument or human error, diet, or differences in output of spigots. Rather, the results strongly suggested that the chemical composition of MaAS is neither constant within species nor from a single spider. The search for causes was directed elsewhere (see Work 1984) and more samples were collected for analyses.

Table 3.—Analyses of amino acid composition of major ampullate silk samples: ND = Not determined. TR = Trace. Column headings and code numbering are explained in the Results section of the text.

OBS	SF	G	SP	SPIDER	SAMPLE	GROUP	ANAL	ASP	THR	SER	GLU	PRO	GLY	ALA	CYS	VAL	ILE	LEU	TYR	PHE	HIS	LYS	ARG	TRY	MET
1	1	1	1	8037	391		D	1.68	0.74	4.95	10.22	7.84	43.10	21.30	0.10	0.86	0.67	2.31	3.94	0.40	0.79	0.49	0.60	ND	0.00
2	1	1	1	8038	343		D	0.77	0.43	3.16	11.93	8.90	34.24	20.93	0.17	1.02	0.45	1.59	4.95	9.85	1.06	0.21	0.33	ND	0.00
3	1	1	1	8039	347		D	0.79	0.22	6.12	13.44	11.92	46.56	12.67	0.20	0.83	0.46	1.39	4.25	0.25	0.19	0.14	0.55	ND	0.00
4	1	1	2	7931	232		D	0.91	0.21	4.17	17.99	11.70	44.23	13.10	0.06	0.91	0.41	1.31	2.82	0.33	0.64	0.20	0.66	ND	0.35
5	1	3	5	8011	304		D	1.06	0.09	6.60	9.78	11.05	50.74	13.00	0.03	0.75	0.38	1.64	3.82	0.27	0.25	0.12	0.42	ND	0.00
6	1	3	5	8015	315		D	1.10	0.10	7.51	8.01	11.43	51.37	13.22	0.03	0.89	0.50	1.40	3.18	0.20	0.54	0.16	0.36	ND	0.00
7	1	3	10	8030	332		D	0.90	0.07	4.24	11.34	12.00	49.08	14.71	0.03	0.75	0.55	1.56	3.82	0.18	0.20	0.07	0.50	ND	0.00
8	1	7	9	8017	316		D	1.13	0.11	6.52	9.19	11.86	43.09	20.53	0.18	0.96	0.61	0.74	3.65	0.20	0.40	0.08	0.69	ND	0.06
9	1	8	11	7907	136		B	0.87	1.31	5.65	12.38	12.78	38.36	19.64	0.06	1.40	0.50	1.31	3.97	TR	TR	0.58	0.76	0.00	0.42
10	1	8	11	8205	386	1A	D	0.96	0.56	5.18	10.74	10.42	41.23	19.59	0.98	3.24	0.57	1.09	2.64	0.34	2.21	0.26	0.00	ND	0.00
11	1	8	11	8205	390	1C	D	1.05	0.64	6.51	10.62	8.58	43.95	21.23	0.50	1.53	0.49	1.16	1.32	0.09	2.05	0.26	0.00	ND	0.00
12	1	8	11	8205	393	2A	D	1.01	0.65	5.97	10.81	8.08	45.47	20.12	0.40	1.39	0.51	1.26	2.02	0.29	1.81	0.22	0.00	ND	0.00
13	1	8	11	8205	400	3A	D	0.90	0.65	5.12	11.87	9.98	43.88	20.01	0.57	1.40	0.50	1.07	2.35	0.27	1.23	0.20	0.00	ND	0.00
14	1	8	11	8205	402	3C	W	0.82	0.95	4.65	10.46	10.64	42.95	20.98	0.75	1.65	0.56	1.32	0.46	1.85	1.77	0.18	0.92	ND	0.00
15	1	8	11	8205	389	1B	W	1.37	0.60	3.21	12.24	ND	42.18	21.76	0.20	1.41	0.65	1.71	3.26	0.37	0.11	0.53	0.90	0.00	0.00
16	1	8	11	8205	394	2B	W	1.32	0.88	6.77	12.32	ND	41.65	20.84	0.21	1.40	0.66	1.72	1.80	0.62	0.42	0.45	0.84	0.00	0.00
17	1	8	11	8205	401	3B	W	1.03	0.72	4.30	8.15	ND	43.60	22.28	0.00	1.22	0.53	1.65	4.25	0.32	0.21	0.50	0.00	0.00	0.00
18	1	8	11	8206	396	4A	W	0.95	0.67	5.18	12.34	8.06	45.48	19.95	0.51	1.35	0.52	1.19	1.52	0.28	1.79	0.21	0.00	0.00	0.00
19	1	8	11	8206	398	4B	W	1.59	1.29	6.13	12.13	ND	39.48	20.63	0.22	1.76	0.86	2.06	3.35	0.49	0.39	0.45	1.06	0.00	0.00
20	1	8	11	8207	404	5A	W	1.12	0.74	5.76	11.49	5.20	45.72	20.81	0.47	1.58	0.54	1.36	1.78	0.32	2.82	0.30	0.76	0.00	0.00
21	1	8	11	8207	408	5B	W	1.20	0.57	2.20	11.41	ND	46.42	25.41	0.22	1.48	0.61	1.77	2.43	0.00	0.32	0.00	0.76	0.00	0.00
22	2	2	3	7937	279		D	0.97	0.43	4.89	12.06	11.68	38.98	23.96	0.28	0.43	0.38	1.23	0.00	0.13	2.37	0.18	1.54	ND	0.00
23	2	2	3	8012	306		D	0.77	0.21	6.58	11.31	8.67	47.78	16.97	0.13	0.60	0.33	1.61	3.02	0.39	0.51	0.12	0.99	ND	0.00
24	2	2	3	8013	302		D	1.06	0.17	6.10	10.79	5.52	50.99	15.46	0.16	0.70	0.25	2.85	3.71	0.52	0.27	0.19	1.26	ND	0.00
25	2	2	3	8014	313		D	1.07	0.54	4.65	10.48	7.39	44.17	20.73	0.33	0.92	0.23	2.73	3.36	0.90	1.14	0.14	1.22	ND	0.00
26	2	2	4	7917	168		B	0.82	0.65	4.13	11.28	9.92	41.20	22.61	0.11	0.84	0.52	1.58	2.99	0.72	0.00	0.61	1.32	0.00	0.70

#				Cat	No	Code	Type																		
27	2	2	4	7917	179		B	0.91	0.31	3.92	11.14	9.44	44.84	20.16	0.13	0.87	0.48	1.60	3.00	0.82	0.00	0.57	1.33	0.00	0.49
28	2	2	4	7917	215		B	1.13	0.46	4.13	11.30	9.90	36.55	22.34	0.41	1.38	0.90	1.55	3.55	0.88	0.00	2.40	1.43	0.00	1.68
29	2	2	4	7917	164		D	0.83	0.28	2.60	12.26	8.91	32.57	20.85	0.57	1.08	0.21	1.55	6.12	9.62	1.74	0.27	0.54	ND	0.00
30	2	2	4	7917	178		D	0.98	0.40	3.47	11.35	9.42	43.65	20.65	0.20	1.06	0.72	1.85	2.76	1.11	0.40	0.29	1.44	ND	0.27
31	2	2	4	7917	200		D	1.03	0.33	2.82	11.39	9.11	40.40	24.75	0.19	0.91	0.39	2.03	2.64	1.40	1.32	0.37	0.93	ND	0.00
32	2	2	4	7929	243		B	0.83	0.31	3.52	12.06	9.07	40.07	24.90	0.12	0.76	0.48	1.82	3.15	1.07	0.06	0.40	1.36	0.00	0.00
33	2	2	4	7929	239		D	0.73	0.09	3.50	13.86	9.63	48.31	16.82	0.19	1.06	0.17	0.60	1.71	0.68	1.09	0.19	0.78	ND	0.59
34	2	2	4	7933	248		D	0.72	0.12	2.41	12.25	8.12	48.65	19.36	0.13	0.98	0.27	1.29	1.53	1.19	0.71	0.37	1.46	ND	0.43
35	2	2	4	8208	412	6A	D	0.84	0.15	3.86	13.11	8.72	42.42	22.42	0.49	1.82	0.48	1.22	2.00	0.80	1.56	0.29	0.00	0.00	0.00
36	2	2	4	8208	414	6C	D	0.78	0.13	4.19	13.87	7.41	44.42	22.04	0.24	0.89	0.40	1.26	2.14	0.88	1.07	0.28	0.00	0.00	0.00
37	2	2	4	8208	416	7A	D	0.73	0.12	3.68	12.96	5.49	45.90	23.40	0.30	1.10	0.44	1.47	2.27	0.94	0.92	0.30	0.00	0.00	0.00
38	2	2	4	8208	418	7C	D	1.26	0.26	3.66	10.70	5.61	40.24	26.78	0.83	1.67	0.49	2.21	1.10	1.38	3.06	0.48	0.00	0.42	0.00
39	2	2	4	8208	420	8A	D	0.75	0.08	3.58	10.80	9.42	44.33	18.68	0.00	0.80	0.90	2.47	3.46	0.75	0.76	0.32	0.91	0.00	0.00
40	2	2	4	8208	430	10B	D	1.09	0.17	3.21	10.36	5.70	43.22	22.53	0.00	0.88	1.29	4.25	2.30	1.40	0.83	0.44	1.76	0.00	0.00
41	2	2	4	8208	413	6B	W	0.78	0.37	3.97	14.28	ND	38.32	22.10	0.09	0.87	0.46	1.52	3.60	0.99	0.12	0.42	1.12	0.00	0.00
42	2	2	4	8208	417	7B	W	0.97	0.40	3.69	12.75	ND	40.74	25.47	0.18	0.91	0.53	2.33	2.78	1.64	0.19	0.51	1.61	0.00	0.00
43	2	2	4	8208	421	8B	W	0.88	0.45	4.80	12.49	ND	41.19	22.96	0.14	0.88	0.50	1.46	1.41	0.90	0.54	0.47	1.03	0.39	0.00
44	2	2	4	8208	425-27	9A	W	1.04	0.44	4.60	13.53	ND	41.67	24.18	0.17	0.95	0.57	2.14	1.57	1.10	0.58	0.53	1.45	0.19	0.00
45	2	2	4	8208	429	10A	W	0.92	0.35	3.48	11.79	ND	42.47	26.18	0.08	0.74	0.44	2.29	2.71	1.11	0.31	0.00	1.46	0.00	0.00
46	2	3	4	8008	308		D	1.04	0.38	6.23	10.43	6.73	46.63	14.19	0.60	1.31	0.07	3.27	5.45	1.31	1.09	0.20	1.03	ND	0.05
47	2	3	6	8009	310		D	1.06	0.38	5.72	10.19	6.72	47.14	17.52	1.26	1.54	0.07	3.01	2.54	0.40	1.29	0.19	0.96	ND	0.00
48	2	4	6	7913	165		D	1.06	0.34	2.24	11.02	2.04	49.96	22.71	0.06	0.89	0.07	4.26	2.99	0.26	0.21	0.10	1.76	ND	0.04
49	2	4	7	7913	196		D	1.18	0.38	2.39	10.90	1.71	49.34	23.03	0.05	0.95	0.07	4.13	2.83	0.29	0.40	0.11	1.78	ND	0.44
50	2	4	7	7914	199		B	0.79	0.37	0.88	6.20	2.73	42.20	36.63	0.08	0.61	0.35	4.06	2.80	0.30	TR	0.34	1.66	TR	0.00
51	2	4	7	7914	160		D	1.14	0.45	2.92	11.53	4.16	49.52	20.08	0.03	0.93	0.07	3.96	2.29	0.26	0.85	0.09	1.72	ND	0.01
52	2	4	7	7915	180		B	1.11	0.59	2.85	9.71	3.10	41.56	30.20	0.06	0.83	0.49	3.48	3.52	0.33	0.00	0.36	1.77	0.00	0.00
53	2	4	7	7915	250		B	0.49	0.36	0.62	10.13	ND	51.15	26.68	0.06	0.01	0.00	1.50	2.05	0.00	0.58	0.52	3.34	0.00	0.00
54	2	4	7	7916	163		D	0.91	0.40	2.35	11.50	1.75	51.07	21.43	0.05	0.83	0.05	4.38	2.76	0.23	0.43	0.08	1.78	ND	0.00
55	2	4	7	8010	300		D	0.86	0.29	2.05	10.98	0.42	52.40	22.69	0.02	0.77	0.03	4.71	2.23	0.23	0.37	0.15	1.78	ND	0.00
56	2	4	7	8028	329		D	1.03	0.45	2.68	12.45	1.29	51.02	20.16	0.14	0.87	0.04	4.80	2.07	0.24	0.83	0.11	1.83	ND	0.01
57	2	4	8	7934	261		B	0.71	0.54	2.34	8.76	2.44	42.84	32.08	0.00	0.05	0.43	1.76	0.56	0.01	5.76	0.96	0.78	0.00	0.00
58	2	4	8	7934	263		D	1.05	0.51	2.84	9.82	2.24	49.49	25.74	0.02	0.73	0.16	2.02	4.13	0.31	0.17	0.13	0.59	ND	0.05
59	2	4	8	7936	277		D	1.03	0.36	2.63	11.19	2.82	51.42	22.07	0.11	0.66	0.17	2.13	3.85	0.19	0.23	0.13	0.58	ND	0.42

Set 2 samples. Set 2 supplied data on 27 samples from 10 species ("ANAL" = D and Group is blank in Table 3). The most divergent amino acid values are those for phenylalanine in OBS 2 and 29, being 9.85 and 9.62 residues per 100 residues. These unusually high and very similar values came from two species collected over one year apart. The high levels of phenylalanine appear to be associated with low levels of glycine, but the two cannot be confused in the analytical procedure. Nevertheless, these results appeared to be so incongruous that every effort was made to locate some extraneous source of error, but none was found. On the basis of levels of phenylalanine alone, statistical analysis placed these two samples into a statistical population quite separate from all of the other samples in Table 3. Accordingly, the data from them have not been included in the statistical analyses made on the remaining samples.

Set 3 samples. In order to determine whether there are timewise trends in chemical composition as MaAS is generated by spiders, the set 3 samples were secured as groups of chronologically (A to C) related subsamples, each group (1 to 10) representing a single, continuous, forcible silking lasting up to 20 minutes. The inability of the Waters instrument to determine proline complicated, but did not prevent the analysis of the results. In Table 3, it is seen that in each of groups 1, 3, 6 and 7 the Durrum results are far from being identical for subsamples A and C. If there are timewise trends peculiar to a single spider, the increase or decrease or lack of change in the level of each amino acid for subsamples A and C, should be the same or at least in the same direction, in duplicate silkings. Group 1 (OBS 10 and 11) and group 3 (OBS 13 and 14) are duplicates from spider 8205 (*N. hentzii*). The six amino acids which compose about 91% of the total residues provide the following directions of change. Gly increases between OBS 10 and 11 but decreases between OBS 13 and 14. Similarly, Ala increases vs. increases; Glu is essentially unchanged vs. decreases; Pro decreases vs. increases; Ser increases vs. decreases; Val decreases vs. increases. For spider 8208 (*A. aurantia*) group 6 (OBS 35 and 36) vs. group 7 (OBS 37 and 38); Glu increases vs. decreases; Ala essentially unchanged vs. decreases; Gly increases vs. decreases; Pro decreases vs. virtually unchanged; Ser increases vs. identical; Val decreases vs. increases.

From these observations it is reasonable to conclude that there are no systematic trends in the changing chemical compositions during the progression of forcible silkings of individual spiders. This conclusion is reinforced when proline interpolations are put into the Waters data and all of the Set 3 results are submitted to statistical trend analyses.

There is a second method which has the added advantages of reducing theoretical instrument-operator errors and allows the usage of Waters data without taking proline into account. It makes use of dimensionless pair ratios of amino acids from each analysis, of which Gly/Ala, Glu/Pro and Ser/Tyr are useful examples, particularly Gly/Ala, since for the Waters analyses both came from the same aliquot of the primary hydrolysate. The Glu/Pro pair does not exist from the Waters analyses but Glu may be paired with any other amino acid. When these ratios were submitted to statistical analysis, no uniform directional timewise trends were found in compositions of MaAS taken during single forcible silkings.

Taxonomy.—In Table 3, each of 57 usable (omitting OBS 2 and 29) analytical results report upon a maximum of 18 amino acids from 26 spiders, 4 subfamilies,

8 genera, 11 species and 3 instrument-operator combinations, thereby providing an extremely large number of potential sets for statistical analyses. Each taxon-analysis combination ($n = 54$) was taken as a statistical set and submitted to the Duncan Multiple Range Test, programmed for an IBM® 3081 computer at the Triangle Universities Computer Center by SAS®. The results are given in Table 4. The Duncan Test has been described in standard textbooks (example, Steel and Torrie), its computer usage by SAS® (1982) and is summarized (Robert J. Monroe, per. comm. 1986) as follows:

> "The Duncan Multiple Range Procedure was designed to separate a heterogeneous group of mean values into subsets each of which is judged homogeneous in the statistical sense of the word. In its usual form, the procedure identifies each homogeneous subset by a different letter (A, B, C . . .). Since the means are ranked from high to low the letters form a progression from A, B, C . . . depending on the number of different subsets. Hence when a given mean value may belong to two or more subsets, more than one letter may appear beside the mean indicating this fact. In some few instances there may be a clear delineation of subsets but the usual case almost always has some overlapping subsets; thus the source of ambiguity in the interpretation. A common logical error is to equate 'non-significance' (using a test level of Prob. = 0.05) to 'equality'. This reasoning process then always leads to a violation of one of the canons "Things equal to the same thing are equal to each other". A more reasoned use is to impute to 'non-significance' the inability to discriminate among means without concluding equality among them. In this case no logical contradictions occur".

In programming the Duncan procedure, one level of possible error is used for species, two for genera and three for subfamily. For inclusion in Table 4 the more (genera) or most (subfamily) conservative result was selected on the basis of having the greater (-est) mean square error. In examining the letter designations in Table 4, it must be kept in mind that only those within a set may be intercompared.

The only amino acids which help distinguish subfamilies are Pro and Cys. Little weight can be given, however, to the Cys differences, because cysteine is present in very small amounts (Table 3), and n is only 2 for Metinae, the subfamily with unique Cys values. On the other hand, Nephilinae (and its genera and species) is distinct from the other taxa on the basis of Pro which is present in large amounts.

The forcible silkings that provided 59 analyses of MaAS, gave only enough MiAS for the 11 seen in Table 5. These limited results were submitted to statistical analyses, from which it can only be said that these carry the hint that there is less variability of amino acid composition for MiAS, both within species and between species, than for corresponding MaAS. It should be kept in mind, however, that one uncertainty found for MaAS does not exist with MiAS, namely, there is no present evidence that MiAS may exist as two-component systems.

Macromolecular chemistry.—It is generally accepted that in the fibroin of the silk of *Bombyx mori* Linnaeus there is a sequence of (Gly-X-Gly-X-Gly-X)$_n$, where X may be either Ala or Ser, these last being in the ratio of two to one, respectively. Although investigators do not agree upon the exact composition of silk from *B. mori* (Lucas, et al. 1960; Iizuka 1970; Komatzu 1979), the analyses are close to the ratios, Gly = 3; Ala = 2; Ser = 1). As Dickerson and Geis (1969) point out, this allows the glycine side chains to "nestle quite efficiently" opposite to the larger alanine or serine side chains in the antiparallel-chain pleated sheet model of Pauling and Corey (1953). This applies only to the crystalline domains

Table 4.—Duncan Multiple Range Test on major ampullate silk analyses, by taxa: *Number of results secured. **Maximum samples available.

Taxa	n**	ASP 57	THR 57	SER 57	GLU 57	PRO 46	GLY 57	ALA 57	CYS 53	VAL 57	ILE 56	LEU 57	TYR 56	PHE 54	HIS 50	LYS 57	ARG 57	TRY 2	MET 16
SF																			
1	20	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A
2	23	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A
3	2	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	-	A
4	12	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	-	A
Genera																			
1	3	A	BC	A	A	AB	AB	BC	B	AB	A	B	A	A	A	A	B	-	A
2	23	A	BC	A	A	BC	B	ABC	B	AB	A	B	A	A	A	A	B	A	A
3	3	A	C	A	A	AB	A	C	B	AB	A	B	A	A	A	A	B	-	A
4	2	A	BC	A	A	C	AB	BC	A	AB	A	A	A	A	A	A	B	-	A
5	9	A	BC	A	A	D	AB	AB	B	AB	A	A	A	A	A	A	A	-	A
6	3	A	B	A	A	D	AB	A	B	B	A	B	A	A	A	A	B	-	A
7	1	A	C	A	A	A	B	ABC	B	AB	A	B	A	A	A	A	B	A	A
8	13	A	A	A	A	ABC	B	ABC	B	A	A	B	A	A	A	A	B	-	A
Species																			
1	2	A	AB	ABC	BC	AB	AB	BCD	B	ABC	AB	BC	A	B	A	A	B	-	A
2	1	A	B	BCD	A	A	AB	D	B	ABC	ABC	C	A	B	A	A	B	-	A
3	4	A	B	ABC	BC	AB	AB	ABCD	B	BC	ABC	BC	A	AB	A	A	AB	-	A
4	19	A	B	CDE	B	AB	B	AB	B	ABC	AB	BC	A	A	A	A	AB	A	A
5	2	A	B	A	C	A	A	D	B	ABC	ABC	C	A	B	A	A	B	-	A
6	2	A	B	AB	BC	B	AB	BCD	A	AB	C	AB	A	AB	A	A	AB	-	A
7	9	A	AB	E	BC	C	AB	A	B	BC	BC	A	A	B	A	A	A	-	A
8	3	A	AB	DE	BC	C	AB	A	B	C	ABC	BC	A	B	A	A	B	-	A
9	1	A	B	A	BC	A	B	ABCD	B	ABC	A	C	A	B	A	A	B	-	A
10	1	A	B	ABC	BC	A	AB	CD	B	BC	AB	C	A	B	A	A	B	-	A
11	13	A	A	ABC	BC	AB	B	ABC	B	A	AB	C	A	AB	A	A	B	A	A

of *B. mori*, which constitute about 37% to 47% of the total, as defined by x-ray diffraction analysis (Iizuka 1965).

The considerable differences in amino acid compositions of MaAS and MiAS from *Araneus diadematus* and *Argiope aurantia*, respectively, have already been illustrated by Andersen (1970) and Tillinghast (1984), respectively. The former has underscored this by comparing (his Table 2) the residues with short side chains in MaAS and MiAS, being 62.25 and 84.60. In the present study the corresponding figures are 70.47 ($n = 57$) and 83.45 ($n = 11$). It must be mentioned, however, that the C.V.s of the mean values for MaAS are quite large, being Gly = 8.89%, Ala = 20.8%, Ser = 37.4%, and MiAS, the same amino acids, C.V.s are 13.1%, 9.14%, 25.2%. As an extension of this approach, *t-tests* were made to compare the mean values of corresponding amino acids in MaAS (Table 3) vs. those for MiAS (Table 5). It was found that significant or highly significant differences existed for all amino acid residues except for Ser and four of those present in very small amounts, Cys, Met, Phe, and His.

It is evident that when compared with MaAS, the higher levels of short side chain amino acids make it more possible for MiAS to approach the conformational structure of the anti-parallel chain pleated sheet model. To what degree this theoretical condition is attained remains unknown, since the crystalline-amorphous ratios of these two silks have yet to be determined. It would be expected that the relative amounts of amorphous domains, and their chemical and conformational aspects, would be determinative, relative to physico-chemical properties. Some hints relative to this may be revealed by the physical properties of the two types of fibers, investigated many years ago in the pioneering paper by Lucas, et al. (1955). Thus it is not surprising that the 'Hookean' section of the force-elongation curves of MiAS reach higher levels of stress than do MaAS, before inflection (Work 1977, figs. 1 and 2, and ibid., Table 1, section C) and that MiAS possess higher birefringences than MaAS. Levels of this property are considered to be functions of the vectorial degree of alignment of molecular segments parallel to the axis of the fibers, as induced by amounts of 'drawing'. The chemical composition data which suggests that MiAS has greater structural order than MaAS is consistent with the higher birefringences of MiAS.

Tillinghast and Christenson (1984) have already raised the question of the effect of proline on supercontraction. Some light can now be cast on the subject. Because nothing is known regarding sequence of amino acids in either MaAS or MiAS, only average values for amino acids with large side groups may be considered. The Pro in MaAS from the combined subfamilies Araneinae and Argiopinae ($n = 33$) has a mean value of 9.14 (C.V. = 23.1%); for Nephilinae ($n = 11$) mean = 2.25 (C.V. = 40.4%) (Metinae, $n = 2$, will be disregarded). For all MiAS ($n = 11$) mean = 0.46 (C.V. = 74%). Thus, the potentiality exists, on the average, that a proline may occur every 11 amino acid units for the first two subfamilies, every 44 for Nephilinae, and only every 220 for MiAS. Glutamic acid is another amino acid with a large side group. When similar calculations are made on its presence in MaAS and MiAS, it is found that based on average contents, it may occur about every nine and 50 units in these two polypeptides, respectively. Work (1981b, Table 1), has shown that combined Araneinae and Argiopinae ($n = 180$) mean supercontraction ratio = 0.546; for *Nephila clavipes* ($n = 29$) mean ratio = 0.639; and for *Nephilengys cruentata*, ($n = 22$), mean ratio = 0.817. The contraction ratio of MiAS was 0.956 ($n = 35$). Thus, there is an

Table 5.—Analyses of amino acid composition of minor ampullate silk samples: ND = Not determined. Column headings and code numbering are explained in the Results section of the text.

OBS	SF	G	SPIDER	SAMPLE	GROUP	ANAL	ASP	THR	SER	GLU	PRO	GLY	ALA	CYS	VAL	ILE	LEU	TYR	PHE	HIS	LYS	ARG	TRY	MET
1	1	1	8039	345		D	1.71	1.65	4.15	1.98	0.38	47.46	30.26	0.39	1.65	0.33	1.35	5.63	0.74	0.77	0.11	1.44	ND	0.00
2	1	1	8040	340		D	1.87	1.48	4.60	1.89	0.58	51.09	29.56	0.44	1.38	0.27	0.60	2.35	0.59	1.53	0.20	1.57	ND	0.00
3	1	5	8011	303		D	0.95	1.83	4.02	0.98	0.39	54.70	28.16	0.02	0.96	1.02	1.07	4.49	0.24	0.24	0.06	0.73	ND	0.15
4	1	3	8015	314		D	0.98	1.68	3.75	0.96	0.34	54.07	28.68	0.04	1.14	0.97	1.01	4.98	0.41	0.18	0.07	0.71	ND	0.02
5	1	3	8030	333		D	1.00	1.52	3.62	1.01	0.20	55.75	28.37	0.03	0.92	0.78	1.08	4.36	0.25	0.25	0.04	0.77	ND	0.06
6	1	8	8207	407	5	D	1.19	0.72	2.29	0.75	0.00	58.33	29.51	0.25	1.14	0.91	0.62	3.36	0.17	0.68	0.08	0.00	ND	0.00
7	2	2	7937	256 & 265		B	1.85	1.70	5.27	2.99	1.12	41.98	31.88	0.12	1.38	1.24	1.77	4.68	0.77	0.00	1.08	2.17	0.00	0.00
8	2	4	7929	236 & 240		B	1.82	1.87	4.52	1.46	0.00	40.95	35.49	0.08	1.69	1.15	1.93	4.72	0.65	0.00	0.71	2.22	0.00	0.00
9	5	7	8028	330		D	2.32	2.12	4.46	3.60	0.62	45.86	27.63	0.13	2.84	1.34	1.78	3.77	0.58	0.80	0.29	1.82	ND	0.04
10	6	8	7934	259		B	1.50	1.32	2.86	2.93	0.56	39.95	35.21	0.01	1.62	0.71	1.00	5.04	0.65	2.67	1.81	1.61	ND	0.44
11	6	8	7936	275		D	1.23	0.88	2.35	3.31	0.85	52.81	28.34	0.03	1.39	0.82	0.99	4.59	0.42	0.42	0.08	1.49	ND	0.00

inverse relationship between the presence of the large side groups of proline and glutamic acid in the polypeptide molecules and the degree of their axial stability, when wetted in an unrestrained state.

The physical characteristics of MaAS, strength, extensibility, moduli, and viscoelastic behavior, regardless of source of these fibers, are very similar (Work 1976, 1977, 1981b, 1985). Because the knowledge of these is infinitesimally small as compared with the published literature on man-made fibers, it is appropriate to consider the latter as the basis of speculation about the former. Among man-made fibers, very small differences in chemical composition tend to produce considerable dissimilarities in physico-chemical properties, as is well known to polymer chemists who have attempted to duplicate the properties of commercially acceptable man-made fibers without infringing patents. In view of this it may be speculated that perhaps the core dominates physical properties, even as it alone supercontracts. It is of interest to note that MiAS and the skin of MaAS neither supercontract nor possess a known function in the orb web. One can only conjecture concerning all of these phenomena, and suggest that their study, especially their individual chemical compositions and amino acid sequencing, offer a challenge for future study.

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THE MECHANISM OF HABITAT SELECTION IN
THE LONG-JAWED ORB-WEAVING SPIDER
TETRAGNATHA ELONGATA (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT

Tetragnatha elongata is associated exclusively with riparian habitats. The physiological suitability of
a given environment is determined by accessibility to open water. When this is denied, spiders suffer
dehydration, the rate of which is determined by the temperature and relative humidity. Where the
abiotic environment is suitable, spiders build webs on any available structural support. The webs of *T.
elongata* are short lived. Once a web has been built, a spider may rebuild at the same site or move to
a new site. Prey availability appears to be the primary determinant as to which of these alternatives is
adopted.

INTRODUCTION

One of the most important decisions web-building spiders make during their
life is that of selecting a site in which to build. These decisions are known to
strongly influence spider growth, survival and reproduction (Riechert and Tracy
1975). Habitat utilization has been described in a large number of spiders, strong
associations being found with abiotic factors such as structural features,
temperature, wind, rain and humidity; similar associations have been found with
areas of high prey availability (Riechert and Gillespie 1986). Such associations
need not, however, imply habitat selection: ballooning may allow spiders to be
carried to different areas using wind currents. But, as shown by Tolbert (1976),
spiderlings may reinitiate ballooning, presumably after sampling the local
environment encountered following initial dispersal. Changing environmental
conditions have also been found to cue dispersal in later life history stages in, for
example, linyphiids (Duffey 1956, 1963, Wingerden and Vughts 1974, Vughts and
Wingerden 1976). Chance encounter is therefore insufficient to account for the
habitat ultimately occupied by these spiders.
A number of spider species have also been shown to exhibit active preference
for a specific abiotic environment reflective of their natural habitat (Norgaard
1951, Cloudsley-Thompson 1957, Riechert 1976). Similarly, several groups have
been shown to exhibit active site selection on the basis of prey availability

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(Turnbull 1964, Dabrowska Prot et al. 1968, Holldobler 1970, Luczak 1970, Riechert 1976, Gillespie 1981, MacKay 1982, Morse & Fritz 1982, Olive 1982). In this paper I examine the extent to which habitat utilization involves active site selection, using the long-jawed orb-weaving spider *Tetragnatha elongata* Walckenaer (Levi 1981). This species, in common with other tetragnathids, builds delicate, short-lived orb webs which are taken down and ingested daily if not more frequently. Webs are built by immatures and mature females. *T. elongata* is associated exclusively with aquatic habitats. The present study was conducted in North Carolina during the summers of 1982-1984. I first looked at the distributional pattern of the spiders—the organization of a population through the spatial arrangement of its individuals in the environment (Pielou 1969). The technique used was the same as that employed to examine the patterns of distribution of the desert funnel-web spider *Agelenopsis aperta* (Gertsch) (Riechert et al. 1973; Riechert 1974). The second part of this study examines whether the observed pattern of distribution is a consequence of differential survival, or is rather caused by active habitat selection.

METHODS

Two study areas were established in the vicinity of Highlands Biological Station in western North Carolina. The first was in a cool, sheltered woodern with a creek. The other was an exposed area near the edge of a lake where dead twigs and branches jut out of the water.

Pattern.—*Field Methods.* Two plots—one on the creek (64 m x 16 m) and the other on the lake (16 m x 16 m)—were selected and mapped in July 1982. Plot sizes were selected in order to include comparable areas (approx. 25 m²) of surface water in the different habitats. Each plot was divided into quadrats of 1.0 m² for mapping. Webs on the creek were examined, and their location within a quadrat recorded, over a period of 32 days. An index of web site suitability was obtained by using the frequency with which each site was used over this period. Webs on the lake were far more dense. Data on web locations here were taken from censuses on two consecutive days, during which time approximately the same number of webs were recorded as in the creek habitat. In each plot, the distribution of habitat features and microclimate characteristics were also mapped. Measurements were then taken in each quadrat of: water, sand, moss and leaf litter; twigs (branches less than 2 cm diameter) and branches (more than 2 cm diameter) at heights of 0-50 cm, 50 cm-1 m, 1-2 m and 2-4 m. Microclimate characteristics (light intensity, temperature, humidity, wind speed and water flow rate) were also measured on three occasions (each on clear, sunny days) in each plot.

Methods of Analysis. Block size analysis of variance was used to examine the distribution of webs in the study areas. This type of pattern analysis was developed by Greig-Smith (1952, 1961, 1964) and Kershaw (1960, 1964) for measuring departure from randomness. It is useful in dealing with most natural situations in which not only presence or absence are involved but also ranges of density (Greig-Smith 1961). Covariance was calculated between web distribution and that of each of the habitat features mentioned above in all plots. This allowed the determination of pattern scales as well as significant associations.

Factors responsible for survival and web building.—In order to determine whether *T. elongata* was exhibiting active selection of web sites, it was necessary to examine (1) those parameters which allowed survival; (2) those required for construction of the web trap; and (3) the probability that a spider would move from a site where it had built a web versus situations where no web was built. The variables I chose to examine (on the basis of the results from the pattern analysis) were: (1) temperature (2) light intensity (3) humidity (4) presence of open water and (5) prey availability. Within its natural distributional area, the parameter most likely to have an immediate effect on individual survival is desiccation (caused by high temperature, low humidity or the absence of water). The relative effects of each of these parameters was measured through a series of experiments (Table 1): A, high temperature, low humidity, no water; B, high temperature, high humidity, water present; C, high temperature, high humidity, no water; D, lower temperature, low humidity, no water; E, lower temperature, high humidity, water present; F, lower temperature, high humidity, no water. For each treatment (A-F) six spiders were used. After being weighed, individuals were placed in small, cylindrical, plastic vials (height 5 cm, diameter 2.5 cm) covered with cheesecloth. The weight of each spider was recorded at quarter hour intervals during a 10 hour treatment. For spiders that died, recordings were taken up until death.

The most likely parameters to exert a direct effect on web-building behavior in *T. elongata* were considered to be one or more of the following: (1) vulnerability to desiccation (i.e. the combined effects of temperature, humidity and open water); (2) light intensity (acting as a cue to humidity) and (3) prey availability. Results from the tests on survivorship (Table 1) showed that direct access to open water was needed to prevent desiccation. Field cage experimentation was used to examine this. Two cages were set up—identical except that the floor of one was covered with wire mesh (to allow the passage of small emergent aquatic insects, but prevent direct access to the water by spiders); the other was open to the water's surface. These cages were 1.5 m x 0.6 m x 0.6 m, and were placed at the same orientation (with respect to incident sunlight), separated by a distance of approximately 2 m. The sides were covered with clear polythene and the top with fine wire netting. Wooden bars crisscrossed the cages to provide structural support. The effects of incident solar radiation were examined by dividing each of the cages into two equal portions along their length by means of a polythene sheet. One of these sections in each cage was covered with aluminum foil and black polyethelene to block out a large portion of both visible and infrared wavelengths of the solar spectrum. Any time that measurements were made on the spiders, recordings were taken of temperature (°C) and illuminescence (lumens m^{-2}) in both covered and open sections of the cages. In order to control for any differences in these variables that might exist between the two cages, recordings were taken from both at approximately the same time. Humidity was also measured.

Two separate experimental procedures were employed to examine the respective effects of desiccation and light intensity on web-building. In the first, a total of 12 adult female spiders were collected, weighed and marked, and six were placed in each section on a clear, sunny day. Individuals were weighed hourly from 0600 to 2100 h. (To do this, in order to minimize time out of the cage, spiders were taken in rotation.) The experiment was replicated on the next clear,

Table 1.—Set of experiments to test survivorship under various extremes of the abiotic environment: Weighed spiders were placed individually in small cylindrical vials (height 5 cm, diameter 2.5 cm) covered with cheesecloth, and were then subjected to one of six treatments. Water (up to 5 mm in the vial) was added to four of the vials, but was covered over with wire mesh (to prevent direct access by the spider) in two of these. Half the vials were placed in a desiccator (temperature 37.5° C, humidity 4%) and the other half were kept in the laboratory (temperature 18.0° C, humidity 75%). Six spiders were tested under each of these sets of conditions.

	TREATMENT					
	A	B	C	D	E	F
TEMPERATURE	37.5	37.5	37.5	18.0	18.0	18.0
ACCESSIBILITY OF OPEN WATER	NO	YES	NO	NO	YES	NO
HUMIDITY	4%	75%	75%	4%	75%	75%
EXPERIMENTAL SET UP						
Desiccator	yes	yes	yes	no	no	no
Water	none	present	covered	none	present	covered

sunny day with 12 new spiders. In the second experiment, 12 new spiders were collected and six weighed and marked individuals placed, as before, in each section. Spider activity and web lifespan were monitored at hourly intervals each day for a 16-day period. The procedure was replicated over the next 16 days.

In order to determine the effect of prey availability on web-building, a series of small cages (39.3 cm x 39.3 cm x 11.4 cm) were set up along a stream bed, where the incidence of solar radiation was very low (midday peak approx. 37.20 lumens m^{-2}). Individual spiders were weighed and then placed in these cages, where they had direct access to open water. The spiders were fed on field-collected fruit flies (*Drosophila* spp.) caught from a culture of rotten fruit just prior to feeding. Spiders were fed at 2000 h daily, insects being placed in the cages by means of specifically designed apertures in their tops. The stoppers in these apertures were removed, and tubes containing the insects inverted over the top. Although the presence of soft tissue paper in the tubes prevented the insects from just dropping into the water, prey capture success was low: spiders caught approximately 30% of the insects administered. The tubes were left in the inverted position until the next day. In order to find the relationship between prey availability and web-building, spiders were subjected to one of three treatments for a period of ten days: insects administered at a rate of 20, 5 and 0. The extent to which web-building occurs in the absence of any stimuli from either light or prey was examined by daily monitoring of spiders in a dark room without insects (six weighed spiders in a 1.2 m x 0.6 m x 0.5 m cage placed in a basin of water).

Finally, the probability that a spider would move from a site where it had built a web versus a situation where no web was built, was examined using a wood-framed cage (1.2 m x 1.2 m x 0.6 m high) with clear plastic sides and provided with wooden struts for web-building. The top was covered with cheesecloth and the bottom was open to the surface of a shallow pool of water. Eight marked spiders were placed in the cage and monitored throughout the season by recording the number of webs, mapping their specific locations and noting the identity of the spider occupant every day. This allowed a comparison of the numbers that changed site subsequent to building versus those that moved from a site where no web was built.

RESULTS

Pattern.—Analysis of web pattern showed *T. elongata* to be associated exclusively with areas of open water, provided that suitable structural supports (twigs, branches, etc.) are available (Table 2). Comparing the two habitats used in the study, webs were found to be more intimately associated with twigs on the lake, which reflects the higher web density in this population. Neither habitat exhibited significant associations of webs with other abiotic features measured such as light intensity, temperature, humidity or wind speed.

Factors responsible for survival and web building.—The results from experiments to determine the effect of abiotic parameters on survival are shown in Table 3. Spiders were found to tolerate a maximum dehydration weight loss of approximately 15%. The rate of desiccation appears to be more a function of temperature than humidity, although the rate of weight loss was considerably reduced at high humidities. In any situation where spiders are denied direct access to water, however, desiccation appears to occur. But, even at high temperatures, virtually no weight loss was detected if individuals had direct access to open water.

The water loss suffered at different times of the day, and—at corresponding times—the effect of light intensity and temperature on web-building is shown in Table 4 for situations where water is, and where it is not, accessible. The primary determinant of web-building appears to be access to open water. When they cannot reach water, spiders suffer desiccation (the rate of which is determined by the temperature) and never build webs. Light intensity, although it does not appear to exert a significant effect on the presence of a web, does determine the activity pattern of the spider: at high light intensities spiders move off the hub of the orb. They do, however, continue to monitor prey impinging on the orb through tarsal contact with one of the bridge lines.

Total movement was also documented by recording the position of individuals in the uncovered (illuminated) sections of both cages each day. The average distance moved by an individual on any given day (averaged over 6 days) was found to be 74.0 cm in the cage with the bottom covered, and 29.6cm in the cage providing accessibility to open water (*t-test:* $t = 18.41$, $p < 0.01$). The effect of prey availability on web-building was determined by counting the number of days on which webs were built for each spider. Results (Table 5) showed tht spiders

Table 2.— Spider web associations: Correlation coefficients were computed on covariance between the distribution of webs and that of habitat features and microclimate characteristics on both the creek and the lake. The following associations were found to be significant (* : $p < 0.05$; ** : $p < 0.01$).

	CREEK	LAKE
WATER	**	**
MOSS	*	
BRANCHES Low, 0-50 cm		**
Middle, 50-100 cm	*	*
TWIGS Low, 0-50 cm	*	**
Middle, 50-100 cm	*	**
High, 100-200 cm		**

Table 3.—The effect of temperature, humidity and open water on dehydration of spiders: Individual spiders ($n = 36$) were subjected to one of six treatments (see Table 1). Water (height 5 mm up vial of height 5 cm) was placed in four of the vials, but was covered over (to prevent direct access by the spider) in two of these. Half the vials were kept in a desiccator (temperature 37.5°C, humidity 4%); the other half in the laboratory (temperature 18.0°C, humidity 75%). The weight of each spider was recorded at quarter hourly intervals during each 10 hour treatment, and allowed an estimate of the rate of desiccation shown here (mean, SD), along with the original weight of the spider (mean, SD). The weight loss suffered by spiders just prior to death allowed estimation of the % weight loss tolerated.

TREATMENT	DESICCATION RATE	INITIAL WT.	%WT.LOSS
	(wt.loss,mg/h) (mean, SD)	(mg) (mean, SD)	before death (mean, SD)
High temperature, low humidity, no water.	5.15 (±0.66)	56.13 (±14.51)	14.82 (±2.81)
High temperature, high humidity, no water.	4.42 (±0.83)	59.30 (±13.95)	15.12 (±1.01)
High temperature, high humidity, open water.	0.05 (±0.05)	60.93 (±13.59)	—
Low temperature, low humidity, no water.	0.13 (±0.05)	55.80 (±12.65)	—
Low temperature, high humidity, no water.	0.21 (±0.10)	60.35 (±11.58)	—
Low temperature, high humidity, open water.	0.00	64.08 (±13.92)	—

would generally build webs daily when administered 20 flies a day. At very low prey administration levels (five or zero) web-building frequency was found to drop sharply, though even when prey were absent spiders still built orbs, albeit at a very low frequency. Indeed, where spiders were deprived of all external stimuli, webs were still built, though very infrequently: of six spiders, only four webs were built (by different spiders) over a ten-day period; none of these were maintained for more than 1.5 days (average 1.25 days).

The final experiment was a comparison of translocation frequency in spiders that had built webs versus those that moved from a site where they had not built. This showed that 27% of spiders ($n = 132$) would move after they had built an orb. On the other hand, of those that did not build orbs ($n = 187$) 83% moved.

DISCUSSION

The results from this study show: (1) The pattern of distribution of *T. elongata* is non-random, spiders being found to be positively associated with areas over water that are suitable for web-building. (2) In terms of abiotic parameters, the ability of a spider to survive in a given environment is determined by the rate of desiccation, this being a function of humidity and temperature. The effects of desiccation can be counteracted by access to open water. (3) Where abiotic

Table 4.—Daily variation in water loss, light intensity, web-building and occupation of the hub of an orb where water is and is not accessible.

TIME (hrs)	Mean light reading (lumens/m²)	Mean temp. °C	WATER ACCESSIBLE		WATER NOT ACCESSIBLE	
			Mean water loss(mg)	% at hub (mean web #=2.8±0.5)	Mean water loss(mg)	% at hub: # webs built
0600	—	0.00	—	100	11.0	—
0900	0.08	5.58	0	73	14.5	—
1200	0.34	6.05	0	70	19.5	—
1500	0.46	5.58	0	74	19.0	—
1800	0.21	3.72	0	80	19.0	—
2100	0.02	0.00	0	100	17.0	—
0600	—	0.00	—	100	11.0	—
0900	0.06	46.50	0	0	20.0	—
1200	5.34	186.00	0	0	29.5	—
1500	4.42	186.00	0	0	28.5	—
1800	2.83	65.10	0	0	19.0	—
2100	0.00	1.86	0	0	17.0	—

conditions are suitable, spiders will build orbs on a daily basis provided there is adequate prey available. (4) The probability of changing site is much higher where no web has been built. A three component mechanism of habitat selection in *T. elongata* may occur as spiders operate by the parameters identified in this study. (1) Random movement curtailed upon encountering a favorable abiotic environment. Alternatively, if they do not move, temporal variability may cause the environment surrounding the spider to change. The end result of either spatial or temporal change might trigger off (2) active search for a specific microhabitat within this environment which satisfies the requirements for web construction. (3) Site sampling occurs once the web has been built and leads to a repetition of the process if the spider's immediate foraging requirements necessary for survival are not satisfied. (*T. elongata* loses weight and will die when administered prey at a level much below 10 per day; see Gillespie and Caraco, in press).

The first component—the random search phase—has been recognized and described in a number of spider groups (Riechert and Gillespie 1986). The mechanism behind this procedure has been considered in terms of negative feedback (Sale 1969): where the environment is inadequate, low intensity feedback causes a high level of exploratory activity. As shown in this study, *T. elongata* does not build webs where the environment is unfavorable (i.e. there is no open water accessible). During this period, their activity may be largely non-directed exploratory movement, which would frequently enable them to locate a suitable environment. It may be that a similar mechanism is used by other species that are associated with specific forms and strata of vegetation that permit efficient perception and capture of prey (Hallander 1967, 1970, Kronk and Riechert 1979).

The second component involves active search for a specific microhabitat. The importance of spatial/architectural features of the habitat in determining the specific location of webs has been documented in araneids (Colebourn 1974) and linyphiids (Schaefer 1978). In this study, twigs appeared to be the structures of primary necessity for web-building in *T. elongata*. LeSar and Unzicker (1978), working with the closely related *T. laboriosa*, came to similar conclusions.

Table 5.—The effect of prey availability on web-building.

TREATMENT (No. of insects)	AV. NO. WEBS BUILT (Mean & C.L.: taken over 10 day period)	NO. SPIDERS USED
20	10.92 (±1.33)	18
5	3.75 (±1.88)	9
0	1.28 (±0.53)	16

The final component considered to be involved in the habitat selection process of *T. elongata* is web relocation if the insect availability is insufficient to allow survival (Gillespie and Caraco, in press). It differs from the first component of random search in that it cannot be explained by the idea of negative feedback (Sale 1969). Rather, it is a continual trial and error procedure. Also, due to the effect of temporal variation superimposed on spatial variation, no one site can be optimal for any length of time. This component of the habitat selection process has been documented in many species that require web traps to be built before they can estimate the availability of prey in particular patches. Hildrew and Townsend (1980) report this type of behavior in the caddis fly larva *Plectrocnemia conspersa*. Amongst spiders, Turnbull (1964) found that individuals of the house spider *Achaearanea tepidariorum* (C. L. Koch), when released into an empty room, will continue to change web locations until all have built webs in the vicinity of a localized prey source (in this case a window, where flies were attracted to the light). In two studies on theridiid ant specialists, a change in web location has been shown to be associated with predation avoidance tactics of the ants: Holldobler (1970) noted that *Steatoda fulva* (Keyserling) changes web location from one ant mound to another following cessation of ant usage of particular entrances. MacKay (1982) found that *Latrodectus hesperus* Chamberlin and Ivie migrates from a nest of ants that have ceased to forage. The crab spider *Misumena vatia* (Clerck) leaves flowers that yield insufficient prey (Morse and Fritz 1982). And amongst tetragnathids, *T. montana* Simon has been shown to base its web-building activity on mosquito abundance (Dabrowska Prot et al. 1968, Luczak 1970). Olive (1982) has shown that this process of web relocation occurs when the current rations a spider is receiving fall below its previous rations, and the effect of this tendency is aggregation of animals in quadrats with high ration levels.

This type of three-component sequence of habitat selection may well explain the mechanism by which a suitable habitat is located by most web-building spiders. The method of prey sampling will, however, vary depending on web investment at any given site (Rypstra 1983). Spiders with a high investment are unlikely to build complete webs to sample prey availability, as the cost incurred by such behavior would be inordinately high. Gillespie (1981) showed that the cribellate spider *Amaurobius similis* (Blackwall) (which has a very high web investment) continually lays single silk threads during the sampling period. This may be the standard sampling technique used when web investment is high.

ACKNOWLEDGEMENTS

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SYSTEMATICS AND NATURAL HISTORY
OF *WADOTES* (ARANEAE, AGELENIDAE)[1]

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ABSTRACT

The coelotine agelenid genus *Wadotes*, exclusive of the single described Palaearctic species *W. primus*, is a monophyletic assemblage of species endemic to eastern North America. Diagnoses, descriptions, distributions, natural history notes, a key, and a phylogeny are presented for eleven species, five of which (*W. carinidactylus, W. deceptis, W. mumai, W. saturnus,* and *W. willsi*) are described as new. *W. convolutus* and *W. carolinus* are synonymized with *W. bimucronatus*. The male palpal tarsus and the female epigynum of the Nearctic group is described in detail. Mating behavior of *Wadotes* is described for the first time.

INTRODUCTION

North American spiders of the genus *Wadotes* Chamberlin, 1925 form a monophyletic assemblage occurring east of the Mississippi River from Nova Scotia, New Brunswick, eastern Ontario, and adjacent Quebec south to the central regions of Alabama and Georgia. These medium- to large-sized araneomorph spiders are commonly found in leaf litter or under various objects on forest floors. In parts of the range, some species have been shown to be among the most common spiders of the forest floor and consequently may be of great importance in the dynamics of such ecosystems (see Coyle 1981).

In 1925 Chamberlin named the genus *Wadotes* for three North American coelotine agelenid species originally described in the genus *Coelotes* Blackwall, 1841 (*Coelotes bimucronatus* Simon, 1898a; *C. calcaratus* Keyserling, 1887; and *C. hybridus* Emerton, 1889). He separated these species from both *Coelotes* and the related genus *Coras* Simon, 1898b by the following characters: two teeth on the retromarginal cheliceral fang furrow; "anterior median eyes much smaller than the laterals"; a posteriorly projecting, anteriorly attached scape; and variously developed processes on the proximal margin of the cymbium.

Subsequently *W. tennesseensis* Gertsch, 1936; *W. convolutus* Muma, 1947; and *W. georgiensis* Howell, 1974 from North America were described. Muma (1947)

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revised the taxonomy of the North American species of *Wadotes*. *Wadotes primus* Fox, 1937 from east Asia, is the only non-North American species described in the genus.

Eleven Nearctic species are described and figured in this revision, including five new species (*W. carinidactylus, W. deceptis, W. willsi, W. mumai*, and *W. saturnus*). The status of *Wadotes primus*, which may not belong in *Wadotes* (Lehtinen 1967), is discussed.

MATERIALS AND METHODS

This paper is the result of my own field observations and collecting, and the examination of approximately 1,500 specimens generously lent by museums and individuals listed in the Acknowledgments.

All measurements were made from specimens immersed in 80% ethanol and examined under a stereo dissecting microscope with an ocular micrometer mounted in one eyepiece. Measurements are accurate to 0.1 mm for carapace length (CL) and width (CW) (and also sternum length and width in *W. hybridus, W. saturnus*, and *W. mumai*) and to 0.025 mm for sternum length (SL) and width (SW) (except as noted above). Statistics are presented in the following fashion; sample range (mean±standard deviation). The ratios DL/DW and EL/LAE, used in the diagnoses of various species and in the key to species, compare respectively the length (DL) and width (DW) of the connecting ducts (Fig. 26) and the total length (EL) and length from the atrial slit to the epigastric furrow (LAE) of the epigynum (Fig. 22).

In the genus description, the position and number of macrosetae on a particular face of a leg segment are presented as a series of three numbers (separated by hyphens) which represents the number of macrosetae on the proximal, medial, and distal portions, respectively.

Except where noted, a left palpus was used for drawing male palpal characters. Palpi, or their dissected parts, were drawn while immersed in 80% ethanol. Internal characteristics of epigyna were drawn after being cleared in clove oil. All drawings were executed with the aid of a 10x10 squared grid eyepiece reticle. Figures of morphologically similar species are grouped together to facilitate the identification of specimens.

For simplicity in applying names to the various faces of the species-specific terminal apophysis (ventral, retrolateral, prolateral, and dorsal), the conductor and terminal apophysis have been visualized straightened out to lie along the anterior/posterior axis of the palpus and directly lateral to each other.

Expanded species and genus descriptions and discussions of palpal and epigynal structure are in Bennett (1984). Detailed lists of synonymies and literature records of *Wadotes* spiders can be found in Bennett (1984), Roewer (1954), or especially Bonnet (1959).

Abbreviations and acronyms not explained as they appear in the paper are listed below. Standard postal abbreviations are used for state and province names. Abbreviations used in figures are defined in the legend of the first figure in which they appear. RGB—R.G. Bennett, BRPWY—Blue Ridge Parkway, GSMNP—Great Smoky Mountains National Park, and JKMF—Joyce Kilmer Memorial Forest.
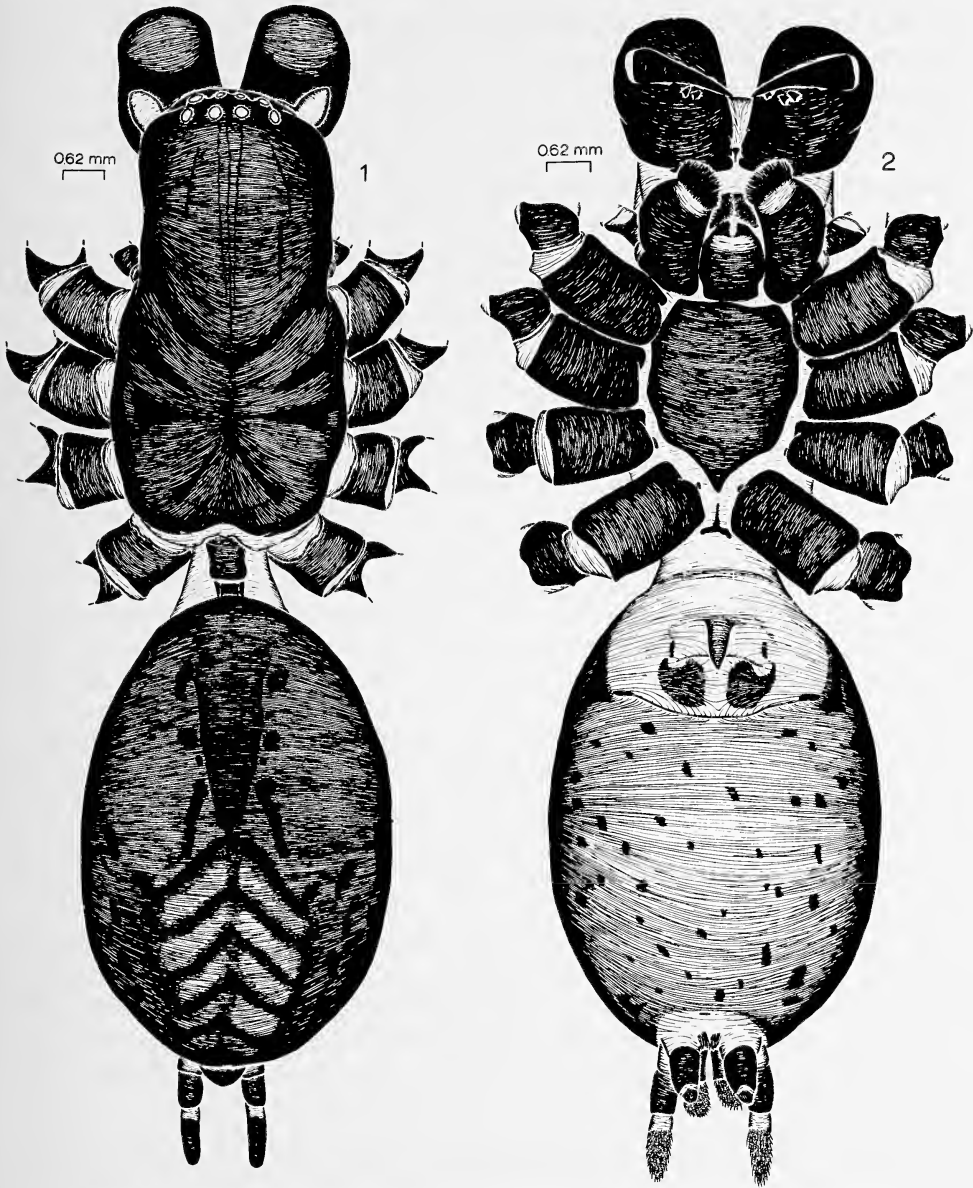
Figs. 1,2.—*Wadotes hybridus*, female, Cullowhee NC: 1, dorsal view; 2, ventral view.

MATING BEHAVIOR

Mating behavior was observed (under low power stereoscopic magnification) in *W. bimucronatus* on one occasion during this study (19.X.1983). A male and female already in some stage of a presumably post-courtship, pre-copulatory embrace were recovered live from a Berlese funnel. The ensuing sequence of events was similar to that described for *Agelenopsis* by Gering (1953).

When first observed, both were immobile with the male above the female and facing in the same direction. Her legs were tightly folded above her carapace and under her sternum (in the manner of a spider "feigning death") such that the male

was able to grip her by the patella/tibia joints securely with his chelicerae. The female was cataleptic at this stage and for most of the proceedings. The male spent several minutes dragging the female about, occasionally releasing his hold of her legs and repositioning himself. Most often the male returned to the superior position, oriented the same way as the female, but periodically he would approach her from either side at various angles. He rolled the female several times from side to side to angles of about 45 degrees. Some pauses in this general activity occurred during which both spiders were motionless for a minute or two, or the male would groom his palps and/or the tarsi and metatarsi of the first two pairs of legs with his chelicerae.

Copulation was initiated when the male approached the female from her left side and grasped her, facing in the opposite direction and in the superior position. He then rolled her onto her right side exposing the ventral surface of her abdomen. This corresponds to a modification of a "Type 2" mating position according to Kaston (1948, see figs. 2006 and 2010) or "Type 3" according to Foelix (1982). The male maneuvered the female's abdomen, contary to the statement of Foelix (1982:196) that the female adjusts the orientation of her abdomen herself. The male then rapidly rubbed the retrolateral edge of the left cymbium laterally back and forth across the epigynum. This was repeated a few times with the same palpus and was alternated with grooming of both palpi. Following this, the male suddenly inserted the left palpal embolus into the atrial slit.

Insertion was achieved with the dorsal side of the cymbium oriented towards the posterior end of the female and with its proximal dorsal margin pressed against the ventral surface of the female's abdomen in the vicinity of the epigastric groove. The prolateral cymbial process was tightly pushed against the female abdomen at initiation and sank within the epigastric groove as insertion was effected.

Following this rapid sequence of events, inflation of the basal haematodocha was accomplished through a rhythmic and cumulative series of haematodochal pulsations until full expansion of the haematodocha was achieved. Once fully expanded, the basal haematodocha continued to pulsate rhythmically at about 4-second intervals with 1 to 1.5 seconds of maximal expansion followed by 2 or 3 seconds of slight relaxation.

Four consecutive copulatory events involving the left palpus were observed, each separated by short intervals of palpal grooming during which the male retained his basic mating position. Each copulation was preceded by an identical process of rubbing the epigynal surface with the retrolateral edge of the cymbium. The initial event lasted about 45 seconds. Two further events of short duration followed, one about 5 minutes in length and another of 5 to 10 seconds. The fourth event was terminated by the observer after approximately 40 minutes. As this event proceeded, the haematodochal pulsation rate slowed to about once every 5 or 6 seconds. The basal haematococha remained in a fully expanded state, obliterating all other features of the genital bulb.

While the two were *in copula* the female was always in a cataleptic state lying on her right side with her legs folded over her cephalothorax and the male straddling her. The only obvious point of contact between the two spiders was of the palpal tarsus and the epigynum.

PHYLOGENY

North American *Wadotes* are probably closely related to both North American *Coras* and East Asian *Wadotes* (for the reasons discussed below). Until a better understanding of the latter group (and other coelotines) is achieved this relationship will remain an unresolved trichotomy. The following phylogeny is based upon a cladistic analysis of North American *Wadotes* using *Coras* and east Asian *Wadotes* (*W. primus*) as out-groups to establish character state polarity. Clades are numbered on Figure 119 and discussed below by number.

The presence of a membranous embolus support on the conductor (Figs. 5, 7, 12) is a possible synapomorphy linking *Coras* and North American *Wadotes*. Convoluted, matrix-bound connecting ducts with distinct primary loops (Figs. 24, 110) tie *Coras* and *Wadotes primus* to North American *Wadotes* but both characters may be synapomorphic at the subfamily level (the male of *W. primus* is unknown and I have not examined non-Nearctic coelotines). Three other weak synapomorphies support the monophyly of a group including *Wadotes* and *W. primus*: small anterior median eyes (Fig. 3), two retromarginal cheliceral fang furrow teeth (Fig. 2), and an epigynal scape (Figs. 1, 109, 111). These characters have arisen independently in various araneomorph genera (e.g. a scape occurs, within the Agelenidae, in such divergent agelenid genera as *Ethobuella* and *Calilena*).

Synapomorphies of the Nearctic species of *Wadotes* include the reduced sclerotization of the connecting duct matrices, a single transverse atrial slit (Fig. 21), and the sickle-like form of the conductor sclerite (Figs. 15, 16). Within this group, *W. tennesseensis, W. calcaratus*, and *W. willsi* (component 2) are linked by two synapomorphies: a roughened terminal apophysis surface (Figs. 38, 43, 47) and reduced and separate connecting duct matrices (Figs. 50, 58, 62).

Component 3 (*W. calcaratus* and *W. willsi*) is defined by three apomorphies: the large and conspicuous retrolateral cymbial process (Figs. 35, 41), lateral support sclerites (Figs. 49, 58), and the position of the spermathecae ventral to the secondary loops of the connecting ducts (Figs. 50, 58).

All the remaining species (component 4) are united by the following synapomorphies: a furcate terminal apophysis with a conspicuous median retrolateral process (Figs. 15, 97), a bisected prolateral cymbial process (Figs. 13, 93), and a reduced support sclerite not fused with the lateral plates of the superficial epigynal sclerotization (Fig. 23). (In *W. hybridus* the support sclerite has been lost.) Within this clade two monophyletic sub-groupings are evident: one composed of *W. bimucronatus* and *W. georgiensis* (component 5) and the other *W. carinidactylus, W. deceptis, W. dixiensis, W. hybridus, W. mumai*, and *W. saturnus* (component 6).

The presence of a reduced prolateral arm of the terminal apophysis (Figs. 15, 19), a deeply and narrowly bisected prolateral cymbial process (Figs. 13, 17), and the anterodorsal orientation of the connecting duct matrices (Figs. 24, 32) are autapomorphies of component 5. Despite the lack of females of *W. carinidactylus, W. deceptis*, and *W. mumai* these species are included in component 6 which is defined by the presence of relatively broad connecting duct matrices (Figs. 78, 84, 104). No defensible synapomorphies are known which bind either *W. carinidactylus* or *W. deceptis* to any of the lineages within component 6. They are placed there on the basis of their closer similarity to species of this component

than to those of component 5. A better understanding of the polarity of male character states (particularly the form of the prolateral cymbial process and the relative development of the terminal apophysis arms) will help resolve species relationships within component 6.

Synapomorphies of *W. hybridus, W. mumai,* and *W. saturnus* (component 7) are the lack of superficial epigynal sclerotization anterior to the atrial slit (Figs. 70, 76, 82—probably independently evolved in *W. tennesseensis* [Fig. 60]) and the presence of a ridge on the ventral surface of the prolateral arm of the terminal apophysis.

Finally, the reduction of the ventral arm of the prolateral cymbial process (Figs. 68, 85) and the elongation of the dorsal prolateral tibial extension to form an apophysis (Figs. 68, 86) constitute synapomorphies uniting *W. mumai* and *W. saturnus* (component 8). The development of this apophysis may be functionally correlated with the reduction of the prolateral arm of the cymbial process.

The ranges of *W. hybridus, W. mumai,* and *W. saturnus* (Fig. 118) are in accordance with the close relationship of these three species. *W. hybridus* and *W. saturnus* almost certainly have parapatric distributions. Possibly *W. hybridus* and the common ancestor of *W. saturnus* and *W. mumai* evolved from an ancient species with a range in the southern Appalachians. Subsequently, perhaps, *W. hybridus* expanded its range northward (after the retreat of the last of the Pleistocene glaciers) and *W. saturnus* and *W. mumai* differentiated from their common ancestor.

TAXONOMY

Genus *Wadotes* Chamberlin, 1925

Wadotes Chamberlin, 1925:120. Type species *Wadotes dixiensis* Chamberlin by original designation.

The following diagnosis and description of the genus pertain to the Nearctic species group. The single Palaearctic species, *W. primus,* is discussed following the species descriptions.

Diagnosis.—Spiders of the genus *Wadotes* can be distinguished from all other coelotine agelenids by the presence of two retromarginal cheliceral fang furrow teeth (Fig. 2); variously developed, caudally projecting processes proximally on the prolateral and retrolateral margins of the male palpal cymbium (Figs. 13, 14, 34, 35, 45, 46); a caudally projecting, anteriorly attached scape on the ventral surface of the epigynum (Fig. 2); and a single, transverse, slit-like atrial orifice on the posterior two-thirds of the epigynum (Figs. 48, 82).

Description.—Species with carapaces averaging 3.9 to 6.7 mm in length; longer than wide, widest at coxae II, with well defined longitudinal thoracic groove; sparsely setose; ground color pale yellowish-brown to dark reddish-brown (usually darker anteriorly) (Fig. 1). Pars cephalica slightly elevated (Fig. 4). Eight eyes in two rows, rows straight in dorsal view (Fig. 1), slightly procurved in frontal view (Fig. 3); anterior median eyes smallest, other eyes subequal; median ocular quadrangle wider posteriorly than anteriorly, slightly higher than clypeus.

Chelicerae (Figs. 1-4) dark brown, robust, strongly geniculate; each with conspicuous, proximal, yellowish-brown boss retrolaterally (Fig. 4); two fang furrow teeth retromarginally (Fig. 2); three promarginally (Fig. 3), middle one
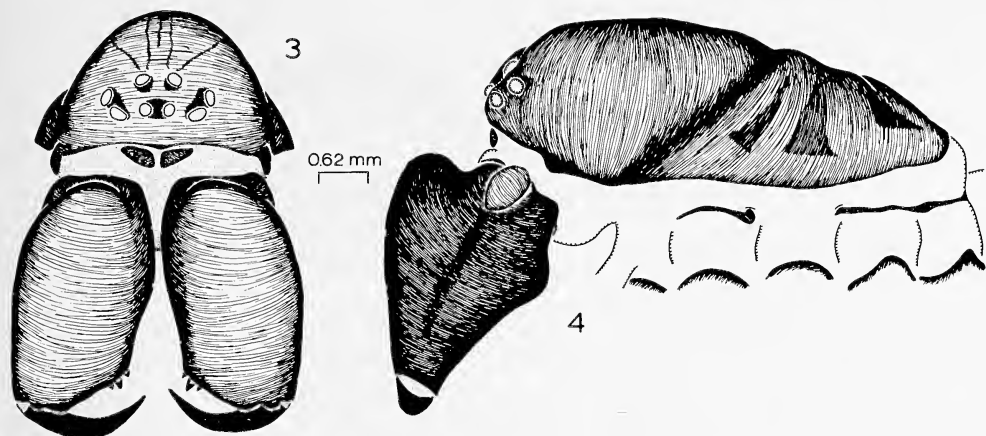
Figs. 3,4.—*Wadotes hybridus*, female, Cullowhee NC: 3, face and chelicerae, frontal view; 4, carapace and chelicerae, lateral view.

largest. Endites (Fig. 2) slightly convergent. Labium (Fig. 2) ca 0.7 times as long as endites, constricted basally. Endites and labium dark colored except narrow, lightly pigmented borders distally. Sternum colored as in carapace, longer than wide, widest between coxae II, with short caudal projection extending partly between coxae IV.

Abdomen (Figs. 1, 2) longer than wide, clothed with short setae, base coloration ranging intraspecifically from very light gray to dark gray. Anterodorsal "heart mark," posterodorsal chevrons, and other abdominal markings also of variable coloration and intensity.

Spiracle minute, located anterior to two groups of less than ten colular setae each. Anterior spinnerets (Fig. 2) slightly separated, median and anterior spinnerets subequal, posterior spinnerets twice as long as others (Figs. 1, 2).

Legs in order of decreasing length, 4123; femora, tibia, and metatarsi with numerous macrosetae. Femur I usually with one (*W. calcaratus* and *W. willsi*) or two prolateral macrosetae distally. Tibiae I, III, and IV usually 2-2-2 ventrally. Tibia II either 2-2-2 or 1-2-2 ventrally with proximal ventral prolateral macroseta absent or reduced. Metatarsi I to IV all 2-2-2 ventrally (*W. tennesseensis*) or metatarsi I and II 2-2-3 and metatarsi III and IV 2-2-2. Tarsi with three claws; six to nine trichobothria dorsally, normally tarsi II and III each with one less trichobothrium than tarsi I and IV.

Male palpal patella distally with well developed retrolateral apophysis (Figs. 36, 37), dorsodistal macroseta arising from short dorsal apophysis (*W. calcaratus*— Fig. 36) or slight prominence. Tibia with three conspicuous prolateral megasetae (Figs. 72, 73, 93, 94); ventral retrolateral carina along length of tibia terminating in dorsoventral ridge distally; dorsal prolateral extension of tibia simple (Figs. 17, 34) or terminating in apophysis (*W. mumai*—Fig. 68).

Structure of the male palpal tarsus.—An understanding of the palpal tarsus is required in order to identify male *Wadotes*. Terminology used here is based on Gering's (1953) discussion of *Agelenopsis* and other agelenid genera.

The tarsus is comprised of the cymbium (CY; Figs. 9, 10) and the various components of the genital bulb or palpal organ which protrude from the alveolus (AL) on the ventral surface of the cymbium (Figs. 9-12).
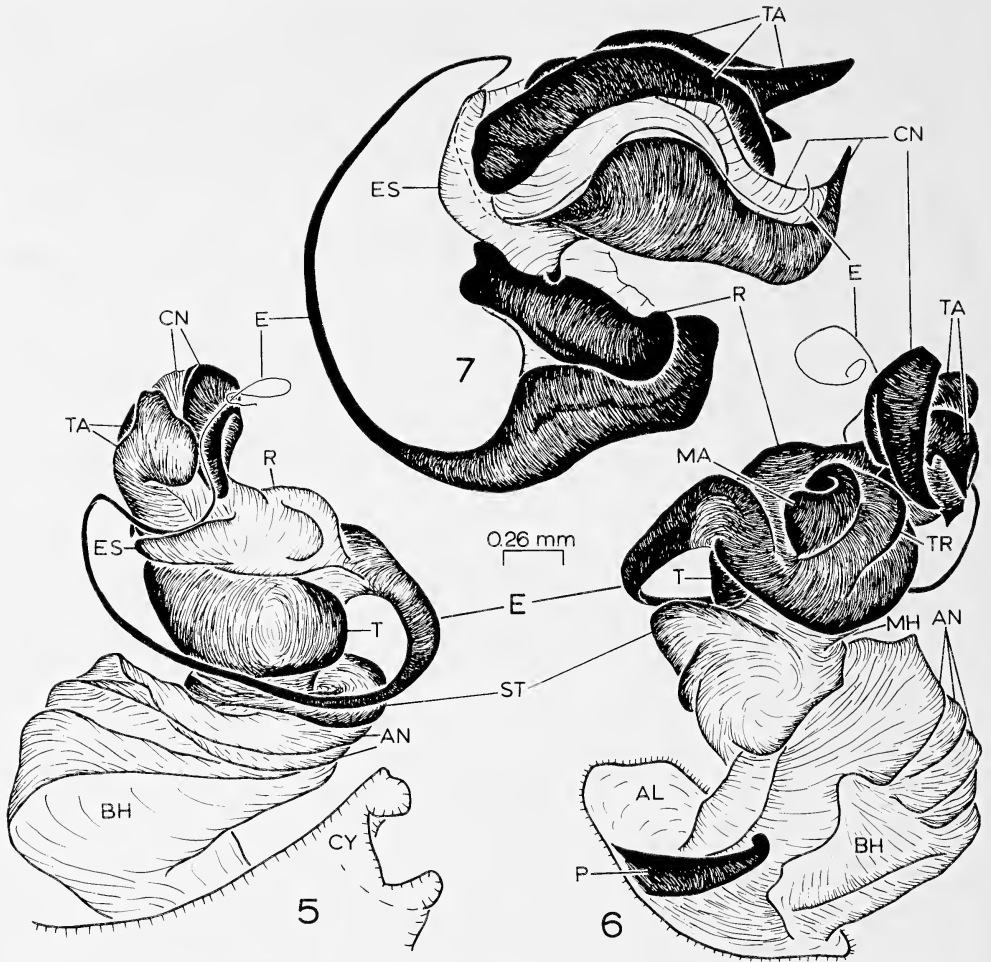
Figs. 5,6.—*Wadotes saturnus*, expanded left genital bulb, Vogel State Park GA: 5, prolateral view; 6, retrolateral view. Fig. 7. *W. georgiensis*, terminal division of left genital bulb, ventral view, Vogel State Park GA. AL—alveolus, AN-anneli of subtegulum, BH—basal haematodocha, CN—conductor sclerite and/or membrane, CY—cymbium, E—embolus, ES—embolus support of conductor, MA—median apophysis, MH—median haematodocha, P—petiole, R—radix, ST—subtegulum, T—tegulum, TA—terminal apophysis, TR—tegular ridge.

Retrolaterally on the proximal half of the cymbium, there is a well developed, dorsally ridged concavity. The proximal margin of this is notched, and articulates with a dorsoventral retrolateral ridge on the tibia. The dorsal ridge of the concavity terminates proximally on or adjacent to a variously developed retrolateral cymbial process (RC; Fig. 14). This process is conspicuous in *W. calcaratus* and *W. willsi* (Figs. 35, 41), but is only a short knob in all other species. The proximal prolateral margin of the cymbium (PC; Fig. 13) is modified into a caudally oriented process which is obvious in all species except *W. calcaratus* and *W. tennesseensis* (Figs. 13, 93, 98). When present, this process is variously bifurcated, except in *W. willsi* where it is a simple extension of the cymbial margin (Figs. 40, 42).

The genital bulb occupies the alveolar cavity and is attached to its margins by means of the membranous and highly extensible basal haematodocha (BH; Figs.

5, 6, 10). A triangular, flattened sclerite, the petiole (P), is attached to the surface of the haematodocha near its proximal retrolateral boundary with the margin of the alveolus (Figs. 6, 10).

Distally, the basal haematodocha merges with the anneli of the subtegulum (AN, ST; Figs. 5, 6, 9, 10). Gering (1953:32-33) stated that "the subtegulum is virtually wanting as a sclerotized structure" and "the anneli are entirely obliterated" in *Wadotes*. These structures can, however, be readily observed by carefully dissecting an uncleared palpus (Fig. 10) or by drawing the genital bulb out from the alveolus with needles.

The anneli are approximately four long, narrow, lightly sclerotized, parallel bands interconnected by expansible membranes (Fig. 10). They form a nearly complete revolution before merging with the sclerotized ring of the subtegulum. In the unexpanded bulb, part of this ring is usually evident as a band of sclerotization between the proximal prolateral margin of the alveolus and the tegulum (Figs. 8, 9).

Collectively, the basal haematodocha, petiole, and components of the subtegulum comprise the basal division of the genital bulb (Comstock 1912, Gering 1953). Likewise, the middle haematodocha, tegulum, and median apophysis form the middle division in *Wadotes*.

The membranous, inconspicuous middle haematodocha forms a flexible union between the ventral margin of the subtegulum and the dorsal margin of the tegulum (MH; Figs. 6, 10).

The tegulum is a bowl-shaped, heavily sclerotized structure (T; Figs. 5, 6, 9, 11). It is readily obvious in the unexpanded bulb (Figs. 8, 9). All remaining components distal to the tegulum are associated with its ventral surface. Upon its ventral surface it bears a bevelled tegular ridge and the median apophysis (TR, MA; Figs. 6, 11).

The median apophysis, as defined by Gering (1953) for *Agelenopsis*, does not appear to exist in *Wadotes*. Here, Lehtinen (1967) and Roth and Brame (1972) are followed in naming, as the median apophysis, the sclerotized structure located in a ventral retrolateral excavation of the margin of the tegulum and joined to it by a narrow membrane (MA; Figs. 6, 11). This apophysis protrudes ventrally from the surface of the genital bulb and is shaped like one half of a bivalve shell. The ventral anterior margin of the median apophysis is distinctly and deeply notched.

In *Wadotes* the terminal division of the genital bulb is made up of the embolus, radix, conductor, terminal apophysis, and the membranes joining them to each other and to the ventral margins of the tegulum. The radix is an oblong, round-surfaced sclerite between the embolus and the conductor and adjacent to the median apophysis (R; Figs. 5-9). It is not rigidly attached to any sclerite as it is in *Agelenopsis* (Gering 1953).

The embolus, attached directly to the caudal margin of the tegulum, is long, slender, and flexible beyond the broad base (E; Figs. 5-7, 9, 11). Only the proximal third of this distal portion (the truncus) is visible in ventral view of the unexpanded bulb (Figs. 8, 9). Distally the truncus is enclosed by the embolus support (ES) and the conductor membrane joining the ventral surfaces of the terminal apophysis (TA) and conductor sclerite (CN; Fig. 7).

The conductor is the combined hyaline embolus support membrane, the crescent-shaped, pointed conductor sclerite caudal to the terminal apophysis, and
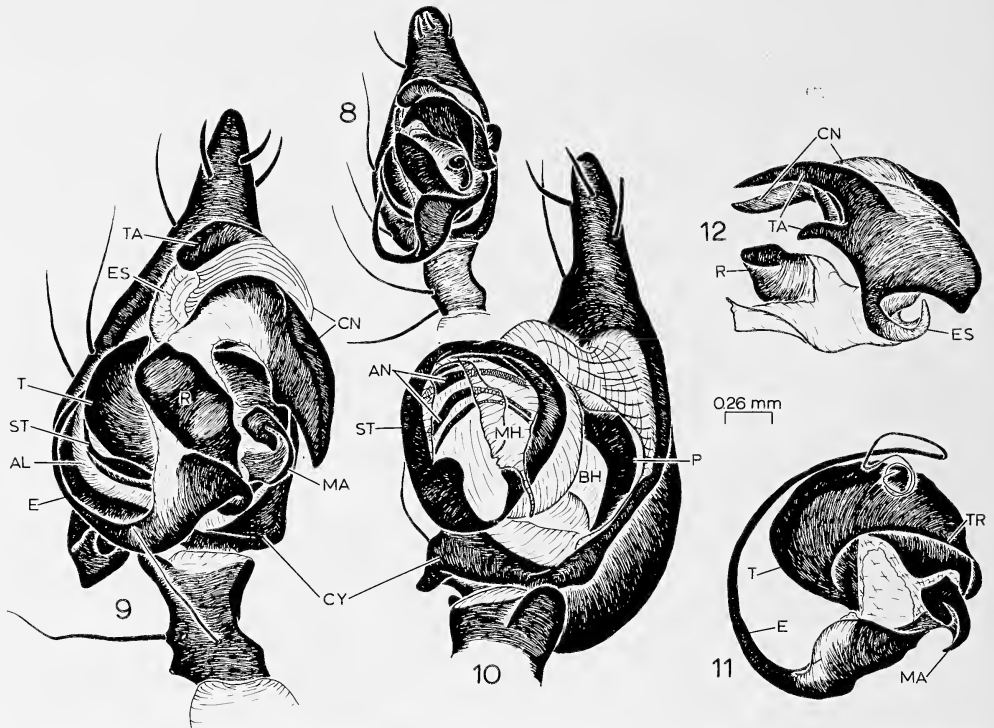
Fig. 8.—*Wadotes tennesseensis*, left palpal tibia and tarsus, ventral view, Newfound Gap (GSMNP) NC/TN. Figs. 9-12. *W. saturnus*, Vogel State Park GA: 9, left palpal tibia and tarsus, ventral view; 10, same, ventral retrolateral view, components of genital bulb distal to subtegulum removed; 11, tegulum, median apophysis, and embolus of left genital bulb, anteroventral view; 12, radix (interior surface), terminal apophysis, and conductor of left genital bulb, prolateral view.

the flexible membrane connecting this sclerite to the terminal apophysis (CN, ES; Figs. 5-7, 9, 12). Many terms have been applied to these components. The conductor sclerite is the embolic conductor of Muma (1947), the secondary terminal apophysis of Howell (1974), and the fulcrum of Lehtinen (1967). Roth and Brame (1972), feeling that a true conductor is lacking in *Wadotes* (and *Coras*), preferred to call the conductor, as here defined, the functional conductor (which, in combination with the terminal apophysis, forms the embolic process). Howell (1974) mistakenly believed that Muma (1947) had not mentioned the conductor sclerite, and that the embolic process of Roth and Brame (1972) included only the terminal apophysis.

The terminal apophysis is the primary conductor of Lehtinen (1967), and the functional conductor of terminal apophysis of Howell (1974). It is the only component of the genital bulb of *Wadotes* that exhibits apparent species-specific variation. Shear (1967) and Lehtinen (1967) incorrectly felt that this structure and the conductor sclerite are fused together (at least in *W. calcaratus*).

The terminal apophysis in its simplest form (*W. calcaratus, W. willsi,* and *W. tennesseensis*) (TA; Figs. 38, 39, 43, 44, 47) is truncate distally, laterally compressed, rough surfaced, and, except for a median retrolateral process (MRP; Fig. 38) projecting ventrally in the region of the embolus support and a dorsal extension supporting the latter structure, is unadorned by arms or other apophyses. The males of all other species possess complex terminal apophyses.

The complex type also bears a median retrolateral process (MRP; Fig. 15) and a dorsal extension bracing the embolus support as well as a long, pointed ventral arm (VT; Figs. 15, 19, 95, 100) and less obvious retrolateral (RT; Figs. 15, 19) and prolateral arms (PT). The retrolateral arm is either fused to the ventral retrolateral edge of the ventral arm (Figs. 87, 88, 91, 92) or to the prolateral arm by means of a variously-developed dorsal plate (Figs. 15, 101). The prolateral arm may be distinct (Fig. 12), an integral part of the dorsal plate (Fig. 97), or greatly reduced (Fig. 19).

The ventral, retrolateral, and prolateral arms are the median, basal, and apical apices, respectively, of Muma (1947). Howell (1974), in his description of *W. georgiensis*, mistakenly interpreted the median retrolateral process (discussed below) of that species as Muma's basal apex and the retrolateral arm (basal apex) as the apical apex. As well, he did not mention the very inconspicuous prolateral arm (Fig. 19) which is Muma's apical apex.

Muma (1947) did not discuss the median retrolateral process (MRP) of the terminal apophysis. This prominent feature of the dorsal surface of complex terminal apophyses (Figs. 15, 87) is inconspicuous in simple terminal apophyses (Fig. 38). It is broadly triangular and not attached to any of the nearby membranes as is the adjacent process which strengthens the embolus support.

In ventral view, the terminal apophysis is inconspicuous and overlain by the conductor (Figs. 8, 9) with only the proximal knob and the distal end of the ventral arm (or truncated tip in simple terminal apophyses) visible. These features are the only parts of the genital bulb which may be visible in dorsal view (TA; Figs. 14, 35, 94), other than the proximal loop of the embolus in *W. tennesseensis* (Fig. 46).

Among North American agelenids, the tarsal components of *Wadotes* are morphologically most similar to those displayed by the genus *Coras* (see Muma 1946). The genital bulbs of *Wadotes* and *Coras* differ markedly only in the structure of the conductor and terminal apophysis. In *Wadotes* the conductor exhibits a fairly constant morphology and the terminal apophysis is variable. In *Coras* the terminal apophysis is usually blunt and rounded and the conductor sclerite is variable. Muma (1946) used the latter to partially define the species of *Coras*. The embolus support is similar in both *Coras* and *Wadotes*.

Structure of the epigynum.—The epigyna of *Wadotes* are simple organs but are difficult to describe as there are few well pigmented or sclerotized structures and the internal epigynal characters are enveloped by soft tissue.

In *Wadotes* the epigynum is characterized externally by a scape, a transverse atrial slit, and a variable amount of superficial sclerotization (SC, AS, SES; Fig. 21). The scape (atrial guide [Gering 1953], stylus [Chamberlain and Ivie 1941]) projects caudally from the inside medial edge of the anterior epigynal margin across a central unsclerotized area as a dorsoventrally flattened, finger-like cuticular evagination. Scape morphology is highly variable within species (Figs. 53-57). Dorsal to the scape, the central region of the epigynum is unsclerotized.

The caudal end of the scape lies in the vicinity of the atrial slit which is a single, inconspicuous, transverse fissure located in the posterior one-quarter (Fig. 48) to two-thirds (Figs. 76, 77) of the epigynum. Its position is of some importance in species determinations.

Posterior to the atrial slit the median unsclerotized area (MUA), which corresponds to the posterior median sclerite of Gering (1953) and Chamberlin and

Ivie (1941), extends into the epigastric groove (Figs. 22, 23). Posteriorly, on the lateral margins of the median unsclerotized area, a pair of slight longitudinal depressions is present in *W. tennesseensis* (DN; Fig. 60). These are of variable occurrence in other species (Figs. 21, 83).

The superficial epigynal sclerotization is composed of a pair of large (SES; Fig. 22) or small (Fig. 48) sclerotized plates (lateral to the median unsclerotized area) and, connecting them, a band of sclerotization delimiting the lateral and anterior margins of the epigynum (SES; Fig. 21). This band is reduced or absent in some species (Figs. 76, 77).

In most species of *Wadotes* a support sclerite, perhaps a reduction of Gering's (1953) posterior median sclerite, lies within the epigastric groove on the caudal surface of the epigynum (SS; Figs. 23, 61). *Wadotes hybridus* has no support sclerite and in *W. calcaratus* and *W. willsi* it is a pair of narrow lateral bands running from the vicinity of the spermathecae to the posterior margins of the lateral plates (SS; Figs. 49, 50).

Internally the atrial slit becomes an anterodorsally oriented, shallow, flattened atrium (AT; Figs. 24, 27). The atrium terminates as two lightly sclerotized pockets which are inconspicuously connected to the anterior ends of the connecting ducts (Fig. 27).

The long, narrow connecting ducts (CT; Fig. 26) and the matrices (MX; Fig. 24) in which they are imbedded correspond to Gering's (1953) bursa copulatrix. Since the term bursa implies the presence of a pouch or sac it is not used here. The anterior-most 'S'-shaped section comprises the primary loops (PL; Fig. 25) and the remaining length the secondary loops of the connecting duct. The matrices are lightly sclerotized but tough and durable, and contiguous (Figs. 24, 104) or separated (Figs. 50, 78). In *W. bimucronatus* and *W. georgiensis* the matrices are strongly convex dorsally and extend somewhat posterodorsally from the atrium (Figs. 24, 32).

The oblong, lobed spermathecae (SP; Figs. 23, 24) have thick walls and large lumina and are the only heavily sclerotized internal components of the epigynum. In *W. calcaratus, W. tennesseenis,* and *W. willsi* the spermathecae are ventral (as opposed to caudal) to the posterior ends of the matrices (Figs. 50, 58, 62). From the posterodorsal margin of each spermatheca emanates a short, curved, and inconspicuous fertilization duct (FD; Fig. 24) which lies very close to the spermathecal surface and is best observed in profile.

Natural History.—*Wadotes* specimens are usually found on the floor of deciduous or coniferous forests but may also be common in clearcut areas within forests (see Coyle 1981). They have been collected from leaf litter, within rotting logs, under bark or moss on logs, on the underside of and underneath rocks and other objects, and through the use of pitfall traps and Berlese funnels.

The web of *Wadotes* is normally flimsy, tubular, several cm in length and often branched with one or more openings. It is always hidden with only the entrance(s) visible.

KEY TO NEARCTIC SPECIES OF *WADOTES*

(Females of *W. carinidactylus, W. mumai* and *W. deceptis* unknown.)

2 (1).   Prolateral cymbial margin bisected (Figs. 17, 98); terminal apophysis with variously
          developed arms (Figs. 19, 95)...5
          Prolateral cymbial margin entire (Figs. 40, 45); terminal apophysis blunt (Figs. 39, 47).....3

3 (2).   Retrolateral cymbial margin strongly developed, produced over tibia (Figs. 35, 41); embolus
          not visible in dorsal view...4
          Retrolateral cymbial margin inconspicuous, not produced over tibia (Fig. 46), basal third of
          embolus visible in dorsal view...*tennesseensis*

4 (3).   Prolateral cymbial margin not developed (Fig. 34); species widespread...........*calcaratus*
          Prolateral cymbial margin well developed (Figs. 40-42) species probably restricted to vicinity
          of Mount Rogers, Virginia...*willsi*

5 (2).   Prolateral cymbial margin deeply bisected by narrow cleft (Figs. 13, 17); in dorsal view
          prolateral usually slightly longer (Fig. 14) to twice as long as retrolateral cymbial margin
          (Fig. 18). Prolateral arm of terminal apophysis inconspicuous (Fig. 19) or reduced to a
          short dorsal plate (Fig. 15)...6
          Prolateral cymbial margin bisected other than by deep, narrow cleft (Figs. 68, 72, 89); in
          dorsal view prolateral and retrolateral cymbial margins subequal or prolateral slightly
          longer than retrolateral margin. Prolateral arm of terminal apophysis well developed (Figs.
          87, 100)...7

6 (5).   Base of retrolateral arm of terminal apophysis fused to flattened, short, triangular,
          prolateral arm (Fig. 15); species widespread in southern Appalachians and surrounding
          Piedmont..*bimucronatus*
          Base of retrolateral arm of terminal apophysis fused to base of ventral arm; prolateral arm
          an inconspicuous projection on dorsal base of ventral arm (Fig. 19); range probably
          restricted to vicinity of Vogel State Park, Union County, Georgia..............*georgiensis*

7 (5).   Retrolateral arm of terminal apophysis fused to base of ventral arm (Figs. 88, 92).........8
          Retrolateral arm of terminal apophysis otherwise (Figs. 70, 75, 97, 101).................9

8 (7).   Bisection of prolateral cymbial margin wide in prolateral view (Fig. 85), ventral and dorsal
          arms well separated...*saturnus*
          Bisection of prolateral cymbial margin triangular in prolateral view (Figs. 89, 90), ventral
          and dorsal arms close together..*deceptis*

9 (7).   Ventral arm of terminal apophysis with a conspicuous ventral keel (Fig. 95); prolateral and
          retrolateral arms forming a broad, conspicuous plate with retrolateral keel ventrally...*carini-
          dactylus*
          Ventral arm of terminal apophysis long and slender with no ventral development; prolateral
          and retrolateral arms otherwise (Figs. 70, 75, 100)....................................10

10 (9).   Retrolateral arm of terminal apophysis with a basal flange dorsally which connects it
          broadly to prolateral arm (Figs. 69, 75)...11
          Retrolateral arm of terminal apophysis broadly connected to prolateral arm from tip to tip
          forming a smooth crescent-shaped dorsal plate (Figs. 100-101)..................*dixiensis*

11 (10). Ventral arm of prolateral cymbial margin as large as or larger than dorsal arm in prolateral
          view (Fig. 72), species widespread...*hybridus*
          Ventral arm of prolateral cymbial margin greatly reduced (Fig. 68), dorsal arm large and
          conspicuous (Fig. 66); species apparently restricted to north-central Georgia.........*mumai*

12 (1).   Superficial epigynal sclerotization present as two well developed plates posterior to the
          atrial slit, separated by a narrow median unsclerotized area and joined by a sclerotized band
          passing anterior to the scape (Figs. 21, 102)..13
          Either median unsclerotized area (posterior to atrial slit) wide, greater than one-half width
          of epigynum (Fig. 48), or anterior sclerotized band lacking (Figs. 76, 82)..............14

13 (12). Connecting duct matrices wide (Fig. 104), length and width subequal, DL/DW=0.87-1.29, *N*=20 . . . . *dixiensis*
Connecting duct matrices narrower (Figs. 24, 32), much longer than wide, DL/DW=1.30-1.89, *N*=15 (*bimucronatus*), or 1.38-1.67, *N*=9 (*georgiensis*) . . . . . . *bimucronatus* or *georgiensis*

14 (12). Median unsclerotized area (posterior to atrial slit) wide, > one-half width of epigynum; LAE about one-fifth to one-quarter of EL; anterior sclerotized band present (Fig. 48); caudal support sclerotization inconspicuous, lateral to position of spermathecae (Figs. 49, 50); species widespread (*calcaratus*) or restricted to vicinity of Mt. Rogers, Virginia (*willsi*) . . . . *calcaratus* or *willsi*
Median unsclerotized area narrow (sclerotization posterior to atrial slit well developed) (Figs. 60, 76, 82); LAE > one-quarter of EL; anterior sclerotized band absent or weakly developed; caudal support sclerotization lacking or located between position of spermathecae (Fig. 83) 15

15 (14). Caudal support sclerotization lacking, species widespread . . . . *hybridus*
Caudal support sclerotization present between position of spermathecae (Fig. 83) 16

16 (15). LAE between one-quarter and one-third of EL (Fig. 60), duct matrices separate, slender (Fig. 62) . . . . *tennesseensis*
LAE one-half or more of EL (Fig. 82); duct matrices large, wide and contiguous (Fig. 84) . . . . *saturnus*

Wadotes bimucronatus (Simon)
Figs. 13-16, 21-31, 115, 117

Coelotes bimucronatus Simon 1898a:6.
Wadotes bimucronatus: Chamberlin 1925:121.
W. carolinus Chamberlin; 1925:121; Muma 1947:6, figs. 5, 6, 18, 19, 35, 36, **NEW SYNONYMY**.
W. convolutus Muma 1947:8 (male only), **NEW SYNONYMY**.

Diagnosis.—Males of *W. bimucronatus* are distinguishable from all other *Wadotes* except *W. georgiensis* by the combined presence of a strongly bifurcate terminal apophysis (Figs. 15, 16) and a proximal prolateral cymbial process laterally divided by a long, narrow cleft (Fig. 13). The prolateral cymbial process of *W. bimucronatus* is shorter in dorsal view (about 1 to 1.5 times as long as the retrolateral process) than that of *W. georgiensis* (compare Figs. 14, 18). The terminal apophysis in *W. bimucronatus* has a conspicuous, somewhat triangular, flattened process dorsally (Fig. 15) which is represented in *W. georgiensis* by only a very slight projection (Fig. 19).

Females of *W. bimucronatus* are distinguishable from all other *Wadotes* except *W. georgiensis* and *W. dixiensis* by the complete superficial epigynal sclerotization, both anterior and posterior to the atrial slit (Figs. 21, 22). *Wadotes bimucronatus* can be separated from *W. dixiensis* by the presence, in the former, of collecting duct matrices which are about 1.5 times as long as their combined width (DL/DW=1.30-1.89, *N*=15) (Figs. 24-28). No morphological characteristics have been observed which serve to adequately distinguish females of *W. bimucronatus* from *W. georgiensis*. Howell (1974) stated that the relative shape of the boundaries of the median unsclerotized area posterior to the atrial slit distinguishes the two species. This character is highly variable in both species and cannot reliably separate the two.
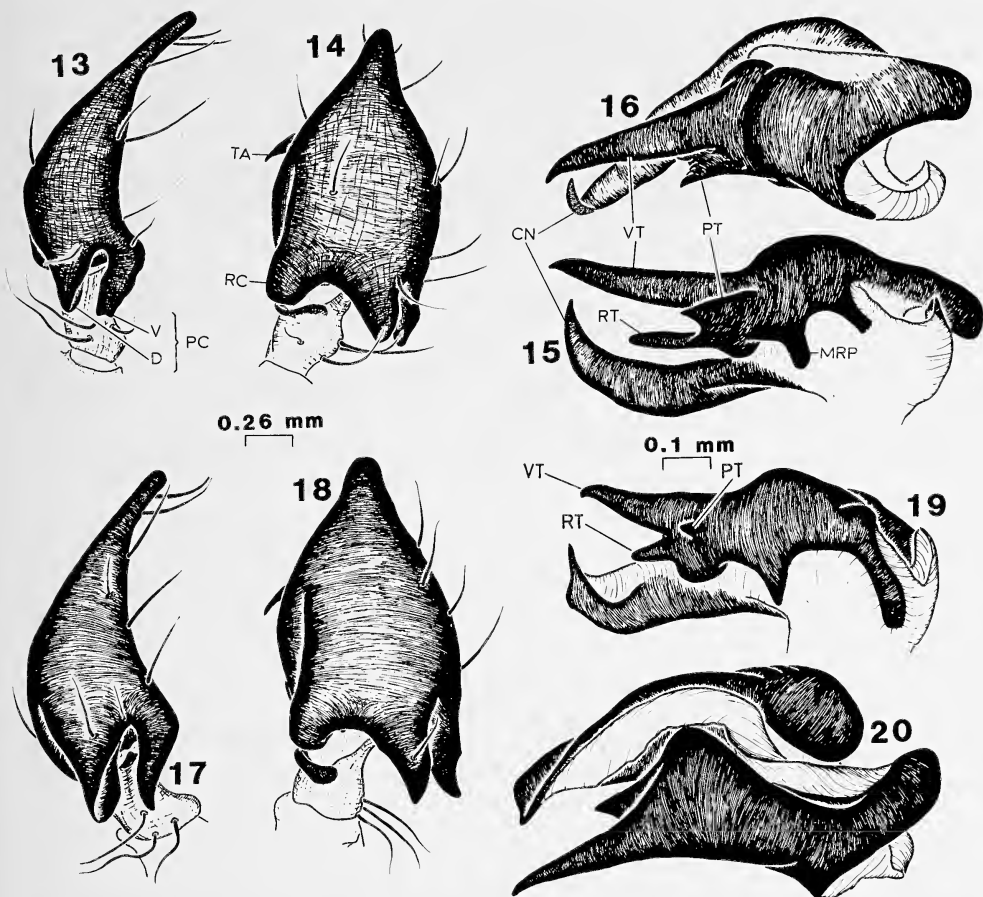
Figs. 13-16.—*Wadotes bimucronatus*, Cataloochee NC: 13, left palpal tibia and cymbium, prolateral view; 14, same, dorsal view; 15, terminal apophysis and conductor of left genital bulb, dorsal view; 16, same, prolateral view. Figs. 17-20. *W. georgiensis*, Vogel State Park GA: 17, left palpal tibia and cymbium, prolateral view; 18, same, dorsal view; 19, conductor and terminal apophysis of left genital bulb, dorsal view; 20, same, ventral view. D—dorsal arm of PC, MRP—median retrolateral process of TA, PC—prolateral cymbial extension, PT—prolateral arm of TA, RC—retrolateral cymbial extension, RT—retrolateral arm of TA, V—ventral arm of PC, VT—ventral arm of TA.

Description.—*Male:* Figs. 13-16. 40 specimens measured. CL 3.2-4.9(4.2±0.39), CW 2.1-3.2(2.7±0.29), SL 1.63-2.40(2.05±0.18), SW 1.33-1.75(1.58±0.11). Holotype of *C. bimucronatus* CL 5.0, CW 3.3, SL 2.43, SW 1.8. (This specimen was not on hand when the statistics were compiled and, thus, was not included in the sample. Simon's measurement [1898b] of 6.0 mm total length for this specimen is either a mistake or a misprint.)

Female: Figs. 21-31. 40 specimens measured. CL 2.9-5.4(4.0±0.46), CW 1.9-3.3(2.5±0.27), SL 1.55-2.50(1.95±0.19), SW 1.25-1.95(1.56±0.14). LAE about two-fifths of EL, EL/LAE=2.13-2.83(2.54±0.21), *N*=16.

Variation: Considerable variation is found in the form and pattern of the connecting ducts, even among specimens from the same locale. One specimen (from Monroe County, Georgia, on the present southern boundary of the range of this species) has duct matrices wider than average for *W. bimucronatus* (width ca 0.75 times length [Fig. 28]), resembling those of *W. dixiensis*. The matrices

lack the overall squarish, "fat" appearance of those of *W. dixiensis* (Fig. 104), however, so this specimen is tentatively considered to be *W. bimucronatus*.

The tip of the ventral arm of the prolateral cymbial process may be bluntly pointed, rounded, or truncated. The scape (Figs. 21, 23, 29-31) is variously tapered to a blunt, bifid, or pointed tip.

Distribution.—Figs. 115, 117. *Wadotes bimucronatus* is the most common *Wadotes* collected in the southern Appalachians of western North Carolina and northern Georgia, and is found at least as far south as central Georgia as shown by the pitfall trapping of Howell (1976) and a single record from southern Alabama. A population from the north panhandle of West Virginia may be isolated from the southern aggregations as no *W. bimucronatus* have been recorded from the rest of West Virginia except for Mercer County (far to the south on the Virginia border).

Natural History Notes.—*Wadotes bimucronatus* is a very common spider of the hardwood forest floor in the southern Appalachians. At high elevations it becomes rare and is probably absent from the spruce/fir community on the high peaks of the region. This spider has been collected syntopically with *W. hybridus, W. dixiensis, W. mumai,* and *W. carinidactylus*. It may also be syntopic with *W. calcaratus* and *W. saturnus*, but is probably not sympatric with the closely related *W. georgiensis*.

Mature males have been collected from mid-September to late March. Mature females are present all year.

One dipterous pupa (Acroceridae) emerged from the abdomen of a penultimate male *W. bimucronatus* being reared in the laboratory. The spider had been collected sometime previously as a penultimate in Cullowhee, North Carolina. On 3 November 1983 the spider was dead and a small cocoon containing the acrocerid pupa was observed in the spider's webbing. On 5 November the pupa had left the cocoon but was still encased in a puparium. It was removed at this time for examination and then placed in a vial to contain the emergent adult. Shortly thereafter the pupa died, a result that probably illustrates the importance of E. I. Schlinger's advice (pers. comm.) to avoid manipulating or handling acrocerid pupae during attempts to rear them to adulthood.

Types.—*Coelotes bimucronatus* Simon, male holotype, North Carolina, in MNHN, examined. *Wadotes carolinus* Chamberlin, male holotype, North Carolina, Polk Co., Tryon, XI 1913 (W. M. Wheeler), in MCZ, examined. *Wadotes convolutus* Muma, female holotype, Alabama, Marshall Co., Bishop Cave (Ms5), Bishop Mtn., 1.5 mi S. of highway, 12 I 1933 (A. F. Archer), in AMNH, examined.

Discussion.—Muma (1947) misidentified specimens which properly belong in *W. dixiensis* Chamberlin as *W. bimucronatus* Simon.

Wadotes calcaratus (Keyserling)
Figs. 34-39, 48-57, 112, 113, 118

Coelotes calcaratus Keyserling 1887:470 (in part), fig. 32 (not fig. 32a [Kaston 1948]).
C. longitarsus Emerton 1889:192 (in part), fig. 2 (not fig. 2a [Kaston 1948]).
C. nigriceps Banks 1895:82.
Wadotes calcaratus: Chamberlin 1925:121; Muma 1947:2, figs. 3, 4, 16, 17, 33, 34; Kaston 1948:282, figs. 903, 904, 916.
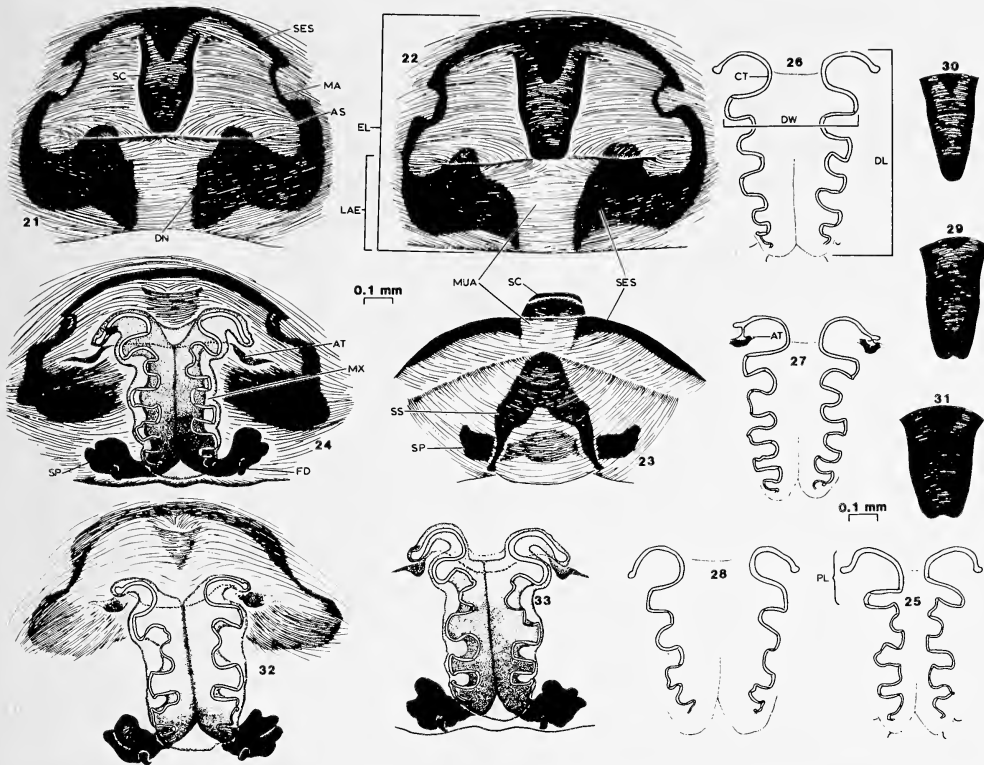
Figs. 21-31.—*Wadotes bimucronatus*: 21-22, epigyna, Cullowhee NC, ventral views; 23, same, caudal view; 24, same, anterodorsal view; 25, connecting ducts, anterodorsal view, Bryson City NC; 26, same, Wheeling WV; 27, same, Bryson City NC; 28, same, Monroe County GA; 29, scape, ventral view, Cartersville GA; 30, same, Cullowhee NC; 31, same, Highlands NC. Figs. 32,33. *W. georgiensis*, Vogel State Park GA: 32, epigynum, anterodorsal view; 33, same, ventral superficial features excluded. AS—atrial slit, AT—atrium, CT—connecting duct, DL—length of CT, DN—depression, DW—width of duct matrices, EL—epigynum length, FD—fertilization duct, LAE—EL from AS to epigastric groove, MA—muscle attachment sclerotization, MUA—median unsclerotized area, MX—CT matrix, PL—primary loops of CT, SC—scape, SES—superficial epigynal sclerotization, SP—spermatheca, SS—support sclerite.

Diagnosis.—*Wadotes calcaratus* can be separated from all other *Wadotes* except *W. willsi* by the presence of, in males, a long proximal retrolateral cymbial process (Fig. 35) and a short dorsodistal patellar apophysis (Figs. 36, 37); and in females, EL 4 to 6 times as long as LAE (EL/LAE=3.70-6.00, N=11) (Fig. 48) and caudally on epigynum a pair of weak support sclerites lateral to spermathecae (Fig. 49). *Wadotes calcaratus* males can be distinguished from *W. willsi* by their lack of a pronounced dorsodistal tibial apophysis and the relatively undeveloped nature of the proximal prolateral cymbial margin (Fig. 34). Females of *W. willsi* and *W. calcaratus* show no apparent structural differences.

Description.—*Male:* Figs. 34-39. 40 specimens measured including lectotype. CL 3.5-4.7(4.1±0.32), CW 2.3-3.0(2.7±0.19), SL 1.75-2.33(2.04±0.13), SW 1.35-1.78(1.57±0.05). Lectotype CL 4.5, CW 3.1, SL 2.25, SW 1.63. Tibia with a small, proximal, dorsal apophysis (Fig. 37).
Female: Figs. 48-57. 40 specimens measured. CL 3.1-5.2(4.2±0.43), CW 2.1-3.3(2.6±0.28), SL 1.55-2.38(2.02±0.18), SW 1.28-1.88(1.61±0.13).

Variation: The retrolateral cymbial process varies in length and curvature from slightly shorter than in Figure 35 to slightly longer with an abrupt, truncate, prolaterally bent terminus. The epigynal scape varies widely (Figs. 48, 53-57). The connecting ducts vary considerably in the orientation of the primary loops.

Distribution.—Figs. 112, 113, 118. The range of *W. calcaratus* corresponds fairly closely to a region delimited in the south, south-east, and south-west by the northern boundary of the Gulf and Atlantic Coastal Plains, and in the north by the southern boundary of the boreal forest.

Specimens are reported to have been collected in Nebraska (Worley and Pickwell 1927), Wyoming and Colorado (Keyserling 1887, in Bonnet 1959), and Oklahoma and Arizona (Muma 1947). All these records are old and the Nebraska record is of an immature specimen. Roth and Brame (1972) stated that all western records for this species listed in Muma (1947) are based on mislabelled specimens. This is probably true at least for the Arizona and Colorado collections. Marx, who supplied Keyserling's (1887) type material, is known to have frequently put erroneous locality data with specimens (see Coyle 1971:345).

This species becomes rare south of the North Carolina-Georgia border. One specimen is known from Georgia and one from Alabama.

Natural History Notes.—Although widespread and common throughout much of its range, *W. calcaratus* is not common in pine forests and has not been collected from the isolated spruce/fir forests of the southern Appalachians.

Mature females (and mature males, at least in the northern part of the range) are present year-round.

Specimens of all other species of *Wadotes* have been collected from within the range of *W. calcaratus*, but only *W. tennesseensis* has been shown to exist syntopically with *W. calcaratus*. Specimens of both these species were recovered from a leaf litter sample from Jackson County, North Carolina.

One egg case (from Aylmer, southern Ontario, 21 April 1975) containing 17 eggs was examined.

Types.—*Coelotes calcaratus* Keyserling, two male snytypes, Colorado, Valmont and Minnesota, Olmstead Co., Rochester (G. Marx), in NMNH, examined, here designated paralectotype and lectotype respectively. *Coelotes longitarsus* Emerton, male holotype, New Hampshire, Mt. Carmel, 9 X (J. H. Emerton), in MCZ, examined. *Coelotes nigriceps* Banks, two female syntypes, New York, Roslyn, in MCZ, examined.

Wadotes carinidactylus, new species
Figs. 93-97, 112, 117

Etymology.—The species name is derived from the Latin adjective *carinatus* meaning "keeled" and the Greek noun *daktylos* meaning "finger" and refers to the diagnostic character described below.

Diagnosis.—This species is readily separated from all other *Wadotes* species by the presence of a conspicuous ventral keel on the ventral arm of the terminal apophysis (Fig. 95).

Description.—Known only from four males.

Male: Figs. 93-97. All specimens measured. CL 41.-4.8(4.4±0.31), CW 2.7-3.1(2.9±0.17), SL 2.05-2.33(2.16±0.13), SW 1.55-1.80(1.63±0.11). Holotype CL 4.1, CW 2.7, SL 2.05, SW 1.58.
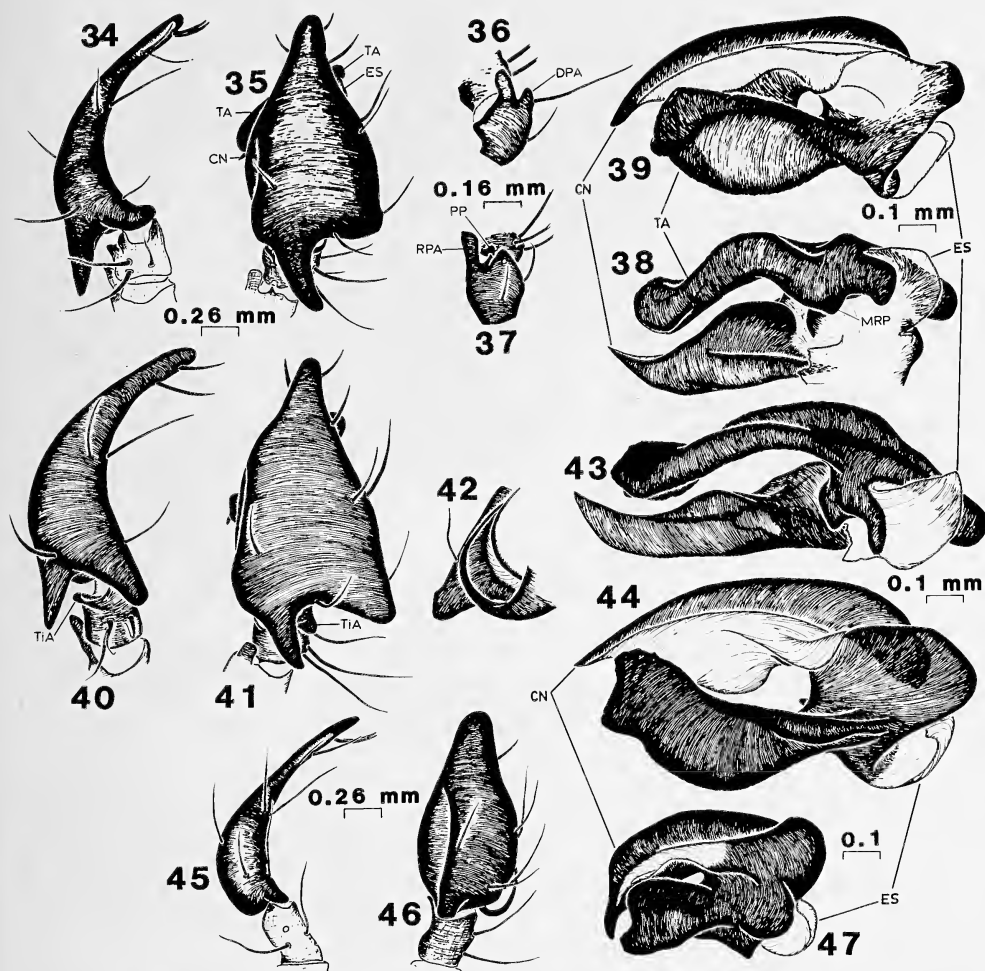
Figs. 34-39.—*Wadotes calcaratus*, locality unknown: 34, left palpal tibia and cymbium, prolateral view; 35, same, dorsal view; 36, left palpal patella and base of tibia, retrolateral view; 37, same, dorsal view; 38, conductor and terminal apophysis of left genital bulb, dorsal view; 39, same, ventral prolateral view. Figs. 40-44. *W. willsi*, Mount Rogers VA (holotype): 40, left palpal tibia and cymbium, prolateral view; 41, same, dorsal view; 42, prolateral margin of tarsus including part of embolus and subtegulum, ventral view; 43, conductor and terminal apophysis of left genital bulb, dorsal view; 44, same, ventral prolateral view. Figs. 45-47. *W. tennesseensis*, Newfound Gap (GSMNP) NC/TN: 45, left palpal tibia and cymbium, prolateral view; 46, same dorsal view; 47, conductor and terminal apophysis of left genital bulb, ventral view. DPA—dorsal patellar apophysis, PP—proximal dorsal tibial prominence, RPA—retrolateral patellar apophysis, TiA—dorsal prolateral tibial apophysis.

Retrolateral patellar apophysis short, ca. 0.25 times total patella length. In dorsal view, cymbial processes subequal (Fig. 94). In prolateral view (Fig. 93), prolateral process laterally bisected by somewhat triangular cleft, ventral arm angular ventrally, smoothly and slightly convex dorsally; dorsal arm short and broadly triangular dorsally with shallow ventral cleft.

Ventral arm of terminal apophysis well developed with a high, narrow, longitudinal keel ventrally (Fig. 95); prolateral and retrolateral arms fused into heavy, broad plate (Figs. 96, 97) with strong retrolateral ridge ventrally running
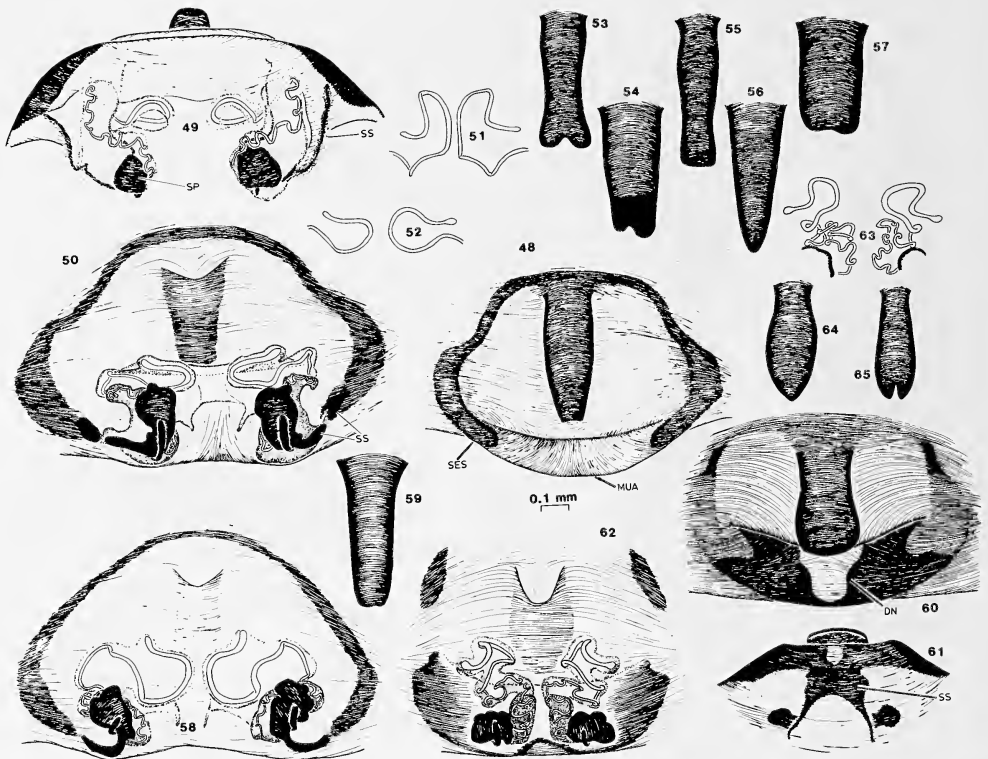
Figs. 48-57.—*Wadotes calcaratus*: 48, epigynum, Pumpkintown NC, ventral view; 49, same, Cataloochee NC, caudal view; 50, same, dorsal view; 51, primary loops of connecting ducts, dorsal view, Washington County VA; 52, same, Pocahontas County WV. Figs. 58, 59. *W. willsi*, Mount Rogers VA: 58, epigynum, dorsal view; 59, scape, ventral view. Figs. 60-65. *W. tennesseensis*: 60, epigynum, Mount Le Conte (GSMNP) TN, ventral view; 61, same, caudal view; 62, same, Rough Butt Bald Trail (BRPWY) NC, dorsal view; 63, connecting ducts, Mount Le Conte TN, dorsal view; 64, scape, ventral view, GSMNP; 65, same, Mount Le Conte (GSMNP) TN.

longitudinally and curving prolaterally proximal to base of ventral arm. Median retrolateral process pronounced, bluntly pointed, triangular (Fig. 96).

Distributions.—Figs. 112, 117. *Wadotes carinidactylus* is known only from the type locality in the southern ridges of the southern Appalachians in Georgia and from the Piedmont in the Atlanta, Georgia area.

Natural History Notes.—The holotype and paratype males were collected from within a well rotted pine log on a westerly facing slope of a shallow ravine in the east face of Taylor Ridge. The surrounding forest was composed of mixed pines and hardwoods with pines dominating on the immediate ridges. A female, identical to those of *W. bimucronatus*, was captured from the same log. Given the possibility that this specimen could be the female of *W. carinidactylus* it has been left in the vial containing the paratype male of *W. carinidactylus*.

Type Series.—Male holotype and paratype, Georgia, Chattooga Co., Mackwhite Gap, Taylor Ridge, 3 mi E Summerville (1200'), 13 I 1984 (R. G. Bennett) in MCZ.

Collection Data.—U.S.A.: GEORGIA; *Fulton Co.*, Atlanta, 20 I 1944 (P. W. Fattig), 1 male (AMNH), 12 I 1946 (1 XII 1946?) (P. W. Fattig), 1 male (AMNH).
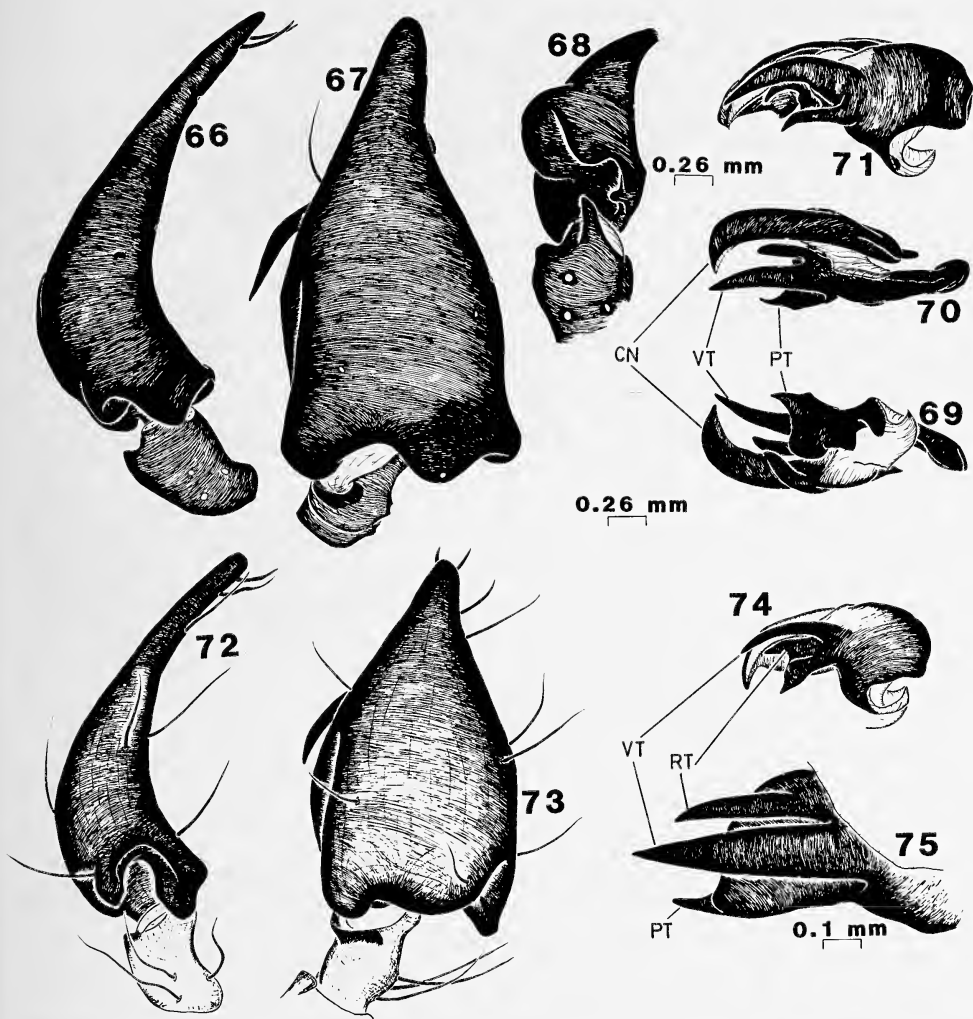
Figs. 66-71.—*Wadotes mumai*, Blue Ridge Mountains GA (holotype): 66, left palpal tibia and cymbium, prolateral view; 67, same, dorsal view; 68, same, posterior prolateral view; 69, conductor and terminal apophysis of left genital bulb, dorsal view; 70, same, ventral view; 71, same, prolateral view. Note: left palpal cymbium of holotype damaged. Figs. 66-68 are of right palpus drawn as mirror images to simulate appearance of left palpus. Figs. 72-75. *W. hybridus*: 72, left palpal tibia and cymbium, Cullowhee NC, prolateral view; 73, same, dorsal view; 74, conductor and terminal apophysis of left genital bulb, Cataloochee NC, prolateral view; 75, distal section of terminal apophysis, Cullowhee NC, ventral view.

Wadotes deceptis, new species
Figs. 89-92, 114, 118

Etymology.—The specific name is a Latin adjective meaning "deceptive."

Diagnosis.—The bisection of the prolateral cymbial process by a wedge-shaped cleft (Figs. 89, 90) combined with the fusion of the retrolateral arm of the terminal apophysis to the base of the ventral arm (Figs. 91, 92) serve to distinguish this species from all other *Wadotes*.

Description.—Known only from seven males.

Male: Figs. 89-92. Five specimens measured including holotype. CL 4.0-4.8(4.4±0.35), CW 2.7-3.3(3.0±0.26), SL 2.0-2.4(2.2±0.16), SW 1.6-1.8(1.7±0.1). Holotype CL 4.7, CW 3.1, SL 2.3, SW 1.7.

Retrolateral patellar apophysis short, stout, about one-quarter of total patella length. Distal prolateral tibial extension not produced as an apophysis. Cymbial processes subequal in dorsal view. Prolateral cymbial process similar to *W. dixiensis*, laterally bisected by a wedge-shaped cleft (Figs. 89, 90), ventral arm rounded terminally with smoothly curving margins, dorsal arm broadly triangular to somewhat rectangular with shallow ventral cleft.

Terminal apophysis (Figs. 91, 92) similar to *W. saturnus*; long ventral arm tapering to fine point; retrolateral arm fused to retrolateral base of ventral arm; prolateral arm pointed, broadly triangular, connecting with dorsal base of retrolateral arm by means of a narrow flange (Fig. 91); longitudinal ridge on prolateral arm very reduced and more prolateral than ventral. Median retrolateral process well developed, triangular (Fig. 91).

In the GSMNP a male of this species was collected with two females that are morphologically indistinguishable from *W. dixiensis*. These may be *W. deceptis* females.

Variation: The prolateral cymbial process varies as diagrammed (Figs. 89, 90); the JKMF specimens differ from the Little River (GSMNP) specimens in the width of the cleft and the relative shape of the arms. The fused retrolateral arm of the terminal apophysis is shorter in the Little River specimens than in those from the JKMF. Distally on femur I there may be one or two prolateral macrosetae.

Distribution.—Figs. 114, 118. This species is known only from southwestern North Carolina (JKMF) and from adjacent eastern Tennessee (southwestern GSMNP).

Natural History Notes.—Three males, including the holotype, were collected by sifting leaf litter in a hardwood forest. Two more came from underneath rotting logs in a mixed forest of pine, hemlock, and hardwoods.

Holotype.—Male, North Carolina, Graham Co., Poplar Cove, JKMF, 30 X 1971 (F. A. Coyle) in MCZ.

Collection Data.—U.S.A.: TENNESSEE; *Blount Co.*, Parson's Branch Road at Sam's Gap, GSMNP, 7 XI 1984 (R. G. Bennett), 1 male (RGB), Parson's Branch Rd., 2 mi E of Sam's Gap, GSMNP, 7 XI 1984 (R. G. Bennett), 1 male (RGB); *Sevier Co.*, Little River, GSMNP, 3 IX 1936 (W.M.B.), 2 males (AMNH). NORTH CAROLINA; *Graham Co.*, Poplar Cove, JKMF, 25 IX 1971 (F. A. Coyle), 2 males (MCZ).

Wadotes dixiensis Chamberlin
Figs. 98-108, 116, 117

Wadotes dixiensis Chamberlin 1925:120, (not *Wadotes dixiensis:* Muma, 1947 or subsequent authors).
W. bimucronatus: Muma 1947:5, figs. 8, 9, 20, 21, 39, 40, (misidentification).

Diagnosis.—*Wadotes dixiensis* can be distinguished from all other species of *Wadotes* by the presence of an elongate ventral arm underlying a pronounced, smooth, crescent-shaped dorsal plate on the terminal apophysis of the male palpus (Figs. 100, 101) and, in the female, by the combined presence of complete superficial epigynal sclerotization (Figs. 102, 103) and relatively stout, contiguous duct matrices (Fig. 104) which are, together, nearly as wide as long (DL/DW=0.87-1.29, *N*=20).
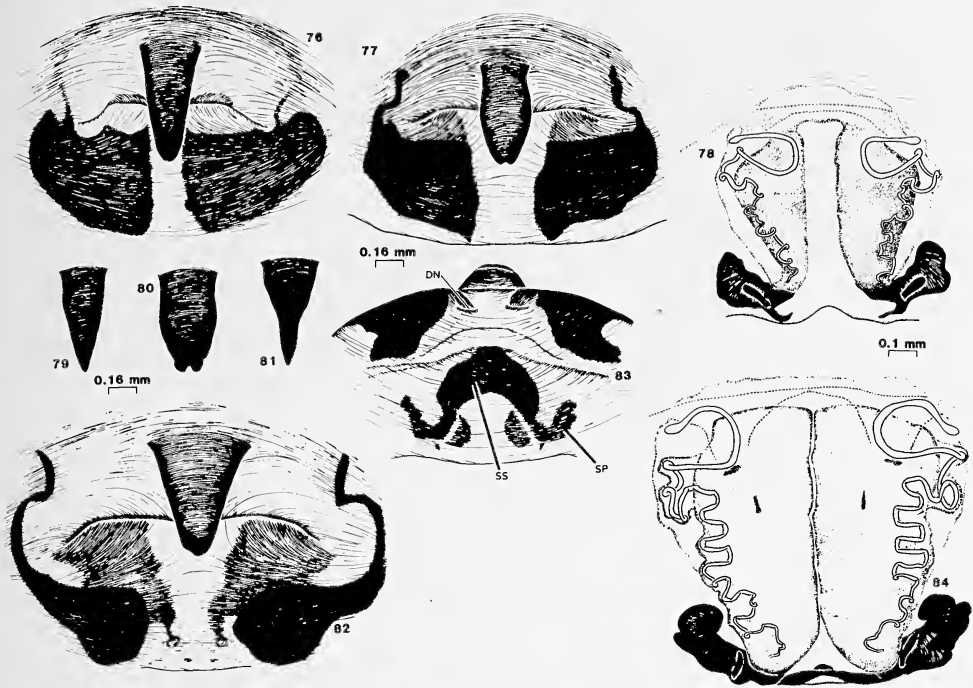
Figs. 76-81.—*Wadotes hybridus*: 76, epigynum, ventral view, Ithaca NY (*Coelotes altilis* syntype); 77, same, Randolph NH; 78, same, dorsal view, ventral superficial features excluded, Straight Fork Creek (GSMNP) NC; 79, scape, ventral view, Straight Fork Creek NC; 80, same, Cullowhee NC; 81, same, Highlands NC. Figs. 82-84. *W. saturnus*, Gainesville GA: 82, epigynum, ventral view; 83, same, caudal view; 84, same, dorsal view, ventral superficial features excluded.

Description.—*Male:* Figs. 98-101. 11 specimens measured including holotype. CL 3.8-5.5(4.7±0.6), CW 2.5-3.7(3.1±0.39), SL 1.88-2.70(2.32±0.26), SW 1.43-2.00(1.78±0.19). Holotype CL 4.7, CW 3.2, SL 2.33, SW 1.80.
Female: Figs. 102-108. 22 specimens measured. CL 3.2-5.7(4.2±0.69), CW 2.0-3.7(2.6±0.48), SL 1.53-2.73(2.03±0.32), SW 1.25-2.08(1.64±0.25). LAE about one-half of EL (Figs. 102, 103) EL/LAE=1.36-2.43(2.05±0.27), N=18.
Variation: The scape varies widely in form (Figs. 102, 103, 105-108). The connecting ducts converge rapidly or gradually posteriorly.

There is considerable size variation in both sexes which appears to be related to geographic distribution. The females can be divided arbitrarily into two groups, one (from the northern part of the range in southwestern North Carolina) with carapace lengths < 4.0 mm (3.2-3.9[3.5±0.27], N=8) and the other (found primarily in the southern region and to some extent in the north, > 4.0 mm (4.1-5.7[4.7±0.41], N=14). There is, however, a continuum of less commonly collected intermediate sizes. At Wayah Bald, Macon County, North Carolina (the northern range boundary in that region), four females which have a continuous range of carapace lengths from 3.2 to 4.7 mm were collected together. Insufficient males are available for analysis.

The specimens here included in *W. dixiensis* may comprise two species. Because of the difficulty of assigning intermediate-sized specimens to one size class or the other, the wide and continuous size range in the Wayah Bald sample, and the absence of any other character with a concordant variation pattern, I conclude that all these *W. dixiensis* specimens are conspecific.
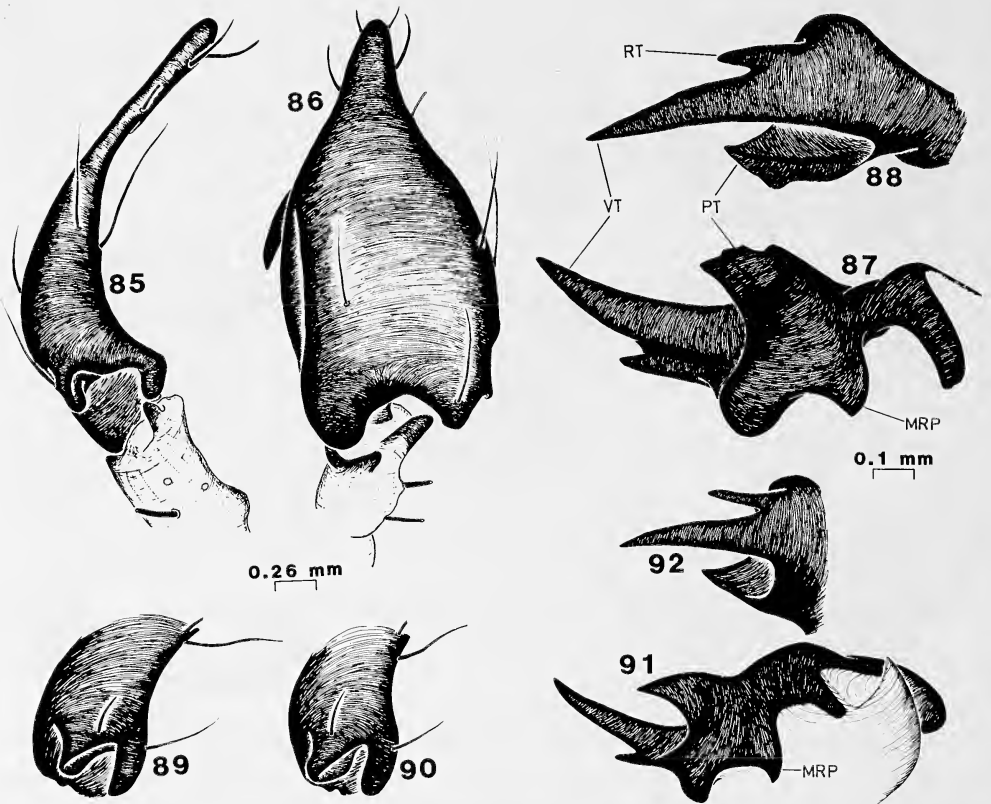
Figs. 85-88.—*Wadotes saturnus*: 85, left palpal tibia and cymbium, Vogel State Park GA, prolateral view; 86, same, dorsal view; 87, terminal apophysis, dorsal view, Indian Springs State Park GA; 88, same, distal section, ventral view, Vogel State Park GA. Figs. 89-92. *W. deceptis*: 89, proximal portion of left palpal cymbium, prolateral view, Graham County (JKMF) NC; 90, same, Little River (GSMNP) TN; 91, terminal apophysis and embolus support of left genital bulb, dorsal view, Little River TN; 92, distal section of terminal apophysis of left genital bulb, ventral view, Graham County (JKMF) NC.

Distribution.—Figs. 116, 117. *Wadotes dixiensis* has been collected from scattered locales through much of the northern half of Alabama into the highlands of southwestern North Carolina and southeastern Tennessee. No specimens are known from northern Georgia.

Natural History Notes.—Within its rather restricted range, this species exploits a variety of habitats from the low oak/pine forests of the northern Gulf Coastal Plain to the high elevation hardwood forests of the southern Appalachians.

Along the Bartram Trail at Wayah Bald, Macon County, North Carolina, *W. dixiensis* is well established in hardwood forests at elevations around 5200 feet and occurs syntopically with *W. bimucronatus* within and beneath rotted logs. In Alabama, *W. dixiensis* and *W. saturnus* both occur at De Soto State Park (De Kalb County).

Mature males have been collected from late September to early May, and adult females throughout the year.

Holotype.—Male, Alabama, Lee Co., Auburn (N. Banks), in MCZ, examined.
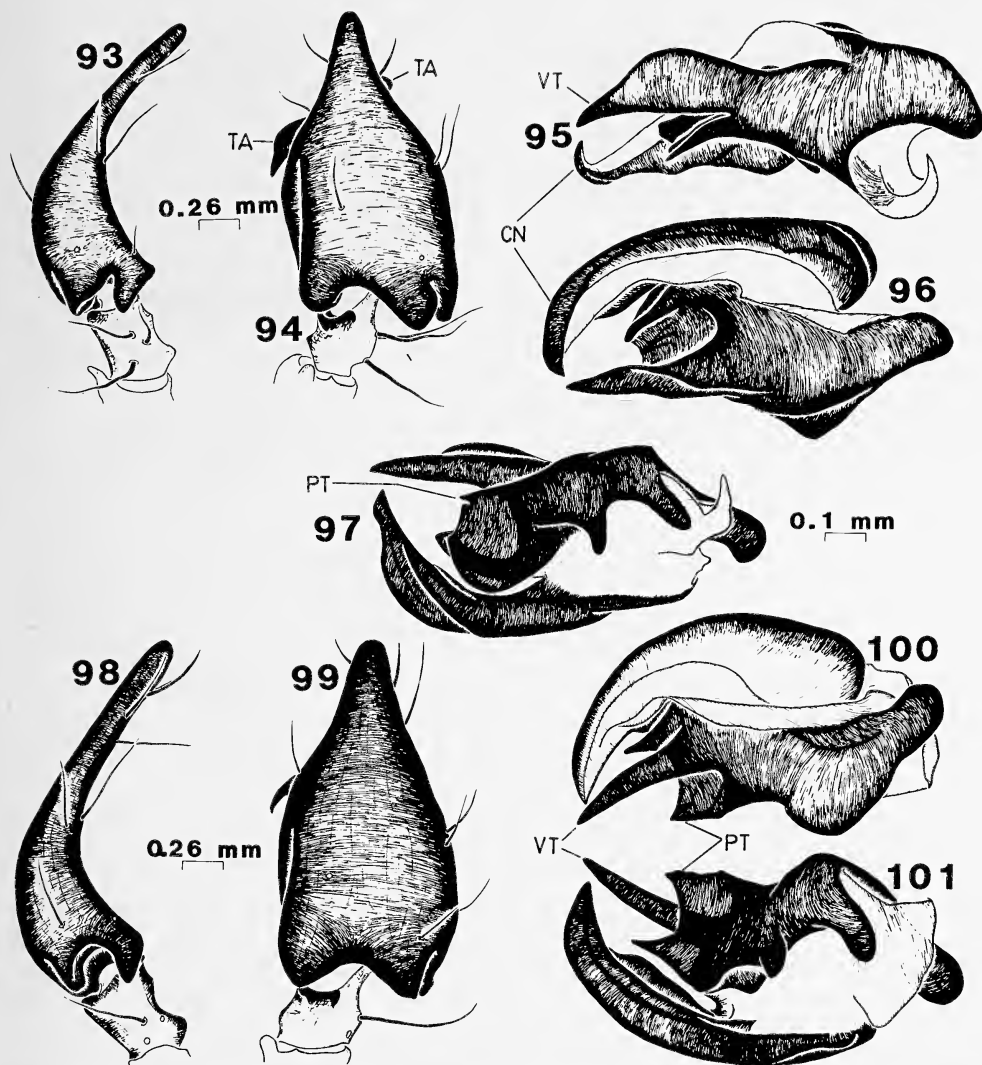
Figs. 93-97.—*Wadotes carinidactylus*, Atlanta GA: 93, left palpal tibia and cymbium, prolateral view; 94, same, dorsal; 95, conductor and terminal apophysis of left genital bulb, prolateral view; 96, same, ventral view; 97, same, dorsal view. Figs. 98-101. *W. dixiensis*, De Soto State Park AL: 98, left palpal tibia and cymbium, prolateral view; 99, same, dorsal view; 100, conductor and terminal apophysis of left genital bulb, ventral view; 101, same, dorsal view.

Wadotes georgiensis Howell
Figs. 7, 17-20, 32, 33, 115, 117

Wadotes georgiensis Howell 1974:728, fig. 1 (a-f).

Diagnosis.—*Wadotes georgiensis* can be distinguished from all congeners except *W. bimucronatus* by a combination of a deeply and narrowly bisected prolateral cymbial process (Fig. 17) and a bifurcate terminal apophysis in the male (Fig. 19), and the complete superficial epigynal sclerotization combined with the narrow collecting duct matrix in the female (Figs. 32, 33), DL/DW=1.38-1.67, N=9. Females of *W. georgiensis* and *W. bimucronatus* are evidently indistinguisha-

ble on morphological grounds. Males of *W. georgiensis* differ from *W. bimucronatus* in having the prolateral cymbial process much longer then the retrolateral cymbial process in dorsal view (Fig. 18); the prolateral arm of the terminal apophysis reduced to a slight, inconspicuous dorsal projection (Fig. 19) (best observed in profile at magnifications of 40X or greater); and a short retrolateral arm extending from the base of the ventral arm (Figs. 19, 20).

Description.—*Male:* Figs. 7, 17-20. 13 specimens measured including holotype. CL 3.7-4.4(4.0±0.26), CW 2.4-3.0(2.7±0.18), SL 1.80-2.18(1.99±0.13), SW 1.38-1.63(1.52±0.08). Holotype CL 4.1, CW 2.7, SL 2.1, SW 1.55.

Female: Figs. 32, 33. 14 specimens measured. CL 3.4-5.0(3.9±0.44), CW 2.1-3.3(2.5±0.29), SL 1.63-2.30(1.90±0.18), SW 1.33-1.88(1.53±0.14). EL/LAE=2.27-2.82(2.52±0.16), N=13. Characteristics as for *W. bimucronatus* except that scape varies only slightly, tending towards a thickening of the terminus.

Distribution.—Figs. 115, 117. *Wadotes georgiensis* is known only from the area of Vogel State Park, Union County, Georgia. Due to my inability to separate females of this species and *W. bimucronatus* and the lack of male specimens from other nearby areas, all *W. bimucronatus/georgiensis*-type females collected from the neighboring areas have been conservatively identified as *W. bimucronatus*.

Natural History Notes.—Adults examined were collected from mid-September to early May. Howell (1974) reported a June collection of one female as well and stated that this species was most often encountered "in thick stands of white pine" but could also be collected from "rhododendron thickets and on the slopes of open hardwoods." Most specimens have been recovered from pitfall traps or by sifting leaf litter.

Type Series.—Male holotype and female allotype, Georgia, Union Co., Vogel St. Pk., 8 mi (13 km) S Blairsville, 9 III 1972 (J. O. Howell), in AMNH, examined.

Collection Data.—U.S.A.: GEORGIA; *Lumpkin/Union Co.* line, 1/2 mi W of Neels Gap on App. Trail (3500'), 13 IX 1975 (J. D. Pittillo), 3 males, 4 females (FAC); *Union Co.*, Vogel St. Pk., 23 III 1972 (J. O. Howell), 3 males, 3 females (AMNH and JOH), 20 IV 1972 (J. O. Howell), 3 males, 2 females (JOH), 4 V 1972 (J. O. Howell), 3 males, 2 females (JOH), Vogel St. Pk. (2300'), 12 I 1984 (R. G. Bennett), 1 male, 2 females (RGB).

Wadotes hybridus (Emerton)
Figs. 1-4, 72-81, 114, 118

Coelotes hybridus Emerton 1889:193, figs, 4, 4a (in Bonnet 1959 and Banks 1910 as Emerton 1890).
C. altilis Banks 1892:25, figs. 74, 74a.
Wadotes hybridus: Chamberlin 1925:122; Muma 1947:7, figs. 10, 11, 24, 25, 41, 42; Kaston 1948:283, figs. 917-919.

Diagnosis.—Males of *W. hybridus* can be distinguished from all male *Wadotes* except *W. mumai* by the combined presence of three distinct arms on the terminal apophysis (Fig. 75), the free ventral arm, and the retrolateral arm joined from its base dorsally to the prolateral arm by a broad plate (Figs. 74, 75). From *W. mumai*, male *W. hybridus* differ in the presence of a strongly developed ventral arm of the prolateral cymbial process (Fig. 72). Female *W. hybridus* are distinguishable from all *Wadotes* females except *W. saturnus* by a combination of the restriction of superficial epigynal sclerotization to two broad plates posterior to the atrial slit and EL about 1.5 to 2 times as long as LAE (EL/LAE=1.55-2.06,
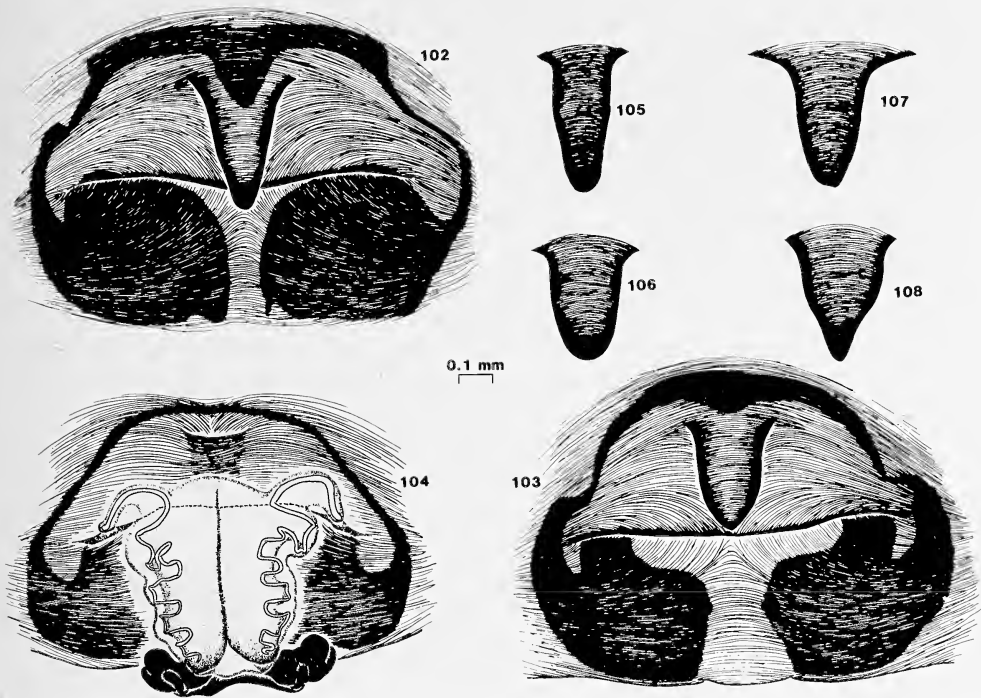
Figs. 102-108.—*Wadotes dixiensis*: 102, epigynum, ventral view, The Sinks (GSMNP) TN; 103, same, Maud AL; 104, same, dorsal view, Clay County NC; 105, scape, ventral view, Graham County (JKMF) NC; 106, same, Clay County NC; 107, same, Acton AL; 108, same, Alberta City AL.

N=12) (Figs. 76, 77). From female *W. saturnus, W. hybridus* is readily separated by its lack of support sclerotization on the caudal surface of the epigynum within the epigastric groove.

Description.—*Male:* Figs. 72-75. 40 specimens measured including holotype. CL 4.6-6.2(5.6±0.40), CW 3.0-4.3(3.6±0.30), SL 2.3-3.1(2.7±0.20), SW 1.7-2.3(2.0±0.13). Holotype CL 5.1, CW 3.5, SL 2.45, SW 1.88.

Female: Figs. 1-4, 76-81. 40 specimens measured. CL 4.1-6.9(5.7±0.72), CW 2.9-4.6(3.6±0.46), SL 2.2-3.3(2.7±0.30), SW 1.8-2.5(2.1±0.21).

Variation: Aside from scape variability (Figs. 79-81) and a wide range of size (especially in the females), *W. hybridus* exhibits fairly constant morphological characteristics throughout its range.

Distribution.—Figs. 114, 118. Next to *W. calcaratus, W. hybridus* has the largest range of all *Wadotes* species and is the most commonly collected species. South of Long Island, *W. hybridus* is absent from the Coastal Plain and Piedmont regions. Specimens from the west central part of the range are rare and thus the western boundary cannot be determined with any accuracy.

The extreme southern boundary of the range of *W. hybridus* passes through Sevier County, Tennessee and Swain and Jackson Counties, North Carolina. Immediately north of this boundary, *W. hybridus* is very common, but it disappears abruptly to the south of this area, where it is replaced by its rarely collected sister species, *W. saturnus* and *W. mumai.*

Natural History Notes.—*Wadotes hybridus* shares its range with *W. calcaratus, W. willsi, W. dixiensis,* and *W. bimucronatus* but only is known to be syntopic

with the latter species. It is absent from the high elevation spruce/fir forests of the southern Appalachians within its range.

Mature males have been collected from early August until late November. They apparently do not overwinter. Mature females can be collected throughout the year. Twelve egg cases, collected (with females) between mid-April and early July, contained 17 to 151 eggs or spiderlings.

One case from Summers County, West Virginia contained 125 eggs and more than 20 dipterous egg predators in an early instar larval stage. H. J. Teskey (CNC) identified these as acalyptrate diptera, probably chloropids.

At "The Sinks" (GSMNP), Sevier/Blount County line, Tennessee, on one occasion several mature females, with egg cases, were collected from underneath large flat rocks. Each female and her egg case were in a small depression in the ground at the end of a short silk tube extending to the edge of the rock. The females, normally relatively shy and retiring, vigorously defended their egg cases by repeatedly attacking and biting at fingers and forceps. Similar behavior was noted for another female collected with an egg case from underneath rotting bark on a log in Jackson County, North Carolina.

Types.—*Coelotes hybridus* Emerton, male holotype, New York, Chateaugay Lk., Adirondacks (F. A. Bowditch), in MCZ, examined. *Coelotes altilis* Banks, three female syntypes, New York, Ithaca (N. Banks), in MCZ, examined.

Wadotes mumai, new species
Figs. 66-71, 112, 118

Wadotes convolutus Muma 1947:8 (in part, not female holotype of *W. convolutus* Muma [= *W. bimucronatus* Simon]), figs. 26, 27, 43, 44.

Etymology.—The specific name is a patronym in honor of Martin H. Muma who first described this specimen.

Diagnosis.—*Wadotes mumai* can be distinguished from the males of all other species of *Wadotes* by the greatly reduced ventral arm of the prolateral cymbial process (Fig. 68).

Description.—Known from a single male.
Male: Figs. 66-71. CL 6.2, CW 4.1, SL 3.1, SW 2.2.

Retrolateral patellar apophysis ca 0.2-0.3 times total patella length. Distal prolateral edge of tibia extended into short, thin apophysis (Fig. 68). In dorsal view (Fig. 67) cymbial processes subequal. Retrolateral process short. Prolateral process greatly bisected laterally such that ventral arm is reduced to short, inconspicuous projection (Fig. 68) on proximal margin of cymbium; dorsal arm large, conspicuous; broadly convex dorsally with deep, wide, longitudinal ventral cleft.

Terminal apophysis (Figs. 69-71) with three conspicuous arms; ventral arm long, thin, pointed; retrolateral arm laterally flattened, twisted slightly, with a basal flange dorsally connecting by way of a broad, curving plate with prolateral arm (Fig. 69); prolateral arm in dorsal view triangular and pointed (Fig. 70), with a low longitudinal ridge ventrally (Fig. 71). Median retrolateral process (Fig. 70) pronounced, broadly triangular (broken on left terminal apophysis).

Distribution.—Figs. 112, 118. Known only from the type locality in north central Georgia. The original label accompanying this specimen (and the paratype
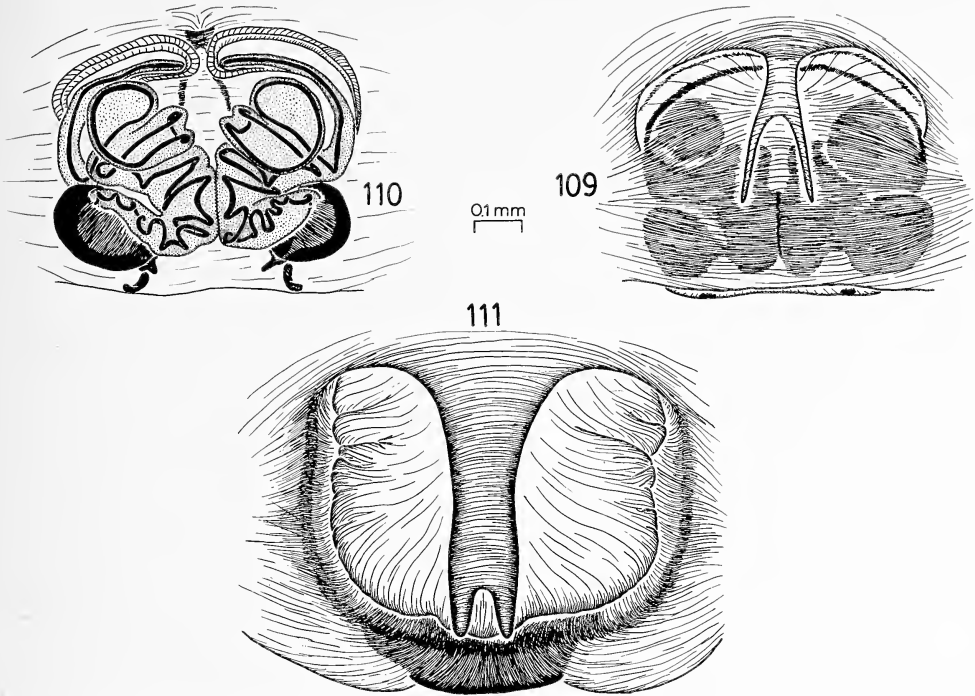
Figs. 109, 110.—*Wadotes primus*, epigynum, Hong Kong (holotype): 109, ventral view; 110, dorsal view. Fig. 111. "*Wadotes* new species near *primus*," epigynum, ventral view, Nanking China.

female of *W. convolutus*) is apparently missing. A more recent label lists the collection locale as Blue Ridge Mountains, Georgia with no additional data. This is the locality cited by Muma (1947) in his description of *W. convolutus*. It is possible that the original label referred to the small town of Blue Ridge (Fannin County), Georgia.

Holotype.—male (allotype of *W. convolutus* Muma), Georgia, Blue Ridge Mtns., in AMNH.

<center>

Wadotes saturnus, new species

Figs. 5, 6, 9-12, 82-88, 114, 118

</center>

Etymology.—The specific name is a noun in apposition after *Saturnus*, the ancient Italic god of agriculture.

Diagnosis.—Males of *W. saturnus* are distinguished from all congeners by the combined presence, on the terminal apophysis, of a short retrolateral arm fused to the base of the ventral arm (Figs. 87, 88) and, distally on the prolateral edge of the palpal tibia, a short but definite apophysis (as in *W. mumai*, Fig. 68). Females closely resemble females of *W. hybridus* but differ from the latter in the possession of a well defined area of support sclerotization medially on the caudal surface of the epigynum within the epigastric groove (Fig. 83). Female *W. saturnus* are distinguished from all other *Wadotes* females by the restriction of the superficial epigynal sclerotization to two broad plates posterior to the atrial slit and EL/LAE=1.63-1.97, *N*=5 (Fig. 82).

Figs. 112, 113.—Distributions of *Wadotes calcaratus*, dark circles; *W. carinidactylus*, open inverted triangles; *W. mumai*, slashed circle; and *W. willsi*, dark triangle: 112, southeastern Canada and eastern United States; 113, southeastern Canadian Maritime provinces. Dark circle with overhead arrow indicates collection locale beyond boundary of map of *W. calcaratus* syntype (Rochester MN).
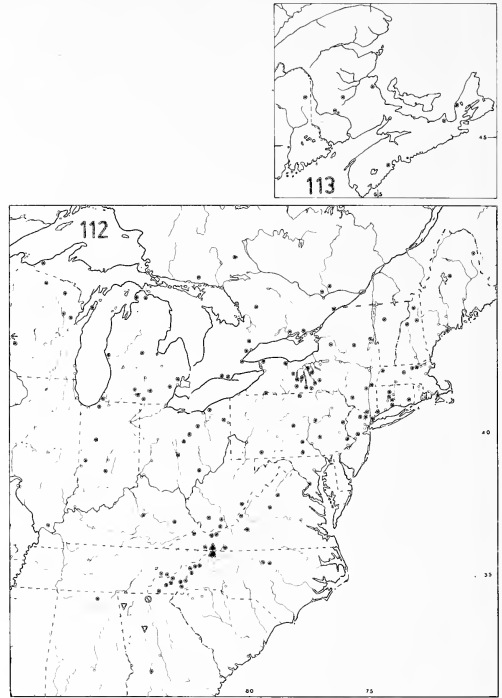
Description.—*Male:* Figs. 5, 6, 9-12, 85-88. 13 specimens measured including holotype. CL 5.5-6.8(6.2±0.43), CW 3.5-4.4(4.1±0.27), SL 2.7-3.3(3.0±0.18), SW 2.1-2.4(2.2±0.13). Holotype CL 6.4, CW 4.3, SL 3.1, SW 2.4.

Retrolateral patellar apophysis long, about one-third of total patella length. Prolateral tibial extension terminating in short but conspicuous apophysis. Cymbial processes subequal in dorsal view (Fig. 86). Prolateral cymbial process broadly bisected laterally (Fig. 85); ventral arm reduced to a short caudally or prolaterally produced projection; dorsal arm short and broad in dorsal view, concave ventrally.

Terminal apophysis trifurcate (Figs. 87, 88); retrolateral arm short, smoothly fused to middle of retrolateral edge of long, pointed ventral arm; prolateral arm short, with low longitudinal ridge running along entire ventral length (Figs. 12, 88), fused to ventral base of retrolateral arm by a narrow, crescent-shaped, flanged plate (Fig. 87). Median retrolateral process well developed, broadly triangular with dull point (Fig. 87).

Female: Figs. 82-84. 13 specimens measured. CL 5.3-7.4(6.7±0.57), CW 3.5-4.6(4.2±0.32), SL 2.7-3.3(3.1±0.19), SW 2.2-2.8(2.5±0.19).

Posterior plates of superficial epigynal sclerotization usually two-toned (sometimes inconspicuously), with area of lighter sclerotization extending anteriorly into atrial slit (Fig. 82). Internally, duct matrices broad, contiguous; ducts convergent posteriorly and restricted to lateral margins of matrices (Fig. 84).

Variation: Female *W. saturnus* show considerable variation in size. Scape form is also variable: broadly or narrowly triangular with the tip blunt, rounded, or pointed. The superficial epigynal sclerotization is usually confined to the posterior plates but may extend laterally and anteriorly to the muscle attachment

sclerites. The ventral arm of the prolateral cymbial process in males from the Guntersville, Alabama area is bent prolaterally. Males from the rest of the range tend to display a slightly larger and caudally directed ventral arm. Distally on femur I there may be one or three prolateral macrosetae instead of two.

Distribution.—Figs. 114, 118. *Wadotes saturnus* has been collected from locales in northeastern Alabama, northern Georgia and extreme southwestern North Carolina.

Natural History Notes.—Specimens of *W. dixiensis, W. georgiensis, W. bimucronatus,* and *W. deceptis* have come from the same collecting locales as *W. saturnus.*

One female was collected in early January from a silk lined circular diapause chamber in the earth underneath a log in Unicoi State Park, White County, Georgia. This spider produced a large egg case in the laboratory in late January but consumed the case shortly thereafter.

Mature females are probably present year-round. Mature males have been collected from late fall to early winter.

Type Series.—Male holotype, female allotype, Alabama, Marshall Co., Little Mtn. St. Pk. (now Lk. Guntersville St. Pk.), E of Guntersville, 13 IX 1970 (J. A. Beatty), in MCZ.

Discussion.—Muma (1947) incorrectly associated members of this species with *W. dixiensis* Chamberlin.

Collection Data.—U.S.A.: ALABAMA; *De Kalb Co.,* De Soto St. Pk., X 1937, 4 males (AMNH); *Marshall Co.,* Little Mtn. St. Pk., E of Guntersville, 11 VI 1963 (J. A. Beatty), 1 female, 5 imms (JAB), 13 IX 1970 (J. A. Beatty), 2 males, 3 females (JAB), 13 IX 1970 (T. N. Trudeau) 1 male, 2 females (RGB), 3 VI 1975 (J. A. Beatty), 1 female (JAB). GEORGIA: *Butts Co.,* Indian Springs St. Pk., 2 XI 1972 (J. O. Howell), 2 males, (JOH); *Habersham Co.,* Clarksville, 27 IV 1943 (W. Ivie), 1 female, (AMNH); *Hall Co.,* Gainesville, 23 IV 1939 (B. J. Kaston), 1 female (AMNH); *Union Co.,* Vogel St. Pk., 27 I 1972 (J. O. Howell), 1 male, (JOH), 23 III 1972 (J. O. Howell), 1 female (JOH), 15 XI 1972 (J. O. Howell), 1 male (MCZ); *White Co.,* near Ana Ruby Falls, Unicoi St. Pk. (1800′), 12 I 1984 (R. G. Bennett), 1 female (RGB). NORTH CAROLINA: *Graham Co.,* JKMF, Poplar Cove, 30 X 1971 (F. A. Coyle), 1 female (FAC).

Wadotes tennesseensis Gertsch
Figs. 8, 45-47, 60-65, 116, 117

Wadotes tennesseensis Gertsch 1936:14, fig. 27; Muma 1947:4, figs. 1, 2, 14, 15, 31, 32.

Diagnosis.—*Wadotes tennesseensis* can be distinguished from all other *Wadotes* by its lack of well developed proximal lateral cymbial processes in males (Fig. 46); and in females, by a combination of EL ca three times as long as LAE (EL/LAE=2.70-3.61, *N*=19) and normally a complete lack of sclerotization anterior to the atrial slit (Fig. 60).

Description.—*Male:* Figs. 8, 45-47. 16 specimens measured including holotype. CL 3.4-4.6(4.0±0.35), CW 2.3-3.0(2.6±0.20), SL 1.68-2.20(1.93±0.13), SW 1.43-1.78(1.58±0.10). Holotype CL 4.0, CW 2.6, SL 1.93, SW 1.58.
Female: Figs. 60-65. 20 specimens measured. CL 3.3-4.8(3.9±0.36), CW 2.1-3.1(2.6±0.25), SL 1.58-2.25(1.89±0.16), SW 1.35-1.83(1.55±0.12).
Variation: The scape varies dramatically even among specimens from a single locale (Figs. 60, 65). The superficial epigynal sclerotization is normally restricted to the area posterior to the atrial slit, however, one specimen from Mount Pisgah,

Fig. 114.—Distributions of *Wadotes deceptis*, encircled triangles; *W. hybridus*, dark circles; and *W. saturnus*, triangles with extended apices; in southeastern Canada and eastern United States. Fig. 115. Distributions of *W. bimucronatus*, dark circles; and *W. georgiensis*, triangle; in eastern United States. Fig. 116. Distributions of *W. dixiensis*, triangles; and *W. tennesseensis*, circles; in southeastern United States.
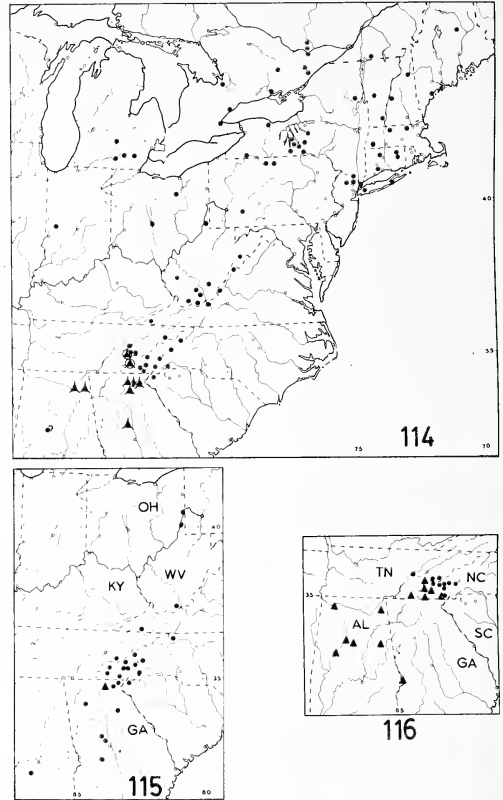
North Carolina has a narrow encircling band of sclerotization passing around the anterior end of the scape and a few other specimens exhibit a very faint band. Males do not exhibit significant variation.

Distribution.—Figs. 116, 117. One specimen of *W. tennesseensis* has been collected at Kingston, Roane County, Tennessee near the confluence of the Clinch and Tennessee Rivers in the lowlands east of the Cumberland Plateau. With this exception, this species appears to be restricted to higher elevations (probably over 900 m) in the Great Smoky Mountains of Tennessee (Sevier and Blount Counties) and North Carolina (Haywood and Swain Counties) and in adjacent areas in the Plott Balsams, Pisgah Range, and the Blue Ridge Mountains of North Carolina from Mount Pisgah (Buncombe County) to Highlands (Macon County).

Natural History Notes.—*Wadotes tennesseensis* is most common in the high elevation oak and spruce/fir forests within its range but is also present in the lower elevation mixed hardwood forests down to about 900 m above sea level.

Overwintering females have been collected from small diapause chambers, not much larger than themselves, which they have constructed in rotting wood under the bark of fir logs. In the spring females construct single egg cases in these cavities and remain with them at least until the young emerge. Two egg cases collected in June contained 19 and 65 eggs.

Adult males appear considerably earlier than do those of other *Wadotes* occurring in the same vicinity and do not appear to overwinter. They have been collected from early July to early September.

Wadotes calcaratus, *W. hybridus*, *W. dixiensis*, and *W. bimucronatus* are all possibly sympatric with *W. tennesseensis*, but *W. dixiensis* and *W. bimucronatus* have been collected only from lower elevations than has *W. tennesseensis*. Specimens of *W. calcaratus* and *W. tennesseensis* were found in the same sample of hardwood leaf litter.

Wadotes tennesseensis may be the sole *Wadotes* found in the southern spruce/fir forest stands within its range. Although both *W. calcaratus* and *W. hybridus* are characteristically northern species, the latter has not been found at the higher elevations of the southern Appalachians and the former, although collected from nearby spruce/fir forests, such as at Mount Mitchell, North Carolina, has not been discovered in this habitat within the range of *W. tennesseensis*.

Populations in the vicinity of Kingston, Tennessee and Highlands, North Carolina (only one specimen is known from each locale) are possibly disjunct from the apparently contiguous populations in the Great Smoky, Plott Balsam and Pisgah Mountains. If the former populations are peripheral isolates, this could indicate that this species has had a larger range in the past. Its range may have been shrinking since the last glacial maximum. The present rapid destruction of spruce/fir habitat throughout the Southern Appalachians may hasten this process and significantly reduce the already restricted range of this species.

Type Series.—Male holotype, female allotype, 6 male and 2 female paratypes, Tennessee, Sevier Co., Mt. Le Conte, GSMNP, 8-9 VII 1933 (W. J. Gertsch), in AMNH, examined.

Collection Data.—U.S.A.: NORTH CAROLINA; *Buncombe Co.*, Mt. Pisgah, 14 X 1926, 1 female (AMNH), no date, 2 females (AMNH); *Haywood Co.*, Waterrock Knob, 30 X 1969 (W. A. Shear), 1 female (MCZ), no locale, 28 V 1934 (A. F. Carr), 1 female, 1 imm (FSCA); *Jackson Co.*, BRPWY, Cherokee Indian Reserve, 3 X 1960 (W. Gertsch, W. Ivie), 1 male (AMNH), BRPWY, Richland Balsam (6000′), 7-20 VIII 1965 (S. Peck), 1 male (AMNH), 25 IX 1982 (R. G. Bennett), 1 female (RGB), BRPWY, Bearpen Gap (5400′), 23 VII 1975 (F. A. Coyle), 2 females (FAC), BRPWY, W slope of Campbell Lick (4700′), 9 VI 1983 (R. G. Bennett), 1 female (RGB), BRPWY, NE slope of Yellow Face (5800′), 9 VI 1983 (R. G. Bennett), 1 female, 19 eggs (RGB), BRPWY, above Grassy Ridge Mine (5200′), 11 IX 1983 (R. G. Bennett), 1 female (RGB), BRPWY, along trail from Haywood Gap to Rough Butt Bald, 27 VI 1984 (R. G. Bennett), 1 female, 65 eggs (RGB); *Macon Co.*, Highlands, 6 IV 1929 (Bishop), 1 female (AMNH); *Swain Co.*, GSMNP, Deep Creek nr. Bryson City, 26 VII 1930 (P. L. Darlington), 1 male (MCZ), GSMNP, Newfound Gap (5200′), 31 VIII 1930 (P. L. Darlington), 4 males, 1 imm (MCZ), GSMNP, Mt. Kephart (6000′), 23 IV 1952, 1 female (MCZ). TENNESSEE: *Blount Co.*, no locale, IX 1931 (W. M. Barrows), 3 females (AMNH); *Roane Co.*, Kingston, 12 VII 1933, 1 female (AMNH); *Sevier Co.*, GSMNP, Mt. Le Conte, 9 IX 1928 (W. M. Barrows), 1 male, 3 females (AMNH), no dates, 11 females, 35 imms (AMNH), GSMNP, Little Pigeon Ck., 9 VII 1933 (W. Ivie), 1 male, 2 females (AMNH), GSMNP, Clingman's Dome, 22 VI 1941 (C. and M. Goodnight), 1 female, 1 imm (AMNH), GSMNP, Elkmont, 8 VIII 1960 (T. C. Barr), 1 female (AMNH), GSMNP, Rt. 441, Buckeye Nature Trl., 8 VIII 1981, (L. N. Sorkin and A.A.S.), 2 males, 3 imms (AMNH), no locale, no date, 1 female (AMNH).

Wadotes willsi, new species
Figs. 40-44, 58, 59, 112, 118

Etymology.—The specific name is a patronym honoring the late band leader Bob Wills.

Diagnosis.—*Wadotes willsi* is only likely to be confused with *W. calcaratus* with which it is closely related. It can be distinguished from all *Wadotes* including *W. calcaratus* by the combination of a dorsodistal prolateral tibial apophysis and

Fig. 117.—Ranges of *Wadotes bimucronatus*, horizontal bars; *W. carinidactylus*, dots; *W. dixiensis*, vertical bars; *W. georgiensis*, encircled 1; and *W. tennesseensis*, flecks; in eastern United States.
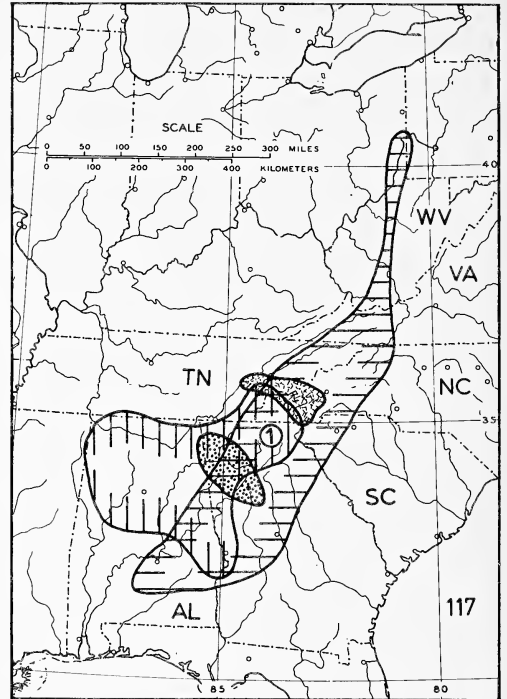
a well-developed but unbisected prolateral cymbial process in the male (Figs. 40-42. Females (Figs. 58, 59) are apparently indistinguishable from female *W. calcaratus* but can be separated from all other *Wadotes* by the diagnostic characters of *W. calcaratus*.

Description.—*Male:* Figs. 40-44. Four specimens known. CL 3.8-4.3(4.0±0.22), CW 2.4-2.8(2.6±0.17), SL 1.85-2.13(1.98±0.12), SW 1.45-1.65(1.58±0.09). Holotype CL 4.0, CW 2.5, SL 1.95, SW 1.6.

Retrolateral patellar apophysis long, about one-third of total patella length. Pronounced dorsodistal prolateral tibial apophysis (Figs. 40, 41) extending from dorsal surface of prolateral tibial extension. Retrolateral cymbial process (Fig. 41) long, arched prolaterally, but shorter and less robust than in *W. calcaratus*. Proximal loop of embolus closely associated with ventral surface of prolateral process (Fig. 42). Terminal apophysis (Figs. 43, 44) laterally flattened (Fig. 43) with surface roughened distally.

Female: Figs. 58, 59. Two specimens known. CL 3.8, 4.7; CW 2.3, 2.8; SL 1.85, 2.25; SW 1.48, 1.70. LAE about one-quarter of EL (EL/LAE=4.44). Median unsclerotized area very wide, occupying most of region posterior to atrial slit. Narrow band of superficial epigynal sclerotization extends around anterior end of scape from region posterolateral to atrial slit. Spermathecal support sclerotization (Fig. 58) conspicuous only when specimen is cleared.

These female specimens have been paired with the males of *W. willsi* on the assumption that the population located on and around Mount Rogers is allopatric with and distinct from surrounding *W. calcaratus* populations. This area has been poorly collected. Both species may exist sympatrically on Mount Rogers.
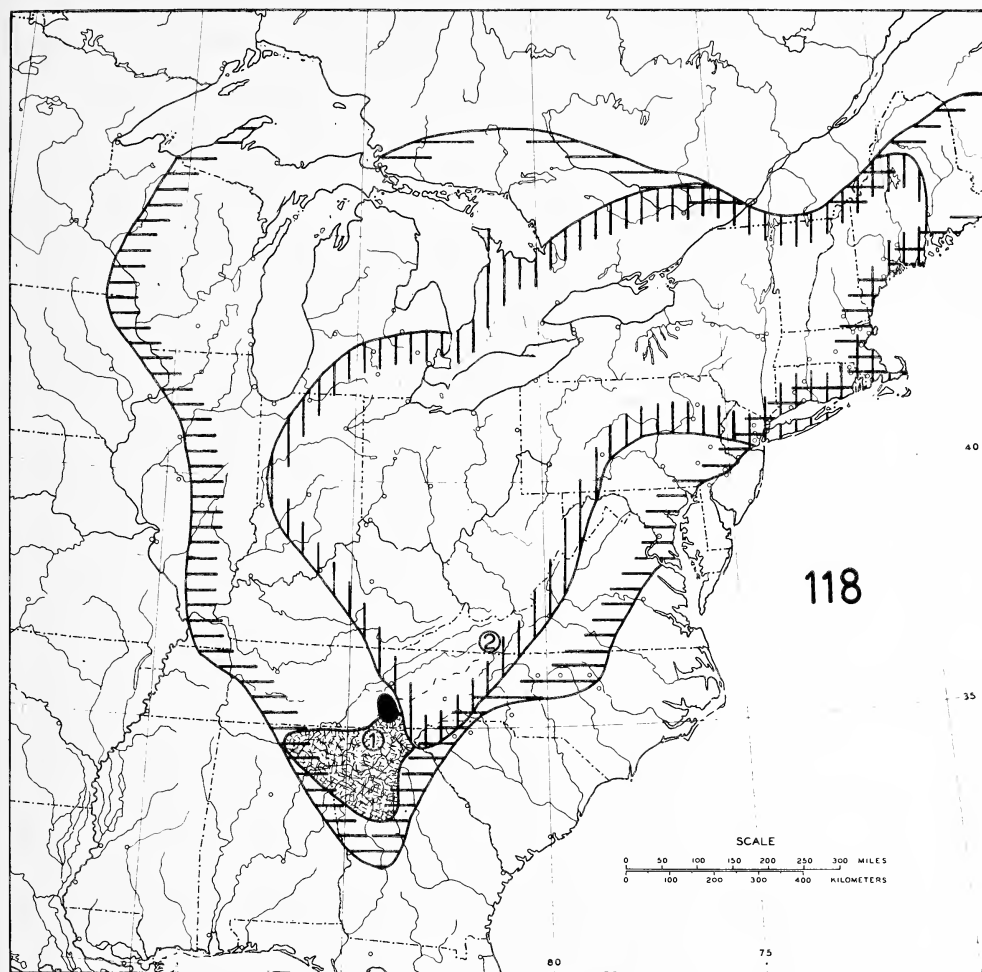
Fig. 118.—Ranges of *Wadotes calcaratus*, horizontal bars; *W. deceptis*, darkened area; *W. hybridus*, vertical bars; *W. mumai*, encircled 1; *W. saturnus*, flecks; and *W. willsi*, encircled 2; in southeastern Canada and eastern United States.

Variation: One female has the primary loops of the connecting ducts oriented nearly at right angles to the main axis of the body such that the anterior terminus of each duct points cephalad (Fig. 58). The ducts of the other specimen exhibit a more *W. calcaratus*-like pattern of looping.

Distribution.—Figs. 112, 118. *Wadotes willsi* is presently known only from the slopes of Mount Rogers in Smyth and Grayson Counties, southwestern Virginia, and from adjacent Ashe County, North Carolina.

Natural History Notes.—Mount Rogers is characterized by a Fraser fir forest and grass and blackberry/hawthorn balds at the higher elevations with northern hardwoods (especially sugar maple, beech, and yellow birch) predominant below (Pittillo 1976). One male was collected from a beech/maple forest near Deep Gap on the west slope of the mountain.

Holotype.—Male, Virginia, Grayson Co., S side Mt. Rogers, 4500′, 27 IX 1969, in AMNH.

Collection Data.—U.S.A.: NORTH CAROLINA; *Ashe Co.*, 3 mi NW of Lansing, 13 X 1963 (R. L. Hoffman), 1 male (NMNH). VIRGINIA; *Grayson Co.*, Mt. Rogers (5000′-6000′), 20 VIII 1955
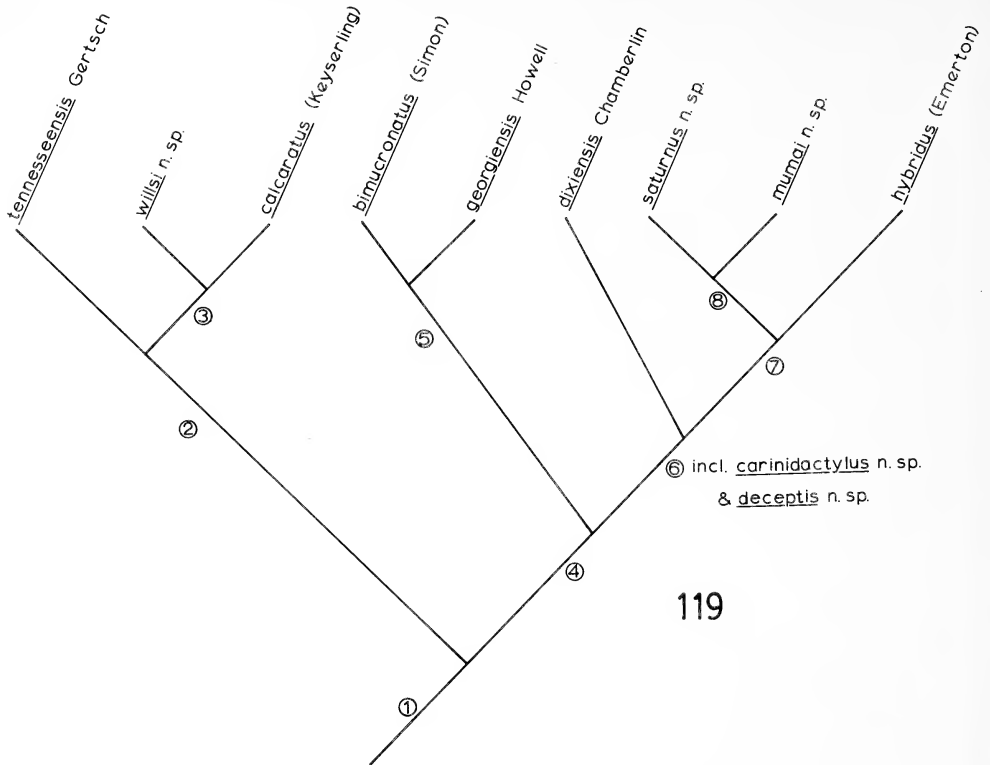
Fig. 119.—Cladogram of hypothesized *Wadotes* species relationships.

(Hanson, Muka, Turner, Hoffman), 1 female (AMNH), Mt. Rogers, 11 XI 1957 (VPI expedition), 1 female (NMNH), Mt. Rogers (4500′), 12 IX 1962 (R. L. Hoffman), 1 male (NMNH); *Smyth Co.*, nr. Deep Gap Shelter on Appalachian Trail (4920′), 2 IX 1975 (F. A. Coyle), 1 male (FAC).

Status of *Wadotes primus* Fox

Wadotes primus Fox 1937 from Hong Kong exhibits several characteristics in common with North American *Wadotes*: two retromarginal cheliceral fang furrow teeth, small anterior median eyes, and an anteriorly attached epignal scape. The male is unknown. Lehtinen (1967) stated, without discussion, that this species "belongs to an undescribed genus." The female holotype of this species and a female of another species from China (both in AMNH) identified by V. Roth as "*Wadotes* n. sp. near *primus*" have been examined and neither possess any of the putative synapomorphies of the North American species of *Wadotes*.

The following characters of *W. primus* are distinct from those of the North American species of *Wadotes*: epigynum (Fig. 109) with a deeply forked, slender scape; transverse atrial slit near anterior edge of epigynum in region of base of scape, divided such that each half extends from lateral margin of epigynum to edge of scape base; connecting ducts in posteriorly contiguous, heavily sclerotized matrices (Fig. 110), ducts very convoluted, loops traversing entire width of each matrix; anterior terminals of ducts facing each other; spermathecae oval, support sclerotization not apparent on caudal boundary of epigynum.

The female specimen of "*Wadotes* n. sp. near *primus*" (Fig. 111) is superficially similar to *W. primus* (and North American *Wadotes*): scape long and slender, weakly forked posteriorly; atrial slit strongly developed and 'U'-shaped, extending from anterior lateral margins of epigynum to posterior boundary; uncoiled, strongly sclerotized, widely separated connecting ducts extend along dorsal margins of invaginated edge of atrial slit laterally; spermathecae contiguous, located medially at posterior margin of epigynum; (apparent) support sclerite extends from medial posterior lip of atrial slit around posterior boundary of epigynum. This latter species wil probably prove to be a member of *Paracoelotes* Brignoli, 1982.

No defensible synapomorphies are known which warrant the continued inclusion of *W. primus* in *Wadotes*, but unless *W. primus* can be shown to belong cladistically to another group, there is no good reason to remove it from that genus. Further decisions as to the generic status of this species must await new data on Palaearctic coelotines, in particular the discovery of Asian *Wadotes* males.

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RESEARCH NOTES

AN INQUILINE RELATIONSHIP BETWEEN THE TAILLESS WHIP-SCORPION *PHRYNUS GERVAISII* AND THE GIANT TROPICAL ANT *PARAPONERA CLAVATA*

Tailless Whip-Scorpions (Amblypygi, Phrynidae) are widely distributed in the Neotropics, but their natural histories are poorly known (Quintero, D. 1981. J. Arachnol., 9:117-166). *Phrynus gervaisii* (Pocock) is common in moist lowland forests from Venezuela through Costa Rica, where it is often found in leaf litter, under bark and fallen trees, or between the fronds and trunk of the corozo palm, *Schellea zonensis* (Quintero, D. 1981. J. Arachnol., 9:117-166). In this paper we report possible commensalism of *P. gervaisii* with the giant tropical ant *Paraponera clavata* (F.).

In May, 1984, the western half of a 50 ha forest plot on Barro Colorado Island (Hubbell, S. and R. Foster. 1983. pp. 25-41 *In* Tropical Rain Forest: Ecology and Management; S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, eds. Spec. Publ. No. 2, British Ecol. Soc., Blackwell Scientific Publications, Oxford) was surveyed for the distribution of *P. clavata* colonies at the bases of trees. *Phrynus gervaisii* was detected in the entrances to some of the 96 ant nests observed. (Only two specimens of tailless whip-scorpions were collected for identification so there remains the possibility that *Paraphrynus laevifrons*, known to occur in habitats similar to *P. gervaisii* (Quintero, per. comm.), may have been identified as *P. gervaisii*.) Re-examination of these colonies and 120 more found on the eastern half of the plot in May 1985 included behavioral observations of *P. gervaisii*. The nest entrances were examined using a flashlight; if a tailless whip-scorpion was not observed within 5-10 sec, the colony was gently disturbed with a probe, often resulting in the emergence of a tailless whip-scorpion.

Of 178 active *Paraponera* colonies examined in 1985, *P. gervaisii* was observed in 76 (42.7%) of the nest entrances. Two each were observed in the entrances of 8 nests, and immatures were present in 6. When the *P. clavata* colonies located in 1984 were recensused, 46.2% (30) of those still active had *P. gervaisii* associated with them. Only one colony that had become inactive since 1984 harbored a tailless whip-scorpion ($p < 0.001$, Binomial Test). Since we made no effort to excavate the nests and seldom remained more than 60 sec at each, our observations were probably rather conservative regarding the frequency of association between these two species.

P. gervaisii usually clung motionlessly to the sides of the entrances, out of the path of the rather large worker ants, when observed in undisturbed entrances. When disturbed ants erupted from the nest in defense, *P. gervaisii* usually remained in the sides of the entrance unless ant activity became too intense, in which case they moved to accommodate the ants. Accommodation included

lifting their long legs and body off the surface of the tunnel allowing ants to freely pass underneath. When *P. gervaisii* was gently touched they typically retreated deeper into the entrance. If ant activities blocked the nest entrance, *P. gervaisii* often moved a short distance (< 50.0 cm) up or around the trunk of the tree, where it remained motionless until the ant activity subsided. It then returned to the nest entrance and soon disappeared into the nest interior. We never saw the ants attempting to sting or bite a *P. gervaisii*, even when the ants had been disturbed into a frenzy of colony defense.

We suggest that *P. gervaisii* may opportunistically select *P. clavata* nests for diurnal refuge. These arachnids may derive protection from the well defended ant colonies. Their presence in *P. clavata* nests occurred too frequently to be accidental, particularly when they were found so rarely in inactive ant nests or other cavaties around the base of tree trunks. The close association between *P. gervaisii* and *P. clavata* may have gone largely unnoticed due to human avoidance of these large ants, whose sting is extremely painful (Hermann, H. and M. Blum. 1966. Ann. Entomol. Soc. Amer., 59:397-407; Hermann, H. and M. Douglas 1976. Ann. Entomol. Soc. Amer., 69:681-86).

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EGG PRODUCTION OF *ACHAEARANEA TEPIDARIORUM* (C.L. KOCH) (ARANEAE, THERIDIIDAE) IN THE FIELD IN JAPAN

This field survey on the egg production of *Achaearanea tepidariorum* (C. L. Koch) in Japan was made in 1984 to compare with the results of a laboratory investigation which was reported separately (Miyashita, K. 1987. J. Arachnol. 15:51-58.

The survey was conducted in a vacant house in Abiko City (140°02′E, 35°52′N), Chiba Prefecture. Adult females, which spun webs on the wall, at the edges of the verandah, and under the floor, were carefully observed and censused daily from May to September. When new females were found, they were recorded and marked with colored paint, and the dates of egg sac productions and disappearances of females themselves were recorded. Egg sacs were removed from webs on the 7th or 8th day after oviposition and kept separately in glass vials. The number of spiderlings that emerged was considered as an indicator of the number of eggs in the sac, since healthy egg sacs rarely contained non-viable eggs.
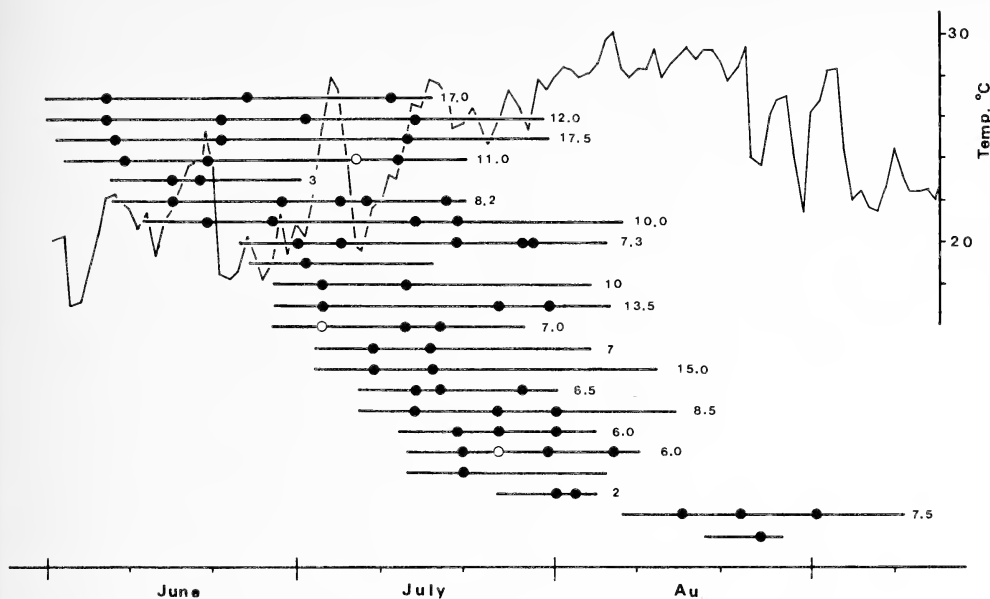
Fig. 1.—Seasonal changes in the resident periods and egg sac production of 22 females *Achearanea lepidariorum* in the field. Horizontal lines indicate length of resident periods in days. Solid or hollow circles show healthy or sterile egg sacs, respectively. The figures following each line are the mean interval(days) between egg sacs. The fine line shows the change of daily mean temperatures.

Figure 1 shows the seasonal changes in length of the resident periods of females and the intervals between egg sacs. "Resident period" means the period from the date of first appearance to that of disappearance of each female. The cause(s) of disappearances were not ascertained. The rate of appearance of adult females increased gradually from early June to late July, and decreased sharply thereafter. The total number of adult female residents was 22, some were residents as juveniles and others were invaders from outside. The resident period became shorter for individuals that appeared late in the season (mean = 35.1 ± 14.0 days).

Egg sac production began in early June, reached a peak in the middle of July, and ceased by early September. Observations outside the survey site, however, showed sporadic egg sac production from the middle of May to late October, although that production was rare. It appears that temperature changes had no apparent effect upon the egg sac production (Fig. 1).

The number of egg sacs per female varied from 1 to 5, (mean = 2.9) including sterile egg sacs produced by three females. The mean interval between egg sacs was 9.4 ± 5.6 days. The number of eggs per sac varied from 150 to 650, (mean = 310.8) excluding sterile egg sacs. In 14 among the 64 egg sacs examined in total,

Table 1.—"Egg periods" in days examined in June, July and August.

Season	No. of egg sacs	Mean	Range
Early June	4	15.4	14-18
Early July	7	11.3	8-15
Early Aug.	6	10.4	8-13

females produced egg sacs a few days after they had captured a large prey. The interval between egg sacs and the number of eggs per sac seemed to be influenced by the nutritional condition of the female. The number of total eggs produced per female varied from 242 to 1866 (mean = 881.7).

In the laboratory, each of 15 females produced 9.7 egg sacs containing a total of 1812.7 eggs at intervals of 8.1 days in average (Miyashita, K. 1987. J. Arachnol. 15:51-58).

Valerio (1976. Bull. British Arachnol. Soc., 3:194-198) examined egg sac production in tropical Costa Rica and reported that, although one female produced 20 sacs, the mean number of sacs per female was 14.1, and that the mean number of eggs per female was 3211.9. Valerio's search of the literature showed that the number of egg sacs produced per female in the temperate regions ranged from 4 to 7 except for one record of 17 reported by Bonnet (1935. Bull. Soc. Hist. Nat. Toulouse, 68:335-386).

As shown in Table 1, the "egg period", which means the number of days from egg sac production to the spiderlings' emergence, became shorter later in the season. This may be influenced by rising temperatures at that time. In the laboratory at 25°C, the mean egg period was 11.0 days.

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PREDATION BY *CHEIRACANTHIUM MILDEI* (ARANEAE, CLUBIONIDAE) ON LARVAL *PHYLLONORYCTER BLANCARDELLA* (LEPIDOPTERA, GRACILLARIIDAE) IN A GREENHOUSE

The spotted tentiform leafminer, *Phyllonorycter blancardella* (F.) (Lepidoptera, Gracillariidae), has become an important pest in commercial apple orchards in eastern North America since its introduction from Europe (Pottinger and LeRoux 1971). The larvae form tentiform mines in leaf tissues of apple (*Malus pumila* Mill.) and other closely related plants (Pottinger and LeRoux 1971). Although many insect parasitoids of this insect have been recorded (Laing 1984, Ridgeway and Mahr 1985), little attention has been directed towards predators of larval *P. blancardella*.

Cheiracanthium mildei L. Koch, a native of Europe, is a clubionid spider commonly found in synanthropic habitats in eastern North America (Dondale and Redner 1982). In Israel, this species was found to be very common in unsprayed apple orchards where it is important for control of various insect pests, especially the larvae of *Spodoptera littoralis* (Boisd.) (Lepidoptera, Noctuidae) (Mansour et al. 1980a,b). Mansour et al. (1980a) indicated that *C. mildei* preys on larvae and adults of *P. blancardella* under laboratory conditions.

This note reports our observations of specialized predation by *C. mildei* on the larvae of *P. blancardella* in a greenhouse.

In the winter of 1985, as part of an ongoing parasitization study, larval *P. blancardella* were reared on young apple trees in the greenhouse of the Biological Control Laboratory, University of Guelph, Ontario. The trees were put in sleeve cages and adult *P. blancardella* were released into the cages for oviposition on apple leaves. A high level of predation on the larval leafminers was found in some cages, although the rate was not quantified. Predation was indicated by single triangular rents (1-2 X 2-3 mm) in the undersurfaces of mines and the absence of larvae. Larval losses in the greenhouse sleeve cages were severe and hampered the rearing program for the spotted tentiform leafminer.

Various unidentified species of Salticidae, Araneidae, Linyphiidae, Philodromidae, and Theridiidae were also present in the greenhouse, but only *C. mildei* was found regularly on leaves in the vicinity of attacked mines. Individuals of these clubionid spiders spun (and were found within) silken retreats on the lower surface of mined apple leaves. Many clubionids construct and inhabit similar retreats (Dondale and Redner 1982).

We suspected that *C. mildei* actively sought out trees infested with leafminers. *C. mildei* was rarely found on uninfested trees in the greenhouse. Although other species of spiders (unidentified salticids especially) were found in some sleeve cages, predation on larval leafminers was observed only in cages containing *C. mildei*.

Two or three individuals of each of the various hunting spiders found in the greenhouse were isolated in covered plastic petri plates with freshly picked apple leaves that contained mines formed by the tissue-feeding instars. Because of the relatively sedentary habits and the nature of prey capture behavior generally observed in web-building spiders, predation on leafminers by web-building species present in the greenhouse (such as araneids and linyphiids) was considered to be unlikely. Spider attacks on larvae were not observed directly, but only leaves isolated with *C. mildei* received characteristic mine damage and predation on the leafminer larvae.

Predation is typically difficult to quantify because predators often do not leave evidence of their work (J. E. Laing pers. comm.). However, predation on leaf-mining larvae is detectable because the mines are damaged (Pottinger and LeRoux 1971) and the type of damage often is characteristic of the predator. For example, the larvae of chrysopids feed on *P. blancardella* through the top surface of the mine and do not remove their prey (J. M. Heraty pers. comm.). Birds also attack the larvae through the top of the leaf leaving a large entrance hole (Pottinger and LeRoux 1971). On the other hand, *C. mildei* attacks through the bottom surface of the mine. Thus, it is possible to identify the predator *in absentia* by its mode of entry into the mine. Presently, predation by spiders may be incorrectly attributed to more obvious predators such as entomophagous birds.

Although larval *P. blancardella* are infrequently attacked by invertebrate predators because of the concealment afforded by their mines, *C. mildei* apparently is able to detect and attack the larvae through the leaf epidermis. This phenomenon of search and extraction of a cryptic food source has not been previously reported for *C. mildei*. Because of this specialized feeding behavior, we suspect that *C. mildei* may prove to be an important predator of *P. blancardella* and worth considering in integrated control programs for this insect.

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ORTHOLASMA SETULIPES SHEAR AND GRUBER IS A SYNONYM OF *ORTHOLASMA CORONADENSE* COCKERELL

In our recent revision of the opilionid subfamily Ortholasmatinae (1983. Amer. Mus. Novitates no. 2757:1-65), we described *Ortholasma setulipes* as a new species from southern California (type specimens from Borrego Palm Canyon, San Diego County, deposited in AMNH). We thought at that time that the name might fall as a synonym of *O. coronadense* Cockerell (Cockerell, T. 1916. Ent. News 27:158), if the types of that species (from South Island, Coronados Group, Baja California, Mexico) ever were to turn up. Our requests to all major American museums failed to locate the specimens, and so, since Cockerell's original description lacked the information needed to place the species, we listed *O. coronadense* with a few comments and described our southern California material as new. We might have recognized the synonymy given here at that time but for the occurance in southern California (syntopically in two instances) of two species (the other is *O. levipes* Shear and Gruber).

Some time after our paper had appeared, our colleague James Cokendolpher made us aware that Ralph Crabill, curator of arachnids (since retired) at the National Museum of Natural History, Smithsonian Institution, had written him that the holotype specimen was in the collection there, even providing a catalog number. We borrowed the specimen courtesy of the present curator, Jonathan

Coddington. It proved to be a typical female of what we had described as *O. setulipes*. Cockerell's statement that the animal had a rounded hood, like that found in *O. pictipes*, was mistaken.

Therefore the name *Ortholasma setulipes* Shear and Gruber 1983 is placed as a junior subjective synonym of *Ortholasma coronadense* Cockerell 1916.

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A PROPOS DU MALE D'*ANANTERIS LUCIAE* (SCORPIONES, BUTHIDAE)

Dans un article récent (Lourenço, W. R., 1984, J. Arachnol., 12:279-282), *Ananteris luciae* a été décrite comme espèce nouvelle, fondée sur deux femelles adultes et huit immatures, provenant de Santarém dans l'Etat de Pará au Brésil.

L'étude d'un matériel de Scorpions de Tucurui, également dans l'Etat de Pará, de la collection de l'Institut Butantan(IB), a permis l'identification d'un mâle adulte, appartenant à l'espèce *A. luciae*; ainsi, il nous a paru utile de compléter à présent la diagnose de l'espèce.

Dans la diagnose proposée pour le mâle, seuls les caractères qui le différencient des femelles sont donnés; la pigmentation des chélicères, caractère important dans la diagnose des espèces (Lourenço, W. R., 1982, Bull. Mus. natn. Hist. nat., Paris, 4è sér., 4:119-151.), est illustrée pour la première fois (Fig. 1). Les illustrations sont de M. Gaillard.

1   **2**
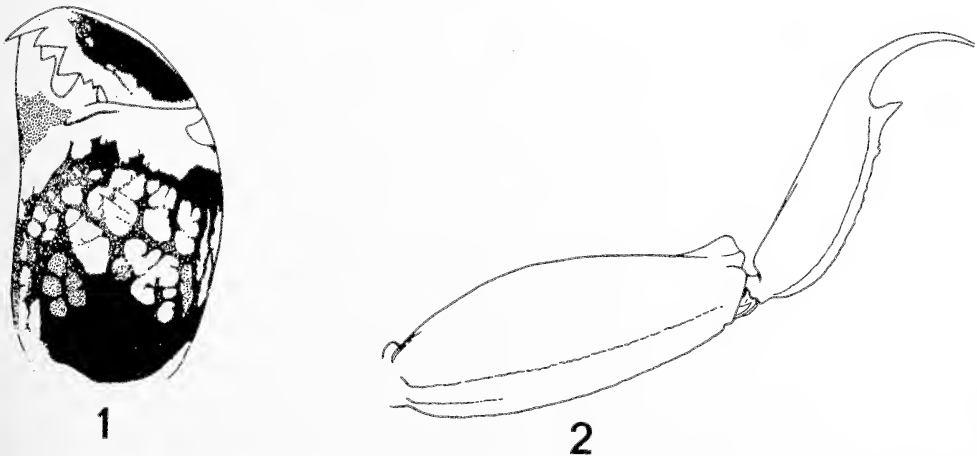
Figs. 1 et 2.—*Ananteris luciae*, mâle de Tucurui: 1, chélicère droite. 2, cinquième anneau du metasoma et telson, vue latérale.

Tableau 1.—Mensurations (en mm) du mâle d'*Ananteris luciae*.

Longueur totale	18,0
Prosoma	
longueur	2,3
largeur antérieure	1,5
largeur postérieure	2,2
Mesosoma	
longueur	4,0
Metasoma	
longueur	11,7
anneau caudal I, longueur/largeur	1,3/1,3
anneau caudal II, longueur/largeur	1,3/1,2
anneau caudal III, longueur/largeur	1,5/1,2
anneau caudal IV, longueur/largeur	1,8/1,2
anneau caudal V, longueur/largeur/hauteur	3,0/1,2/1,2
Telson	
longueur	2,8
vésicule, longueur/largeur/hauteur	1,8/0,7/0,7
aiguillon, longueur	1,0
Pédipalpe	
longueur	7,3
fémur, longueur/largeur	2,0/0,5
tibia, longueur/largeur	2,7/0,7
pince, longueur/largeur/hauteur	3,2/0,5/0,5
doigt mobile, longueur	2,3

Ananteris luciae Lourenço
Figs. 1,2

Ananteris luciae Lourenço, 1984:279.

Coloration.—La distribution de la pigmentation est identique à celle de la femelle.

Morphologie.—Le corps du mâle est plus fin, et les appendices ainsi que le metasoma sont plus allongés que ceux de la femelle; les granulations et les carènes du corps et des appendices sont moins accentuées que celles de la femelle; le tégument est plus lisse. Peignes plus grands chez le mâle avec 16-15 dents. Tranchant des doigts mobiles avec 7-7 séries longitudinales de granules, légèrement obliques. Les valeurs morphométriques du mâle sont données dans le tableau I.

La répartition connue d'*A. luciae* se limite à Santarém et Tucurui dans l'Etat de Pará, Brésil.

Matériel examiné.—BRESIL: PARÁ; Tucurui, 5 août 1984, (J. Knysak et M. Costa), 1 mâle (IB-SC-1496).

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AQUATIC SUBMERGENCE OF *ACANTHEPEIRA VENUSTA* (BANKS) (ARANEAE, ARANEIDAE)

Few spiders are known to move about effectively on or under water. The European water spider, *Argyroneta aquatica* (Clerck), which lives entirely in water and maintains an underwater air supply in a silken sac, is the only known spider capable of swimming under water. However, many pisurids and lycosids that live near water (e.g. *Dolomedes, Pardosa, Pirata*) are quite adept at moving about on the water surface. The common fishing spiders, *Dolomedes* spp., also are capable of submerging by clinging to underwater vegetation. Adaptations to an aquatic mode of life are virtually unknown in other spiders.

Our recent observations of the araneid spider, *Acanthepeira venusta* (Banks), however, indicate that this species is capable of aquatic submergence. On November 1, 1985, behavioral observations of *A. venusta* were made where it occurred abundantly in the sawgrass (*Cladium jamaicense* Crantz) marshes of Everglades National Park and two other similar sites in Dade County, Florida. The water depth at each location was approximately 15 cm. All observations were made between 1300 and 1500 h.

Female spiders were found clinging to flowering stalks of sawgrass and other plants, just beneath one or a series of egg sacs. None were found on the more flexible leaf blades. The globular egg sacs were 5.5 to 6.0 mm in diameter with a smooth, papery outer covering and were tightly appressed to the plant stalks. They occurred most commonly in groups of 3 but up to as many as 7. A few stray lines of silk were usually evident but none of the spiders possesed complete orbs. The spiders clung tenaciously to the plants when attempts were made to remove them. No males were observed.

When disturbed, several individuals dropped into the water. Others crawled down the plant and entered the water with no apparent difficulty. Once beneath the surface, they clung motionlessly to underwater stems or other submerged objects. The periods spent under water by three spiders timed were 38 seconds, 2 minutes 20 seconds, and 2 minutes 58 seconds. After this period of submergence, the spiders quickly reemerged by crawling out of the water on adjacent emergent vegetation.

Acanthepeira venusta, the smallest member of this American genus, is found from Virginia to Florida and Cuba where it inhabits tall grassy areas of fields, roadsides and swamps. It has been frequently collected in sawgrass of the Florida Everglades and in floating-island vegetation of wet areas in southern Georgia (Levi, H. W. 1976. Bull. Mus. Comp. Zool., 147:351-391). Although it is not restricted to wet areas, vegetation emerging from standing water appears to be a common habitat for this species.

Although the ability to submerge may be important in predator evasion, it might also represent an adaptation to wind. In open grassy areas over water the spiders are subject to frequent strong winds as evidenced by their severely damaged orb webs. Submergence behavior would allow a dislodged spider to gain access to the substrate without being blown across the water surface. Additional characteristics which may be adaptations to frequent winds include the egg sacs tightly appressed to the plants, the spiders clinging tenaciously to the plant stems, and their location only on the more rigid plant parts.

Although submergence behavior is unusual among araneids, certain other orb-weaving species frequently build their webs over water. These include *Argiope argentata* (Fabricius), *Gasteracantha cancriformis* (L.), *Leucauge venusta* (Walckenaer), *Nephila clavipes* (L.), and most *Tetragnatha* spp. With the possible exception of some *tetragnatha* spp. (Foelix, R. F. 1982. Biology of Spiders. Harvard University Press), these spiders move clumsily about when forced onto or into the water. They typically inhabit wooded areas where they are shielded from winds and therefore are not subjected to the same selective pressures as *A. venusta*.

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SUPPLEMENTARY DESCRIPTIVE NOTES ON
SCHIZOMUS LIBERIENSIS (COOK)
(SCHIZOMIDA, SCHIZOMIDAE)

The name *Artacarus liberiensis* Cook was used [*nomen nudum*] by Kraepelin (1897). Abh. Naturw. Ver. Hamburg, 15:1-60), but the new genus and new species remained undescribed for two years. Cook (1899. Proc. Entomol. Soc. Washington, 4:249-261) briefly diagnosed the species, but it remained a *nomen dubium* until Kraus (1960. Senck. biol., 41:103-107) designated a lectotype and published a redescription based on specimens in the National Museum of Natural History, Washington, DC. At that time he also transferred the species to the genus *Schizomus* Cook.

In the present note we provide a description and illustration of the female spermathecae and flagellum and add some additional descriptive data.

We wish to thank Dr. Jonathan Coddington, National Museum of Natural History (USNM), Washington, DC, for permitting us to examine the type-series of the species.

Schizomus liberiensis (Cook)
Figs. 1, 2

Artacaris liberiensis Cook, 1899. Proc. Entomol. Soc. Washington, 4:254, 255.
Schizomus liberiensis: Kraus, 1960. Senck. biol., 41:103-107, figs. 1-5.

Material examined.—Male lectotype and three female paralectotypes from Mt. Coffee, by the St. Paul River, Montserrado County, Liberia (USNM No. T-1:1903).

Supplementary description.—The female paralectotypes are in poor condition, being shriveled and largely cleared. The male lectotype is broken at the base of the metapeltidium but is in somewhat better condition than the females.
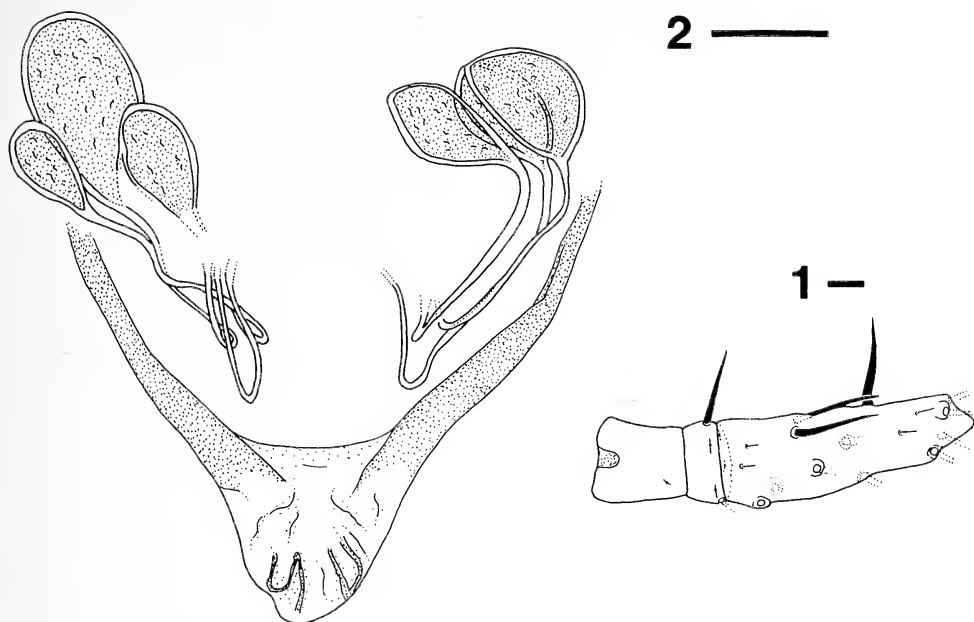
Figs. 1-2.—*Schizomus liberiensis*, female paralectotype: 1, flagellum, dorsolateral view; 2, spermathecae, ventral view. Scale lines =0.2 mm for Fig. 1, 0.05 mm for Fig. 2.

Prosoma: Anterior process ends in a down-turned point; one seta on and a pair of setae at base of process; three pair dorsal setae on prosoma.

Opisthosoma: Male with tergites I-VIII with one pair of dorsal setae on each; tergite IX with one pair dorsal and one pair lateral setae. The condition of the females did not allow an accurate count of the opisthosomal setae. Female flagellum (Fig. 1) of one female with two annulations, the posterior segment more than twice as long as two basal segments combined. The most basal annulation could not be seen in a second female but is probably present. No annulations could be seen in the flagellum of the third female due to extreme clearing.

Spermathecae (Fig. 2): The spermathecae consist of three pair of expanded ovate lobes with long, curved stalks.

Comments.—This is the first illustration of the spermathecae of an African species of *Schizomus* to be published. Reddell and Cokendolpher (1985, Oriental Ins., 18:43-52) illustrated the spermathecae of *Megaschizomus mossambicus* (Lawrence 1958). In that species the spermathecae consist of one pair of slightly rugose lobes. The relationships of *S. liberiensis* to other African species must await examination of the spermathecae of additional species.

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Research Notes

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MORPHOLOGY AND ALLOMETRY OF THE PURSE-WEB OF
SPHODROS ABBOTI (ARANEAE, ATYPIDAE):
RESPIRATORY AND ENERGETIC CONSIDERATIONS

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ABSTRACT

The influence of web morphology and allometry on respiration and energetics was investigated in the purse-web spider, *Sphodros abboti*. Carbon dioxide and oxygen concentrations in gas samples from underground portions of the nest where these spiders normally reside did not differ significantly from those in atmospheric air. Web dimensions such as length, diameter, and surface area scaled geometrically to body size. The scaling of these relationships differed from expected. Since the surface area of the web functions in prey detection, I anticipated it would scale in parallel with increases in energy demand that accompany size increases. Rates of oxygen consumption serve as an index of the latter and scale in direct proportion to body size whereas web surface area scales only to the two-thirds power. The weight of the web scaled to a power less than predicted by simple geometry, a result interpreted as an adaptation towards reducing costs of web construction. These results and comparisons suggest the web and its morphology do not restrict respiratory gas exchange nor limit energy acquisition in this species. Conversely, the standard rates of metabolism in this species were not higher than those of related species that also burrow but do not use a web for prey capture.

INTRODUCTION

The purse-webs of the atypid spiders found in temperate zones of North America are tubular structures attached vertically to the sides of hardwood trees (Gertsch and Platnick 1980). These webs extend above and below ground with the spiders normally residing in the subterranean portion. The aerial part of the web serves to alert the resident spider of potential prey walking or landing on its surface. The alerted spider proceeds upward within the web and attacks the prey through the web with long fangs. Once immobilized, the prey is pulled through a slit in the web and eaten.

This type of web can be considered as an extension of the silken lining of the spider's burrow into the aerial environment. Nentwig and Heimer (1983) suggested that evolution of webs extending above ground level allows for more effective prey detection and capture. Increased prey capture may permit increases in rates of energy expenditure thus increasing rates of growth and reproduction (Anderson 1970; Anderson and Prestwich 1982). If this interpretation is correct, one should be able to detect and correlate differences in standard rates of metabolism between atypid spiders and other tarantulas that do not use webs for prey capture. My aim was to make such a comparison. I selected *Sphodros abboti* Walckenaer for study as it is common in mesic hardwood habitats in north Florida.

The nature of the web in atypid spiders complicates interpretation of such comparisons. The gas composition within the underground portion of the web may differ significantly from atmospheric air and therefore rates of metabolism may be under selective pressures in addition to those assumed to be operating. These spiders spend virtually all of their lives within the web. Soil particles and other debris are incorporated into the wall of the tubular web (Gertsch 1979; Gertsch and Platnick 1980; Coyle and Shear 1981) during construction. Living material such as mosses are passively incorporated within the web, particularly those of older individuals. Underground, where the spider normally resides, the walls of the silken tube are thicker than in aerial portions (Coyle and Shear 1981). These spiders construct their nests in moist sandy soils with a high humus and loam content. The ground is usually covered by a continuous layer of leaf litter. Restricted gas exchange, decomposition of organic matter, high water content in these soils, and respiration of symbiotic organisms and spiders may promote hypercarbic and hypoxic conditions within the burrow (Levy and Toutain 1982) and thus affect their rates of metabolism (Withers 1978; Tanaka and Saito 1984). I believed it necessary to measure O_2 and CO_2 levels within the bottom of the purse web to provide a more valid interpretation of their rates of metabolism.

An additional aim was to determine the relationship between size of the web and size of the spider. Coyle and Shear (1981) reported that web size is a function of body size and conditions at the nest site. The web serves as a nest for the entire life of the individual spider and is enlarged to accommodate growth. Since energy demands increase with increases in size, one would expect web size to reflect these demands. A similar question has been evaluated in mammals (Harestad and Bunnell 1979; McNab 1983) and other vertebrates (Peters 1983; Calder 1984). Home range has been used as a measure of the minimum size necessary for obtaining the energy required to support the organism. Its relationship to body size has been determined for a large number of vertebrates (Peters 1983; Calder 1984) and compared to metabolism-body weight regressions to provide a more complete understanding of their ecological energetics.

Although the energetic constraints appear important in determining territory size and other relevant variables in some spiders (Kronk and Riechert 1979; Riechert 1974, 1978), no comparisons have been made of metabolism and web size regressions. My aim was to explore these relationships in *S. abboti*. Previous reports (Anderson and Prestwich 1980, 1982) indicate that morphological parameters of the book-lungs of spiders do not scale to maintain geometric similarity (isometric scaling) as spiders increase in size, but exhibit increases consistent with metabolism-body size regressions. As such, I anticipated that the surface area of atypid webs would scale in parallel with increases in rates of metabolism as these animals increase in size.

An alternative hypothesis involves consideration of the costs of web production. If larger web size does increase the efficacy of prey capture, spiders should produce very large webs. However, as many have suggested (Lubin 1973; Denny 1976; Nentwig 1983; Nentwig and Heimer 1983), selective pressures would operate towards reduction of these costs. Here I would expect web parameters to increase isometrically for a given web shape with all characteristic linear dimensions (L) of the web scaling to the one-third power of body mass, surface area (L^2) scaling to two-thirds power of body mass, and volume or weight of the

web (L^3) scaling in direct proportion to body mass. Since the major cost of web production is its mass (Prestwich 1977), I also planned to obtain the data necessary to determine its scaling relationship with body size.

METHODS AND MATERIALS

Animals.—Specimens of *S. abboti* were collected from Florida State Parks at Ichetucknee Springs, Suwannee County, and O'leno, Columbia County. Selection of specimens was made from the size of their webs taking care that a representative sample of body sizes was collected. The specimens were obtained by removal of the soil surrounding the underground portions of the tube webs and then cutting any of the latters' attachments to trees. The webs containing the resident spiders were transported to the lab.

Rates of metabolism.—Rates of oxygen consumption (μL O_2/hour, STPD, at 20ºC) for individuals over the size range found in this species were obtained from a previous study (Anderson and Prestwich 1982). I selected 20ºC as it represents, on an annual basis, an average thermal environment for this long-lived species in north Florida. These rates were determined using a Gilson Differential Respirometer following the procedures reported earlier (Anderson 1970).

Burrow gas composition.—The air within the below-ground portions of the purse-webs was analyzed for oxygen and carbon dioxide using a Scholander 0.5 cc Gas Analyzer (Scholander 1947). A 1.0 cc glass syringe with attached 3-way valve, syringe needle and length of catheter tubing (PE-90) was used to obtain gas samples. The catheter tubing was inserted through a small hole in the web at ground level and slowly pushed to the bottom of the burrow. A 1.0 cc sample was taken and partially ejected via the 3-way valve to clear the dead space of the sampler. The remainder was immediately analyzed for O_2 and CO_2 dry gas composition. These determinations were made in the field with only a short delay of a few minutes between collection and analysis of samples. Comparisons of analysis of atmospheric air ($N = 10$) with known values indicated average deviations of +0.03% (SE $\pm$ 0.004) and −0.17% (SE $\pm$ 0.15) for CO_2 and O_2, respectively.

Morphological measurements.—Webs were slit open to extract the spiders. Specimens were weighed to the nearest mg or, in the case of the smaller animals, to the nearest 0.1 mg. All were returned to where captured and released. Their webs were used either for measurements of their dimensions or cleaned and dried prior to determination of their weight. Webs were mounted flat on paper, taking care to avoid stretching, and traced. Measurements included length of web, diameter at ground level, and surface area. The latter was determined using a polar compensating planimeter. Webs were washed repeatedly with agitation to remove, as much as possible, humus soil particles, and other extraneous material. They were dried at 105ºC to a constant weight.

Data analysis.—Rates of oxygen consumption and web measurements were related to body size by regression analysis. I used live body mass (in milligrams) as an index of size. As Günther (1975) and Calder (1984) both emphasize, body mass is the most appropriate measure of size in most animals. Since most regression studies indicate physiological and morphological variables do not increase in direct proportion with increases in body size (Peters 1983; Calder

Table 1.—Composition of gas in the burrow of *Sphodros abboti*.

VARIABLE	N	$\bar{x}$	SE	RANGE
Depth of Sample	8	8.4 cm	1.3	3.9 - 14.0 cm
Percent CO_2	8	0.25	0.04	0.15 - 0.50
Percent O_2	8	20.62	0.03	20.50 - 20.73

1984; Schmidt-Nielsen 1984), I fitted my data to the power function $Y = aM^b$. Here Y is the parameter in question in relation to size, M; a is a proportionality constant characteristic of the particular group of organisms; and b is the exponent of the function that describes the effect of size on the variable. The parameters, a and b, were calculated by least squares analysis of the paired data after transformation to common logarithms. I followed the recommendations of Peters (1983) and Smith (1984) and calculated the standard error (Sb) and 95% confidence limits for b, r^2, and Sy·x as indices of fit for each regression.

RESULTS AND DISCUSSION

The concentrations of CO_2 and O_2 in burrows of *S. abboti* are reported in Table 1. Comparison with given values and measured values (in %) for CO_2 and O_2 in atmospheric air (0.03 and 20.95 and 0.06 and 20.78, respectively) indicates these animals experience only mild hypercarbia and hypoxia while in their nests. These burrow concentrations are not as different from atmospheric air as are those found in termite nests (Lee and Wood 1971) and the deeper burrows of tiger beetle larvae (unpublished data). Since CO_2 and O_2 levels in the burrows of *S. abboti* do not approach those reported to affect respiratory processes in spiders (Dresco-Derouet 1960; Tanaka and Saito 1984), I do not believe they are important in affecting their rates of metabolism and could be eliminated as a consideration in my analysis.

I compared rates of metabolism of *S. abboti* with those reported for theraphosids (tarantulas) to determine whether this parameter is correlated with use of webs in prey capture. Although tarantulas live in natural cavities or make burrows whose upper regions are lined with silk, most do not use this material to construct devices to capture prey. I calculated a regression using the available data (Anderson 1970; Dresco-Derouet 1971, 1972, 1973; Greenstone and Bennett 1980) for use in predicting rates of metabolism for *S. abboti* of adult size. The regression included data from 13 species ranging in size from 142 to 36,000 mg. It predicts a rate of metabolism of 28 μL O_2/h for an individual weighing 500 mg: this predicted value is equal to that observed for adults of this species. This similarity suggests rates of metabolism in *S. abboti* are not correlated with use of a web. This conclusion should be considered tentative until additional data from other related species becomes available for comparison. One problem of using theraphosids for comparison is that most species are much larger than *S. abboti*, thus complicating the analysis. Unfortunately rates of metabolism of other related spiders of similar size, e.g., trap-door spiders (Ctenizidae), are not available.

The parameters of the regressions describing relationships between rates of metabolism and web measurements to live body mass are reported in Table 2 and shown in Figs. 1-5. The metabolism and web weight regressions include outlying

Table 2.—Relationships of oxygen consumption and web morphology to body mass in *Sphodros abboti*.

| RELATIONSHIP | N | RANGE IN BODY MASS (mg) | $Y = aM^b$ | | | | | |
			a	b	Sb	95% CL for b	r^2	Sy·x
$\dot{V}O_2$ at 20°C (μL O_2/h)	18	22 - 625	0.082	0.94	0.039	0.86 - 1.02	0.97	0.053
Web Weight (mg)	20	0.7 - 715	8.8	0.74	0.040	0.66 - 0.82	0.95	0.118
Web Length (cm)	29	7.9 - 577	3.72	0.38	0.030	0.32 - 0.44	0.85	0.089
Web Diameter (cm)	29	7.9 - 577	0.18	0.31	0.021	0.27 - 0.35	0.89	0.061
Web Surface area (cm^2)	29	7.9 - 577	2.37	0.65	0.038	0.57 - 0.73	0.92	0.110

values at lower body size (Figs. 1 and 2, respectively) and I was concerned they might bias these relationships. Recalculation after exclusion of the outlying values resulted in insignificant changes in slope values; from 0.94 to 0.90 and from 0.74 and 0.71 for the metabolism and web weight regressions, respectively. Inclusion of extreme values decreases the standard errors of the slopes (Sb) from 0.063 to 0.039 and from 0.058 to 0.040, respectively, thus supporting the view that these equations, as given in Table 2, are valid estimates of these relationships.
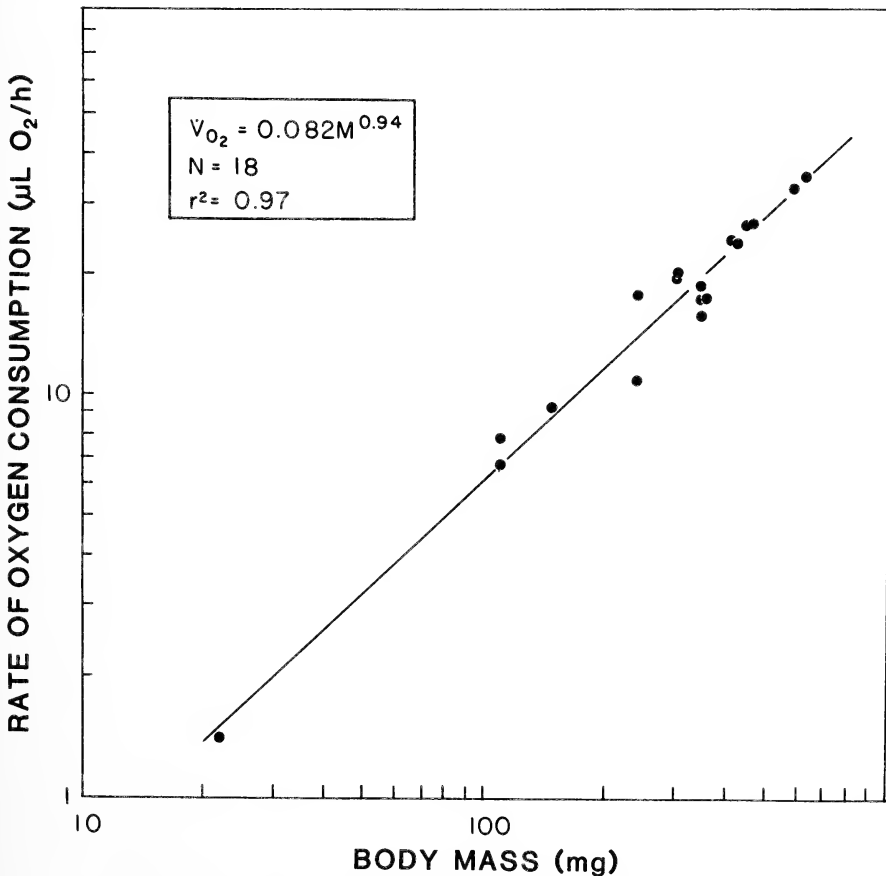
Fig. 1.—Relationship between rates of oxygen consumption and live body mass in *Sphodros abboti* at 20°C.
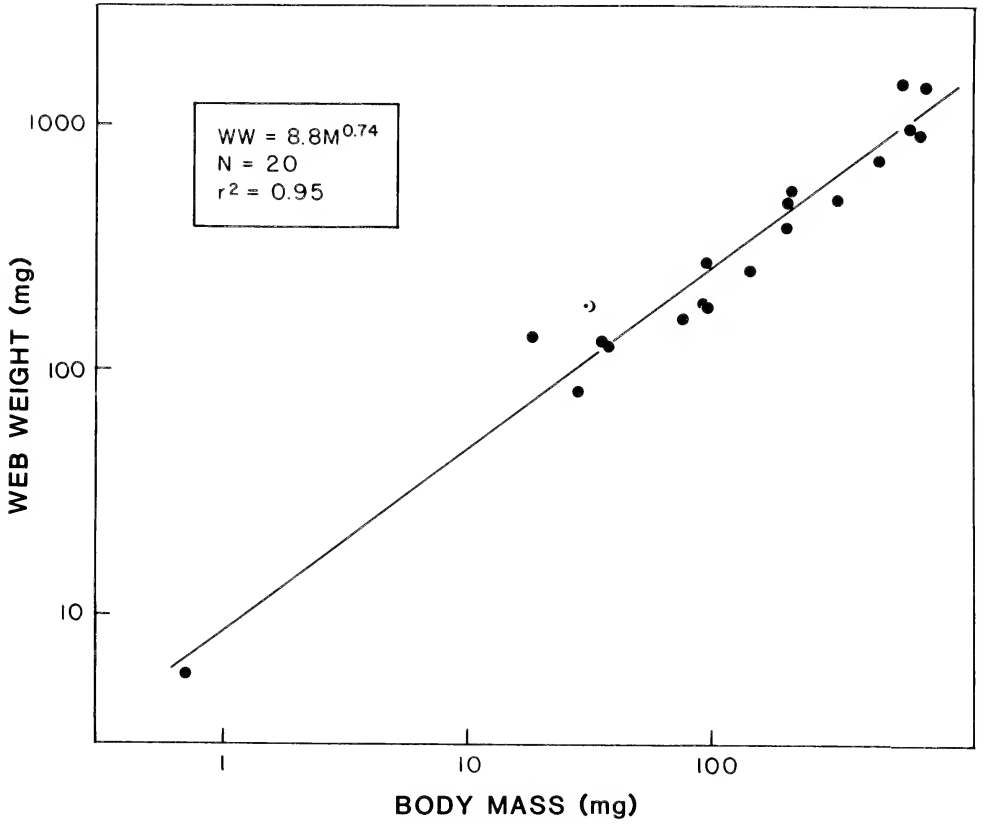
Fig. 2.—Relationship between web weight and live body mass in *Sphodros abboti*.
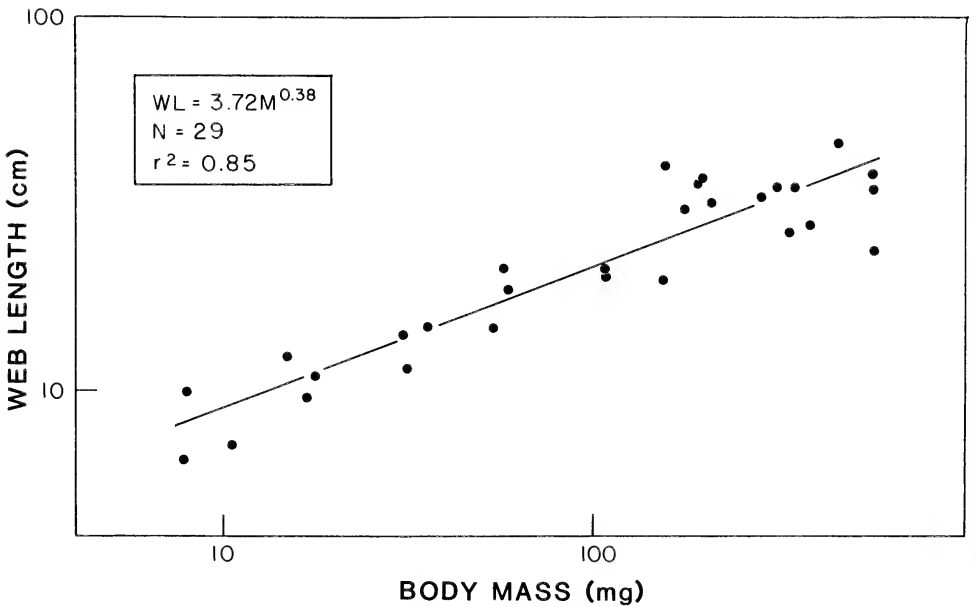
Fig. 3.—Relationship between web length and live body mass in *Sphodros abboti*.
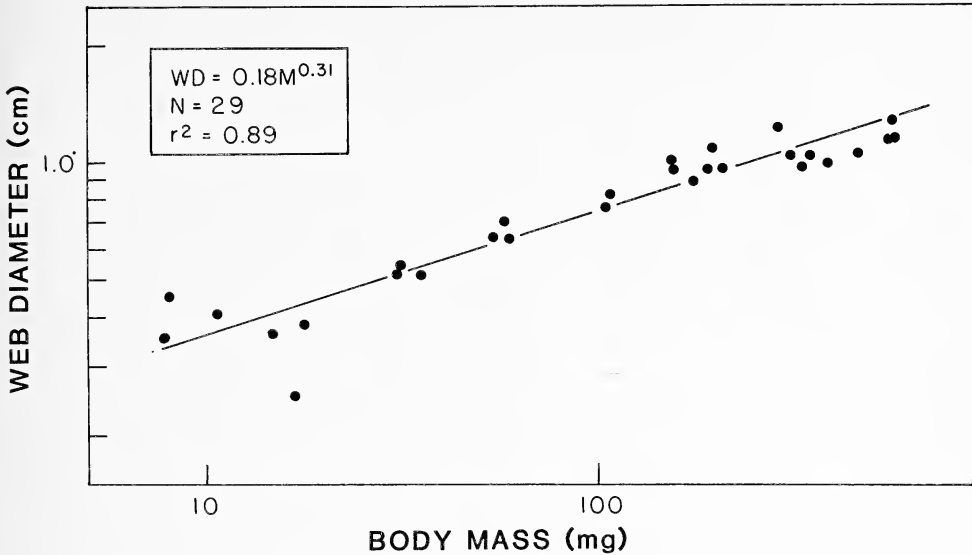
Fig. 4.—Relationship between web diameter and live body mass in *Sphodros abboti*.

The regressions relating length, diameter, and surface area of the web to body mass (Table 2, Figs. 3, 4, and 5) indicate they scale isometrically. The slopes of each equation do not differ significantly from those predicted for geometrically similar structures of different size where web length and diameter scale to the one-third power of body mass ($P = 0.11$ and 0.35, respectively) and surface area scales to the two-thirds power of body mass ($P = 0.60$).

This was an unexpected result. Although the isometric model is frequently used for such comparisons, isometric scaling is not commonly observed (Schmidt-Nielsen 1984). Departures from isometric scaling have been documented for respiratory and circulatory parameters in spiders (Anderson and Prestwich 1980, 1982) with the deviations in a direction consistent with meeting demands for respiratory gas exchange and transport. Consequently I expected the surface area of the web would scale to body size in parallel with scaling of rates of metabolism. I did consider the possibility that the surface area of only the aerial portion of the web might scale differently from that of the entire web as it is the former that is involved in prey detection and capture. Calculation, however, yields an equation whose slope and confidence intervals are almost indistinguishable from those obtained for the surface area equation listed in Table 2.

A comparison with the regression describing the relationship between rates of oxygen consumption and size in *S. abboti* is germane to the goals of this study. The scaling exponents of web surface area and oxygen consumption regressions are significantly different from one another ($P = 0.003$). The increase in surface area and presumably its effectiveness in prey capture does not increase as fast as do rates of metabolism during ontogeny in this species. For a ten-fold increase in body size, the demand for energy or rates of metabolism increase about nine times (antilog $0.94 = 8.7$) while surface area increases only 4.5 times (antilog $0.65 = 4.5$). A number of studies have related web parameters to body size in orb-weaving spiders (Howell and Ellender 1984 and citations therein). Although the nature of their data precludes complete regression analysis, it does indicate that the web surface area to body size ratios decrease with increases in spider size. In
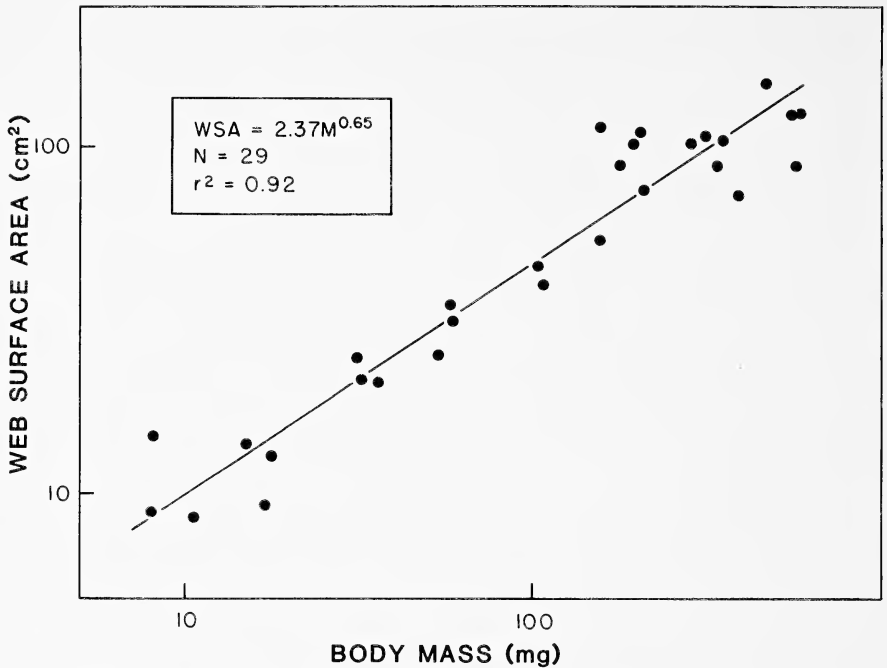
Fig. 5.—Relationship between web surface area and live body mass in *Sphodros abboti*.

araneids, as in *S. abboti*, metabolism scales in direct proportion to body size (Anderson and Prestwich 1982).

These results suggest the web of *S. abboti* and possibly other spiders are not limiting in their ability to capture prey in amounts required to support metabolic requirements. Obviously adult *S. abboti* are successful in obtaining enough energy to maintain themselves for years in this long-lived species. Of significance here is the observation that the European atypid of similar size to *S. abboti*, *Atypus affinis* Eichwald, builds a very short aerial web, about 20% of total tube length (Locket and Millidge 1951). In *S. abboti*, the length of the aerial portion is about 67% (Coyle and Shear 1981; this study). This comparison also suggests that web size is not energetically limiting in atypid spiders.

This situation differs from that found in mammals where home range scales to a higher power of body mass than do rates of metabolism (Harestad and Bunnell 1979). Although the reasons explaining this difference between the two relationships in the direction indicated are not completely known (McNab 1983), most discussions involve energetic considerations. The difference between spiders and mammals may serve to emphasize the adaptive significance of the low rates of metabolism in spiders (Anderson 1970; Greenstone and Bennett 1980; Anderson and Prestwich 1982). Most spiders have rates of metabolism about 50% lower than those of other poikilotherms of comparable size. The difference between observed and expected rates of metabolism is even larger in adult *S. abboti* with females exhibiting rates only 34% expected for their size (Anderson and Prestwich 1982). This reduced level of metabolism may provide freedom from energetic constraints (Greenstone and Bennett 1980) and represents an adaptation to buffer fluctuations in food availability. To put this adaptation into a more meaningful context, I calculated that an adult *S. abboti* (500 mg), at a rate of

metabolism predicted using the appropriate equation (Table 2), would have to eat its weight in insect tissue only once about every 170 days to remain in energy balance. Even if completely unsuccessful in obtaining prey, they would not succumb to starvation until after 200 days or more. Data used to make these estimates such as energy content of insect tissue, ingestion efficiency, etc., were obtained from various sources (Golley 1961; Anderson 1974; Riechert and Tracy 1975).

This adaptation would allow these spiders to reduce the cost of web construction without compromising effectiveness of prey capture. Since most of the cost in web production is in the amount of silk used (Prestwich 1977), savings would accrue if the larger webs of adults used smaller amounts of silk than required by web design features. One can predict how web weight would scale to body mass from the product of the regression equations relating surface area and length of the web to body mass, i.e.,: web weight is proportional to web surface area x web length. Using the weight exponents for each of these expressions (Table 2) indicates web weight should scale in direct proportion to body mass. This is not the observed result (Table 2, Fig. 2). Web weight scales to a power significantly less than one, the predicted value, (b = 0.74, $P \lll 0.001$). This difference between expected and observed is explained by the observation that the thickness of the silken tube decreases in the aerial portion of the tube web (Coyle and Shear 1981). I suggest the departure from proportional scaling of web weight is an adaptation to reduce costs (and possibly conserve amino acids) in web construction.

Although the data and analysis have emphasized energetic considerations, I believe the tubular web of *S. abboti* is the result of a complex evolutionary history and therefore subject to selective constraints in addition to those involving energy. Obviously such constraints need further study to fully understand the functional advantages of this type of web.

ACKNOWLEDGMENTS

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A NEW SPECIES OF *DIPLOCENTRUS* PETERS
FROM TEXAS (SCORPIONES, DIPLOCENTRIDAE)

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ABSTRACT

Diplocentrus diablo, new species, is described from the Rio Grande Valley of Texas, U.S.A., and northern Tamaulipas, México

INTRODUCTION

The genus *Diplocentrus* is a poorly understood assemblage of meso-American scorpions, most of which are described from southern and central México. Species known to occur in the U.S.A. are *Diplocentrus spitzeri* Stahnke from Arizona (Stahnke 1970a), *Diplocentrus peloncillensis* Francke from Arizona and New Mexico (Francke 1975), and *Diplocentrus whitei* (Gervais) (= *Diplocentrus bigbendensis* Stahnke) from Texas (Ewing 1928; Gertsch 1939; Stahnke 1967). No species of *Diplocentrus* are recorded from Tamaulipas, but *D. whitei* is known to occur in Coahuila and Neuvo León, and *Diplocentrus colwelli* Sissom is found in central Neuvo León (Sissom 1986). In the present paper, we describe a new species of *Diplocentrus* from the Rio Grande Valley area of Texas, U.S.A and Tamaulipas, México.

METHODS

The measurements and terminology follow that of Stahnke (1970b), except for trichobothriotaxia, which follows that of Vachon (1974), and metasomal and pedipalpal carination, which follows that of Francke (1978). Hemispermatophores were removed and observed in 100% clove oil. All measurements and drawings were made using a Wild Model 7A® dissecting microscope equipped with an ocular micrometer and a drawing tube. Acronyms for collections from which

[1]Current address: Department of Entomology, University of California, Berkeley, CA 94720.
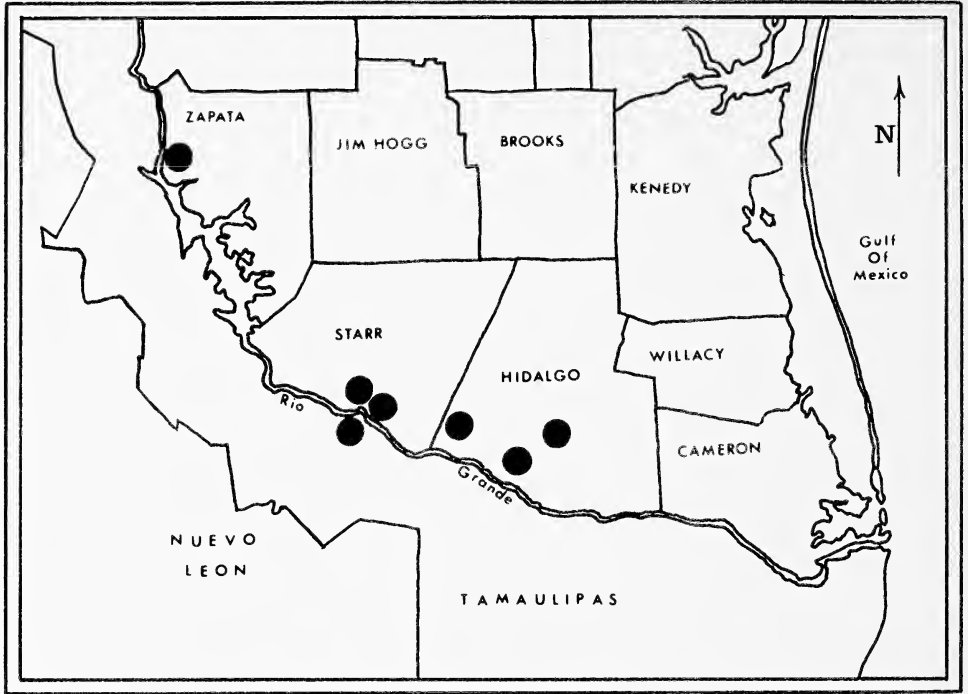
Fig. 1.—Map of the lower Rio Grande Valley showing the distribution of *Diplocentrus diablo*, new species.

specimens were examined are given in the acknowledgements. Specimens from the junior author's collection are listed "JAN."

Diplocentrus diablo, new species
Figs. 1-8

Diplocentrus whitei Hoffman 1931:308-309 (in part).

Type data.—Holotype male from Santa Cruz, Starr County, Texas, 18 August 1985 (Jan A. Nilsson), deposited in the American Museum of Natural History, New York. Paratypes are listed under "Specimens Examined".

Etymology.—The specific epithet is taken from the Spanish word, *diablo*, and is inspired by the belief of the Hispanic locals that these scorpions are the consorts of evil forces. The word is used as a noun in apposition.

Distribution.—Known only from the lower Rio Grande Valley, including Hidalgo, Starr, and Zapata counties in the state of Texas, U.S.A., and the state of Tamaulipas, México (Fig. 1).

Diagnosis.—Dark scorpions, 40 to 50 mm in total length; carapace smooth to weakly, minutely granular; pectinal tooth count 12-14 in males, 9-11 in females; modal tarsomere II spine formula 4/4: 4/5: 5/6: 5/6. Males with moderate to weak reticulate costate pattern on pedipalp; female pedipalp with vestigal to obsolete reticulation. Sexes morphometrically similar (Table 1); metasomal segment I wider than long; pedipalp chela length approximately equal to twice its depth.

Table 1.—Morphometric ratios of *Diplocentrus diablo*, new species. M = male, F = female.

Ratio	Sex	Range	Mean	SD
Pedipalp chela length/pedipalp chela depth	M	1.86-2.00	1.92	0.060
	F	1.91-2.09	1.97	0.083
Pedipalp chela length/carapace length	M	1.65-1.67	1.66	0.009
	F	1.61-1.66	1.63	0.022
Pedipalp chela length/fixed finger length	M	2.31-2.37	2.33	0.026
	F	2.21-2.33	2.26	0.051
Carapace length/fixed finger length	M	1.39-1.43	1.40	0.019
	F	1.33-1.45	1.38	0.050
Fixed finger length/pedipalp femur length	M	0.97-0.99	0.98	0.008
	F	1.00-1.06	1.04	0.028
Fixed finger length/metasomal V length	M	0.75-0.80	0.78	0.026
	F	0.88-0.97	0.93	0.039

Description.—Males. Color brown with variable dark brown marbling (Fig. 2). Carapace smooth to weakly minutely granular; posterior width typically greater than its length; prosomal venter lustrous, weakly punctate; pectinal tooth count 12-14 (mode 13). Tergites with small to minute irregular granulation; tergite VII moderately bilobed, submedian and lateral carinae weak, with a few irregularly positioned granules. Sternites smooth, moderately punctate; sternite VII with submedian and lateral carinae weak, subcrenate.

Hemispermatophore lamelliform; lamalla not noticeably elongate; external lateral margin of capsular lobe weakly dentate (Fig. 3).

Metasoma intercarinal spaces shagreened, vestigially reticulate. Dorsal lateral carinae moderate, granulose on segments I-III; moderate, vestigially granulose on IV. Lateral supramedian carinae strong to moderate, granulose on segments I-IV. Lateral inframedian and ventral lateral carinae moderate on segments I-III; weak on IV; granulose. Ventral submedian carinae moderate, granulose on I, II; weak to vestigal, subgranulose on III, IV. Metasomal segment V dorsal lateral carinae moderate, subgranulose; lateral median carinae vestigal, vestigially granulose; ventral lateral, ventral median, and ventral transverse carinae weak to moderate, moderately tuberculate; anal subterminal carina moderate, tuberculate; anal terminal carina weak, granulose. Telson smooth except for a few tubercles on the ventral anterior surface, sparsely setose.

Pedipalps not noticeably elongate, orthobothriotaxy C (Vachon 1974). Femur with internal face irregularly tuberculate; other faces weakly, minutely granular;

Fig. 2.—*Diplocentrus diablo*, adult male, dorsal aspect.
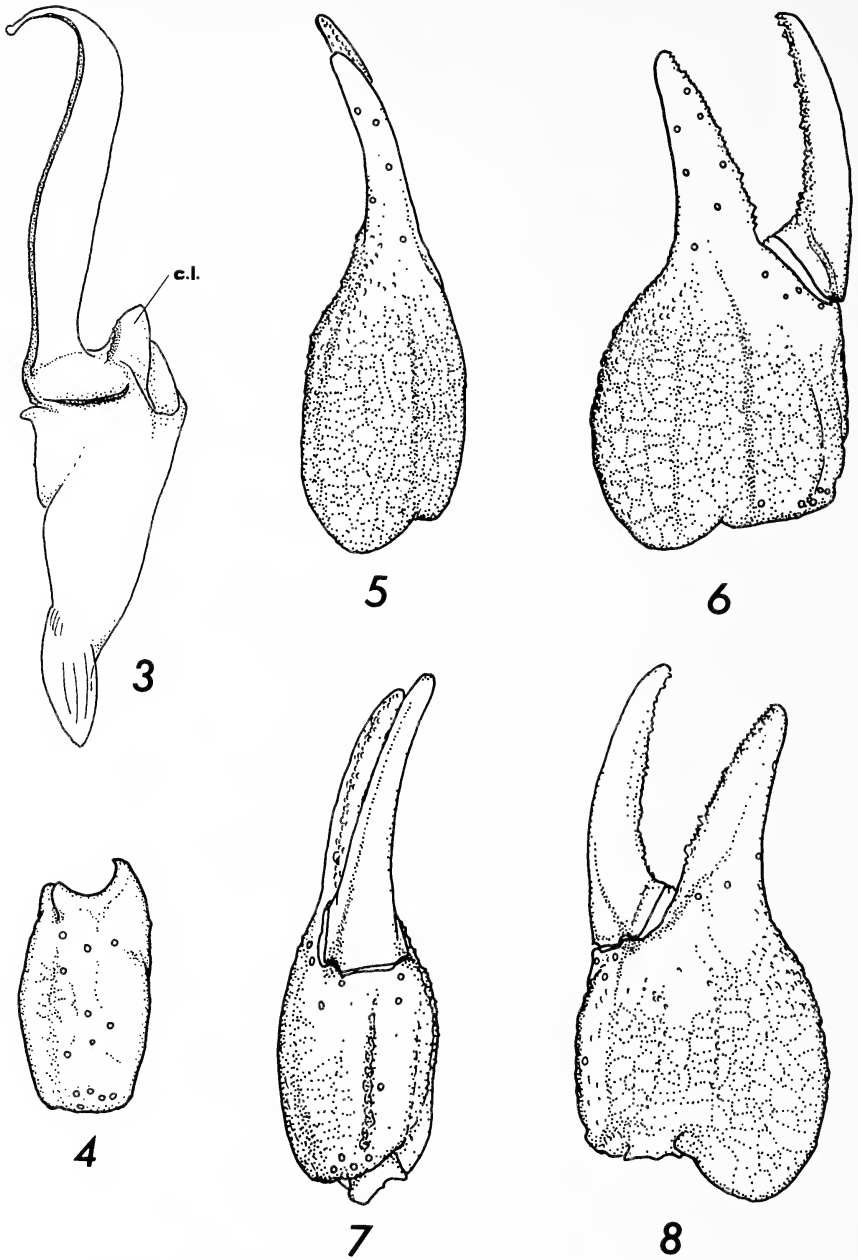
Figs. 3-8.—*Diplocentrus diablo*, adult male: 3, right hemispermatophore, lateral (external) aspect; 4, right pedipalp patella, external aspect showing trichobothrial pattern, c.l. = capsular lobe; 5, right pedipalp chela of adult male showing trichobothrial pattern, dorsal aspect; 6, pedipalp chela, external aspect; 7, pedipalp chela, ventral aspect; 8, pedipalp chela, internal aspect.

dorsal internal carina moderate, granulose to tuberculate; dorsal external carina moderate, tuberculate proximally to obsolete distally; ventral external carina obsolete; ventral internal carina moderate, granulose. Patella (Fig. 4) with ventral and external faces weakly reticulate; internal face irregularly granular; basal tubercle moderate, consisting of a single pointed tubercle; dorsal median carina strong, smooth; ventral external carina moderate to weak, smooth; ventral

Table 2.—Variation in tarsomere II spine counts of *Diplocentrus diablo*, new species. Missing tarsomeres are indicated in column X.

No. of spines in row	3	4	5	6	7	X
Leg I						
Prolateral row	6	27	1			2
Retrolateral row		32	2			2
Leg II						
Prolateral row		33	3			
Retrolateral row			36			
Leg III						
Prolateral row			26	7	1	2
Retrolateral row				33	1	2
Leg IV						
Prolateral row			27	6		3
Retrolateral row			5	27	1	3

internal carina weak to moderate, granulose; other carinae obsolete. Chela (Figs. 5-8) with dorsal and external faces moderately to weakly reticulate; other faces weakly to vestigially reticulate; dorsal marginal carina weak to moderate, granulose; dorsal secondary and external secondary carinae weak; digital carina moderate; ventral external carina obsolete; ventral median carina strong, crenulate; ventral internal carina vestigal; internal carinae weak, sparsely granular. Unless otherwise noted, the carinae of the chela are smooth, except where a continuation of the reticulate pattern occurs.

Legs typical, sparsely granular to smooth. Tarsomere II spine formula 4/4: 4/5: 5/6: 5/6.

Females differ from males as follows. Carapace and tergites smooth; pedipalps and metasoma without reticulate costate pattern; pectinal tooth count 9-11 (mode 10).

Morphometrics.—Sexes are morphometrically similar; carapace wider than long; pedipalp chela length approximately equal to or less than two times chela depth; pedipalp chelae of males slightly shorter and deeper than those of females; metasomal segment I wider than long; remaining segments longer than wide. The ranges, means, and standard deviations of six taxonomically important morphometric ratios from three adult males and four adult females are given in Table 1.

Variation.—Specimens varied in pectinal tooth counts as follows: in males, three combs had 12 teeth, six combs had 13 teeth, and three combs had 14 teeth; in females, four combs had nine teeth, 15 combs had 10 teeth, and seven combs had 11 teeth. Variation in tarsomere II spine counts is shown in Table 2. One female specimen had metasomal segment II wider than long.

Habitat.—The new species, like all species of *Diplocentrus*, is an obligate burrower but may be found under large surface objects in rocky areas of the Rio Grande Valley.

Comparisons.—The only known species of *Diplocentrus* that is closely related to *D. diablo* is *D. colwelli* Sissom, found in the state of Nuevo León, México. The latter is distinguished from the new species by its smaller size, slightly higher tarsomere II spine formula (5/5-6: 5/6: 6/7: 6/7), smaller pedipalp chela length/ depth (males 1.78-1.88, females 1.86-1.96), and vestigially dentate external lateral margin of dorsal lobe of hemispermatophore. *Diplocentrus whitei*, the only other

species of the genus known to occur in Texas, is easily separated from the new species by its larger size, higher pectional tooth counts (females 14-18, males 16-20), higher tarsomere II spine formula (5-6/7: 6/7-8: 7/8: 7/8), larger pedipalp length/depth (females 2.05-2.33, males 2.41-2.79), and strongly dentate external lateral margin of dorsal lobe of hemispermatophore.

Specimens examined.—All specimens designated paratypes. U.S.A.: Texas; *Zapata County*, 32 mi SE of Laredo, 12 September 1940 (S. D. Mulaik), one female (AMNH); *Starr County*, Rio Grande City, 4 May 1934 (S. D. Mulaik), one male, one female (AMNH); Rio Grande City, 9 April 1939 (S. D. Mulaik), 1 female (AMNH); Santa Cruz, 21 August 1985 (J. A. Nilsson), one male (JAN), Santa Cruz, 2 March 1986, two females (JAN), Santa Cruz, 8 March 1986, one female (JAN); Dreamland, 19 April 1985 (J. A. Nilsson), one female (JAN); *Hidalgo County*, NW Mission, March 1933 (S. D. Mulaik), one female (AMNH); Edinburg, December 1939 (S. D. Mulaik), one female (AMNH); 5 km N of La Joya, 22 October 1984 (J. A. Nilsson), one female (JAN), 5 km N of La Joya, 8 March 1986. MÉXICO: Tamaulipas; Ciudad Camargo, no date (C. C. Hoffmann), two males (AMNH).

Three specimens obtained from the Naturhistorisches Museum Wien also belong to this taxon. These are labelled "Central America, acquis. no. 1871.IV.I (Schenzer leg.)," one male, two females (NMW). The locality data accompanying these specimens is somewhat problematical, however, it is not uncommon for such old material from this part of the New World to possess erroneous or very general locality data.

ACKNOWLEDGMENTS

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COMMUNICATION BY CUTICULAR PHEROMONES
IN A LINYPHIID SPIDER

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ABSTRACT

The bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae), receives information
about its world primarily through its senses of touch (including vibrations) and taste. We report here
that when a male touches the carcass of a conspecific mounted on the web of an adult female, the
male receives information about the sex of the carcass. Moreover, the information is encoded in
chemical form on the cuticles of both sexes of adult spiders. Tarsal contact with the carcass of a male
elicits many abdomen flexions but few foreleg waves from an assay male. In contrast, tarsal contact
with the carcass of a female elicits far fewer abdomen flexions but many foreleg waves. Both
intersexual differences are lost when the carcass has been washed in solvent.

INTRODUCTION

A growing literature on communication by web-building spiders suggests that
the vibratory (reviewed by Barth 1982) and chemical (reviewed by Tietjen and
Rovner 1982) channels are of primary importance. Among the solitary web-
builders, vibratory and/or pheromonal communication are usually associated
with agonistic interactions (e.g., Christenson and Goist 1979; Riechert 1984), mate
attraction and courtship (e.g., Krafft 1978; Olive 1982; Roland 1984), or parent/
offspring relations (e.g., Norgaard 1956; Tretzel 1961; Krafft and Horel 1980),
those being the only situations in which intraspecific communication typically
occurs. The literature on communication in social spiders is more sparse, but
there, too, the same two channels appear to be of primary importance (Kullmann
and Zimmermann 1971; Buskirk 1975; Lubin in press).

The bowl and doily spider, *Frontinella pyramitela* (Walckenaer) (Araneae,
Linyphiidae), is a solitary spider that also appears to utilize vibrations and
pheromones as its primary communication signals. This spider's male-male
agonistic interactions are characterized by nearly continuous vibratory signalling
which may culminate in tactile displays (Austad 1983; Suter and Keiley 1984).
Female-female agonistic interactions are also known in this species and they, too,
are primarily vibratory (Hodge 1987). The seasonally frequent male-female
agonistic interactions that occur during disputes over access to prey in this species
are also mediated by vibratory signals (Suter 1985). It has heretofor been unclear
whether the communication during any of these agonistic interactions might
involve pheromones in addition to vibrations, and whether the direct contact
between contestants was chemically informative.

The courtship of bowl and doily spiders involves pheromonal and vibratory signals as well as direct contact (Suter and Renkes 1982, 1984). As with the agonistic interactions, it has not been clear whether direct contact between the prospective mates was functional as communication and whether, if so, it was purely tactile or was chemotactile.

Work on other spiders, both non-social and social, has suggested that chemicals borne on the integument may act as pheromones (Krafft 1975, 1982; Lubin in press). In the work reported here, we sought to determine whether the outer surfaces on adult *F. pyramitela* bear chemicals that function as pheromones in either agonistic or courtship contexts.

MATERIALS AND METHODS

Bowl and doily spiders are common inhabitants of fields and forest edges throughout much of North America. They are easily captured as adults from their concave upward, bowl-shaped webs, and can be maintained in the laboratory for weeks and sometimes months. Techniques used to maintain the animals in captivity are described elsewhere (Suter and Keiley 1984; Suter 1985).

In the laboratory, healthy female *F. pyramitela* build new webs every day if they are removed from their old ones and if they are well fed. By such removals and frequent feeding, we accumulated a number of clean (no prey carcasses or other debris) webs which later served as the arenas on which behavioral assays were run.

The complete assay arena consisted of a female-produced web and, cemented to it, the carcass of either a male or a female bowl and doily spider. The carcass was prepared in one of two ways: a live spider was dropped into absolute methanol and then into hexane, each for 30 minutes, and then was air dried for at least 24 h, or a live spider was impaled through the cephalothorax with a fine pin and then placed in a desiccator to dry for 24 h. Dried carcasses were mounted on the underside of the bowl of a web, the normal location of either sex of the species, with droplets of Testor's paint applied to the spider's tarsi. Several hours after carcass mounting, the completed arena was used in behavioral tests. (Preliminary testing of the dried paint indicated that it neither attracted nor repelled nor otherwise affected the behavior of bowl and doily spiders.)

At the start of a behavioral assay, the assay spider, a male, was swung at the end of its dragline onto the upper strands of the web. In response to a web-borne pheromone (Suter and Renkes 1982), it would then proceed downward until it made contact with the silk of the bowl and then laterally until it could reach the lip. Once on the underside of the bowl, the assay spider would, through oriented search behavior (Suter 1984), quickly arrive at the center and make contact with the carcass mounted there. The timing of a 5-minute behavioral assay began upon contact with the carcass. The initial contact and all subsequent behaviors were videotaped from above while a voice record of the behaviors visible from the side of the web was made on one of the tape's audio channels.

We analyzed the videotapes with respect to two stereotyped male behaviors. One behavior, the abdomen flexion, is known to be characteristic of males both during courtship (Suter and Renkes 1982, 1984) and during agonistic interactions (Austad 1983; Suter and Keiley 1984). The other, the foreleg wave, is seen only during courtship and then usually late in courtship (Suter and Renkes 1984).

RESULTS

Initial contact of the assay male with a carcass usually involved the tarsi of the assay animal and the legs of the carcass. Subsequent contacts, especially during tests in which the assay male was foreleg waving, also involved contact with the body of the carcass, and occasionally the assay animal's pedipalps and mouthparts touched the carcass. Rarely, the assay male fed for a brief period on a carcass.

Untreated male carcasses and untreated female carcasses elicited significantly different numbers of abdomen flexions (Fig. 1a) as well as significantly different amounts of foreleg waving (Fig. 1b) from assay males. During 5 minutes of post-contact activity, the male assay spiders produced nearly four times as many abdomen flexions in response to unwashed male carcasses (median = 224) as in response to unwashed female carcasses (median = 65.5; Mann-Whitney U test, $P < 0.01$). During the same test period, assay males did 27 times as much foreleg waving in response to unwashed female carcasses (median = 27 s) as in response to unwashed male carcasses (median = 1 s; Mann-Whitney U test, $P < 0.01$).

Treating male and female carcasses with methanol and hexane washes rendered them much more similar to each other than were the untreated carcasses. With respect to abdomen flexions, there remained a significant difference between washed males and washed females, but the direction of the difference was reversed. The washed carcasses of males elicited fewer abdomen flexions from assay males than did the washed carcasses of females (male median = 100, female median = 37; Mann-Whitney U test, $P = 0.03$). With respect to foreleg waves, the solvent treatment eliminated the difference between the sexes of the carcasses. The washed carcasses of both males and females elicited very little foreleg waving (median for each = O s; Mann-Whitney U test, $P = 0.82$) from the assay males.

DISCUSSION

The data presented here demonstrate clearly that male bowl and doily spiders perceive differences, based on touch alone, between male and female conspecifics. There is no a priori reason to assume that the sex discrimination is based upon chemical rather than structural differences, except that other aspects of the spider's behavior are strongly influenced by pheromones (see references in the introduction). Tests of solvent-washed male and female carcasses reveal that it is chemical differences between their surfaces, not structural differences, that elicit distinct behaviors from assay males: the untreated carcasses of males release far more abdomen flexions in assay males than do untreated carcasses of females (Fig. 1a), while both sexes of carcasses, when washed, release similar numbers of abdomen flexions; similarly, untreated carcasses of females release far more foreleg waving than do untreated male carcasses (Fig. 1b), while neither sex of carcass elicits much foreleg waving when it has been washed.

The assay male's response to contact with a dead spider on the web is consistent with its responses to contact with living conspecifics under natural conditions. When a male first contacts the web of a female, that contact releases abdomen flexions, which the male continues to produce until he contacts the female (Suter and Renkes 1982). The sequence of behaviors that follows contact is very complex, but in all cases that sequence includes foreleg waves whose
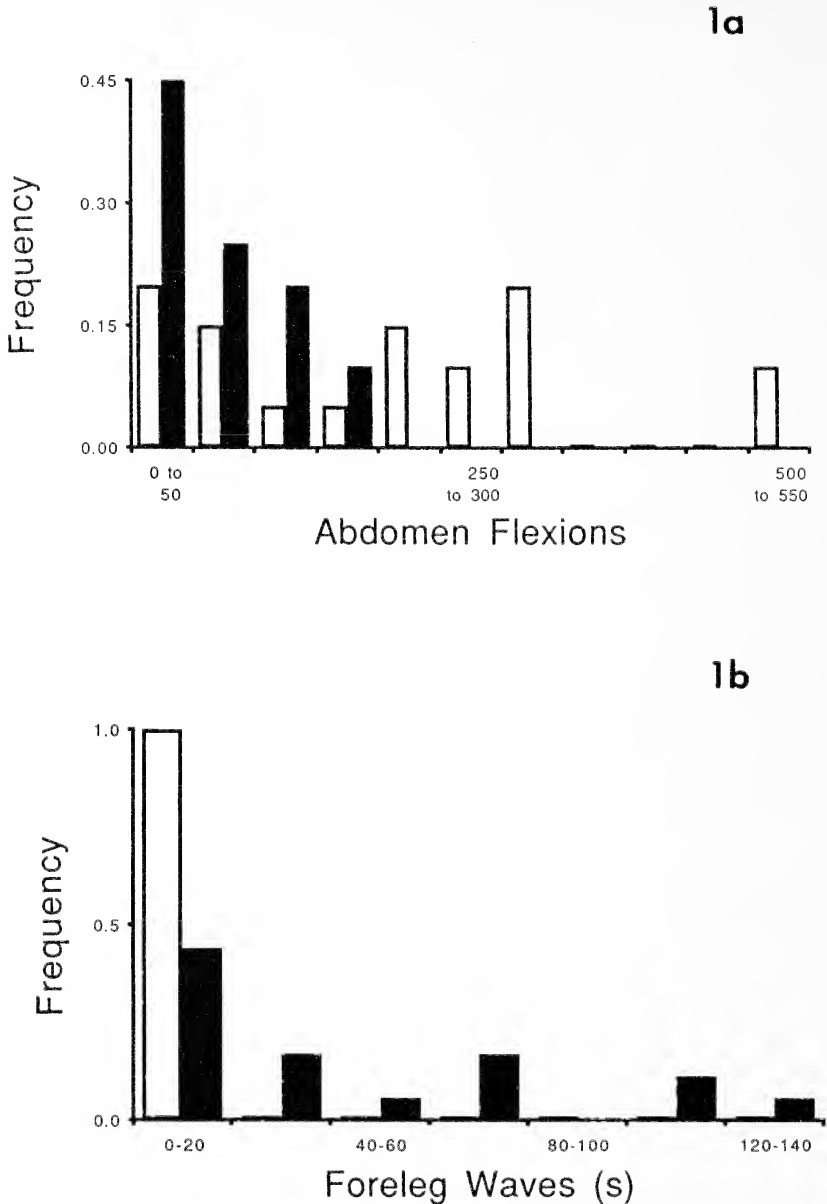
Fig. 1.—Behaviors performed by male assay spiders during the first 5 min following contact with the carcass of a conspecific. (a) Untreated male carcasses (open bars) elicited far more abdomen flexions than did female carcasses (filled bars), but (b) untreated female carcasses elicited much more foreleg waving (in seconds) than did male carcasses. With respect to both behaviors, when the carcasses had been washed in methanol and hexane, the sex-specific differences disappeared (see text).

frequency increases as courtship progresses (Suter and Renkes 1984). Thus it is not surprising that, if contact with a female's carcass is to elicit any sex-specific behavior, the behavior should be foreleg waving.

Parallel logic can be applied to the behavior of a male after contact with another male. The presence of a living male on a female's web ultimately leads, under natural conditions, to a stereotyped, agonistic interaction between the intruding male and the resident male (Suter and Keiley 1984). Such interactions,

though they may escalate to more intense displays and overt combat (Austad 1983; Suter and Keiley 1984), always include persistent abdomen flexion production. Again, it is no surprise that a male's contact with a dead male spider, if it is to elicit any sex-specific behavior, should elicit the production of more abdomen flexions.

Both courtship and male-male agonistic interactions in bowl and doily spiders are complex chains of behavioral events that involve vibratory communication as well as the contact chemical communication that we have now demonstrated. We deduce from this study and from our observation of attempted copulations by males on dead females and on female exuviae (Suter and Renkes 1984), that from the male's perspective, chemical confirmation that the resident spider is a female is both necessary and sufficient for courtship to reach completion. (It will be very difficult to similarly separate the roles of vibrations and chemicals either from the female's perspective in courtship or from either male's perspective in agonistic interactions.)

That the chemical confirmation is *sufficient* suggests that the role of the female in courtship is to delay copulation until she is fully ready, either physiologically or behaviorally, to mate. That the confirmation is *necessary* suggests that males are cautious, because prior to contact with the female they already have two sources of information about her identity. First, the webs of adult bowl and doily spiders are chemically marked such that an adult male knows whether a web it encounters was built by an adult male or by an adult female (Suter and Hirscheimer 1986), though the webs of juveniles are not easily distinguished, chemically, from those of adult females. Vibratory information, also available to the male spider shortly after he makes contact with an inhabited web, is similarly sex-specific (Suter and Renkes 1984; Suter and Keiley 1984) and thereby provides a second level of information about the probable identities of the inhabitants of a web. Now we have demonstrated that chemotactic information provides a third level.

That the third level is necessary for courtship to be completed implies that male *F. pyramitela* are cautious because of the detrimental consequences of close contact with a larger adult male or with a spider of another species. Evidence to be published elsewhere demonstrates that bowl and doily spiders also identify certain of their predators by detecting their cuticular chemicals (Suter et al. in preparation).

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BALLOONING SPIDERS IN MISSOURI, USA, AND NEW SOUTH WALES, AUSTRALIA: FAMILY AND MASS DISTRIBUTIONS

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ABSTRACT

Ballooning spiders were captured during a full growing season over agricultural habitats in Missouri, USA, and one week in New South Wales, Australia, using sticky traps in Missouri and tow nets in Australia. More than 2,000 spiders in Missouri and more than 800 spiders in Australia were identified to family and estimates made of their live masses. Both aeronaut faunas are dominated by the family Linyphiidae, with the remaining families making up different proportions at the two sites. The vast majority of aeronauts weighed between 0.2 and 1.0 mg, with the mass-frequency distributions at both sites tailing off rapidly beyond 2.0 mg. The most massive Missouri aeronaut weighed 25.5 mg, and the most massive Australian aeronaut 19.1 mg. These are the first published extensive data on the live masses of ballooning spiders from the field and this is the first taxonomic analysis of a Southern Hemisphere aeronaut fauna.

INTRODUCTION

There is a large and well established literature on aerial migration of terrestrial arthropods (see Johnson 1969 and Dingle 1978 and 1980 for reviews). Not surprisingly it is dominated by the insects, whose large size, instances of mass seasonal dispersal, and agricultural pest status call attention to them. However insects are not the only aerially dispersing terrestrial arthropods (Southwood 1962). The most conspicuous of the remaining groups are the spiders (Arachnida: Araneae). Like the insects, spiders disperse aerially in enormous numbers (Comstock 1948), often seasonally (Emerton 1908; Bristowe 1929; Duffey 1956), and may in this way travel hundreds of kilometers (Holzapfel and Perkins 1969; Okumo and Kisimoto 1981). Unlike the insects, they lack wings, being instead lifted and carried passively on silken threads in the process known as ballooning. Spiders have considerable potential as agents of biological control of pests (Riechert and Lockley 1984), so their capacity to disperse is of more than theoretical interest, especially in annual crop systems which they must recolonize

at the beginning of each growing season along with the insect pests on which they feed.

Insects lighter than aphids and as massive as plague locusts are known to disperse aerially. There has only been one restricted data set available on the masses of ballooning spiders (Coyle et al. 1985). We have been able to gather large samples of such data as a part of long-term studies on terrestrial arthropod dispersal in Missouri, USA and New South Wales, Australia. Since all previous taxonomic data on aeronauts are exclusively from the Northern Hemisphere, we also feel it is valuable to present the family distributions of aeronauts from both sites.

METHODS

The Missouri site was a 2.0 ha field at the University of Missouri South Farms, 9.7 km SE of the city of Columbia in Boone Co., planted to soybeans with varying admixtures of sunflowers as part of a study on the influence of cropping scheme on natural enemy diversity (N. L. Marston, pers. comm.). Panel sticky traps made of 12.7 mm (1/2 in) and 6.35 mm (1/4 in) galvanized hardware cloth coated with the adhesive Tack Trap® (Animal Repellents, Inc., Griffin, GA.) were run for eighteen consecutive one-week periods beginning on June 15, 1983. The traps were mounted on an open frame and covered a total area of 3.0 m² between 0.5 and 2.0 m elevation. All vegetation was cleared from within 3.0 m of all traps by application of the herbicide Roundup® (Monsanto Co., St. Louis, MO) to maximize the probability that all trapped spiders had been ballooning rather than travelling on bridge lines. For the same reason the trap supports were coated with adhesive to ensure that walking spiders would be intercepted rather than spuriously trapped (see Greenstone et al. 1985a, for complete description of trapping system). The traps were returned to the laboratory for examination at 6X with a stereo microscope, and the spiders placed in paint thinner to remove the adhesive. After four days the spiders were transferred to toluene and after a further four days to 70% ethanol for final preservation. The traps were cleaned with solvent, recoated in the laboratory and replaced in the field each week.

The Australian site was at Trangie in the Central Western Plains of New South Wales, in native pastures derived from cleared savannah woodland adjacent to fields of wheat and dryland lucerne. Spiders were sampled by tow net from both the surface boundary layer, at 3.0 m, and the planetary boundary layer, between 100 and 300 m elevation. The net, which had a 1.0 m² opening, was supported by a mast at the lower elevation and by a kite in the upper air. The kite was deployed in a way which minimized arthropod catches during ascent and descent (Farrow and Dowse 1984). The samples of arthropods were immediately preserved in 70% ethanol and the spiders were subsequently separated in the laboratory. Unlike the Missouri sampler the net is dependent upon favorable winds for its deployment, so that sampling at the Australian site was not continuous and the individual sampling periods were relatively short (1-6 h). We present only data from November 23-30, 1979, which had the largest proportion of spiders of the samples taken in the Trangie sampling program.

After the spiders had been preserved in ethanol for at least three months, the masses of all of the Australian spiders and a representative sample of the

Missouri spiders were estimated by means of a volumetric mass estimate derived from a series of linear measurements (Greenstone et al. 1985b); this estimate is not affected by the differences in methods of trapping and preservation at the two sites and stabilizes after six weeks of ethanol preservation (Greenstone et al. 1985c). We also identified the spiders to family. Although a few species can be confidently identified to genus and even species (e.g. the *Oxyopes* and *Tetragnatha* species, which were represented by one or a few species at each site), the vast majority of aeronauts are minute immatures so that genus or species level identification would require a major basic research effort in systematics (J. Coddington pers. comm.).

RESULTS AND DISCUSSION

Family-frequency distributions for the Missouri and Trangie samples are shown in Figs. 1A and 1B, respectively. The family Linyphiidae dominates in both cases, with 42% and 52% of the individuals, respectively (we follow Millidge 1980 in including the Erigonidae and Micryphantidae of some authors in this family). The Araneidae and Oxyopidae each make up between 9% and 17% of the total, with the remaining families differing in dominance between the two sites. The same proportion of unidentifiable ‘animals, about seven percent, was found at both sites, reflecting comparable incidences of damage to spiders whether collected by sticky trap or tow net.

The mass-frequency distributions are shown in Figs. 2A and 2B. More than half of the aeronauts at both sites are in the first two mass classes (0.21 and 0.60 mg) and the vast majority, 85% in Missouri and 94% in Trangie, weigh 1.0 mg or less. The most massive spiders collected weighed 25.5 mg and 19.1 mg, respectively.

About 14% of identified Missouri aeronauts and 32% of identified Trangie aeronauts were adults (Table 1). However the percentages for linyphiids alone are 31 and 58, respectively. In both cases the sex ratio is not significantly different from 1.0 ($p > 0.15$ and $p > 0.99$, Binomial Test, Siegel 1956). The large proportion of adults among linyphiid aeronauts has been noted by other workers but females have predominated in these earlier studies (Duffey 1956; Meijer 1977; Salmon and Horner 1977).

The Trangie collection is the first from the Southern Hemisphere to be analyzed taxonomically. Because it covers only one week’s data, no detailed comparisons with Northern Hemisphere collections are made here. However the same families appear to be involved in the aeronaut fauna of the most isolated of Southern Hemisphere continents as in the better-studied Holarctic, so that the ecology and evolution of ballooning behavior are probably little influenced by Australian endemicity.

The linyphiids dominate most of the ballooning literature, which has emphasized mid to high latitude Northern Hemisphere sites, where the linyphiids predominate on the ground as well as in the air (Bristowe 1929; Enders 1975). Their domination of the Missouri (N. Latitude 38° 58′) samples was therefore to be expected. The linyphiids are of particular interest because a high proportion balloon as adults, when they have high reproductive value and hence high colonizing potential (MacArthur and Wilson 1967; Greenstone 1982). Further-
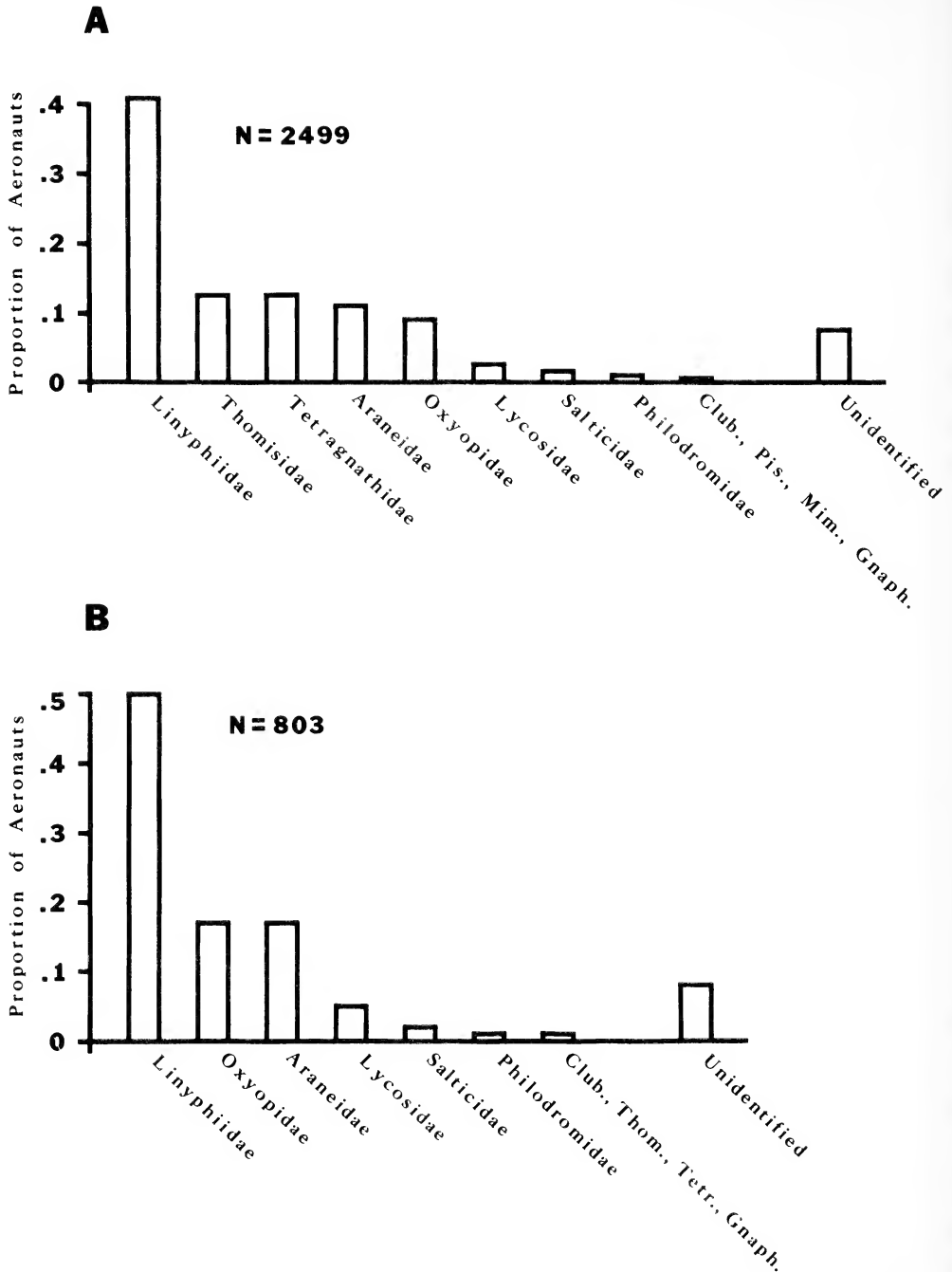
Fig. 1.—Family-frequency distributions for aeronauts captured in Missouri (A) and Trangie (B). Abbreviations: Club. = Clubionidae; Gnaph. = Gnaphosidae; Mim. = Mimetidae; Pis. = Pisauridae; Tetr. = Tetragnathidae; Thom. = Thomisidae.

more they are known to be important predators in at least some agricultural systems (Riechert and Lockley 1984).

Fig. 2A depicts a very large data set collected throughout an entire growing season and is therefore a definitive estimate of the mass frequency distribution of
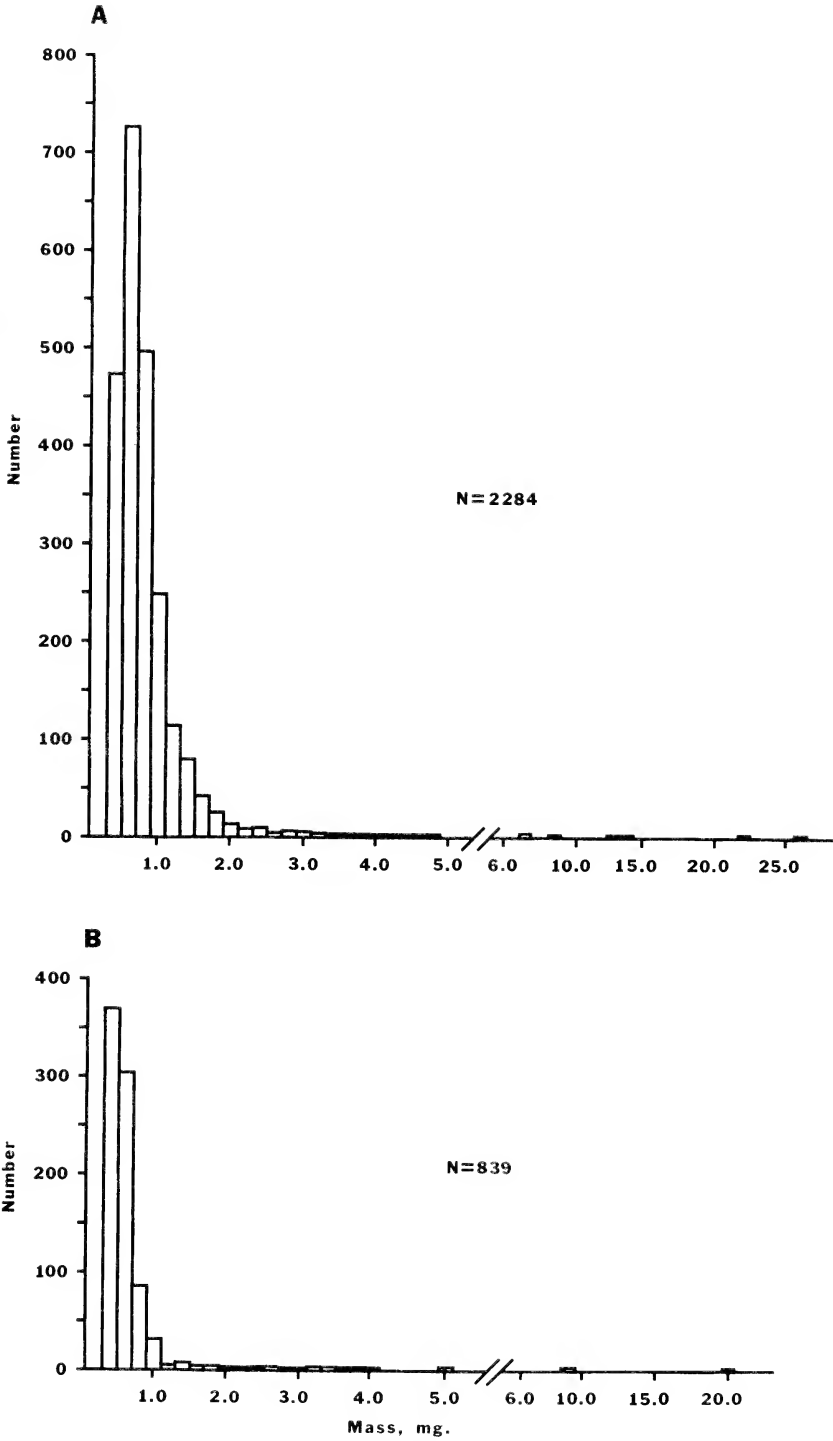
Fig. 2.—Mass-frequency distributions for aeronauts captured in Missouri (A) and Trangie (B). Mass classes are 0.2 mg wide below 6.0 mg and 1.0 mg wide beyond 6.0 mg. Class marks denote upper bound of each mass class.

Table 1.—Age, sex, and taxonomic representation of identified aeronauts. M = male, F = female, I = immature, % = percent of fauna represented by family. Percentages in this table differ from those in Fig. 1 due to exclusion of unidentified animals. *Gnaphosids and mimetids represent less than 0.1% of the identified Missouri animals.

Family	MISSOURI				TRANGIE			
	M	F	I	%	M	F	I	%
Linyphiidae	160	161	716	44.9	105	127	171	54.2
Araneidae	4	0	266	11.7	6	1	131	18.6
Oxyopidae	0	0	231	10.0	0	1	138	18.7
Thomisidae	1	0	314	13.6	0	0	3	0.4
Tetragnathidae	0	0	312	13.5	0	0	1	0.1
Lycosidae	0	0	68	2.9	0	0	37	5.0
Salticidae	1	0	36	1.6	0	0	13	1.8
Philodromidae	0	0	28	1.2	0	0	6	0.8
Clubionidae	1	0	7	0.4	0	0	3	0.4
Gnaphosidae	0	0	1	*	0	1	0	0.1
Pisauridae	0	0	2	0.1	—	—	—	—
Mimetidae	0	0	1	*	—	—	—	—

aeronauts. Clearly most ballooners weigh 1.0 mg or less, and ballooners heavier than 30 mg are unlikely. (Note that there are no aeronauts weighing less than 0.21 mg).

There are three possible contributors to the mass-frequency distributions of aeronauts, viz., the mass-frequency distributions of *potential* aeronauts, the ballooning tendencies of spiders of different mass classes, and the effect of atmospheric lift on the dynamics of ballooning. The mass-frequency distributions of spiders collected from the ground and vegetation do favor smaller animals, but they are not as markedly skewed as those in Fig. 2 (Waldorf 1976; Nentwig 1982), and spiders weighing more than 26 mg are common. Certainly there is no inherent physical barrier to ballooning by more massive animals, which could simply produce more ballooning silk (R. Buskirk and R. B. Suter, pers. comm.). Therefore, the lack of larger ballooners is probably due, at least in part, to reductions in ballooning tendency with increasing mass. Such reductions have been documented by behavioral assays of ballooning in the lycosid genus *Pardosa* (Richter 1970). Variables selecting against ballooning by more massive animals might include enhanced visibility to aerial predators, decreased lift, and increased risk of injury on landing (Coyle et al. 1985).

With few notable exceptions (Glick 1939; Glick and Noble 1961; Holzapfel and Perkins 1969; Okuma and Kisimoto 1981), all aeronaut collections, including those made in this study in Missouri, have been made from elevations less than 3.0 m, where ballooning spiders may be simply drifting back towards the ground following launching from a high take-off point. The ascent of spiders into the upper air depends on convective updrafts and is affected not only by the velocity of the updraft but also by the mass of the spider and by the drag of the silk thread and balloon. Unless updrafts are strong there will be a tendency for the lighter mass classes to be better represented in the upper air compared with the surface due to differential settling rates. We will use a larger Trangie data set to compare upper and lower elevation mass-frequency distributions in a future publication (in preparation).

ACKNOWLEDGMENTS

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DESCRIPCION DE UNA NUEVA ESPECIE
DEL GENERO *VARACOSA* DE MEXICO
(ARANEAE, LYCOSIDAE)

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ABSTRACT

The *avara* group of the genus *Trochosa* (*sensu* Brady), is treated as the genus *Varacosa* (*sensu* Roewer). *V. hoffmannae* n. sp. is illustrated and described from México and *V. avara* is also illustrated.

RESUMEN

El grupo *avara* del género *Trochosa* (*sensu* Brady), es tratado como el género *Varacosa* (*sensu* Roewer). Se hace la descripción de la nueva especie *Varacosa hoffmannae* de México y se ilustra a *V. avara*.

INTRODUCCION

El género *Varacosa* está constituido por cuatro especies descritas para Norte América. Chamberlin e Ivie (1942), propusieron a *Varacosa* como un subgénero de *Trochosa*, considerando a *T. avara* Keyserling 1877, como la especie tipo para esta designación.

El carácter principal en el que se basaron fue la conspicua curvatura de los extremos de la pieza transversa del septo medio.

Roewer (1954) trató al subgénero *Varacosa* a nivel de género, sin embargo, Brady (1979), incluyó al grupo *avara* con el grupo *terricola* en el género *Trochosa*, tomando en cuenta, exclusivamente, la similitud de la coloración del cuerpo y el hábitat compartidos por estas especies, dándole más importancia a estos caracteres que a las diferencias morfológicas de los genitales. No obstante, nuestras observaciones han demostrado que los caracteres de color y hábitat son también encontrados en otros licósidos del género *Hogna*. Los caracteres

principales que consideramos sinapomórficos para el grupo *avara* son: un émbolo aplanado y truncado con la punta torcida (Figs. 1, 2, 5, 7); los extremos de la pieza transversa del septo medio del epiginio, se curvan anteriormente, quedando como puntas angulosas y el atrio presenta a cada lado un abultamiento en forma de burbuja (Figs. 3, 4, 9, 10).

En nuestra opinión, estas características genitales justifican completamente la categoría genérica para el grupo *avara* de Brady (1979).

En este trabajo se describe una nueva especie del génera *Varacosa* de México.

Varacosa hoffmannae, nueva especie
Figs. 5-10

Datos del tipo.—Holotipo macho colectado en Santa Cruz Xochitepec, D.F., México, 2945 m., 15 agosto 1978 (H. Medina); y los siguientes paratipos: 2 diciembre 1979, 11 noviembre 1979, 2 septiembre 1979, 6 julio 1979, 18 noviembre 1979, 15 octubre 1979, 15 septiembre 1979, 11 octubre 1979 de la misma localidad del tipo (M. Jiménez); 9 mayo 1981, Tepeoco, Hgo. (F. Garduño); 20 enero 1978, Tepoztlán, Mor. (E. Méndez); Lagunillas, (C. Martínez). El tipo será depositado en la colección del Laboratorio de Acarología (Facultad de Ciencias, Universidad Nacional Autónoma de México), con excepción de un paratipo que será depositado en la Colección Nacional Canadiense, Ottawa, Canadá.

Macho.—Longitud total 6.6-9.0 mm; longitud del caparazón 3.3-4.5 mm, y anchura 2.3-3.2 mm (6 ejemplares) de color café oscuro con una banda longitudinal media que pasa entre los ojos posterolaterales, en su interior hay una línea oscura y dos manchas tenues, anteriores a cada lado de ésta; lateralmente se observa una banda clara y una oscura cerca del borde del caparazón; área ocular oscura, ojos anteromedios y anterolaterales del mismo tamaño; ojos posterome-dios más grandes que los posterolaterales; los ojos de la línea anterior, levemente procurvados y cuya longitud es menor que la de los ojos lateroposteriores; caparazón sedoso; quelíceros robustos y con sedas largas, claras y oscuras; retromargen y promargen del artejo basal con tres dientes; esternón amarillo café con escasas sedas oscuras, femur I 2.3 mm, con 2 espinas medias dorsales, 3 distodorsales, 0 ventrales; tibia I 2.1-2.8 mm, sin espinas dorsales, 2 lateroexternas, 2 laterointernas, 3 pares ventrales; basitarso I 1.9-2.7 mm, sin espinas dorsales, 2 pares ventrales; 3 distoventrales, escasa escópula blanca; femur II 2.2-2.8 mm, con 3 espinas dorsales, 2 laterointernas, 1 lateroexterna y 0 ventrales; tibia III 1.5-1.8 mm con 2 espinas dorsales, 2 laterointernas, 2 lateroexternas y 3 ventrales; opistosoma café con manchas claras, vientre pálido; émbolo del pedipalpo truncado y con la punta delgada y curva (Fig. 7), palea poco esclerozada, apófisis media con un espolón basal y dirigido distalmente (Fig. 8), lóbulo tegular con dientes en su borde externo (Figs. 5, 6).

Hembra.—Longitud total 7.8-10.7 mm, longitud del caparazón 3.5-4.6 mm y ancho 2.4-3.2 mm, (6 especímenes). Estructura general y color esencial como en el macho. Placa epiginial ancha, con los extremos curvos de la pieza basal del septo medio, atrio ocupado por escleritos cóncavos brillantes; tubos copuladores delgados y espermatecas bulbosas alargadas, extendiéndose hacia los lados cerca del margen del epiginio (Figs. 9, 10).
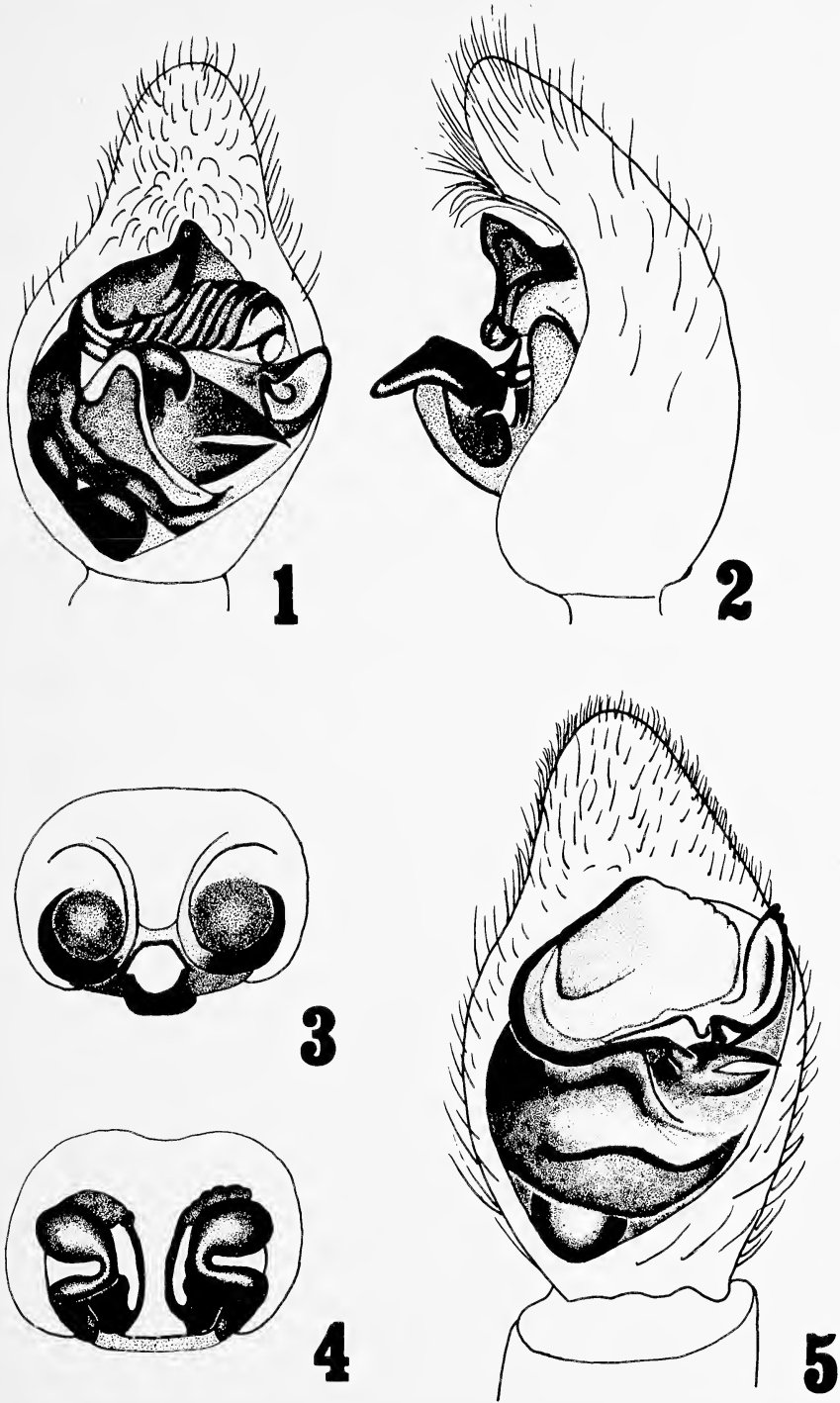
Figs. 1-4.—*Varacosa avara* (Keyserling): 1, pedipalpo vista ventral; 2, pedipalpo vista lateral; 3, epiginio vista ventral; 4, epiginio vista dorsal.
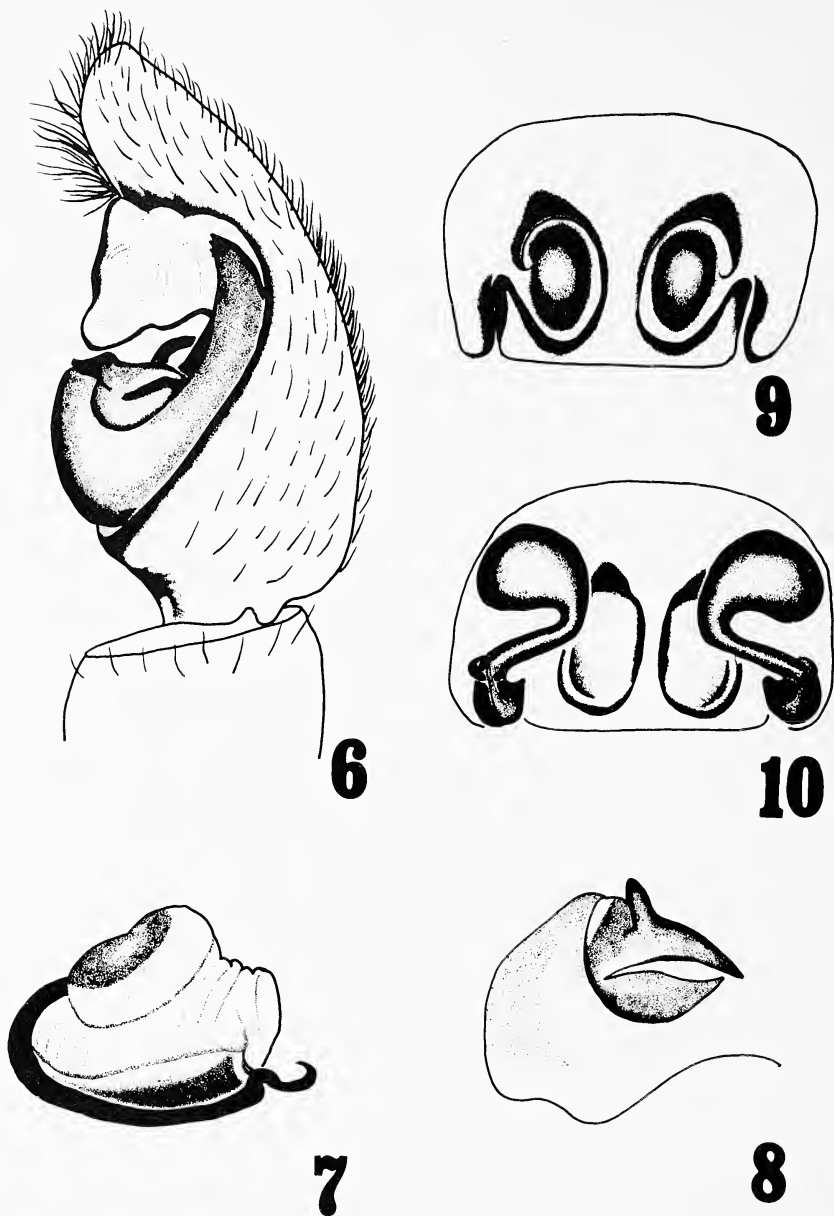
Figs. 5-10.—*Varacosa hoffmannae* sp. nov: 5, pedipalpo vista ventral; 6, pedipalpo vista lateral; 7, émbolo vista ventral; 8, apófisis media, vista ventral; 9, epiginio vista ventral; 10, epiginio vista dorsal.

DISCUSION

La característica común que agrupa a los géneros *Varacosa*, *Trochosa*, *Hogan* (donde inicialmente fueron colocadas las especies americanas de *Schizocosa*), *Geolycosa* y *Schizocosa* es poseer un gran lóbulo tegular. Sin embargo, *Trochosa* se distingue, especialmente del género *Varacosa* por presentar la punta del émbolo en forma de rizo y por tener espermatecas delgadas y aguzadas.

Los especímenes de *Varacosa hoffmannae* sp. nov. se parecen a los de las otras especies de *Varacosa*, pero se distinguen por presenter un lóbulo tegular delgado;

el espolón basal de la apófisis media se dirige distalmente; espermatecas alargadas que se extienden hacia los lados cerca de las márgenes del epiginio.

Distribución.—Conocida sólo para las localidades de los tipos y paratipos.

Etimología.—Se dedica esta especie a la Dra. Anita Hoffmann del Laboratorio de Acarología, U.N.A.M., México, por el impulso y el apoyo que ha dado al conocimiento de las arañas mexicanas.

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SENESCENCE OF WEB CONSTRUCTION BEHAVIOR
IN MALE *FRONTINELLA PYRAMITELA*
(ARANEAE, LINYPHIIDAE)

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ABSTRACT

Female bowl and doily spiders, *Frontinella pyramitela*, build species-typical webs throughout their lives. In contrast, males of the species cease the construction of prey capture webs soon after they become adults, though they continue to be capable of producing sperm-induction webs and draglines. In this report we describe the timing of the senescence of web construction, analyze the structure and utility of the webs built by adult males, and eliminate two variables, mass at maturity and adult feeding history, as important contributors to the variability in rate of senescence.

INTRODUCTION

The species-typical prey-capture web of the bowl and doily spider, *Frontinella pyramitela* (Walckenaer), consists of a concave upward, bowl-shaped sheet that lies between two silken meshworks. The upper of these can be vertically quite extensive and acts as a knockdown structure, while the lower of the meshworks (the doily) appears to function primarily as an anchoring structure to which the bowl is attached. Tension in threads (called "tensors") that are attached both to the bowl and to the doily cause deformation of the otherwise flat sheet and give the sheet its characteristic shape and tension profile (Suter 1984).

Until recently, it had appeared that male *F. pyramitela*, like most other male spiders (Savory 1928; Opell 1982), ceased building prey-capture webs upon molting to adulthood, and thereafter built only draglines and sperm-induction webs. But a recent report (Hirscheimer and Suter 1986) has indicated that this species is relatively unusual among the Araneae in that adult males readily build prey-capture webs under laboratory conditions. In that respect, *F. pyramitela* resembles a uloborid species (*Uloborus* sp.) in which adult males also build prey-capture webs (Eberhard 1977).

We report here the results of investigations into the characteristics of webs built by adult male bowl and doily spiders and into the timing of the cessation of prey-capture web-building by males.

MATERIALS AND METHODS

Animal manipulations.—During the last half of April, 1985, 64 immature bowl and doily spiders were captured from webs in the vicinity of Vassar College,

Poughkeepsie, New York. They were reared to adulthood during the subsequent few weeks on webs of their own making and on a diet of vinegar flies (*Drosophila melanogaster*). Every morning and evening, we checked each web for the presence of a newly shed exuvium and the emerged animal, if adult, was weighed under CO_2 anesthesia and sexed. Adult males were immediately transferred to plastic cylinders 10.2 cm in diameter and 15.3 cm long. These enclosures were sealed on both ends with polytheylene plastic wrap held in place with elastic bands and were placed on a platform that kept their long axis in a horizontal orientation. Males so enclosed were checked every 12 h. We evicted (with a water gun) a male from its cylinder if it had built a prey-capture web since the last check or if it had been in the cylinder for more than 48 h without constructing a web. Because the spiders would not, and perhaps could not, attach silk to the plastic wrap that enclosed the cylinders, we could remove the wrap on both ends to facilitate eviction of the spiders without damaging the newly-constructed silk.

We placed each evicted male on the vacant web of an immature conspecific and there fed it one vinegar fly prior to transferring the spider to a fresh cylinder. (A subset consisting of five adult males was manipulated as described, but was not fed at all during adulthood.) Males remained in this build-evict-feed-new cylinder cycle until they failed, during 48 hours of occupancy, to construct anything more complex than draglines.

Web manipulations and analyses.—Webs of adult male spiders were preserved intact in the cylinders in which they had been constructed. We lightly dusted the majority of these with air-blown cornstarch, then photographed them using standardized backlighting, lens, and web-to-focal plane distance. The negatives derived from this procedure were mounted perpendicular to the beam of a helium-neon laser and the intensity of the beam, diminished in proportion to the density of the negative, was measured by a photocell and recorded by computer. The computer recorded between 300 and 1000 data points during the single vertical transection of each negative, smoothed the data by performing continuous averaging of 10-point series, and corrected for the background density of the negative. We analyzed the same negatives by direct measurement to ascertain knockdown diameters (= bowl diameters), knockdown height, and number of tensors attached to the bowl.

On the remainder of the webs, we used a hot needle to destroy the silk that connected a portion of the bowl sheet with both the knockdown meshwork and the underlying "doily". We then caught the freed section of bowl on the perimeter of a circular brass frame (diameter 1.5 cm). It adhered to the frame and could then be removed from the surrounding portions of the sheet without causing any visible distortion of the silken sheet that was attached to the frame. Each mounted bowl section was photographed under a dissecting microscope and the silk threads visible on the resulting negative were counted across two randomly chosen diameters. The two counts from a particular web section were averaged to derive a value of thread density for that bowl sheet.

RESULTS

During this study, 30 adult male bowl and doily spiders constructed 154 webs. Figure 1 shows that all of the males constructed at least one prey-capture web
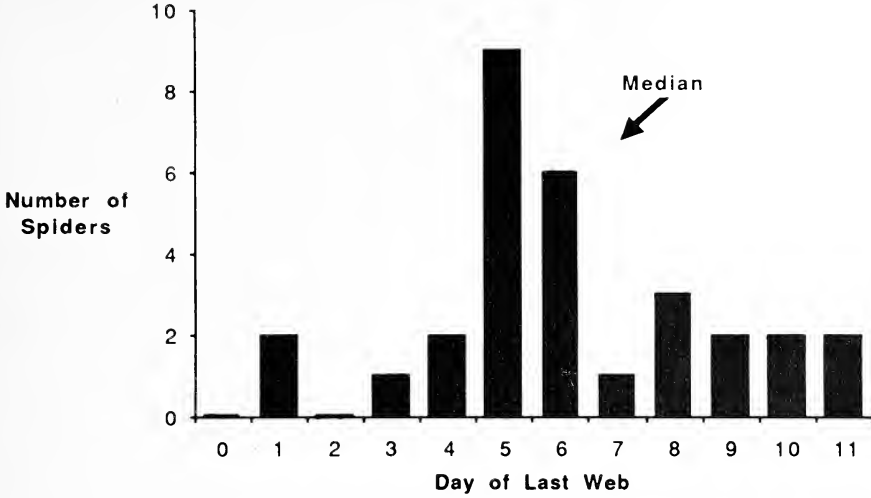
Fig. 1.—Longevity of web-construction behavior. Adult male bowl and doily spiders are capable of constructing prey-capture webs immediately after emergence as adults and under laboratory conditions may continue to build webs for up to 11 days thereafter. Most adult males cease web-construction on day 5 or day 6.

after the final molt, that no spider constructed webs after the 11th post-molt day, and that half the spiders ceased web construction at day 5 or day 6 (median = 6 days). The five spiders that had been starved during adulthood all ceased web construction between 5 and 5.5 days after the final molt (median = 5.5 days). There was no significant difference in the timing of cessation of construction between the starved and fed groups of adult males. Male mass, immediately after the final molt, was not correlated with the number of days of web construction (mean mass $\pm$ SD = 4.38 $\pm$ 0.7 mg; correlation coefficient = -0.006, $P > 0.05$).

Figure 2 shows the first (A) and last (B) webs built by a single spider after its final molt. The first of these is typical of initial prey-capture webs constructed by
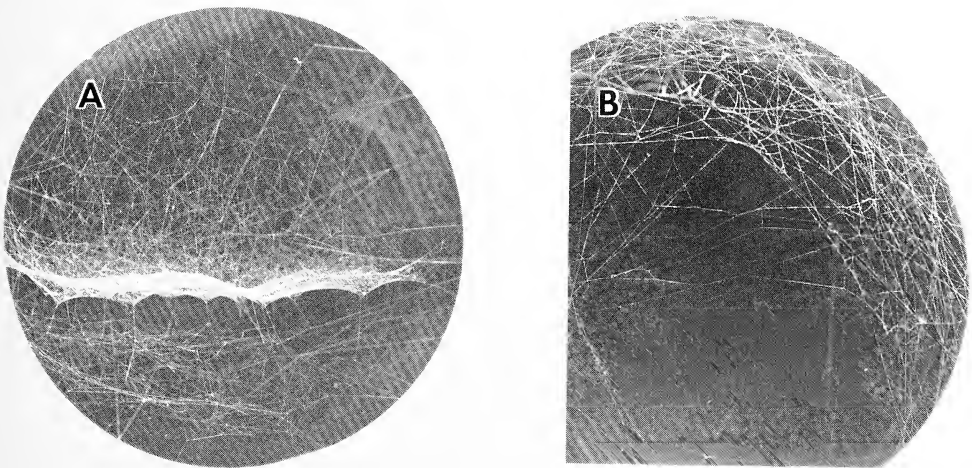
Fig. 2.—The first (A) and last (B) webs constructed by one male that ultimately built seven webs over the first 10 days of adulthood. Densitometric profiles of these and the spider's other five webs are shown in Fig. 3.
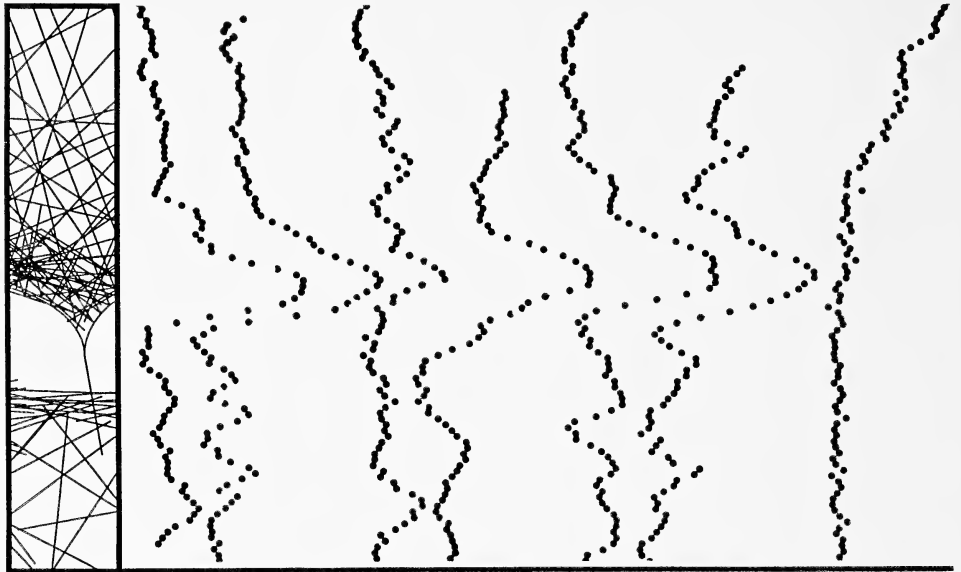
Relative Density

Fig. 3.—Densitometric profiles of the seven webs built by a single adult male over the first 10 days of adulthood. Each profile represents the densities measured along a vertical transect at approximately the middle of the web. For clarity of presentation, the maxima of the profiles are aligned with the maximum density of the schematic web that forms the ordinate. The first (left) and last (right) of these profiles correspond to the webs (A and B) shown in Fig. 2.

newly molted adult males. Though final webs varied more in size and structure, the web shown in Fig. 2B is not atypical. (Some final webs were little more than collections of draglines while others were more obviously prey-capture webs in that they contained a recognizable sheet). The data from densitometric analyses of all of the webs constructed by that spider are shown in Fig. 3. Densitometric profiles of 18 first webs and 21 penultimate webs are shown in Fig. 4 (penultimate rather than ultimate webs were analyzed as "late" webs because often the last web constructed was indistinguishable from a collection of draglines). The profiles represent means and standard deviations of the two sets of individual profiles which were aligned, for analysis, with respect to their maximum (highest density) values.

Of the 154 webs constructed in this study, 93 made up series that could be analyzed with respect to number of tensors, bowl diameter, etc. Using these 93 as our sample, we found that all measures, except bowl-silk density, decreased significantly as number of post-molt webs (and time) increased (Table 1).

DISCUSSION

All adult male bowl and doily spiders appear to be capable of constructing species-typical webs immediately after emergence as adults (Fig. 1). Webs constructed early in a male's adult life are superficially indistinguishable from those built by juveniles and adult females. The penultimate webs, and usually even the last webs of adult males, persist in having a species-typical form
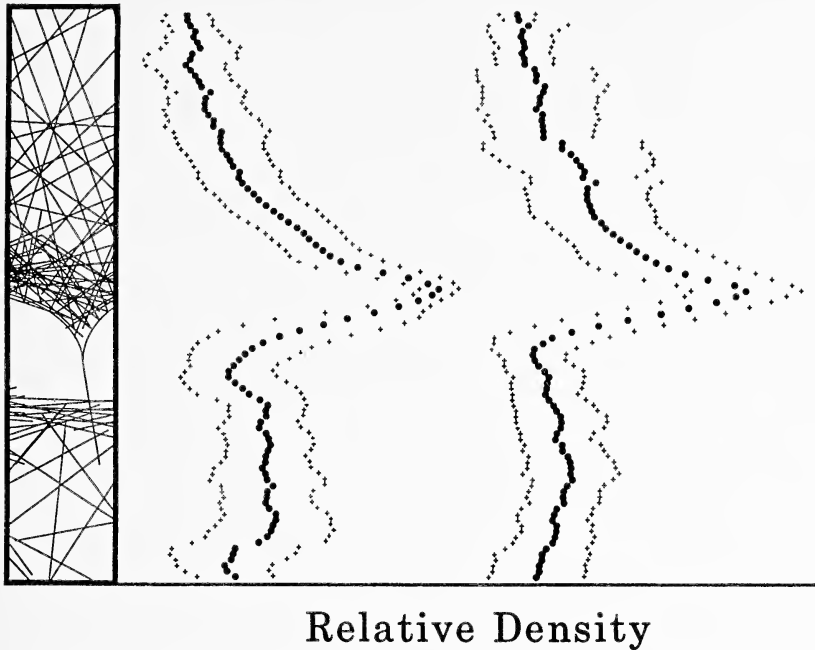
Relative Density

Fig. 4.—Means and standard deviations (point by point) of 18 first (left profile) and 21 penultimate (right profile) webs built by adult male bowl and doily spiders in the laboratory. The maxima of the webs were aligned prior to averaging. In both profiles, the species-typical prey-capture form is evident: an increase in density as the transect approaches the bowl from above, maximum density at the bowl, a rapid decrease in density as the transect leaves the bowl and passes through the space below the bowl where the spider normally rests, and an area of variable density occupied by the doily and its substructure.

consisting of knockdown threads, a bowl sheet, and a doily (Figs. 3 and 4). Despite this persistence of form, new construction by males changes measurably as the male builds additional webs: later webs are progressively smaller (decreased bowl diameters), flatter (fewer tensors), and can intersect the paths of fewer prey (knockdown silk less extensive) that the first web (Table 1). Because the utility of a web as a snare is limited both by its size (smaller webs intersect the paths of fewer prey) and its form (males cannot pursue prey as rapidly in a meshwork of threads as they can under the surface of a sheet), the value of web-construction to a male *F. pyramitela* must decrease as the male ages.

For the males used in this study, which became adults early in the reproductive season, differences in mass did not influence the length of time spent in the web-construction phase of their adulthood. Even with large differences in adult male mass (3.3 to 5.8 mg) we could demonstrate no correlation between mass and web-construction behavior.

Hirscheimer and Suter (1986) suggested that the time and energy spent by an adult male *F. pyramitela* in web construction would be minimized by a male that was large because its chances of discovering and productively fertilizing a female were high. The rationale behind that suggestion was that a larger male has greater nutrient and water reserves for the lengthy search that may be necessary and, if the search is successful, a greater probability of being able to displace a male already in residence (Austad 1983, Suter and Keiley 1984). A smaller male, in contrast, might benefit by increasing its mass through web-construction and

Table 1.—Correlations of web structure variables with sequence of construction. In all tests, N = 93 webs.

Variable	Range	Corr. with Seq.	Probability
Knockdown Height (cm)	0 - 9.5	−0.56	< 0.001
Knockdown Diameter (cm)	0 - 8.4	−0.66	< 0.001
Capture Area (H × D) (cm^2)	0 - 68.7	−0.54	< 0.001
Number of Tensors	0 - 15	−0.61	< 0.001
Bowl Silk Density (threads/mm)	1.3 - 5.2	−0.10	> 0.05

predation, and only then beginning the search. For all sizes of males, there would be pressure to begin the search early because previously inseminated females are reproductively less available to subsequent males - first male sperm priority characterizes the reproductive dynamics of bowl and doily spiders, and a secondary male can fertilize no more than 5-10% of the lifetime reproductive output of a female (Austad 1982).

Apparently, under laboratory conditions at least, the senescence of web-construction behavior is neither significantly hastened in larger male bowl and doily spiders nor delayed in smaller ones. Yet it is unlikely that newly molted males remain on their own webs for five or six days under natural conditions. The first adult males we have found on webs in the spring are found cohabiting with females, not alone on what could be male-constructed webs, and throughout the season adult males are rarely seen alone on webs. Thus we conclude that a) many adult males found on females' webs in the field are physiologically and behaviorally capable of constructing prey-capture webs and b) the conditions that could elicit early abandonment of webs in the field (e.g. unavailability of prey, desiccation, freedom of movement) are not present in strength in the laboratory. Supplemental feeding and misting experiments on marked males in the field may be able to elucidate the variables that stimulate early abandonment of male-constructed webs.

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UTILIZATION OF RESOURCES BY THE MALE GOLDEN ORB-WEAVING SPIDER *NEPHILA CLAVIPES* (ARANEAE)

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ABSTRACT

Two experiments were performed in order to evaluate the influence of female *Nephila* on various aspects of male activity. In the first experiment, the possible benefits of females' presence were measured in terms of male longevity. In the second, food deprived and sated males were offered a choice of mating or feeding with a receptive female.

In the first experiment, groups of individually-housed males were provided with: regularly fed females with which to mate and share prey and silk, freshly killed prey and female silk with no female, female's silk alone, or nothing at all. Solitary males provided with prey and silk lived longer than those in other groups: feeding on silk alone did not affect longevity. Males provided with females lived longer than those without. No significant relationship between body size and longevity was noted in either summer.

In the second experiment, two groups of male *Nephila* were deprived of food for a week. One group was then fed prey partially eaten by a female. Males were then placed on females' webs with prey to determine the influence of deprivation on orientation towards prey or female. Males generally preferred to mate first, even when deprived of food for a long period of time. Observations were made to determine if specific pre-copulatory behaviors exist, and body jerking (violent, rapid shaking with first two sets of legs often jumping on and off the silk) was observed to occur primarily before mating. Other indicators of arousal, such as abdomen wagging or shaking, and exploratory behaviors such as plucking or probing, occurred equally often before mating and feeding.

INTRODUCTION

For most orb-weaving spiders, mating occurs on the female's web, as the adult male ceases building and repairing his own web and adopts a strategy of searching for mates (Christenson and Goist 1979). Though the adult male orb-weaver is not generally considered a predator, he has ways of meeting nutritional needs: feeding on prey that the female has captured (Robinson and Robinson 1980; Christenson et al. 1985), the occasional appropriation of webs from conspecific or related species and trapping prey there (Eberhard, Barreto, and Pfizenmaier 1978), and ingestion of female silk (Vollrath 1980). Female silk ingestion by males have been observed in *Nephila clavipes* (Linnaeus) (Vollrath 1980), in *Leucauge mariana* (Keyserling) (Eberhard pers. comm.) and *Verrucosa arenata* (Walckenaer) (Levi 1976).

It is not clear what males gain from feeding while on the female web. The strategy of searching for a female consumes energy, as does competition between males. The largest male on a given female's web may take up a position in the support strands near the hub, directly above the female (Christenson and Goist

1979). Hub males feed on prey trapped by the female more frequently than do the smaller males who remain on the web periphery (Christenson and Goist 1979).

It is logical to expect that feeding on prey would increase male longevity, but the payoff from silk ingestion is not as clear. In *Araneus diadematus* (Clerck), nearly all of the material the female needs for new web construction can be gotten from consuming, often within a few minutes, the previous day's web (Peakall and Witt 1976). It appears in this case that ingested silk is used for silk production (Foelix 1982); however, silk from naturally occurring webs may be coated with pollen and other microorganisms which may be nutritionally valuable (Smith and Mommsen 1984).

The first question we ask (from census data) is how frequently do males ingest silk and prey and do hub and peripheral males differ in rates of ingestion. Second, we ask (in Exp. 1) if silk and/or prey ingestion influences male and sperm longevity. We exposed males to four feeding conditions: males housed continuously with a regularly fed female, males housed alone but provided with freshly killed prey, males housed alone with female silk, and housed with no prey or silk. As feeding is a variable which contributes to body size, we also asked if male body size is related to longevity.

Female *Nephila* are receptive to the advances of the male in two situations: immediately upon completing her final molt, and when feeding throughout adulthood (Christenson and Goist 1979, Christenson et al. 1985). Robinson and Robinson (1980) note that males feed on the female's prey item or copulate with the female while she is feeding. Virtually nothing is known about the regulation of this male choice, to feed or to mate. The third question we ask (in Exp. 2) is if the immediate feeding status of the male influences his tendency to mate or to feed. Males that were food deprived or recently fed were placed with adult females who were feeding and thus sexually receptive.

As mating may occur while the female is feeding in many species, there is a potential confusion between male courtship behavior and male pre-feeding behaviors. As there is little predation on males by females (Christenson et al. 1985), it is likely that there are cues from which females may be able to distinguish potential mates from potential prey. The fourth question we pose (in Exp. 2) is do males respond differently when mating or feeding on the female's prey item.

METHODS

Census data.—To estimate the frequency of silk and prey ingestion by males in an unrestrained population, free-ranging but individually marked males ($n = 116$) and females ($n = 99$) were observed daily through July and August, 1984, at the Tulane University Hebert Center near Belle Chasse, Louisiana. Incidences of silk and prey consumption by hub and peripheral males were recorded as part of a daily census. A total of about 1425 male/census datum points was gathered. A day's set of observations for each male was considered one male-day. The following summer, 517 additional free-ranging males at Jean LaFitte National Historical Park in Barataria, La. were also observed for incidents of silk and prey consumption. These males were not marked and not followed daily.

Experiment 1—Male and sperm longevity.—In 1984, thirty-eight adult male *Nephila clavipes* were gathered at the Tulane University Hebert Center between

14 and 16 July. In 1985, 45 additional males were gathered at the Barataria site, between 4 and 9 July. All subjects had just completed their final molt, determined by change in palp structure and body coloration, and at least one sperm web was present on their web. Thus, all subjects were of approximately the same age-within a day or two of the final molt. Cephalothorax-abdomen length and tibia-patella lengths were recorded.

Subjects were housed in 123 × 62 × 62 cm boxes, completely enclosed with Fiberglas screen. Males that were to be housed with females were placed one to a box with a randomly selected mate. The subjects in the other groups were housed in three Fiberglas-screened boxes, subdivided into twelve 30 × 30 × 30 cm cells. Each group was housed in a separate box, one male per cell.

Ten subjects were randomly assigned to each of four groups: **Female group**, in which the female was supplied daily with one or two mealworms; **Prey-Silk group** which every other day received a mealworm and female web silk mostly from the viscid spiral; a **Silk group** which every other day received only female silk; and a **Nil group** which received nothing. Subjects to be housed alone were placed in cells counterbalanced by size so that each box contained four small, medium, and large males. Males with a cephalothorax-abdomen length of up to approximately 8.0 mm were classified as small, between approximately 8.0-10.0 mm medium, and greater than 10.0 mm large.

Prey-Silk subjects received web and prey taken from an unrestrained female *Nephila* between 0800 and 1000 hours. A single mealworm was placed in a female's web, and after approximately fifteen minutes of feeding by the female, or when the prey appeared dead, part of the non-sticky barrier strands were removed and a wooden dowel cross (20 cm between the tips of the arms) was swept through the viscid spiral and rotated several times, winding most of the spiral onto the cross. This provided a thick net of support for the mealworm. The cross was then placed upright in the center of the appropriate male's cell. Silk subjects received a cross with female silk obtained in a similar manner, and Nil subjects were given a plain dowl cross.

On the day of prey and/or silk replacement, a one-minute observation of each male was made every hour, beginning fifteen minutes after the last male had been fed. There was approximately four observations each day in which incidents of prey or silk consumption were recorded. A day's set of observations for each boxed male was considered one male-day. Every morning, a census was taken in which feeding, deaths, or disappearances were noted. Data were collected until every animal had died or had disappeared.

Sperm analyses.—One subject from the Prey-Silk group, and one from the Nil group (1985 subjects) were returned to the laboratory every other week for three weeks (total of three from each group) to determine any effect upon sperm development within the palp. Six males were also removed from the Female group over the same period of time. Sperm were evaluated with a Leitz® phase-contrast microscope following methodology described in Christenson, Schlosser, Cohn and Myers (1986).

Ants attracted to the partially eaten prey were a problem, and it was impossible to determine whether missing subjects had escaped, or had died and been carried off. Statistical analyses were conducted on the data from confirmed deaths.

Experiment 2—Male feeding and mating courtship.—Twenty adult male *Nephila* were gathered approximately 20 km south of Belle Chasse at the Jean

Lafitte National Historical Park in Barataria, LA, during August, 1985. Previous mating experience was unknown. They were housed individually in 123 × 62 × 62 cm boxes completely enclosed with Fiberglas screen. Ten adult female *Nephila* were also collected at the Barataria site and housed singly in additional enclosures. Reproductive history of these spiders was also unknown.

All of the males were deprived of prey for one week. On the day of testing, the females were given mealworms and allowed to feed for 15 min, whereupon the mealworms were removed and placed singly in plastic vials. Males were then placed in a vial either alone (unfed group; $n = 10$), or with a partially eaten mealworm for 15 min of observed feeding (fed group; $n = 10$). Individual males were moved to a female's web in which a fresh mealworm had been placed just below the hub. The following male behaviors were recorded during a 30 min period: abdomen wag (tip of abdomen), shake (vibrating the entire body while maintaining contact with the web with all eight legs), body jerk (more violent, rapid shaking with first two sets of legs often jumping on and off the silk), probing and plucking (with forelegs).

To insure that the behaviors were oriented towards prey or female, only behaviors that occurred within the five minutes before copulation or a feeding bout were included in the analyses. During this five minute period, behaviors were scored as 1/0, a 1 given if the behavior occurred, a 0 if not. This was done because of the difficulty in recording each occurrence of some behaviors, for example wags, where a series was recorded as "repeated wags", without an actual count.

RESULTS

Male feeding: Description and frequency.—Males who consumed silk gathered in their chelicerae silk from the upper portions of the viscid spiral or from the outer barrier strands. This silk was formed into a small ball which was continuously worked in the chelicerae until consumed completely in about one hour. Female *Nephila*, in contrast, consume silk at a much faster rate. Portions of their webs are taken down and ingested all within a few minutes. The following are very conservative assessments of the frequency of male ingestion of female silk, since the silk ball is clearly visible only for 15 or 20 minutes after it is formed.

During the census of unrestrained animals, there were nine recorded incidents of silk eating in 240 observations of peripheral *Nephila* males, and six in 1185 observations of hub males over the 1984 summer census of free-ranging males at the Hebert center. There was a significant difference in the rate of observed consumption of silk between hub and peripheral males ($X^2_1 = 19.332$; $p < 0.001$). Peripheral males consummed silk at a rate of 3.7 per 100 male-days. Hub males consummed silk at a rate of one per 200 male-days.

In observations of free-ranging males at the Barataria site (1985), silk ball ingestion was recorded 20 times in 415 observations of hub males, and 9 times in 106 observations of peripheral males. A Chi-square analysis of these data showed no difference in the proportion of hub vs. peripheral males who ate silk ($p = 0.35$). The rate of observed consumption of silk by hub and peripheral males was approximately 8.5 per 100 male-days.

The 1984 census of free-ranging males at the Hebert center resulted in approximately sixty observations of prey items in female's webs. Of these female webs with trapped prey, four observations of males feeding were made. The rate of observed feeding on prey by free-ranging males in this population was approximately seven per 100 male-days.

Feeding and longevity.—There were approximately 1100 male-days of observations of boxed males with access to prey (Prey-Silk, and Female groups). The rate of prey consumption by all boxed males was approximately two per 100 male-days. There were 22 observations of boxed males feeding upon prey (12 in 1984 and 10 in 1985). Fifteen of these observed feedings occurred in males housed with females (seven in 1984 and eight in 1985). The rate of observed feeding males housed alone (Prey-Silk group) was approximately two per 100 male-days. The rate of observed feeding males in boxed males housed with females was also approximately two per 100 male-days.

Over both seasons, two observations of silk eating were made in the Prey-Silk group, and two were made in the Silk group. The rate of observed silk consumption was approximately one per 250 male-days. This was substantially lower than the rate obtained for free-ranging males (eight per 100).

Mean longevity of the males is reported in Table 1. A one-way ANOVA conducted on 1984 males which were housed singly was significant ($F_{2,17} = 5.4531$, $p = 0.015$). Neuman-Keuls analyses of the three groups showed a significant difference between the Prey-Silk and Nil groups ($p = 0.012$), and between the Prey-Silk and Silk group ($p = 0.039$), but not between the Silk and Nil groups ($p = 0.322$). Though the males in the Male-Female group lived almost two weeks longer than the Prey-Silk group, this difference was only suggestive ($p = 0.08$).

In 1985, a significant difference in longevity was found only between the males with females versus those without ($F_{3,21} = 23.855$; $p < 0.0001$). Neuman-Keuls analyses indicated no significant differences in longevity past final molt between the Prey-Silk and Silk groups ($p > 0.99$), Prey-Silk and Nil groups ($p = 0.41$), or the Silk and Nil groups ($p = 0.33$). The mean longevity of the males indicated a slight trend in the predicted direction, identical to the more significant results obtained the previous summer (Table 1).

Effect on sperm.—Analysis of the sperm in palps from deprived and fed males showed no obvious differences in either their number or structure. Slide preparations of sperm from fed and deprived males were filled with coiled sperm.

Size and longevity.—Size was not significantly correlated with longevity in any of the groups. The mean body length for the 30 individually housed males collected at Belle Chasse was 8.8 mm and the mean tibia-patella length was 6.8 mm. The Barataria males' mean body length was 8.9 mm, and mean tibia-patella length was 6.9 mm. When body length and tibia-patella length were correlated with days of survival past final molt, no significant relationship was found in any of the groups.

Male choice: To feed or to mate.—Of twenty males in this study, fifteen preferred to mate first, four preferred to feed first, and one neither fed nor mated ($X^2_2 = 16.3$; $p < 0.001$). Feeding status did not influence males' orientation towards prey or female ($p = 0.36$); they generally preferred to mate even after having been deprived of food for a week. Of ten males in the Fed group, nine mated first, one fed first, and one male neither fed nor mated during the

Table 1.—Mean longevity for males in each group in each season of observation (days). *n* refers to the number of confirmed deaths in each group, SD = standard deviation.

	Nil Group			Silk-Only			Prey-Silk			With Female		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD
1984	22.1	9	7.3	27.3	6	5.3	38.8	5	14.5	52.6	8	13.1
1985	21.6	6	7.2	23.3	7	11.7	28.9	8	8.0	68.8	4	12.7

observation period. Of ten males in the deprived group, seven preferred to mate and three preferred to feed before any other activity.

Male responses when feeding versus mating.—The following analyses were based on 15 males who mated and four who fed when placed on the web with their females. Only data from the males' first activity (either mating or feeding) were counted, although one male (sated) fed first then mated, and three males (deprived) mated first, then fed. The data from the male who neither fed nor mated were dropped from the analyses. Only three males fed without first mating during the observation period, one from the sated group, and two from the deprived group. Abdomen wagging, body jerking, probing, shaking, and plucking were observed in both groups. Their appearance was not dependent upon their feeding status ($p = 0.94$; $p = 0.90$; $p = 0.91$; $p = 0.81$; $p = 0.21$ respectively). However, when the data were collapsed across treatment, it was possible to evaluate whether or not a behavior would occur significantly more often before the subject mated or fed. Wagging, probing, shaking, and plucking were no more likely to occur before mating than before feeding ($p = 0.28$; $p = 0.83$; $p = 0.21$; $p = 0.11$). Body jerking, however, was almost exclusively pre-copulatory and was observed prior to feeding only three times, twice after the male had first copulated ($X^2_1 = 8.872$; $p = 0.003$). Only one incident was observed in which a male copulated without first body jerking.

DISCUSSION

Results indicate that feeding on prey increases male longevity. This should increase the likelihood that a male lives until the female becomes sexually receptive or until he can move from female to female. The costs to the hub male of feeding are minimal since few males are killed by a female while trying to feed on her prey, and since hub males are killed by the female no more frequently than smaller, peripheral males (Christenson and Goist 1979). Silk ingestion, in contrast, appeared to have little affect on male longevity, at least with our subjects who were confined to a cage and not allowed to move long distances. This implies that naturally occurring microorganism attachment to female silk is insufficient to make a significant impact on the longevity of adult male *Nephila*.

Conservative estimate of silk consumption by the boxed males may have been partially responsible for the difference in observed silk ingestion between boxed and free-ranging males, as the Fiberglas screen made it difficult to observe whether the males were consuming silk. Another possibility may be greater silk and/or energy requirements in free-ranging males. As ingested silk is primarily used to produce new silk (Foelix 1982), less would be needed by males whose locomotor activity is reduced through confinement.

The data indicate a substantial difference in the rate of observed silk consumption between the 1984 Belle Chasse census data and the 1985 Barataria data. There are three possible explanations for the difference. First is that there was a seasonal variation in the severity of winter, 1985 being severe and killing most overwintering instars. Prey availability, growth rates, and feeding patterns could have been affected. Second, perhaps there are population differences between the Belle Chasse and Barataria animals. Mating and egg-laying do seem to begin earlier in the summer in the Barataria population. Third, although unlikely, differences in methodology could account for the discrepancy between the Belle Chasse and Barataria data. Belle Chasse males were marked and followed daily over the summer, while the Barataria males were unmarked and from different areas of the park. It is not clear what, if any difference this could make in terms of observation of silk consumption, but it does merit noting.

Males live longer when housed with females. This underscores the importance of females in controlling resources important to male reproductive success. This advantage may be due to female protection from potential predators such as ants, and/or to enhanced ability to feed as prey are located near the female. Vibratory and/or chemical cues provided by the female undoubtedly assist the male in locating available prey (Krafft 1982). The absence of these cues in the three groups of males housed alone might reduce the opportunities to feed in the Prey-Silk group, despite the presence of freshly killed prey.

As a male on a female's web will spend a great deal of energy monitoring her as well as his environment (Christenson and Goist 1979), his nutritional requirements will be higher than that of a male housed alone in a relatively confined space. This may also partially account for the greater number of observed feedings in males housed with females. As the rate of observed prey consumption was approximately the same, however, other as yet undetermined benefits of the presence of females may contribute to increased male longevity.

There was a somewhat large difference in the rate of observed feeding between boxed and free-ranging males. This difference may be related to the frequency of prey availability in each population. The females in the boxes were extremely well fed in comparison to free-ranging *Nephila*. Free-ranging males have fewer opportunities to feed relative to boxed animals, therefore when a free-ranging female is observed with a prey item, the probability of the male attempting to feed with her (as assessed through our census methods) may be higher than what occurs in the boxed animals. It would be necessary to supply free-ranging spiders with prey at a rate comparable to that supplied to the boxed animals in order to obtain a clearer indication on the effect captivity may have on rate of prey consumption by males and females.

Body size is not directly correlated with a specific male's lifespan. However, in a natural setting, size is the predominant factor in determining which male will achieve hub status and the opportunity to feed (Vollrath 1980). It is, therefore, size relative to one's conspecifics on a given female's web which determines mating, feeding, and in part, longevity.

When given a choice between mating and feeding, males prefer to mate. It appears that activities such as abdomen wagging and shaking are not specific pre-copulatory behaviors, but indicative of general arousal. Vibratory signals are integral components of feeding and mating behaviors in orb-weaving spiders (Robinson 1982). Probing and plucking with forelegs were usually observed to

precede contact with either the prey or the female, and probably are used to obtain vibratory cues from the web (Krafft 1982).

The selective occurrence of body jerking suggests that there may be specific pre-copulatory responses in male *Nephila*. The behavior is similar in form to shaking, which seems to be a reaction to arousing stimuli. However, intensity of general arousal is not sufficient to produce the body jerking response, as males do not do it when subjected to significant disturbance. When chased about the web with the tip of a fine paintbrush males will abdomen-wag at a rapid pace, and if tapped lightly with the tip they will shake violently. This activity produces a rapidly vibrating web which makes it difficult to see the animal (personal observations). Body jerking is not observed in these situations and appears to be specific to the mating situation.

ACKNOWLEDGEMENTS

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ATTENDANCE PATTERNS, PREY CAPTURE, CHANGES IN MASS, AND SURVIVAL OF CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE) GUARDING THEIR NESTS

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ABSTRACT

Crab spiders *Misumena vatia* typically guard their nests after laying eggs. Individuals that disappeared from their nests before their young emerged had similar laying dates, pre- or post-laying mass, egg mass, or reproductive effort to those that remained. They included both individuals that actively left the sites and ones that died.

Spiders lost mass constantly through the guarding period, but total losses in the field did not approach those from the laboratory and were unlikely to be the primary source of mortality. Few spiders caught prey during this time, and those captures had little effect on the rate of loss. Small day-to-day fluctuations in mass were largely a result of changes in moisture availability.

INTRODUCTION

The period between which an animal lays its eggs or gives birth and the resulting young become independent is likely to be a time of high vulnerability to these offspring. Not surprisingly, many species protect their reproductive investment during this stage (reviewed by Morse 1980). If an animal produces only one clutch of offspring, the period takes on particular importance. However, a variety of possible trade-offs exists between parental care and reproductive effort (mass of eggs or offspring/mass of parent before laying or birth), if care is not obligate. Animals with a low reproductive effort might guard the eggs or young more effectively than those making a high effort. Individuals that hunted during this period might thereby improve their body condition and thus be able to defend offspring more effectively at other times. Surprisingly, very little information exists on how individuals of a population that differ in their reproductive effort, reproductive output (mass of eggs or newborn offspring), and related variables respond to these differences subsequent to reproduction (e.g., Stearns 1977, 1980). It is thus important to obtain basic behavioral information about individuals that exhibit different reproductive attributes at this stage. In addition to filling vital gaps in our understanding of post-reproductive behavior, such information may eventually even provide valuable insight about the forces dictating the evolution of semelparous and iteroparous reproductive systems.

Here I describe the patterns by which semelparous crab spiders, *Misumena vatia* (Clerck) (Thomisidae), guard their egg masses. I have discussed other

aspects of the life history of this species in detail elsewhere (Morse and Fritz 1982, 1987; Morse 1984, 1985a; Fritz and Morse 1985). These spiders vary in their patterns of attendance at their nests, and they also vary in several attributes related to reproduction: date of laying, mass before and after laying, mass of eggs, and reproductive effort (Fritz and Morse 1985). Specifically I concentrate here on activity and length of attendance at the nests, prey capture, changes in mass during the period of attendance, and survival while at the nests. The results allow me to test the hypothesis that the spiders adjust their nest attendance in a way that accommodates for differences in pre-reproductive success (prey capture: Morse and Fritz 1982) and reproductive success (size of egg mass: Fritz and Morse 1985). Earlier (Morse submitted), I established that guarding increases reproductive success of these nests, largely by lowering the frequency of loss to ichneumonid and dipteran egg predators. Further, large spiders guard more successfully than smaller ones.

All of these results assume additional interest in that differences in body size and egg mass size are a consequence of differences in foraging success and, earlier, in hunting-site decisions (Morse and Fritz 1982; Fritz and Morse 1985). Thus, it is possible to relate the behavior observed about the nest to a few earlier key events in the life cycle and determine if these earlier events strongly influence subsequent performance.

MATERIALS AND METHODS

Adult female *Misumena* reach 10 mm in total length and biomasses of 200-400 mg or more (maximum recorded = 515 mg) prior to egg laying. Before laying their eggs they are sit-and-wait predators at flowers that attract large numbers of insects. Nest-attending females used in this study were observed during the summers of 1980-1985 in Bremen, Lincoln Co., Maine, USA. All of these individuals had hunted on common milkweed (*Asclepias syriaca* L.) flowers, their commonest mid-summer haunt in this region (Morse 1981; Morse and Fritz 1982).

In the study area, a large field with several milkweed clones (described in Morse 1981), spiders almost always built their nests on milkweed leaves (Morse 1985a). A spider about to lay its eggs first rolls under the tip of a medium-sized leaf and secures it with silk. Subsequently, it lays its eggs within the enclosure formed and secures the extremities of the leaf with silk until they are tightly opposed. It then usually rests on the under side of the nest, the former upper side of the leaf tip. Eggs are laid at night. I have described and illustrated the nests and their precise locations in detail elsewhere (Morse 1985a). Subsequently, the spiders guard these nests, sometimes until the young emerge from the nest in the second instar nearly a month later (Morse 1985a), often dying soon after (Gertsch 1939; Levi and Levi 1968).

Spiders were individually numbered on the posterior part of the abdomen with indelible ink prior to egg-laying and subsequently monitored and weighed regularly. As soon as they laid their eggs, they were weighed again, allowing calculation of the mass of the eggs and permitting an estimate of reproductive output and effort. Silk production amounts to only about 1% of the mass of the eggs (Fritz and Morse 1985) and was therefore not included in the calculations.

In 1980 and 1981 the egg masses were collected shortly after laying, weighed, and then dissected to measure egg number (Fritz and Morse 1985). Those parent spiders were brought into the laboratory at that time and, after counting and weighing, kept with their eggs in individual open-topped containers at 18°C-22°C until the eggs hatched. I returned the eggs to their egg sacs after handling; however, since this procedure required collecting the leaves and opening the sacs, the humidity of the eggs' environment was undoubtedly lower than those of egg sacs in the field. A randomly chosen sample of these adult spiders were subsequently weighed every few days, as were a few individuals similarly maintained in 1982.

In 1982-1985 virtually all of the individuals were monitored in the field. Those studied during 1982-1984 were weighed every other day prior to egg-laying, as soon as they laid their eggs, and thereafter every third day, always being returned immediately to their nests. On other days they were censused, and observations made of their location, behavior, and any evidence of prey captured. Information on survival and predation by adult spiders were taken at the time. Treatment of the spiders was similar in 1985, except that they were weighed only once subsequent to egg-laying.

In 1983, 21 spiders were confined to their nest-sites in large bags of white nylon tricot (25 cm wide x 30 cm long, (0.3 mm x 0.3 mm mesh)) as soon as they laid their eggs. They were then monitored similarly to the other spiders. Since ambient temperatures within the bags scarcely differed from those immediately around unmanipulated nests ($\bar{x} \pm SD = 0.1 \pm 0.1°C$, $N = 18$ measurements), these individuals provided a control against which to compare the biomass changes, survival and nest-abandonment of the other individuals monitored in the field.

Sizes of samples differ widely in the results, since many of the spiders were used in other studies that made them appropriate for analysis of only certain of the variables reported here.

RESULTS

Behavior of spiders attending nests.—Spiders usually remained on the under side of their nest, the most likely point of entrance to it by insect predators. During daily censuses in 1982-1985, I saw spiders on top of their nests only 65 times (usually in full sunlight during mid-morning) and in other nearby locations (up to 7 cm away from their nests) 37 times (in 3914 observations on 220 spiders); in all other instances they occupied the under side of the nest. Thus, in only 2.6% of the observations did individuals fail to attend in the commonest way. These were only occasional acts by the spiders exhibiting them, observed in 62 (31%) of the spiders for which census data existed. No individual was observed away from the under side of the nest more than five times. Of individuals seen away from their nest, 65% ($N = 37$) subsequently abandoned that nest, compared to 47% ($N = 183$) never seen away from it ($G = 4.84$, $df = 1$, $P < 0.05$). Individuals seen away from nests and those not seen away from nests did not differ in size before or after egg-laying, size of egg mass, or reproductive effort, however (Table 1).

Effect of handling on adults disappearing from egg masses.—If handling caused spiders to leave their egg masses, the disappearances recorded would be partly or totally an artifact. In that instance, numbers of disappearances recorded on the

Table 1.—Size and reproductive characteristics of spiders that were seen off nest one or more times and ones always seen on next.

Variable	Seen away from nest one or more times		Not seen away from nest			
	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$	N	t^1 or z^2	P
Size before egg laying (mg)	253.3 ± 65.5	32	220.0 ± 75.6	161	1.005[1]	>0.3
Size after egg laying (mg)	77.9 ± 21.1	35	75.2 ± 20.8	182	0.703[1]	>0.4
Size of egg mass (mg)	154.0 ± 49.1	32	146.0 ± 58.8	161	0.710[1]	>0.4
Reproductive effort (%)	65.1 ± 5.4	32	64.7 ± 7.8	161	1.310[2]	>0.1

[1]t-tests, two tailed (df = N-2)
[2]Wilcoxon pairs test, two-tailed

days immediately following weighings should exceed those of other days. In 529 spider-days (number of spiders x number of days censuses during 1982-1984), eight spiders (1.5%) disappeared from their egg masses between weighing and the next census one day later. Fourteen (1.3%) disappeared on the other days, which totaled 1092 spider-days. These two measures do not differ (G = 0.14, $df = 1$, $P > 0.7$, G-test); therefore, I conclude that the weighing procedure did not affect the tendency to abandon egg masses. These results are in accord with my observations that randomly-discovered *Misumena* nests often are unattended; i.e., disappearances occur naturally.

Characteristics of disappearing and remaining adults.—Almost one-third of the spiders disappeared from their nests before their young began to emerge (Table 2). Their lengths of attendance ranged from four days to individuals that disappeared only shortly before the young began to emerge ($\bar{x} \pm SD = 14.9 \pm 9.4$ days). Spiders that disappeared from their egg masses did not differ from those that guarded their egg masses until juvenile emergence (Table 2) in date of egg laying, mass before or after egg-laying, reproductive effort, mass of clutches, or rate of loss in mass subsequent to laying (Table 2).

Length of attendance.—Thirty-nine of the 71 spiders (55%) attending nests that I monitored through the dispersal phase of the young remained until the young

Table 2.—Characteristics of crab spiders that disappeared and remained on their egg masses until young emerged.

Variable[1]	Disappeared from egg masses		Remained on egg masses			
	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$	N	t^3 or z^4	P
Date of laying[2]	211.3 ± 11.6	53	214.4 ± 9.3	131	1.921[3]	>0.05
Size before egg-laying (mg)	215.6 ± 73.5	42	219.1 ± 71.2	118	0.266[3]	>0.7
Size after laying (mg)	72.7 ± 17.3	53	75.6 ± 21.5	131	0.873[3]	>0.3
Size of egg mass (mg)	144.2 ± 58.2	42	143.4 ± 54.6	118	0.095[3]	> 0.9
Reproductive effort (mass of eggs/ mass of spider before laying) (%)	65.3 ± 8.0	42	64.4 ± 7.0	118	1.254[4]	>0.2
% loss/day between egg-laying & disappearance: % loss/day of a random sample of spiders remaining	0.6 ± 0.8	18	0.8 ± 0.7	18	1.220[4]	>0.1

[1]Variables 1-4 did not differ significantly among the years 1982-1985 ($P > 0.5$ in one-way ANOVA for variables 1-3; $P > 0.5$ in a Kruskal-Wallis one-way ANOVA for variable 4)
[2]Julian date: 211 = 31 July, 214 = 3 August
[3]t-tests, two tailed (df = $N-2$)
[4]Wilcoxon pairs tests, (two-tailed)
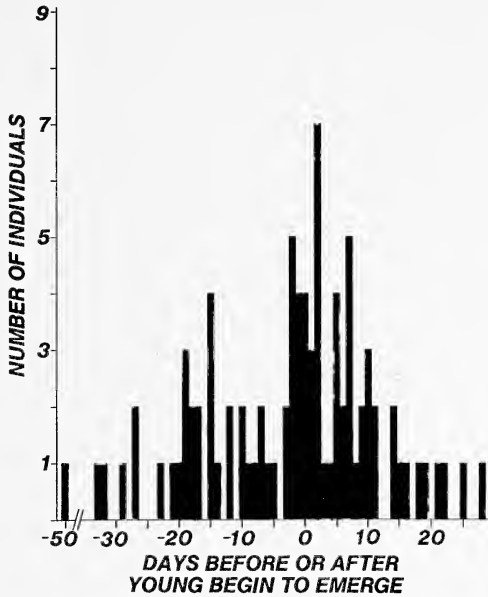
Fig. 1.—Number of adult spiders that ceased guarding their nest before and after the first spiderlings began to emerge. Day of first emergence is 0, negative numbers on abscissa refer to adult spiders that left before the first spiderlings emerged, positive numbers on abscissa refer to adults that remained after the first spiderlings emerged.

began to emerge from their nests (Fig. 1). Their length of stay was not significantly related to pre-laying body mass, or reproductive effort ($r_s < 0.2$ in each Spearman rank correlation, $P > 0.1$, $N = 71$).

Fifteen of the 71 (21%) remained until all the young had dispersed from the nest (Fig. 2). Those post-productive individuals dispersed or died slowly after this period, the last one being noted 13 days after the last young left. Observations were inadequate to tell whether most of these individuals died over this time; however, three were found dead. Many of the individuals thus remained during dispersal of their offspring. Spiders that stayed until their last young left the nest did not differ from the others in pre- or post-laying mass, egg mass, or reproductive effort (Table 3).

Adult mortality.—A minimum of eight spiders, 11% of the total, died before their young emerged from the nest. In most instances I could not separate deaths unambiguously from abandonments, since individuals from either category might simply disappear. The probability of finding dead individuals was low, unless they were found dead on their nest, held by a line of silk in which a limb had become entangled, or picked up directly under the nest shortly after dying. Harvestmen (*Phalangium opilio*) and ants (*Myrmica* sp.) scavenged many corpses of arthropods, including crab spiders, in the milkweed clone (Morse 1985b). Not all that disappeared died, however, since 10 (13% of the total) of these post-reproductive individuals were subsequently found at varying distances away from the nests. Thus, I have retained the distinction between the two categories.

The experiment in which 21 individuals and their nest-sites were covered with nylon tricot bags after egg-laying provided an independent basis for comparing numbers of abandoning and dying spiders. Four of these individuals died before the young were old enough to emerge, and another four individuals abandoned
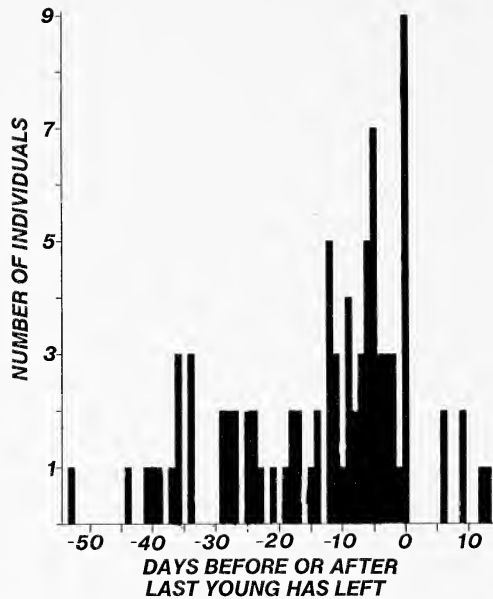
Fig. 2.—Number of adult spiders that ceased guarding their nest before and after the last spiderling left the nest. Day of last departing spiderling is 0, negative numbers on abscissa refer to adult spiders that left before all spiderlings had gone, positive numbers on abscissa refer to adults that remained after all spiderlings had gone. The peak at 0 days is partly an artifact, because several of the nests with adult spiders were collected at that point. These individuals had, however, remained until the last young had left.

their nests, subsequently occupying other parts of the plant covered by the tricot bag. The combined proportion of dead and abandoning spiders in this experiment was not significantly different from the proportion of unrestrained spiders that died or disappeared (Table 2) ($G = 0.74$, $P > 0.3$). Although the sample is small, this result suggests that many of the individuals placed in the "disappeared" category of Table 2 also died.

Loss of biomass and survival.—Survival time could be a consequence of body condition. Observations and experiments on individuals in the laboratory and field provide insight into this question.

At the time that they died, spiders maintained in the laboratory at ambient temperature had lost $39.8 \pm 12.8\%$ ($\bar{x} \pm$ SD) of their biomass subsequent to egg-laying ($N = 16$). Some individuals in the laboratory began to approach this critical level (dashed line of Fig. 3) after as little as 15 days. Despite their high

Table 3.—Size and reproductive characteristics of spiders that remained on nests until after all young left, left before this time.

Variable	Remained until end $\bar{x} \pm$ SD	N	Left before $\bar{x} \pm$ SD	N	t[1] or z[2]	P
Size before egg laying (mg)	209.1 ± 72.8	22	225.5 ± 66.6	88	1.016[1]	>0.3
Size after egg laying (mg)	74.9 ± 22.0	22	75.0 ± 18.0	107	0.025	>0.9
Size of egg mass (mg)	134.2 ± 56.2	22	149.7 ± 52.4	88	1.222[1]	>0.9
Reproductive effort (%)	62.3 ± 10.1	22	65.6 ± 6.3	88	0.975[2]	>0.3

[1] t-tests, two tailed (df = N-2)
[2] Wilcoxon pairs test, two-tailed
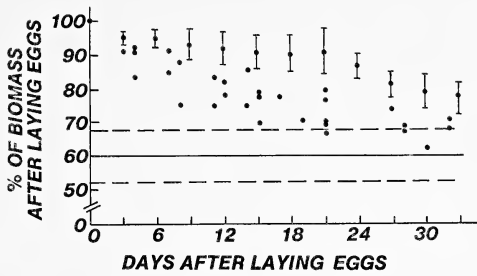
Fig. 3.—Loss in biomass subsequent to egg-laying. Solid line with error estimates is % loss in biomass of spiders monitored in the field ± 2 SE. Twenty spiders were used, N at any one of these points = 12-20. Points immediately below this line are losses in biomass of spiders kept without food or water in the laboratory. Data are from 14 different spiders; in some instances more than one point was obtained from a spider. Shaded area below the points is the mean % loss in biomass at death ± SE in the laboratory, $N = 16$.

rate of decline in biomass, most of the spiders brought into the laboratory with their egg masses survived for long periods without being fed or given moisture ($\overline{x}$ = 32.4 ± 7.8 days, $N = 31$). Survival time in the laboratory was, however, correlated with the mass of individuals after egg-laying ($r_s = 0.43$, $P < 0.05$ in a Spearman rank correlation), but not with mass immediately prior to egg laying ($r_s = 0.30$, $P > 0.2$), or reproductive effort ($r_s = -0.12$, $P > 0.5$).

Since most of the individuals (39/47) followed through the dispersal of young in the field survived until the young began to emerge (24 others disappeared), the results are not directly comparable to the laboratory data. Taking only those spiders known to have died, eight before the young emerged and two after, a significant correlation occurred between survival time and post-laying mass ($r_s <$ 0.63, $P < 0.05$), but not pre-laying mass ($r_s = 0.41$, $P > 0.1$, or reproductive effort ($r_s = -0.40$, $P > 0.1$). Thus, the pattern of adult mortality in the field appeared to resemble that in the laboratory, but longevity was apparently considerably greater in the field, with the result that most spiders survived well in excess of the time that their young emerged from the nest. The disappearance of many of the spiders from their nests precludes a more sensitive analysis.

Condition of adults.—The physiological ability of the spiders to remain on nests in the field could be confounded by a tendency to leave once the young emerge. The individuals maintained in the nylon tricot bags in 1983 provided insight into the potential survival of these individuals in the field. Of the 21 individuals, 17 were still alive 27 or more days after egg-laying, the mean period to the commencement of spiderling emergence in the field. Some survived as long as 39 days, the point at which observations ceased. Although four of these individuals did die over the period, none of them lost percentages of total biomass as great as those dying in the laboratory (losses in the field ranged from 7.3% to 16.4%). The basis for death in these individuals could not be determined, but the differences in loss of mass suggest that it differed from the laboratory individuals.

Basis for changes in mass.—In general, spiders guarding their egg masses in the field lost biomass slowly (Table 2). This result could be the consequence of feeding or of differences in water balance between field and laboratory.

Capture of prey. Given the similar environmental conditions experienced by the sample of 21 spiders confined to the tricot nets in 1983 and the unconfined

spiders, one can test the importance of prey in determining changes in biomass over the season. The confined spiders did not differ in change of biomass over this period from the 12 unconfined spiders measured in 1983 (F = 0.11, $df = 1$, $P > 0.7$ in a repeated measures ANOVA). Neither did the confined individuals differ in loss of biomass from the 20 unconfined spiders measured in 1982 (F = 0.01, $df = 1$, $P > 0.9$) or the 27 unconfined spiders in 1984 (F = 0.51, $df = 1$, $P > 0.4$). Thus, prey do not appear to play a significant role in the maintenance of body mass at this time.

It was possible to investigate and test this result further with observations made on prey visits to the vicinity of the spiders, kills made by the spiders, and fluctuations in patterns of loss in mass. Since most individuals laid their eggs on non-flowering milkweed stems (Morse 1985a), and those using flowering stems usually did so only after the flowers had senesced (three exceptions), these spiders seldom experienced the high densities of insects that they found prior to egg-laying. Only small numbers of insects visited the spiders' nest sites. During 95 hours of observing 27 different brooding spiders, only three insects (a treehopper (Membracidae), a big-headed fly (Pipunculidae), and a tachinid fly (Tachinidae)) visited the leaves upon which nests were placed, or other sites within 5 cm of the nest. The spiders did not attempt to capture any of these insects. During this time an additional 21 insects, also all homopterans and dipterans, alighted elsewhere on plants containing the spiders' nests. Spiders did not attempt to capture any of these insects, either.

Not surprisingly, the spiders captured few prey during this period. In only 23 of 3914 daily census records of spiders (0.6%), involving 220 individuals, was a spider observed feeding on an insect. These prey included an arctiid moth and small hemipterans, membracid homopterans, tachinid flies, halictid bees, and tortricid moths. As a group spiders capturing prey did not differ in mass from non-feeding spiders before and after egg laying, mass of eggs laid, or reproductive effort (Table 4).

Another way to identify possible captures of prey by post-reproductive spiders is to weigh them regularly and search for substantial increases in mass (here defined as greater than 2 mg, the greatest gain shown by the spiders confined with the nylon tricot bags). In the occasional instances in which I observed the spiders feeding on prey, they exhibited such increases at their next weighing, as much as 5-10 mg. However, gains of greater than 2 mg occurred at only 21 of the 354 weighings (5.9%) made every third day in the field. Put another way, these data suggest that on average a guarding spider captured a prey item providing substantial sustenance only once every 51 days (354 weighings, each done every third day = 1062 days, ÷ 21 prey), a period considerably exceeding that of any spider's tenure at a nest.

I divided into three groups spiders monitored more than 10 days: those that registered more than one gain of greater than 2 mg, those that registered one such gain, and those that did not register any gains greater than 2 mg. I then compared their mean percent biomass change per day (Table 5). Individuals of the groups that apparently caught prey did lose mass significantly more slowly than those that did not (H = 19.54, $df = 2$, $P < 0.0001$ in a Kruskal-Wallis one-way ANOVA). Of the three individuals with more than one gain exceeding 2 mg, two roughly maintained their mass over the guarding period, and the third registered a 10% gain. Thus, although spiders apparently measurably slowed their

Table 4.—Size and reproductive characteristics of spiders that captured and did not capture prey while attending their nests.

Variable	Seen with prey 1 ± times $\bar{x} \pm SD$	N	Not seen with prey $\bar{x} \pm SD$	N	t^1 or z^2	P
Size before egg laying (mg)	231.8 ± 80.9	8	222.9 ± 74.0	185	0.329	>0.7
Size after egg laying (mg)	70.9 ± 21.8	10	76.7 ± 25.0	207	0.721	>0.4
Size of egg mass (mg)	160.1 ± 61.5	8	145.8 ± 56.4	185	0.701	>0.4
Reproductive effort (%)	68.3 ± 4.2	8	64.3 ± 8.0	185	0.414^2	>0.6

[1] t-tests, two tailed (df = N-2)
[2] Wilcoxon pairs test, two-tailed

loss in mass if they captured prey, only one of the 47 individuals monitored for more than 10 days registered a persistent gain in mass. Overall, these results do not suggest that feeding appreciably slows loss in mass of most individuals in the field. Spiders registering large gains did not differ significantly from non-gaining spiders in mass before and after egg-laying, in mass of the eggs, or in reproductive effort (Table 6).

Effect of moisture. Another group of spiders was kept in the laboratory without food as a second control, permitting me to assess change of biomass in the absence of both food and the moisture regime normally encountered. Since netted and unnetted individuals in the field did not differ in loss of biomass, this comparison actually provides information about relative water loss. Loss by spiders in the laboratory was roughly linear subsequent to egg-laying, and averaged slightly over 1% per day (1.13 ± 0.20% per day, $N = 12$).

Individuals in the field (confined and unconfined) lost biomass at about two-thirds the rate of the ones confined to the laboratory (Table 2, Fig. 3). The regressions of biomass loss over time differed significantly between the field and laboratory groups in a test for homogeneity of slopes (F = 29.83, $df = 1$, $P < 0.0001$).

The ability of post-reproductive *Misumena* to absorb water can be readily observed in the laboratory. Individuals brought into the laboratory in open containers for 10 days and then placed in a sealed jar with moist paper towels for 24 hours at ambient temperature took up considerable amounts of water, a few increasing up to nearly 30% of their mass immediately previous to treatment ($\bar{x} = 16.8 \pm 6.6\%$, $N = 9$). This uptake recouped most of their loss in mass over the period of their incarceration. None of the gains in the field approached this level, however.

Spiders attending their nests in the field regularly registered small (<2 mg) increases in mass (42 of 354 observations; 11.9%), many probably resulting from changes in their water content. Loss of mass was significantly lower at weighings

Table 5.—Changes in mass/day as a consequence of the number of times spiders gained more than 2 mg between weighings. Each of these spiders was monitored for 10 or more days.

Number of gains > 2 mg	N	% change in mass per day ± SD
0	29	−0.86 ± 0.50
1	15	−0.29 ± 0.29
2	3	−0.04 ± 0.25

Table 6.—Size and reproductive characteristics of attending spiders that registered gains of over 2 mg mass, spiders that did not register gains of this size.

Variable	Gain of > 2 mg $\bar{x} \pm$ SD	N	No gains of > 2 mg $\bar{x} \pm$ SD	N	t^1 or z^2	P
Size before egg laying (mg)	195.0 ± 53.4	22	224.9 ± 74.8	87	1.765[1]	>0.05
Size after egg laying (mg)	67.0 ± 15.3	23	76.0 ± 21.0	91	1.925[1]	>0.05
Size of egg mass (mg)	128.3 ± 41.6	22	147.3 ± 58.0	87	1.444[1]	>0.1
Reproductive effort (%)	64.7 ± 6.5	22	64.2 ± 8.2	87	0.106[2]	>0.9

[1]t-tests, two tailed (df = N-2)
[2]Wilcoxon pairs test, two-tailed

made less than one day after a rainy or foggy period (−0.04 ± 1.2%, 145 observations) than if weighings were preceded by more than three days of dry weather (−0.7 ± 1.4%, 211 observations) ($P < 0.001$ in Wilcoxon two-sample Test). However, such differences soon disappeared, for spiders exposed to rain or fog two or three days (−0.6 ± 1.4%, 276 observations) previously did not differ significantly in mass from those that had experienced only dry weather over that period ($P > 0.1$ in Wilcoxon two-sample Test).

DISCUSSION

Spiders that disappeared from their nests did not differ from those that remained, in laying dates and reproductive variables (Table 1). The significantly higher permanent disappearance rate of individuals seen off their nests once or more (Table 1) might thus be a simple consequence of becoming lost as a result of that activity. Although the spiders habitually lay down a line if they move; which often results in a network of threads about the nest (illustrated in Morse 1985a), chances of losing contact would appear more likely as distance from the nest-site increased. Three of the four abandoning spiders that I found and returned to their nests remained on the nests for a day or more after being returned.

Spiders do not lose a large proportion of their mass before their young leave the nests, at least as judged by the presumably lethal losses of mass incurred in the laboratory. This result suggests that energy and moisture reserves of the females in the field are usually adequate for them to survive until their young emerge. The inability of most hunting individuals to increase their size substantially, in turn probably a consequence of the small number of insects visiting these locations, suggests that the spiders do not depend on food supplements for survival through this stage. The advantage obtained by guarding (Morse, submitted) thus suggests that gains come about as a result of allocating adequate reserves for survival in the first place, rather than obtaining them later. The extremely low metabolic rate of spiders (Anderson 1970) enhances this ability. However, the correlation between length of survival in the field and post-reproductive size, which parallels the pattern found in laboratory survival studies, suggests that selection may act (or has acted) positively on large body size.

The rates of loss of mass in laboratory and field suggest that the principal advantage realized by the spiders in the field is an ability to control their water balance. Spiders seldom exposed themselves on the upper side of the nests, except

early in the morning when sunning themselves in relatively cold conditions. Further, their tendency to gain mass on damp days, and upon occasion to occupy the upper sides of nests on rainy days, suggests that they take in water directly (Volmer and MacMahon 1974). This conclusion is consistent with the changes in mass of those exposed to damp conditions in the laboratory. I have also observed *Misumena* apparently drinking both dew and nectar in the field (Morse, unpublished observations).

Surviving in vigorous condition over this period has clear advantages to the spiders. Nests guarded throughout the nesting period suffered lower predation on their egg masses than unguarded ones; further, large spiders, which probably have larger energy reserves at this time, experienced lower rates of predation on their egg masses than did small ones (Morse, submitted).

Differences in earlier foraging success, characterized at this stage by large female size and large egg mass, thus did not appear to affect any of the behavioral patterns observed in this study (activity about the nest, leaving the nest, hunting); that is, no behavioral trade-offs occurred. However, since large spiders suffered lower levels of egg predation from insects (ichneumonids, dipterans) (Morse, submitted), it seems likely that their ability to defend their nest differs. These size-related differences in success are not a simple consequence of predators choosing small egg masses, because predation was not related to size if spiders were removed immediately after laying their eggs and completing their nests (Morse, submitted). In order to address this factor further, it will probably be necessary to monitor nests with time-lapse photography. No data on these egg predators were obtained during the 95 hours of continually watching the nests noted above.

It is possible that the size-related survival of adults will affect the level of predation on the young as they emerge from the nests over several days after initially making small openings to the outside. Although the results suggested that most spiders could survive until their young began to emerge, the protracted departure of many young might result in a higher proportion of small females dying before all the young left; further, large females might also be more effective at minimizing predation on emerging young than are small females. Considerable predation may occur at this time. Seven times in the regular censuses I have observed jumping spiders (*Metaphidippus insignis* (Banks)) positioned on *Misumena* nests, all without guarding females, and with emerging young. These jumping spiders are abundant in the study area and readily capture second and third-instar *Misumena* presented to them (Morse unpublished).

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NOTES ON THE LIFE HISTORY OF *SITTICUS FASCIGER* (SIMON, 1880) (ARANEIDA, SALTICIDAE)

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ABSTRACT

In the field in Nagano Prefecture, mature females of *Sitticus fasciger* (Simon, 1880) oviposit several times from June to July in their nests. The nest for oviposition is made in a cavity on a wall. The egg-mass size of reared spiders varies from six to 13 eggs. Spiderlings molt five or six times and mature in late July to early August of the next year from hatching. The duration from egg to adult, which includes days of overwintering, varies from 377 to 428 days. A few adults copulate before overwintering, however, the majority copulate in May or June of the year following maturation. All females oviposit in early summer of the year following maturation. It was confirmed that the life history of this species in Nagano Prefecture is a two-year cycle. The population of this species in Nagano Prefecture consists of two groups in which their generation cycles differ from each other. It seems that the mechanism avoiding the reproductive isolation among these two groups is the intergenerational copulation between just matured females and surviving males which matured in the previous year.

INTRODUCTION

In a previous paper (Matsumoto and Chikuni 1980) we described the jumping spider, *Sitticus fasciger* (Simon, 1880), based on Japanese specimens together with its collecting localities. At that time, this spider was little known in Japan. In the present paper, we report the life history of this species.

It was confirmed by rearing that the life history of this species is a two-year cycle. However, in the field in Nagano Prefecture, mature males and females appear every year and oviposition is also found every year. This discrepancy means that there must be two different groups in a population, i.e., one matures in even years, but the other in odd years, respectively. If this is true, reproductive isolation should occur between these two groups. We discuss the mechanism resolving the possibility of reproductive isolation.

METHOD OF REARING

To obtain their eggs, adult females of *Sitticus fasciger* were collected from Toyoshina-cho, Nagano Prefecture, in 1979 and 1980. Nymphs emerging from their egg-cocoons were reared individually in glass vials of 20 mm in diameter. A drosophilid fly was given to each spider as food every day. The temperature and humidity of the rearing room were not controlled. After the rearing from May to October, the spiders were kept in a room without food and water until early spring of the next year, because the spiders in the field disappeared during this period for overwintering. We obtained 10 mature spiders from about 30 nymphs. The following discussion was based on the rearing records of these 10 spiders.

RESULTS

Habitat.—One of the authors, Chikuni, found *Sitticus fasciger* for the first time in a room of a farmhouse in Misato-mura, Nagano Prefecture, in 1937 and thereafter he has often found them on the walls of farmhouses. Collecting sites of the specimens preserved by the other author, Matsumoto, were related to man-made structures, i.e., the campus of Tokyo Education University, a shrine in Kita-Chigasaki of Kanagawa Prefecture, and Tachikawa railway station of Tokyo (Matsumoto and Chikuni 1980). The type specimen of this species had also been collected from a man-made structure, i.e., "les jardins du Palais d'Ete" near Peking, China (Simon 1880). According to Cutler (1965) and Prószyński (1968), this spider lives on stone walls, on rock outcrops, on wooden sheds and in greenhouses. Prószyński (1968) mentioned that this spider and *Sitticus terebratus* (Clerck, 1758) live on the surfaces exposed to the sun, e.g., rocks, tree trunks, walls and fences.

Active period in the field.—In the field in Toyoshina-cho, Nagano Prefecture, *Sitticus fasciger* appears in late May and disappears before November. Abundance of the species becomes highest in July and August. Immatures which seem to be first nymphs are found in July, although both the matures and the immatures are seen in the field throughout their active periods from late May to October.

In other localities than Nagano Prefecture, the active period of the species is unknown. However, a last nymph was collected on April 24 from Tokyo Education University (Tokyo), and a female on April 21 from Kita-Chigasaki (Kanagawa) and a female on May 19 from Tachikawa (Tokyo) (Matsumoto and Chikuni 1980).

Oviposition.—In the field in Nagano Prefecture, mature females oviposit from June to July in their nest made in the cavities on walls. In rearing, a female produces two to six egg-cocoons successively from June to July; the average number of egg-cocoons per female was four. The female stays in her nest for several days after oviposition, and then goes out for hunting. The intervals between respective ovipositions vary from eight to 34 days, and the average was 20 days. The egg-mass sizes were between six and 13 eggs. In one female, the egg-mass size decreased according to the order of oviposition. The egg is whitish yellow, sub-spherical and 1.2 mm in diameter of long axis (Fig. 1).

Hatching and emerging.—Larvae hatch on the average from their eggs simultaneously after 17 days from oviposition and their body length is 1.6 mm
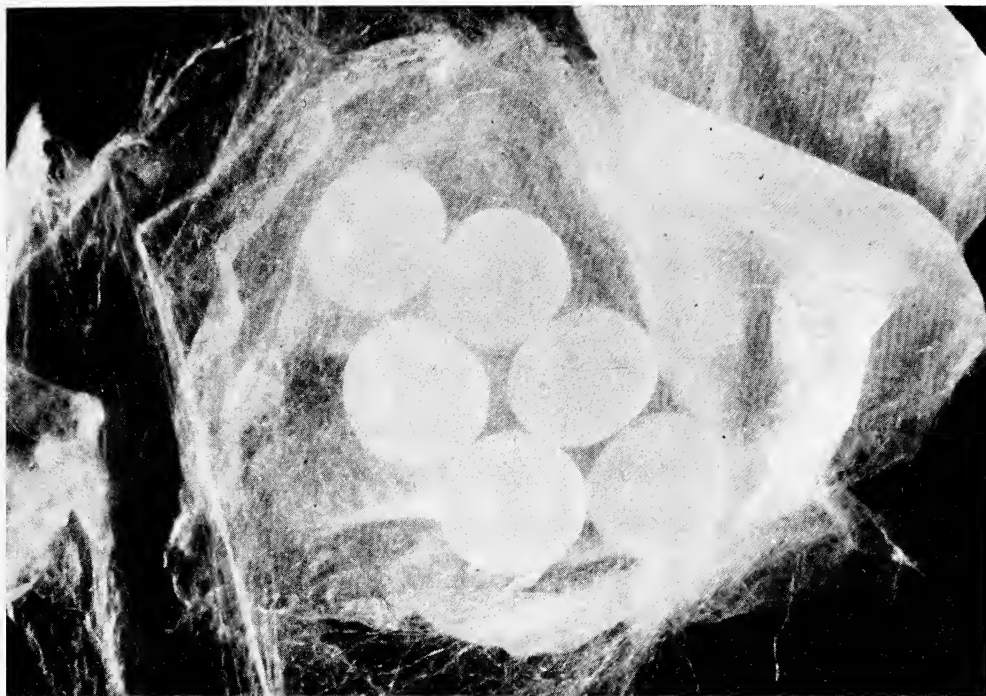
Fig. 1.—Eggs of *Sitticus fasciger*. The egg-cocoon was dissected to show the eggs within.

(Fig. 2). The larvae molt their integuments on the average after 10 days from hatching. The first nymphs stay in the cocoon for an additional five or six days, and then they leave their mother's nest (Fig. 3). Three or four days are required for all nymphs to leave the nest. The first nymphs do not cluster near each other after emerging as those of *Araneus, Argiope, Dolomedes* and some others do (Bristowe 1958; Matsumoto et al. 1976).

Postembryonic development.—Nymphs of the spiders are found throughout the active period of this species from late May to October in the field of Toyoshina-cho. Body sizes of nymphs increase gradually with time. In July, however, the quite small nymphs which are suspected to be the first nymphs are observed together with much larger nymphs.

It is found from rearing that the second molt occurs after 20 to 53 days from emerging. Two individuals molted again within the year and then overwintered (A and D in Table 1). The second and third nymphs begin to molt in mid-June to early July of the next year. Duration of the third instar varies from 18 to 44 days and that of the fourth instar from 18 to 40 days. After the fifth molting, four spiders matured, but the six remaining molted again after 25 to 32 days and then matured (Table 1).

The mortality of reared individuals was quite high in both the periods of the first instar and overwintering.

Maturation and copulation.—It is difficult to know the maturation season in the field, because mature spiders were always found during the active period from May to October. In rearing, maturation occurred during the period from late July to mid-September (Table 1, Fig. 4). The copulatory organs of the female and the male are shown in Figs. 5-8. The duration from egg to adult containing days of overwintering period varies from 377 to 428 days. Those individuals which

Fig. 2.—Larvae of *Sitticus fasciger*. Two of them are just hatching out of the eggs.
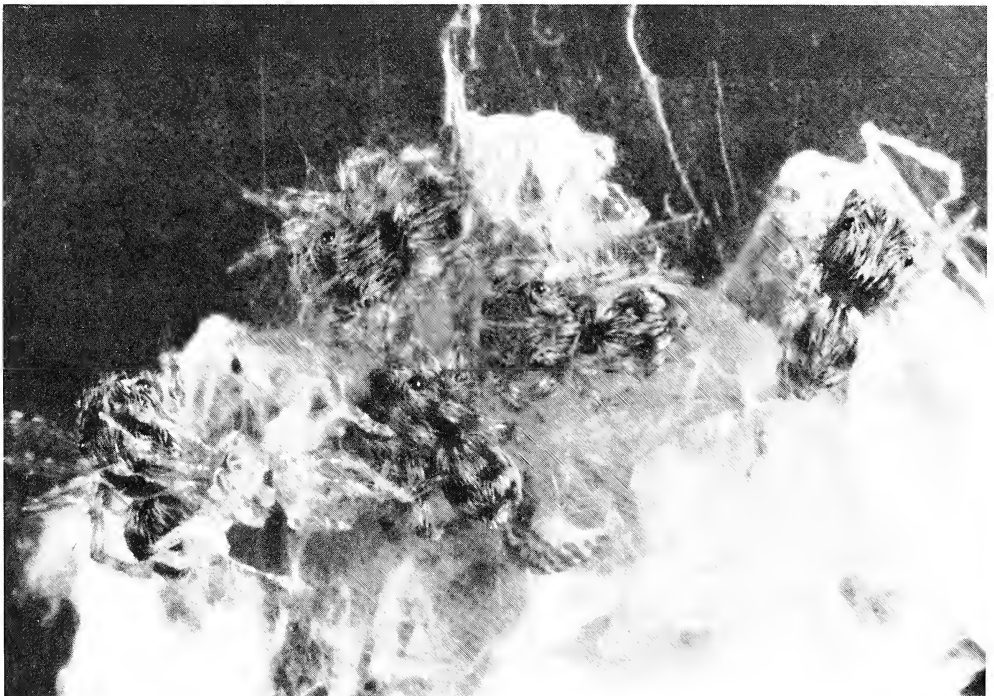
Fig. 3.—The first nymphs of *Sitticus fasciger*. They leave their mother's nest at five or six days after the first molt.

Table 1.—Dates of oviposition, hatching, emerging and molting in the spider, *Sitticus fasciger* (Simon, 1880), collected and reared in Nagano Prefecture, Japan. Spiders (E, F, H & I) matured after the 5th molt and the others after the 6th molt.

	Oviposition	Hatching	1st molt	Emerging	2nd molt	3rd molt	4th molt	5th molt	6th molt
A (♂)	19.JUL.79	5.AUG.79	15.AUG.79	20.AUG.79	9.SEP.79	27.SEP.79	20.JUN.80	10.JUL.80	5.AUG.80
B (♂)	19.JUL.79	5.AUG.79	15.AUG.79	20.AUG.79	30.SEP.79	15.JUN.80	3.JUL.80	26.JUL.80	24.AUG.80
C (♂)	19.JUL.79	5.AUG.79	15.AUG.79	20.AUG.79	22.SEP.79	18.JUN.80	18.JUL.80	12.AUG.80	7.SEP.80
D (♀)	19.JUL.79	5.AUG.79	15.AUG.79	20.AUG.79	9.SEP.79	10.OCT.79	15.JUN.80	25.JUL.80	25.AUG.80
E (♀)	19.JUL.79	5.AUG.79	15.AUG.79	20.AUG.79	30.SEP.79	18.JUN.80	5.JUL.80	30.JUL.80	—
F (♀)	27.JUL.79	12.AUG.79	23.AUG.79	28.AUG.79	28.SEP.79	18.JUN.80	19.JUL.80	16.AUG.80	—
G (♀)	27.JUL.79	12.AUG.79	23.AUG.79	28.AUG.79	10.OCT.79	5.JUL.80	18.JUL.80	10.AUG.80	11.SEP.80
H (♀)	20.JUN.80	7.JUL.80	19.JUL.80	25.JUL.80	4.SEP.80	19.JUN.81	13.JUL.81	31.JUL.81	—
I (♀)	20.JUN.80	7.JUL.80	19.JUL.80	25.JUL.80	16.SEP.80	30.JUN.81	19.JUL.81	22.JUL.81	—
J (♀)	13.JUL.80	31.JUL.80	12.AUG.80	18.AUG.80	29.SEP.80	17.JUN.81	23.JUL.81	15.AUG.81	9.SEP.81
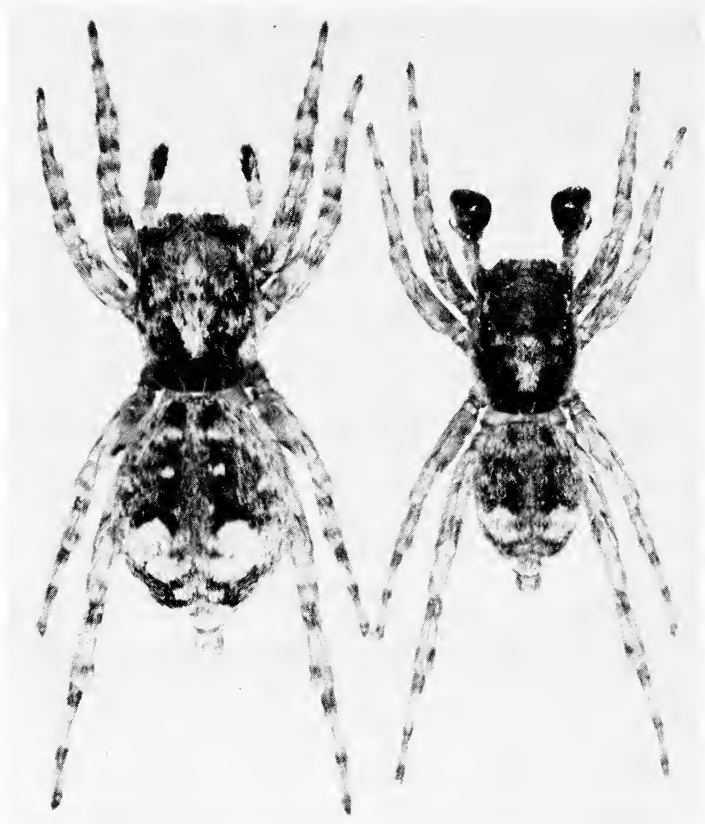
Fig. 4.—Female (left) and male (right) of *Sitticus fasciger*.

matured by early August copulate in some cases before overwintering, although the majority copulate in May or June of the next year.

Longevity.—In rearing, the physiological death of mature spiders occurred during their third overwintering. As a result, the longevity of this spider extends more than 800 days.

DISCUSSION

The habitats of *Sitticus fasciger* are those places which are accompanied by artificial structures, e.g. stone walls, wooden sheds, buildings, greenhouses and farmhouses (Prószyński 1968; Matsumoto and Chikuni 1980). We agree with Gertsch's opinion (in Prószyński 1968) that this spider is really an introduced species to North America, because it is extremely probable that the spider is able to be easily transferred by humans.

According to field observations, it is considered that oviposition occurs every year, since the first nymphs are found every year. On the other hand, it became clear from rearing that maturation is carried out until late summer of the year following hatching, but mating and oviposition seem to be postponed by late spring of the third year. These facts indicate that the population of this species in Nagano Prefecture consists of two groups in which the generation cycles differ from each other. If such a situation becomes perfect, reproductive isolation must
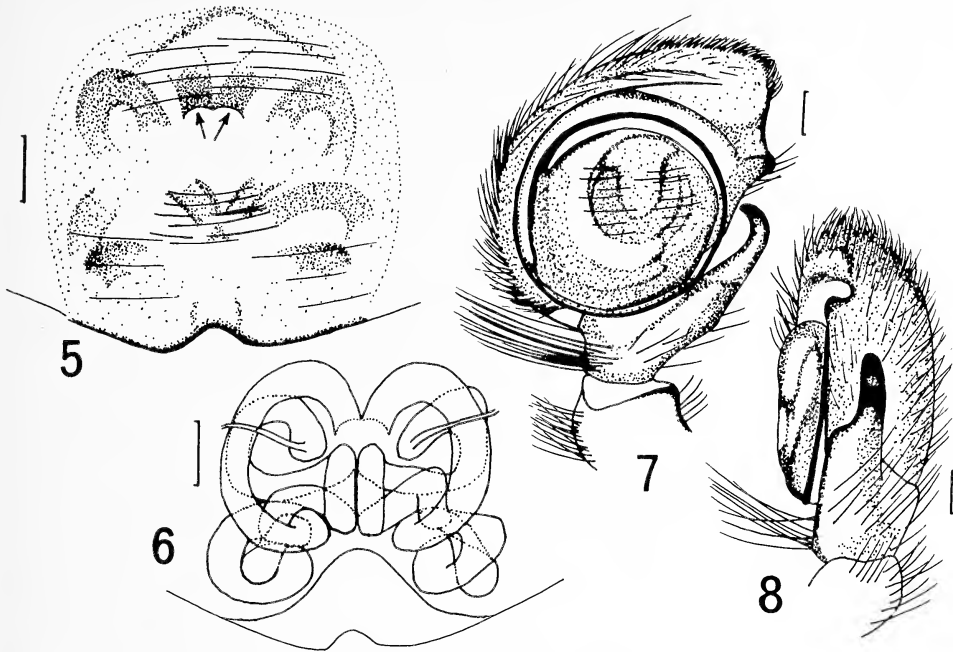
Figs. 5-8.—Copulatory organs of *Sitticus fasciger*: 5,6, female epigynum; 5, ventral view, arrows show the copulatory openings; 6, dorsal view; 7,8 male palpus; 7, ventral view; 8, retrolateral view. All scale lines: 0.1 mm.

be established between these two groups. We have ascertained by rearing that a few spiders copulated in the late summer of their maturation year and that all spiders survived until the winter after copulation and oviposition. These facts
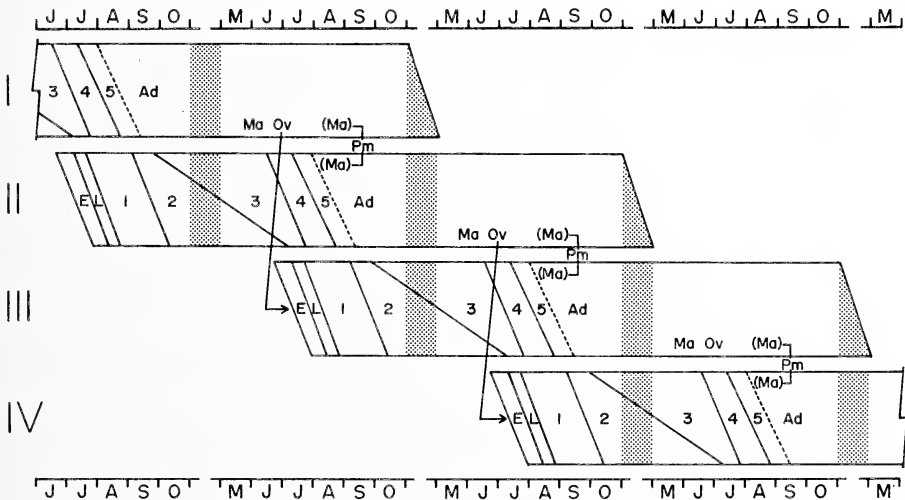
Fig. 9.—Diagram of the life cycle of a Nagano population of *Sitticus fasciger* in four years. E = egg, L = larva, 1, 2, 3, 4 & 5 = 1st, 2nd, 3rd, 4th and 5th nymphs, Ad = adult, Ma = mating in the majority, (Ma) = mating in the minority, Ov = oviposition, Pm = probable mating between different generations. Dotted areas show the periods of overwintering. Scales on the top and the bottom show months of four years.

show the possibility of such intergenerational copulation, i.e., that a few virgin females copulate with the surviving males in the late summer (Pm in Fig. 9).

In Tokyo, a last nymph of a female has been collected on April 24. Tokyo is 4.2°C warmer than Nagano Prefecture in annual mean temperature. Therefore, in Tokyo, spiders must be mature in late spring of the year following hatching and they copulate and oviposit by late summer. This life cycle is identical with that of some other salticids (Gardner 1965; Miyashita 1969; Wild 1969; Horner and Starks 1972).

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WEB MANIPULATION AND TWO STEREOTYPED ATTACK BEHAVIORS IN THE OGRE-FACED SPIDER *DEINOPIS SPINOSUS* MARX (ARANEAE, DEINOPIDAE)

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ABSTRACT

This study shows that *Deinopis spinosus* Marx has at least two stereotyped attack behaviors, each elicited by different stimuli. In "backward" strikes the spider expands the net backward over its cephalothorax and away from the substrate; these strikes capture aerial prey. Vibratory stimuli are sufficient to elicit backward strikes. In "forward" strikes the spider expands the web downward and forward against the substrate; these strikes capture walking prey, and visual rather than vibratory stimuli are more effective. We describe the mechanisms underlying each type of strike and the extraordinary extensibility of the web.

INTRODUCTION

Very few web-spinning spiders actively manipulate their webs to intercept prey. The uloborid genus *Hyptiotes* Walckenaer and the araneoid family Theridiosomatidae tense their webs and release them suddenly after prey strike the web (McCook 1889; Opell 1982; Coddington 1986a), but they do not actively move the webs to intercept near-flying prey. The bolas spiders (*Mastophora* Holmberg and related genera) swing or twirl a tethered viscid silk ball toward near-flying moths (Eberhard 1980, Stowe 1986). All of these spiders catch only aerial prey, whether they manipulate the web in advance or not, and none of them have more than a single stereotyped technique of web manipulation. We report here on a web-spinning spider, *Deinopis spinosus* Marx, that not only actively manipulates its web to intercept prey, but also uses it in at least two distinct attack behaviors—one to catch aerial prey, and one to catch walking prey.

The circum-Caribbean *Deinopis spinosus* belongs to the tropical family Deinopidae, often called "ogre-faced spiders". All deinopids spin architecturally
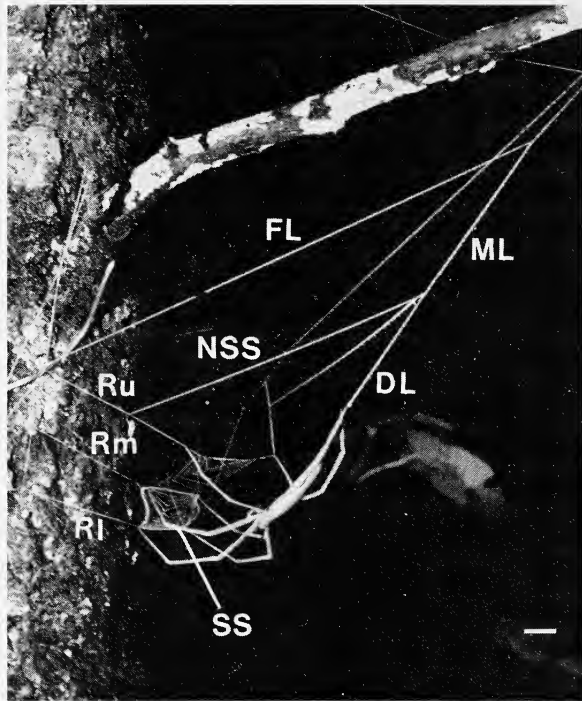
Fig. 1.—*Deinopis spinosus* in prey ready postures. Note 4th legs gripping dragline (DL) attached to midline (ML), 3rd legs on upper radii (Ru), 2nd legs on middle radii (Rm), 1st legs on lower radii (Rl). Legs control the sticky silk portion (SS). Note frame lines (FL) and persistent segments of non-sticky spiral (NSS). Compare this view with Fig. 5. Scale = 1 cm.

uniform, highly specialized webs (Fig. 1). The webs may be called specialized because analysis of the detailed motor patterns used to construct the web shows that they are derived phylogenetically from the classic orb-web, an architecture otherwise found only in the Uloboridae and within the superfamily Araneoidea (Coddington 1986b). The form of deinopid webs is unique to the family, and ever since its discovery (Ackerman 1926) has intrigued and attracted biologists. The web is small compared to the size of the spider, and unless the prey caught are very small (Robinson 1977, 1983), each successful capture usually causes the destruction of the web; to catch more prey, the spider must spin a new web.

Other aspects of deinopid behavior also appear to be fairly uniform throughout the family. All deinopid species observed to date, for example, grasp the corners of the sticky portion of the web with their first two pairs of legs while motionless in their prey-ready posture (Fig. 1), and then simultaneously lunge and push the expanded web as much as 1-2 body lengths away to ensnare prey (*Menneus camelus* Pocock, Ackerman 1926; *M. unifasciatus* (L. Koch), Austin and Blest 1979; *Deinopis subrufus* L. Koch, Baum 1938, Roberts 1954, Austin & Blest 1979; *D. spinosus*, Theuer 1954; *D. longipes* F. O. Pickard-Cambridge, Robinson and Robinson 1971). However, the two most detailed studies to date on *Deinopis* species (Theuer 1954; Robinson and Robinson 1971) differ in their conclusions about the manner in which the web is used, and something of a controversy has developed as to whether they strike forwards against pedestrian prey, or backward toward aerial prey.

A subsidiary mystery (Eberhard, pers. comm. and authors cited above) is the amazing extensibility of the deinopid web. During any strike the web area may expand 10x (compare Figs. 2a, d; 3a, d), which rivals the record for any spider silk (Denny 1976).

This paper seeks to answer 3 questions. (1) Does *D. spinosus* use backward strikes, forward strikes, or both? (2) Can the releasing stimuli for the strikes be elucidated experimentally? (3) How exactly does either kind of strike occur, and how does the architecture of the web and the behavior of the spider enable the strike?

MATERIALS AND METHODS

Web construction and predatory behavior were observed in 19 *D. spinosus* females for a total of 52 hours in outdoor but caged situations, and in 28 individuals for a total of 17 hours in natural field conditions in Gainesville, Florida during August, 1985. Spiders were illuminated with 6 volt headlamps masked with dark red gel filters (no transmittance below 600 nm). In both cages and field we noted web-substrate distances, activity times, and documented prey-ready postures, web placements, and aspects of construction behavior with still photographs. We described all natural predatory strikes seen and also attempted to elicit predatory strikes with various natural and artificial stimuli.

In order to determine the different kinds of strikes used by *D. spinosus* to intercept prey, we elicited predatory strikes with stimuli presented by six means: a vibrating tuning fork held adjacent to the web; audibly humming next to the web; paper models mounted on wires; dead insects mounted on wires; tethered flapping or motionless live prey held adjacent to the web; and releasing live prey into the cages and observing subsequent events. Qualitatively different strikes were characterized by presence or absence of motion patterns during the strike, and by qualitatively different orientations of the web during the strike. We made no attempt to measure quantitative variation in leg extension, body movement, or web orientation. A "strike" was judged to have occurred during a stimulus presentation if the strike occurred within 0.5 sec of the stimulus.

The tuning fork experiments tested if a vibratory stimulus (acoustic or near-field air movement) would elicit a strike. The fork (256 Hertz), either vibrating or not according to the odd-even sequence of a series of random numbers, was presented 36 times to each of nine spiders. In all presentations the animals therefore received the visual stimulus of the tuning fork as a control, but only in some did they receive a vibratory stimulus as well. The tuning fork was positioned behind the spider at a distance of 3-5 cm. The occurrence or absence of a strike was noted, and the fork then removed for about 5 seconds before the next trial. In each presentation of a vibratory stimulus, an effort was made to present roughly the same level of energy.

The vocal humming experiments tested the efficacy of acoustic stimuli in the absence of visual stimuli. A series of 11 "hums" were presented to each of four individuals in the following manner. The observer positioned him or herself ca 30 cm to the side of the web and spider, and emitted at 10 sec intervals a low-pitched hum with the lips closed.
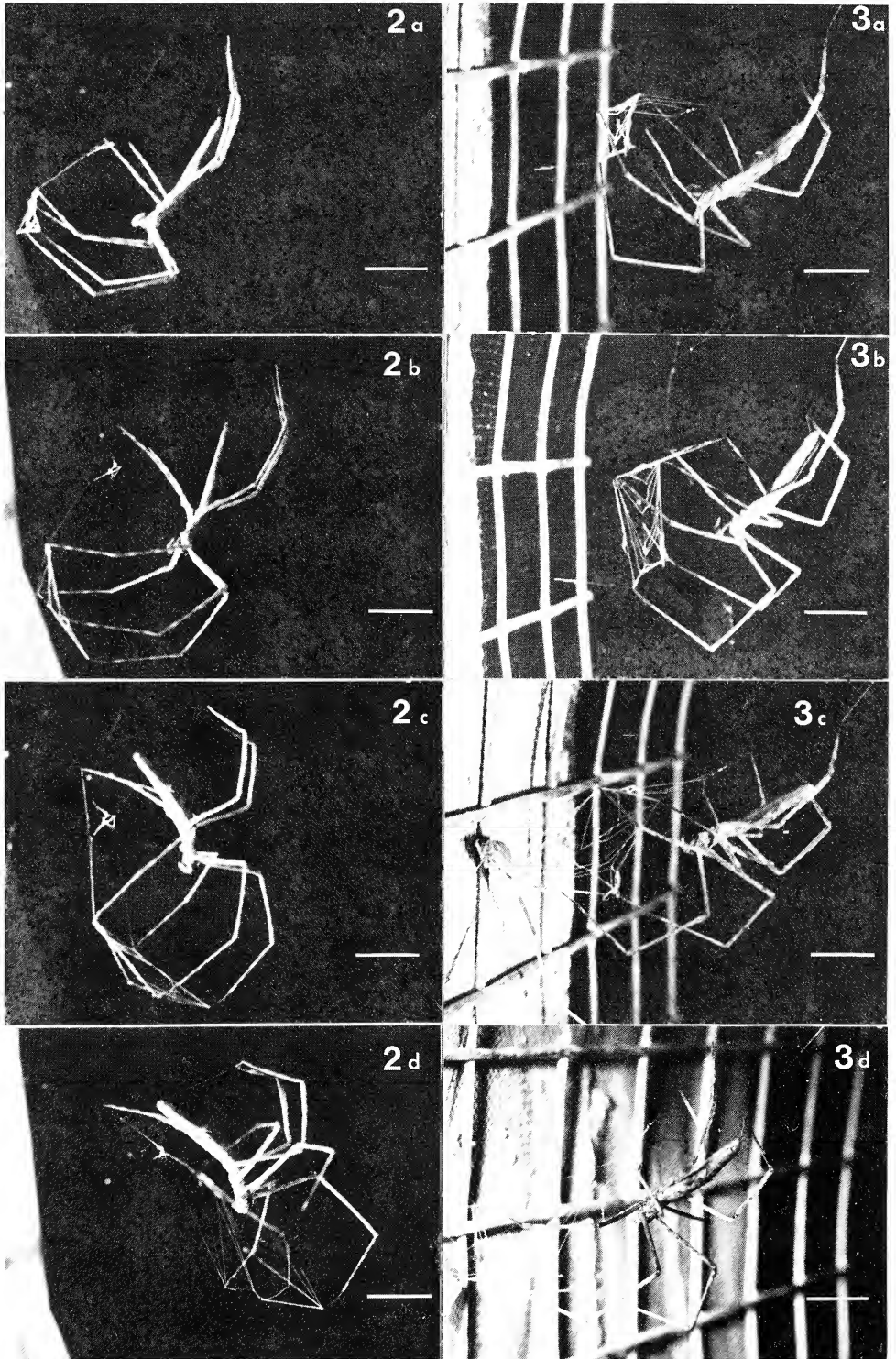
Figs. 2-3.—Stop-action sequences of backward and forward strikes. All photographs are from different strikes, and some may be during web contractions, not extension. Fig. 2, Backward strike: a. prey-ready posture; b. 1st legs moving backward; c. body rotates; d. almost maximum extension (note partly flexed 1st and 2nd legs). Fig. 3, Forward strike: a. prey-ready posture; b. 1st legs extend downwards; c. 4th legs allow movement toward substrate, 1st legs extend further, note moth on wire as lure; d. 2nd legs extended, 1st partly withdrawn. Scales = 1 cm.

Tensions in lines were measured with fine glass filaments used to deflect web lines specified amounts and then later calibrated with known weights (Opell 1985).

RESULTS

Web heights in the field averaged 148 cm (range = 49-300) from the ground. Without exception (n = 28, e.g., Figs. 1, 5) webs were constructed so that the approximately 1 cm square sticky portion was within 1-3 cm of a broad (at least 10 cm) roughly vertical substrate (e.g., tree trunk, palmetto leaf, wooden post). Webs could be found from about 2000 (1 hour after sunset) until at least 0300. No webs were seen during daylight hours under either natural or captive situations. Caged spiders built at roughly the same time as uncaged spiders and the morphology of the webs (n = 65) was indistinguishable. We saw no consistent differences in construction behavior, prey-ready postures, or attack behavior between individuals in cages and those in natural habitats. Our use of dim red light to observe spiders did not seem to perturb spiders in either field or caged situations.

We observed 22 strikes against live prey, and 119 strikes in response to artificial stimuli, totalling 141 instances of attack behavior. All observed strikes were stereotyped, either backward (n = 121) or forward (n = 20) strikes, as described below. In numerous cases, the spiders followed strikes against artificial stimuli with prey wrapping behavior, the normal sequence of actions in deinopid predation (Robinson & Robinson 1971). Thus, the spiders did not seem to be using either strike in a non-predatory behavioral context, such as defensive behavior against a threatening stimulus.

Description of backward strikes.—We call the strike used by *D. spinosus* to catch aerial prey a "backward" strike. During the strike (Figs. 2a-d) the spider retains its grip on the dragline with its 4th legs, rotates the body backward in space, and bends the 1st and 2nd pairs of legs outward and backward past the cephalothorax. In successful backward strikes the prey may be entangled on either surface of the sticky silk sheet, thus caught either on the outward or inward motion of the sheet.

Description of forward strikes.—*D. spinosus* uses a downward, forward strike to catch walking prey on the substrate in front of the web (Figs. 3a-d). We name this a "forward" strike. The animal spreads and extends its 1st and 2nd pairs of legs laterally and frontally, thus expanding the net. A major difference between backward and forward strikes lies in the use of the 4th legs. In forward strikes, the 4th legs allow the dragline to slip rapidly between the claws. The increased length of the dragline allows the spider and expanding web to drop down and forward, pivoting about the upper radius/non-sticky spiral junction and radial attachments to the substrate (Fig. 1, Ru - NSS, Rm, R1) until the front four tarsi of the spider contact the substrate (Fig. 3d).

Mechanism of backward strikes.—During the very brief duration of a backward strike (Fig. 2), the spider's body basically rotates in place rather than moving a substantial distance, as in a forward strike. The forces required to expand and move the web backwards all seem explicable by leg movements of the spider. The contraction of the 4th legs, and the rotation of the body, 1st legs, and 2nd legs downward and backward expands the sheet of the web and moves it about the positions of the 3rd legs, which remain relatively motionless.

Table 1.—Backward strike responses by different spiders to tuning fork vibrations and vocal humming. N = total number of stimulus presentations. * = $P < 0.01$; ** = $P < 0.001$. Tests of individual and pooled responses each had one degree of freedom (df); tuning fork heterogeneity, 8 df; vocal heterogeneity, 3 df.

TUNING FORK					VOCAL HUMMING				
Individual	N	No Vibration	Vibration	G-test	Individual	N	Humming	No Humming	G-test
1	18	1	0	n.s.	10	11	8	0	**
2	18	15	0	**	11	11	11	0	**
3	18	6	0	*	12	11	11	0	**
4	18	2	0	n.s.	13	11	10	0	**
5	18	16	0	**					
6	18	3	0	n.s.					
7	18	6	0	*					
8	18	8	0	**					
9	18	2	0	n.s.					
TOTAL	162	59	0	**	TOTAL	44	40	0	**
HETEROGENEITY				**					n.s.

Mechanism of forward strikes.—The rapid movement of the spider's body towards the substrate during a forward strike (Fig. 3) is powered at least in part, and probably primarily, by gravity. It is possible that the spider pulls on the radii to increase its velocity or to guide its trajectory. Measurements of tensions in the uppermost segments of web midlines (Fig. 1, ML) average 45% more than the spider's body weight ($n = 5$), but the tensions in frame lines (Fig. 1, FL) average 35% less ($n = 3$). Given the geometry of the prey-ready posture (Fig. 1), these magnitudes of tensions would be unlikely to contribute in a major way to the spider's acceleration toward the substrate. Instead, the geometry resembles more a concentrated weight hanging on a lax line (Merriam 1975). Such a cable system cannot act as an efficient "catapult". However, if the spider pulled in on the upper radii (Fig. 1, Ru) with its 3rd legs, it probably could increase its acceleration toward the substrate. Letting the midline slip between the 4th leg claws would still be a necessity.

Elicitation of backward strikes.—Backward strikes were easily elicited with a tuning fork or by humming, and the results of these more controlled experiments are reported below. We also used insect prey (moths, mosquitos, tabanids, tipulids, *Drosophila*) to elicit 14 backward strikes in 19 presentations to a total of 10 spiders. Ten successful elicitations involved freely flying prey (including one unstaged, "natural" strike observed in the field against a tipulid) and four involved flapping prey held by one wing with forceps. Two of the five unsuccessful presentations occurred when motionless (i.e., non-flapping or non-flying) prey were used (predictably inappropriate stimuli). Three occurred during one course of presentations to an apparently unresponsive spider.

In both field and caged animals, the occurrence of a backward strike was highly dependent on vibratory stimuli. In the field, three tuning fork presentations to each of three animals yielded eight backward strikes (not included in Table 1), but many presentations of non-vibrating tuning forks to field animals never elicited a response.

In caged animals, Table 1 shows that mere visual presentation of the tuning fork to caged animals is also completely ineffective in eliciting backward strikes

(none of 162 tries). However, the occurrence of backward strikes was highly dependent on the presentation of a vibratory stimulus ($P < 0.001$, Table 1). The efficacy of a vibratory stimulus in eliciting backward strikes varies significantly among individuals (G of heterogeneity: $P < 0.001$, Table 1). Lastly, animals accommodate significantly to repeated presentations (28 backward strikes summed over all animals in the first six presentations versus 12 strikes in the last six; Chi-square = 10.52, $P < 0.01$).

The above results suggest that a vibratory stimulus is necessary, but do not show that it is sufficient because the animals received a visual stimulus as well. As nearly as possible, the humming experiments presented only an acoustic or vibratory stimulus to the spiders, and successfully elicited backward strikes ($P < 0.001$, Table 1). Although it was more difficult to standardize a humming stimulus than the tuning fork, the results are highly significant and show that a vibratory stimulus is indeed sufficient.

Elicitation of forward strikes.—Experimental elicitation of forward strikes using artificial stimuli proved difficult. Vibrations applied to substrate beneath the web or to web strands were ineffective. The Robinsons (1971) were able to elicit four strikes against shadows projected on cage walls in front of the webs of *D. longipes*, but this stimulus was ineffective with *D. spinosus*. However, we were able to elicit 12 strikes in 12 presentations to two spiders using small paper models ($n = 4$) or dead insects ($n = 8$) mounted on wires (as in Fig. 3c). These results support the inference that visual stimuli are essential to release forward strikes, but the use of dead insects as stimuli might also have provided olfactory cues.

We also saw eight forward strikes against live prey by five spiders. In six instances, three spiders used forward strikes to ensnare termites walking beneath the web, and in two additional instances, two spiders used forward strikes to catch a tethered moth and juvenile cricket.

Web construction as it relates to attack behavior.—The final stages of web construction were observed 12 times and the motion patterns are quite stereotyped. During sticky spiral construction (Fig. 4), the spider is head up with respect to the web, but after completion of the sticky spiral, the spider turns head down, attaches its dragline to the midline (Figs. 1, 5), grasps the web with its four front tarsi, and cuts the lowest midline segment (Fig. 5). The grip of the fourth legs keeps the spider and sticky portion of the web from falling toward the substrate. The spider then lets dragline slip through its fourth tarsi, falls slowly downward, and taps forward and downward with its first legs to contact the substrate (Fig. 6). Finally the fourth legs reel in dragline as the first legs again take up the bottom corners of the sticky web, thus raising spider and web up and away once more from the substrate, and into the prey-ready posture (Fig. 1).

These operations are critical to web function for two reasons. First the cutting of the middle portion of the midline enables the web and spider to fall forward toward the substrate. Second, the attachment of the dragline to the upper midline allows the spider to adjust its distance from the substrate and to control its fall towards the substrate during a forward strike. Third, the final tapping motions (Fig. 6) allows the spider to orient with respect to the substrate, and apparently to gauge distance, immediately before assuming a prey-ready posture.

Sticky silk extensibility.—Examination of sticky spiral construction ($n = 16$) and web samples on slides shows that a hypothesis of extremely extensible silk
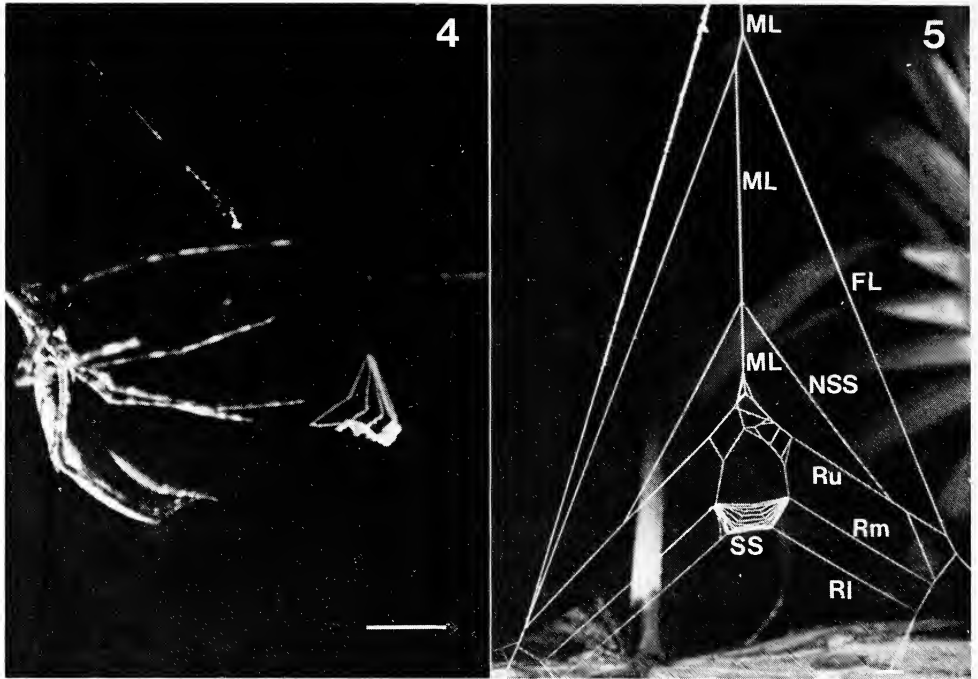
Figs. 4-5.—4, *Deinopis spinosus* constructing sticky spiral. Note the length of the current sticky silk segment; 5, Incomplete *D. spinosus* web showing lowest midline segment not yet removed and incomplete sticky spiral. Abbreviations: midline (ML); frame line (FL); non-sticky spiral (NSS); upper radius (Ru); middle radius (Rm); lower radius (Rl); sticky silk (SS). Scales = 1 cm.

(and thus extraordinary material properties) may not be necessary to explain the ability of the sticky web to expand tremendously. Only the non-sticky radii or the sticky silk segments could potentially resist the efforts of the spider to spread the web. However, *D. spinosus* usually cuts the attachments of the middle and lower radii to each other and of all of these to the upper radii (Figs. 1, 5). These non-sticky lines therefore do not impede expansion of the catching portion of the web, though they do resist the movement of the web as a whole during a backward strike. The upper radii, which do remain attached to each other even after the midline is cut to produce the finished web (Fig. 1), also do not resist the expansion of the web because the expansion is due mainly to movement of the 1st and 2nd pairs of legs which hold the middle and lower radii.

Therefore, the only silk which might constrain web expansion is the sticky silk itself. However, the spider holds its spinnerets well away from the web while it spins the cribellar spiral so that each segment of sticky silk is actually spun longer than its apparent length in an unexpanded web (Fig. 4). In a sense, the spider spins each sticky silk segment at or near its expanded length, only to contract it immediately before final attachment. Examination of sticky silk collected in the contracted state (Fig. 7) shows that it is composed of four components: a doublet of parallel fibers, a mass of much finer paracribellar fibers associated with the straight fibers, a doublet of helically coiled fibers, and a cloud of puffed cribellar silk. The helical fibers confirms that the cribellar silk lines are indeed highly contracted. When one of these complex sticky lines is slowly stretched, the straight fibers snap at about 150% extension, but the helical fibers and the cribellate silk stretch much farther. Thus the remarkable extensibility of deinopid
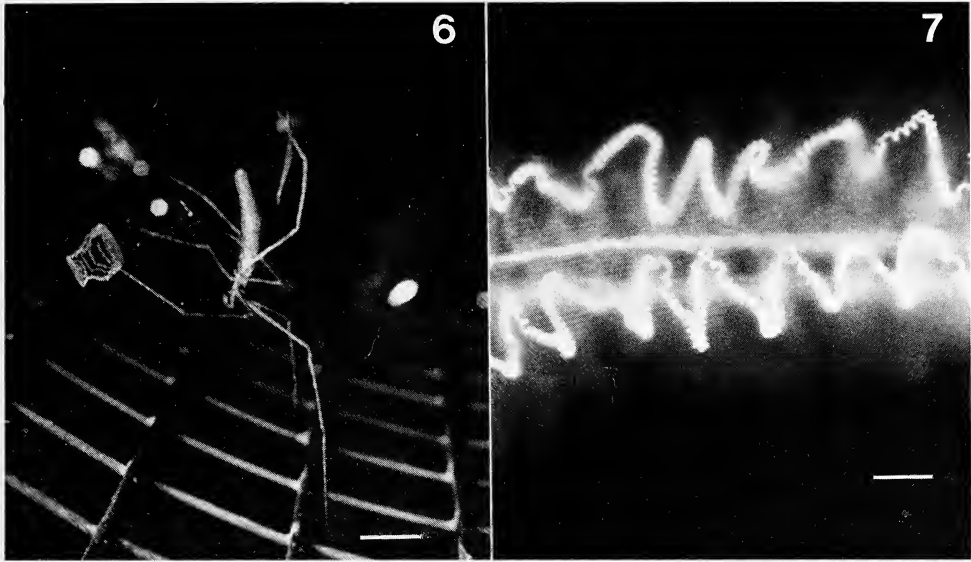
Figs. 6-7.—6, *Deinopis spinosus* tapping downward to locate substrate before assuming ready posture. Scale = 1 cm; 7, Photomicrograph of *D. spinosus* sticky silk in contracted state. Note spiralled fibers. Scale = 0.05 mm.

webs seem adequately explained by particular behaviors during the process of construction.

DISCUSSION

Our results demonstrate two different stereotyped attack behaviors in *D. spinosus*, and resolve a controversy in the literature between Theuer (1954) and Robinson and Robinson (1971). Theuer stated: (1) that *D. spinosus* expands the web with its first two pairs of legs, backward over its carapace and away from the substrate in front of the web; (2) that it "could in no way be construed to be a hurling forward and the throwing down of the net over an insect..." (p. 28); and (3) that "since the entire structure is in one plane and the spider itself does not hold on to any point in another plane, it appears an obvious physical impossibility that either spider or snare can go forward or backward [in space]" (p. 28). The strike described by Theuer seems to be what we call a backward strike, and he also pointed out that it would be effective only against jumping or flying prey. He concluded prior observers of deinopid behavior had been wrong in reporting downward and forward lunges, perhaps because he thought such behavior was physically impossible.

On the other hand, the Robinsons (1971) described in a different species, *D. longipes*, a behavior very similar to what we call a forward strike and pointed out: (1) that Theuer's observations did not agree with theirs or those of any other workers (Ackerman 1926; Baum 1938; Roberts 1954); (2) suggested that Theuer's observations had been based on a false assumption (that neither spider or snare can go forward or backward in space); and (3) questioned Theuer's claim that the kind of strike he described could be effective or frequent.

Our results with *D. spinosus* tend to corroborate some points and refute other points made by these two previous studies. Theuer apparently missed entirely the

occurrence of forward strikes in *D. spinosus*, but he did describe accurately a type of strike which catches aerial prey effectively. The skepticism of the Robinsons concerning the ability or likelihood of deinopids in general to catch aerial prey with backward strikes, on the other hand, seems to be unfounded, although very possibly *D. longipes* does not. Certainly they saw no aerial prey captured, and despite much experience with the species, saw only forward strikes. Theuer was wrong about the inability of a deinopid to move its center of mass during a strike, and the Robinsons may have underestimated the role of fourth legs and gravity in their explanation of how a forward strike occurs, at least judging by our observations on *D. spinosus*. Interestingly, Ackerman (1926) and McKeown (1963) also mention deinopids catching aerial prey, and Austin and Blest (1979) elicited what apparently was a backward strike in *D. subrufus* in response to a clearing of the throat.

Alternative explanations for the mechanics of forward strikes do exist in the literature. Baum (working on *D. subrufus*) said that the radii of the web were under extreme tension, and that if the fourth legs of the spider released the dragline (Fig. 1, DL), the elastic force in the radii would "catapult" the spider and web forward against the substrate. That all extant photographs of deinopids in ready postures show them in lax catenaries would seem to invalidate that hypothesis at the outset. The Robinsons (1971:92, working on *D. longipes*) speculated that"…this movement, presumably, is possible because of the elasticity of the silken web members to which it [the web] is attached. It is more difficult to see what the spider pushes against in order to make the strike. The hackled threads of the net attachment are certainly more elastic than the silk of the supporting framework and this lower elasticity, plus the inertia of the spider's body, presumably makes the lunge possible." We would agree that deinopids have nothing to push against, but see a lesser role for elasticity, either of the sticky or non-sticky threads, in powering a forward strike. Our observations suggest that in *D. spinosus* a forward strike is powered mainly by gravity, but possibly to a subsidiary extent by pulling on the web scaffolding.

One possible reason for the lack of agreement in the literature is that Theuer and the present authors worked on *D. spinosus*, the Robinsons on *D. longipes*, Baum and Roberts on *D. subrufus*, and Ackerman on *Menneus camelus*. However, our research on building behavior in *D. spinosus* (unpubl.) and *Deinopis* sp. (Coddington 1986b) shows a high degree of stereotypy among species, and from that lack of variation in one stereotyped pattern we are inclined to suggest that the genus *Deinopis* shows little diversity in mechanism of attack behavior.

The tuning fork experiments show that both visual and vibratory stimuli together will release backward strikes, and the humming experiments show that vibration alone is probably sufficient. No kind of visual model, nor any of the motionless prey presented to *D. spinosus*, elicited backward strikes, thus corroborating the tuning fork data that visual stimuli alone will not elucidate a backward strike. On the other hand, we were able to elicit forward strikes experimentally with models and mounted insects, mainly visual stimuli, and in their study, the Robinsons (1971) reported that shadows of small round balls projected beneath the web elicited forward strikes from *D. longipes*, also suggesting that visual rather than vibratory cues, are important. Other evidence also strongly implies that visual stimuli are important in eliciting forward strikes.

Fig. 8.—*Deinopis spinosus* "ogre" face. The large eyes are the posterior medians. Scale = 0.5 mm.

Deinopids have posterior median eyes which are probably the largest simple ocelli in arthropods (Fig. 8). With focal lengths of about 0.8 mm and f-numbers of 0.58, they can see in about 1/12 the illumination required by humans, and possess specialized physiological mechanisms to ensure low light sensitivity (Blest 1978; Blest and Land 1977). The resolution of deinopid eyes, on the other hand, is relatively poor (Blest and Land 1977).

The elicitation results do make biological sense. If deinopids see well at night, one would expect that they would use forward strikes on walking prey which they can see, but not "hear." Walking prey very likely impart only the slightest vibrations to the spider, and indeed some spiders spin webs attached to vines rather than directly to the substrate towards which the web is always oriented, and on which prey would move. The bulk of aerial prey, of course, that deinopids would encounter would present both visual and vibratory stimuli. Perhaps only spiders on draglines might be a case of "aerial" yet non-vibratory prey, but given the orientation of the deinopid web, spiders on draglines susceptible to backward strikes seem unlikely. The characteristic femoral trichobothria are likely receptors for near-field air vibrations (B. D. Opell, pers. comm.).

Prey records for deinopids were reviewed and augmented by Austin and Blest (1979). Without doubt, most records are of walking prey. Their own data on 84 prey of *D. subrufus* and *Menneus unifasciatus* suggest that the vast majority were walking, but they do mention a population of *D. subrufus* in Queensland whose main prey items were tipulid flies, and we saw *D. spinosus* ensnare a flying tipulid with a classic backward strike. Nevertheless, the available data clearly affirm that walking prey are more important than flying prey in the diet of deinopid species studied thus far.

The tuning fork experiments also documented significant accomodation to vibratory stimuli in individuals, and significant differences between individuals.

Most animals accomodate to prolonged or repeated exposure of stimuli, and certainly presentation of vibratory stimuli every 5 seconds is a fairly frequent schedule. These results, however, also argue for the effectiveness of vibration as an important component of the releasing stimulus, simply because the response tended to disappear with repeated exposure to vibrations.

Peters (1984) studied the fine structure of uloborid sticky silk, but found only three components: puffed cribellar silk, massed paracribellar fibers, and a doublet of pseudoflagelliform fibers. Uloborids are possibly the sister group of deinopids (Coddington, 1986b, c), and thus should be a good model for interpretation of deinopid sticky silk fine structure. However, deinopid silk exhibits an extra pair of axial fibers. One pair of axial fibers presumably issues from pseudoflagelliform glands, and the other from either major or minor ampullate glands, but it is difficult to say which at this point.

Finally, the extensibility of the web may not be due to any particular ability of the silk itself, but instead to a beautifully functional series of behaviors operating during the process of web construction. That the spider constructs long sticky silk segments and then contracts them seems almost more elegant a solution to the conundrum of the web's extensibility than arcane material properties. One wonders whether the spider precisely adjusts the length of each segment to its role in the extended web during the brief moment of a strike, but such behavior would argue for a degree of functional precision that seems unlikely. Still, the possibility exists, and with recording equipment could be tested. We already know that deinopid webs hold many surprises, and no doubt more remain to test our credulity.

ACKNOWLEDGMENTS

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A SPECIES OF *HEBESTATIS*
(ARANEAE, CTENIZIDAE) FROM COSTA RICA

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ABSTRACT

Hebestatis lanthanus (Araneae, Ctenizidae) is described from Costa Rica. This is the first species added to the genus since its description in 1903 and the first record for the family in Costa Rica.

INTRODUCTION

Among the mygalomorph spiders, only the Theraphosidae, Dipluridae, Idiopidae (*Neocteniza*) and Barychelidae are known from Costa Rica (Valerio 1986; Zúñiga 1980). Although some theraphosids and diplurids are locally abundant, long years of collecting have yielded few specimens of the remaining families. The family Ctenizidae, very diversified in the subtropics, is represented in the Central American region only by the genus *Ummidia* (Bonnet 1957; Brignoli 1983), with no published records from Costa Rica (several specimens from the Museo de Zoología, Universidad de Costa Rica collection, have been sent to N. Platnick for study). I here report the discovery of a new species of the small genus *Hebestatis* Simon, previously known only from the type-species from California.

Genus *Hebestatis* Simon 1903

The genus was established by Simon based on specimens from California that he had previously described as *Cyclocosmia theveneti* (Simon 1891); no additional species has been described since (Brignoli 1983). It is closely allied to the American genus *Ummidia* and to the Indo-Australian genus *Conothele* sharing with both an excavation or depression on the dorsum of tibia III (Fig. 2). It is easily distinguished from *Ummidia* by the absence of notches in trochanters I and II and from *Conothele* by the presence of several sharp denticles (rather than a short one) on the paired claws of tarsi I and II (Fig. 3).

The species here described shares with *Hebestatis theveneti* (Simon), besides the generic features, the eye configuration: compact group with anterior row procurved, PLE smaller than ALE, and PME smaller than ALE (Fig. 4), and the U-shaped thoracic furrow.

The Costa Rican species can be distinguished from the type-species by their small size (carapace length 3.7 to 7.2 mm, vs. 102 mm in *H. theveneti*) and the ovoid abdomen (posteriorly truncate in *H. theveneti*).
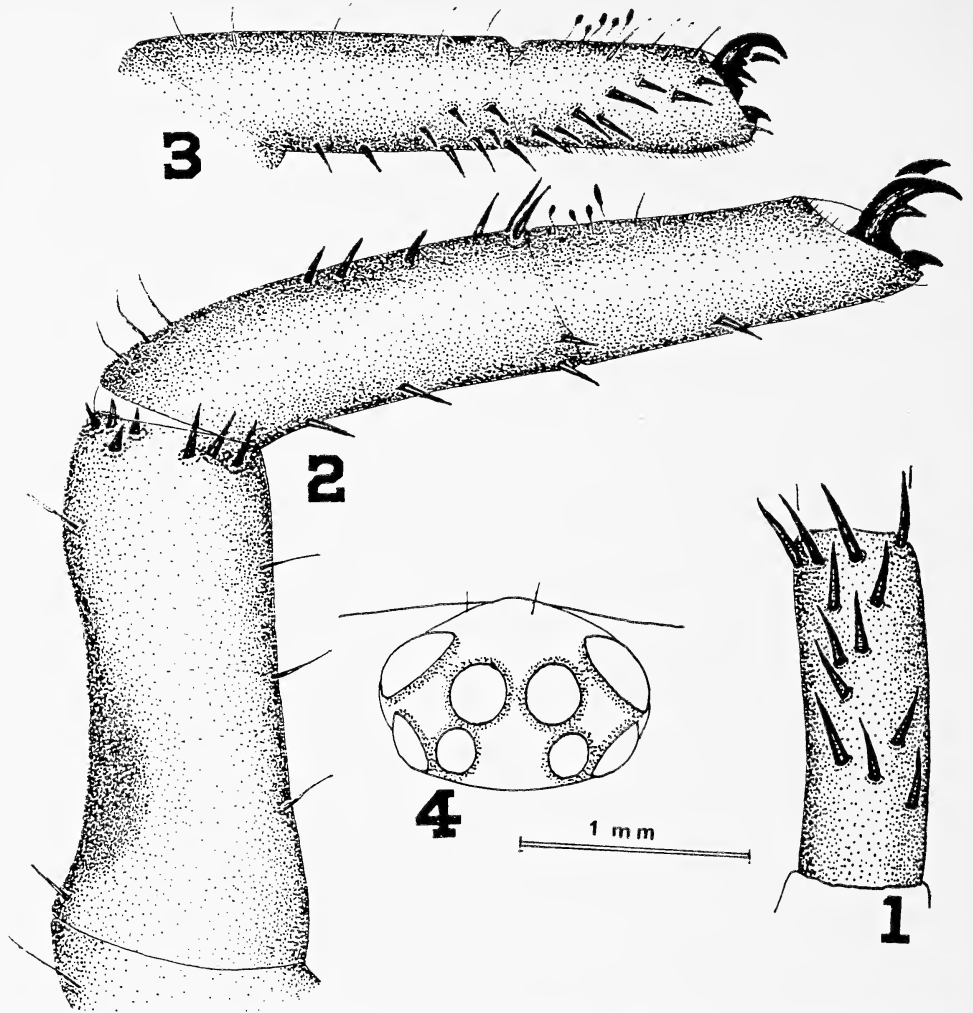
Figs. 1-4.—*Hebestatis lanthanus*, male: 1, third metatarsus, dorsal view; 2, third leg, retrolateral view; 3, second metatarsus and tarsus, retrolateral view; 4, ocular area, dorsal view.

Hebestatis lanthanus, new species
Figs. 1-9

Types.—Male holotype from Ciudad Universitario Rodrigo Facio (Universidad de Costa Rica main campus, 9°57′N 84°04′W), San José Province, collected on April 1981 by R. Aymerich. Female allotype from the same locality, both deposited in the Museo de Zoología, Universidad de Costa Rica. A male and female paratypes deposited in the American Museum of Natural History.

Etymology.—The Greek root indicates surprise that this species has not been discovered before, even though it was found in an area where intensive collecting has been done for many years.

Diagnosis.—Metatarsus III with a row of four strong dorsal spines along distal edge (Fig. 1), tibia I of male with large ventral spines.

Male.—Body glabrous, legs with a conspicuous set of spines on metatarsus and tibia III dorsaly (Figs. 1, 2) and a lateral series of spines on tarsi and metatarsi I-
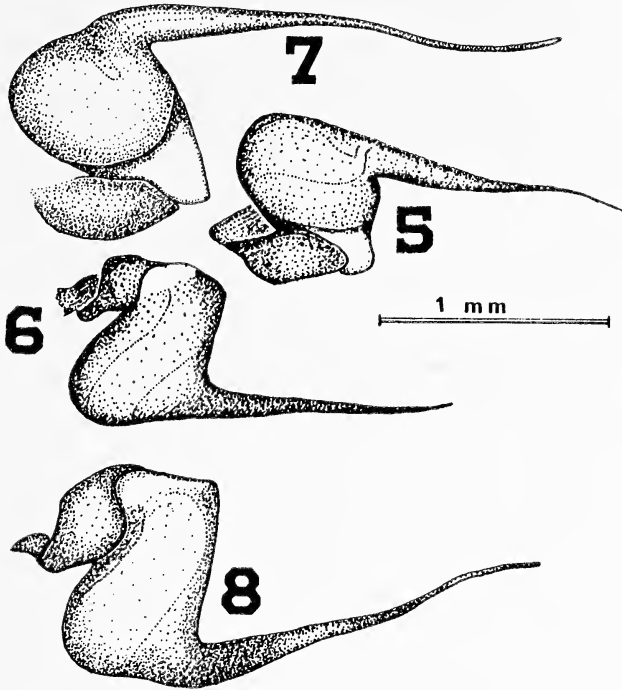
Figs. 5-8.—*Hebestatis lanthanus*, right bulb: 5, Holotype, retrolateral view; 6, Holotype, prolateral view; 7, variation, retrolateral view; 8, variation, prolateral view.

III (Fig. 3), tibia I and II with many (typically more than 20) large spines in ventral view. Weak pad of short hairs on tarsi and distal fourth of metatarsi I and II. Palp and leg tarsi with clavate hairs dorsally (Fig. 3). Paired claws of tarsi with 2-4 denticles (Fig. 3), sometimes only one sharp denticle on those of tarsi III and IV (Fig. 2). Embolus short and straight (Figs. 5-6), sometimes slightly bent (Figs. 7-8). ALE almost touching PLE and AME (Fig. 4). Labium with 6-15 cuspules, sternum lacking cuspules. Carapace shining black; palps, sternum, lungs and genital area light tan; metatarsi and tarsi light brown, remaining leg segments black; abdomen dull black with contrasting white dorsum (white lacking in some individuals). Lengths in mm of 7 specimens, ranges (average in parenthesis): carapace 5.2-6.5 (5.9), sternum 3.1-3.8 (3.5), labium 0.7-0.9 (0.8), abdomen 4.1-6.5, palp 10.3-11.2 (10.6), leg I 12.3-17.4 (15.3), leg II 10.3-15.2 (13.1), leg III 10.3-14.7 (12.6), leg IV 12.2-17.1 (14.9). Bulb total 1.8-2.7 (2.2), embolus 1.2-2.0 (1.9). Carapace width 5.3-6.9 (6.1).

Female.—Similar in coloration to male, except for lighter carapace. Carapace conspicuously narrower than in male. Tibiae lacking ventral spines. Femura III and IV greatly swollen (diameter of tarsi 0.5 mm, diameter of femur 2.7 mm). Adaptations for digging: rastellum consisting of a proturberance bearing many flattened setae, strong flattened setae on both lateral faces of legs I and II (on prolateral face of leg I: 19 on tarsus, 25 on metatarsus and 30 on tibia).

Measurements of allotype.—Carapace length 6.8, carapace width 5.9, sternum length 4.0, labium 0.9, abdomen length 7.1, palp 8.8, leg I 12.1, leg II 10.7, leg III 9.0, leg IV 11.5. Two separated spermathecae with spherical heads and sinuous stalks, covered by ovoid spermathecal glands (Fig. 9).
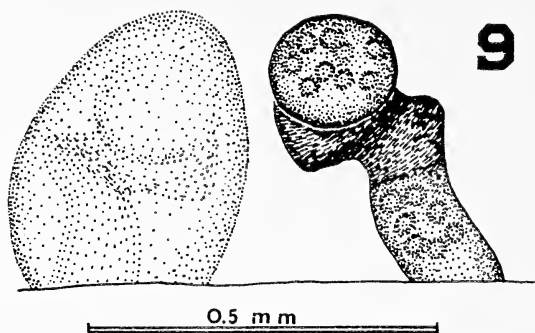
Fig. 9.—*Hebestatis lanthanus*, female genitalia, dorsal view (right spermathecal gland removed).

Distribution.—All localities are in the Central Valley, in Costa Rica, except La Selva, Sarapiquí (a Caribbean lowland site).

Natural history.—The species inhabits the densely populated areas of San José, where it is probably associated with patches of relict forest in a Premontane moist formation. Females inhabit silk-lined tubes, about 10 cm deep. Males wander in May and June.

Specimens examined.—COSTA RICA: *San José Province*, Granadilla, Curridabat, 1 male, 2 females; Barrio La Granja, San Pedro de Montes de Oca, 1 male; San Antonio de Escazú, 1 male; Desampapados, 1 male; Alajuelita, 1 female; *Heredia Province*, Heredia centro, 1 male; La Selva, Sarapiquí, one male.

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GREEN LYNX SPIDER EGG SACS: SOURCES OF MORTALITY AND THE FUNCTION OF FEMALE GUARDING (ARANEAE, OXYOPIDAE)

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ABSTRACT

Guarding green lynx spiders reduce egg sac mortality from two major sources, ants and sac dislodgement, using specific behavior patterns. However, they do not discriminate against egg sacs parasitized by mantispids, which are a third important mortality source. When ants are placed on egg sacs females attack, relocate the sac, or cut attachment lines so that the sac hangs from a minimal number of threads. Egg sacs are also relocated in response to other disturbances. The method of moving the egg sac relies heavily on silk lines and is distinct from that of lycosids and pisaurids.

INTRODUCTION

Numerous functions for female guarding of spider egg sacs and spiderlings have been demonstrated or proposed (Table 1), but the relative importance of these factors for any single species has not been assessed. Many previous observations of maternal behavior, especially in the Lycosidae, have been under laboratory conditions (Bonnet 1947; Higashi and Rovner 1975 and references therein). These studies have uncovered details of egg sac construction, maternal transport of eggs and spiderlings, and feeding of spiderlings. They cannot tell us, however, which of the numerous postulated and demonstrated functions of attending females are the most important under natural conditions. This paper describes the natural sources of egg sac mortality over one reproductive season and the maternal behavior patterns which are variously effective against them, for the green lynx spider *Peucetia viridans* (Hentz) (Oxyopidae) in north Florida.

METHODS

Populations of green lynx spiders in three open fields in Alachua Co., FL were censused at 3-day intervals from July through December 1983 (Fink 1984a, 1986). I followed the fates of 199 females and egg sacs. Egg sacs were marked with plastic flags staked nearby, and females were individually identified with dots of Testor's brand enamel paint. All censuses and observations were made during daylight hours.

The green lynx spider attaches her egg sac to low vegetation and guards the sac and emerged offspring for six to eight weeks until they disperse by ballooning

Table 1.—Presumed or demonstrated functions of the presence of female spiders at egg sacs. Proposed function based on: A = anecdotal field observations, F = field experiments, L = laboratory experiments, H = no data, only hypothesized.

Function		Species (Family)	Reference
Anti-predator	A	*Lyssomanes jemineus* (Salticidae)	Eberhard 1974
Anti-parasite	A	*Cyrtophora moluccensis* (Araneidae)	Lubin 1974
Thermoregulation or humidity regulation	A	*Pardosa amentata* (Lycosidae)	Vlijm et al. 1963
	AL	*Pirata piraticus* (Lycosidae)	Norgaard 1951
	F	*Geolycosa godeffroyi* (Lycosidae)	Humphreys 1974
	A	*Stegodyphus lineatus* (Eresidae)	in Shear 1970
	A	*S. sarasinorum* (Eresidae)	Bradoo 1973
	FL	*Theridion saxatile* (Theridiidae)	Norgaard 1956
Catch spiderling food	AL	*Sosippus floridanus* (Lycosidae)	Brach 1976
	A	*Theridion saxatile* (Theridiidae)	Norgaard 1956
	A	*Stegodyphus sarasinorum* (Eresidae)	in Shear 1970
	L	Other eresids, theridiids	Shear 1970; Kaston 1965
Regurgitate food	L	Several eresids and theridiids	Kaston 1965; Kullmann 1972
	L	*Coelotes terrestris* (Agelenidae)	in Shear 1970
Alert young to danger, food, or water	H	*Theridion saxatile* (Theridiidae)	Norgaard 1956
	H	*Pardosa lapidicina* (Lycosidae)	Eason 1969
Release offspring from sac	L	*Peucetia viridans* (Oxyopidae)	Randall 1977
	L	*Oxyopes salticus* (Oxyopidae)	Whitcomb & Eason 1967
	L	Lycosids, pisaurids	Gertsch 1949

(Gertsch 1949; Whitcomb et al. 1966). Egg sacs that had been recently constructed when first discovered were divided into three groups in each population: (a) females were removed from egg sacs immediately after oviposition ($N = 46$) or (b) after guarding for two weeks ($N = 34$), or (c) females were not removed from their sacs ($N = 58$). The remaining 61 egg sacs were more than a week old when first discovered; although they were not assigned to experimental groups they were censused regularly and used for ant manipulations. Additional observations of unmarked spiders were made in September through December 1984 at various sites in Alachua County.

RESULTS

Source of mortality: Ants.—Three species of ants were observed on or in 13 different unguarded *Peucetia* egg sacs and on the silk surrounding one guarded egg sac: *Crematogaster* sp. (seven egg sacs), *Formica* sp. (three), and *Pseudomyrmex pallidus* (Smith) (five). Holes were chewed through the sac, and each ant carried away a single egg or first instar spiderling at each visit. Up to 10 ants were found in or on a sac, and one sac had both *Formica* and *Pseudomyrmex* removing eggs simultaneously. Seven of these unguarded sacs were completely emptied by the ants, an eighth was emptied except for a mantispid cocoon, and a ninth produced only four spiderlings. Ant damage was distinct from that caused by other predators: attachment lines were undamaged, holes were chewed rather than the silk torn, and whole eggs or spiderlings were removed rather than being damaged or only partly consumed. Based on these

criteria, mortality of at least 20 additional sacs was also attributed to ants. Ants are a major threat to egg sacs both because they are so abundant in *P. viridans* habitat and because they usually destroy the entire contents of the egg sac, resulting in no surviving spiderlings.

Ants are a danger to females as well as to egg sacs. I observed one spider with an ant's head attached to her leg. On four occasions when I placed *Camponotus* and *Crematogaster* ants on unmarked egg sacs and the guarding female attacked, the ant died while clamped onto her leg or chelicera. One female removed the ant and a second autotomized her leg with the ant attached, but the other two females were not able to rid themselves of the corpse. Costs may be associated with having an ant clamped to a leg or chelicera; antlion larvae (Neuroptera) bitten on the mandibles died of starvation if they could not remove the ant (Lucas and Brockmann 1981).

Defense against ants.—A natural encounter between a guarding female and an ant was observed only once, when a female bit and killed a *Crematogaster* ant approaching her on the silk. I staged additional interactions (with females not in the three experimental groups) in order to observe the females' behavior and effectiveness. More than 135 *Solenopsis* sp. and *Crematogaster* sp. ants were collected from nests and introduced one at a time onto the silk surrounding 13 guarded egg sacs. Some ants did not elicit attacks and may not have been noticed by the females before they escaped or fell from the silk. Three distinct behavior patterns were observed: direct attack, sac moving, and sac suspension. Females attacked the first ant(s), but when I continued to supply ants the females initiated one of the other behavior patterns.

a. Direct attack. The females attacked and removed a total of 71 ants. A female did not pursue an ant on the silk or sac, but reacted to it only when it was directly in front of her or walking over her legs or body. When an ant walked on a spider's leg the spider often waved the leg (15 observations), flicking the ant off the plant, and one ant crawling on the spider's abdomen was removed by wiping with a leg. These ants fell from the plant and seemed to be unharmed. Other ants touching the spider or walking directly in front of her were grabbed in the chelicerae (55 observations) and either dropped quickly to the ground or held in a slow bite; none was eaten, but most were moribund or dead.

b. Sac moving. On three occasions when two to five ants had been introduced in succession, the spider cut the silk lines connecting the egg sac to the plant and moved it to a new plant or a new location on the original plant. I watched one female for more than an hour after introducing the ants. After the second ant was introduced the spider began to bite and break individual silk lines near the sac. New lines were spun between the sac and the new site, 10 cm lower on the same plant. Not all lines went directly between the new and old sites; others were spun to two adjacent leaves. These actions, cutting old lines and attaching new, alternated in bouts of several minutes with periods of sac guarding. During this time I continued to introduce ants. Some were attacked, while others triggered new bouts of silk cutting. Within half an hour most of the original lines attaching the sac had been severed, and the sac was suspended on new lines midway between the leaves. By the next census the sac was fastened firmly at its new site, and the attachment lines to the original site had been severed.

The method of moving the sac is different from that used by lycosids, which attach the sac to the spinnerets, or pisaurids, which attach it also to the

chelicerae. In *Peucetia* the move is done entirely by sequentially attaching and detaching lines between the sac and the new and old sites; the female never actually carries the sac.

On 73 occasions guarded egg sacs were relocated to new plants or to new positions on the same plant between censuses. Although the distance moved was not always recorded, most movements were over short distances (< 0.5 m), and movements greater than 1 m were recorded seven times. Twenty-eight of the 73 sac moves (38%) occurred after females were removed for marking and measuring, and therefore indicate that the female moves her sac when disturbed.

c. Sac suspension. Seven spiders began cutting the lines after one to four ants had been placed on the sacs, but did not move the egg sac to a new location. After cutting almost all connections, so that the egg sac dangled from only one to three lines, each female climbed onto the sac and resumed guarding. This behavior is not an aborted attempt to move the egg sac, but a specific response in itself. The effect of silk-cutting is to reduce the probability that a wandering ant will encounter the sac, and to force it to approach from only one direction. This behavior also removes the female herself from the ant's search path, and therefore may lower her own risk.

Source of mortality: Sac disappearance.—The silk attachment lines of eight unguarded egg sacs gradually broke, presumably due to wind and rain. These sacs became loosened from the vegetation and then disappeared. Eight other unguarded sacs also disappeared from their plants, leaving only a few silk lines, and probably had been dislodged similarly. No such loosening and dangling of egg sacs occurred among those that were guarded. Nine guarded egg sacs disappeared simultaneously with their guarding female, but probably were relocated by the female (see b above) rather than dislodged. Alternatively they may have been removed by unidentified predators (such as birds, lizards, or mice), but I have seen no definite evidence of vertebrate predation on egg sacs.

Sac maintenance and prevention of sac dislodgement.—When a female constructs her egg sac the attachment lines are short and inconspicuous, and for several weeks the female does not noticeably alter the sac's appearance. Her spinning, however, prevents the sac from becoming dislodged. Before the spiderlings emerge the female spins more and longer lines, so that the sac is enclosed in a three-dimensional tent of silk. After the spiderlings have emerged the female may spin still more lines, radiating up to 0.3 m from the sac in several directions. The increased number of lines is not necessary to keep the sac attached, and therefore must serve an additional, still undetermined, function.

Other sources of mortality.—*Mantispa viridis* (*Neuroptera: Mantispidae*). *M. viridis* Walker is a generalist brood parasite, appearing in the egg sacs of a number of spider species in Florida (Hieber 1984). Four unguarded, four partially-guarded, and 10 guarded egg sacs contained mantispid cocoons. Fifteen of the broods were completely destroyed by the mantispid, but three had at least one spiderling emerge in addition to the parasite. Five additional sacs, not assigned to the experimental treatments, also produced mantispids.

Mantispid parasitism rates did not differ among the three experimental groups (Fink 1986); however, the proportion of sacs parasitized did vary among sites. At the three sites, 12 of 38 sacs (32%), 5 of 72 sacs (7%), and 6 of 89 sacs (7%) were parasitized (Chi-square = 18.36, df = 2, $p < 0.001$).

Female *P. viridans* do not abandon sacs that contain mantispid larvae or cocoons, or moldy spider eggs, and the behavior of females guarding such sacs was not distinguishable from that of females guarding healthy egg sacs. Females on parasitized sacs guarded for the same length of time (Fink 1984a), spun extra silk lines around the sacs, and bit at the sac to open the seam. Once the seam was open the white cottony mantispid cocoon was visible, as on several occasions was the bright green mantispid within the cocoon. Both cocoon and mantispid are visually quite distinct from a group of globular orange spiderlings. Female green lynx spiders fail to discriminate parasitized sacs not only when the mantispid is invisible within the sac, but also when it is quite obvious to a human observer.

Conspecifics. Peucetia viridans are major predators of immature and mature conspecifics (Turner 1979; personal observation); I found that mature females act as egg sac predators as well. A marked non-parous female was found on another spider's egg sac, which had a hole with a dampened, dark edge unlike the holes made by ants. The partially-digested sac owner was dead on the ground. The non-parous female consumed all of the spiderlings within the sac, and then bit at the sac itself. I observed two other pre-oviposition females adjacent to similarly-damaged egg sacs, but did not see the predation event. The holes in the three egg sacs were distinct from those made by other predators. In each case, the attacking female had not yet constructed her own sac. After a female has oviposited, she is likely to guard another female's egg sac if she encounters it, rather than to eat the eggs (personal observation).

Other predators. In contrast to ants, many arthropods that attack egg sacs and spiderlings cause only partial brood destruction. Five additional species of spiders were observed feeding at or associated with unguarded *Peucetia* egg sacs. *Phidippus pulcherrimus* Keyserling (Salticidae) ate unguarded spiderlings on four occasions, but never consumed an entire brood. *Metaphidippus galathea* (Walckenaer) (Salticidae, two occasions), *Chiracanthium inclusum* (Hentz) (Clubionidae, five), and *Sergiolus bicolor* Banks (Gnaphosidae, four) were found in or on egg sacs but were never seen eating eggs or spiderlings. The clubionid and gnaphosid spiders may have chosen previously-emptied egg sacs as retreat sites.

Unidentified pentatomid bugs (Hemiptera: Pentatomidae) were found on five unguarded egg sacs; at least one had its proboscis piercing the sac and apparently was feeding on eggs. Predaceous larvae of a cantharid beetle (*Chauliognathus* sp.) were found in five unguarded sacs, but were not responsible for their complete mortality. Beetle larvae did consume spider eggs when placed together in a container overnight. A 3 cm long caterpillar (Noctuidae: *Heliothis virescens* (F.)) was found with its head within an unguarded sac. When placed in a container with an undamaged egg sac, it chewed a hole in the side but did not eat any of the sac contents.

Failure to hatch.—Eleven sacs that failed to hatch contained moldy or dried eggs or spiderlings. These unhatched sacs were distributed evenly among the three experimental groups.

Venom spitting.—On at least 15 occasions in 1983 and numerous occasions in 1984, sac-guarding spiders spat venom at me during censuses. This behavior is described in detail elsewhere (Fink 1984b). The intended object of this spitting in natural encounters is unknown; the spiders were never observed spitting at ants or conspecifics.

Interactions between mother and spiderlings.—I found no evidence of a female spider providing any direct care to her emerged spiderlings. Whitcomb et al. (1966) and Randall (1977) have found that the female green lynx spider usually opens the egg sac to allow the spiderlings to emerge, but that spiderlings can emerge unaided. Although I saw at least seven females eating in the presence of their emerged spiderlings, spiderlings did not share the meal, as was reported by Whitcomb et al. (1966). Only two spiderlings were observed feeding while still on the silk surrounding their egg sac; both were eating tiny insects which they probably had captured themselves.

DISCUSSION

This paper has identified several behavior patterns of guarding females. To demonstrate that guarding is adaptive, however, it is necessary to show that females reduce sac mortality and that their overall reproductive success is higher because of their guarding. A companion paper (Fink 1986) proves that the presence of a female significantly increases the survival of her brood. Only 9% of the unguarded egg sacs produced spiderlings, compared with 69% of the guarded sacs. Guarded egg sacs have significantly lower mortality from ants and disappearance but not from mantispids or hatching failure. In addition I showed that under north Florida conditions females have a higher lifetime reproductive success if they guard their first egg sac than if they abandon it and construct a second egg sac.

Although maternal care by *Peucetia viridans* decreases mortality from several sources, I propose that ants were, and continue to be, the major selective factor favoring egg sac guarding. The general importance of ants in the evolution of spider parental behavior has not been assessed. Foelix (1982) and Turnbull (1973) did not include ants in their discussions of spider egg sac predators, and Bristowe (1941) assumed that they were incapable of penetrating the silk sacs. These authors, however, emphasized temperate zone spiders.

Ant predation is more severe in the tropics, and ants can be major selective agents in the evolution of tropical animal adaptations. Jeanne (1975), for example, argues that ant predation has been a major factor in the evolution of social wasp nest architecture. *Peucetia viridans* is a member of a primarily tropical family (Brady 1964), and its range extends through Central America. Some features of its maternal care—in particular severing silk and suspending the sac from a few lines—may be specialized anti-ant adaptations. Additional experiments are necessary before it can be determined if lynx spiders recognize ants as a particular class of danger, and if silk cutting is a specific response.

The fact that a large proportion of unguarded egg sacs were dislodged may be an effect rather than a cause of maternal care. If a female were not going to guard her sac, presumably selection would result in more secure attachment lines. Because the female's presence is selected for by predation, there may be reduced selection for careful attachment behavior. In addition, having fewer attachment lines allows females to move their egg sacs more quickly when disturbed. Although this scenario may be correct, it is also possible that sac dislodgement could not be prevented. During late fall in north Florida the majority of herbaceous plants in *P. viridans* habitats die back, and a plant which provides a

secure substrate for a new egg sac in early October may be prostrate before the spiderlings disperse in mid-November. Christenson et al. (1979; Christenson and Wenzl 1980) found that dislodgement was a major cause of mortality of the egg sacs of *Nephila clavipes* L. in Louisiana, and that it was higher in areas with herbaceous vegetation than in woody areas. Remaining with her egg sac, a green lynx spider can prevent it from falling to the ground by fastening new attachment lines or moving to a safer location.

Some spiders are capable of determining the status of their egg sac contents; thus *Cyrtophora moluccensis* Doleschall females discriminate against parasitized egg sacs (Lubin 1974), and *Agelena consociata* Denis against empty and dead sacs (Krafft 1981). Given that high parasitism rates by *Mantispa viridis* occur (up to 32% of the egg sacs in a particular site), why does *P. viridans* not develop anti-mantispid behavior, or abandon parasitized egg sacs? At least three factors may explain the absence of such behavior in *P. viridans.* (1) At two of three field sites spiderlings emerged from some parasitized sacs. If the probability of successfully producing a second egg sac is lower than the probability that one or a few spiderlings will emerge from a parasitized egg sac, there will be little selection for sac abandonment. This is certainly true for females in north Florida and further north (Fink 1986); however, in south Florida females do produce second sacs successfully (personal observation). (2) Mantispids are active throughout the entire *P. viridans* reproductive season; if a female abandons a sac in a field with a high parasitism rate, then the probability that a second sac would be parasitized is equally high. (3) The mantispid larva, which is approximately 1 mm long when it approaches the egg sac (McKeown and Mincham 1948), initially may be small enough to avoid the female's notice. If a female had a physical rather than a chemical mechanism for checking the status of her egg sac, she might not perceive a mantispid for weeks. Because the weight gain of a female abandoning her egg sac after two weeks of guarding is significantly lower than if she had abandoned immediately, the probability of constructing a second egg sac after perceiving a mantispid in the first would be slight (Fink 1986).

Rovner (1980) has suggested that the Oxyopidae are more closely related to a web-spinning ancestor than to other cursorial families, and Griswold (1983) has described a web-building oxyopid. To my knowledge the green lynx spider's method of moving the egg sac is unlike that of any other hunting spider. Its great reliance on silk lines and the fact that the sac is not carried in its chelicerae or on its spinnerets may be more evidence pointing to a web-building ancestry for the family.

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AGONISTIC INTERACTIONS BETWEEN FEMALE BOWL AND DOILY SPIDERS (ARANEAE, LINYPHIIDAE): OWNER BIASED OUTCOMES

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ABSTRACT

Stereotypic agonistic behavior was observed in induced encounters involving female bowl-and-doily spiders (*Frontinella pyramitela*: Linyphiidae) at natural web sites. Relative size (mass) of opponents, resident status, and web size were examined as possible assessment parameters influencing interaction outcome. Web owners won significantly more interactions than did intruders, regardless of the relative sizes of the spiders. The area of the sheet-web had no relationship to interaction outcome.

INTRODUCTION

Agonistic interactions between spiders occur in two basic contexts: disputes between males over access to a female (Rovner 1968; Dijkstra 1969; Aspey 1976, 1977; Austad 1983; Suter and Keiley 1984) and territorial conflicts over web sites (Buskirk 1975; Ross 1977; Riechert 1978, 1979, 1982; Wise 1983). Among recent approaches to the study of animal conflict behavior is the use of game theory to predict which animal will win or lose (Maynard Smith 1974; Riechert and Hammerstein 1983; Parker 1984). Maynard Smith and Price (1973) have proposed the "hawk-dove" game as a standard paradigm for animal conflict, with the simplest case involving adoption of either an aggressive or a nonaggressive strategy. Use of the appropriate strategy should minimize contest cost and risk of injury to both contestants. The strategy adopted is generally associated with differences in fighting ability and/or in rewards associated with winning. These differences determine the "relative holding power" (RHP = probability of winning) of an individual. Game theory predicts that individuals involved in territorial disputes will assess their own RHP and use the behavioral strategy appropriate to this status (Parker 1974). These concepts have been extensively applied to analysis of contests over web sites in the desert funnel-weaving spider *Agelenopsis aperta* (Gertsch) (Riechert 1978, 1979, 1984; Maynard Smith and Riechert 1984).

In this study, field experiments were conducted to determine: (1) whether individual *Frontinella pyramitela* (Walckenaer) use assessment strategies with regard to their RHP, i.e., relative size (correlated with fighting ability) and resident status, and (2) whether web size contributes to web site value and is thus related to owner defensive behavior.

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METHODS

Bowl-and-doily spiders, *Frontinella pyramitela*, are often present in large numbers on bushes and low vegetation. The web consists of a non-sticky, bowl-shaped sheet of silk (the bowl) with a flat sheet below (the doily) and an irregular meshwork above (the knockdown structure) which deflects prey into the bowl. The spider rests, venter-up, at the center of the underside of the bowl and waits for prey to fall onto the sheet.

This study was conducted from late April through mid May of 1983 and 1984. Penultimate and adult female *F. pyramitela* were collected from low shrubbery and expanses of ivy planted as ground cover on the University of Georgia campus, Clarke Co., Georgia, then taken to the laboratory for marking and weighing. In the laboratory spiders were placed in a holding device and marked on the ventral side of the abdomen with a small dot of enamel paint. Care was taken not to cover the book lungs or the spinnerets. The mark was visible when the spider assumed its characteristic upside-down position on the web. Spiders were than transferred to gelatin capsules and weighed on a Mettler H10/H20® analytical balance to the nearest hundredth of a mg. Spider mass was recorded and each spider was assigned a number (which was marked on the lid of their vial). Spiders were then refrigerated (7°C) to retard water loss and metabolism, thereby minimizing weight loss and possible hunger-drive states that could influence the results of induced encounters (Ross 1977) (however, nothing was known of the hunger state of spiders prior to capture). An experimental group of five spiders was refrigerated for two days and re-weighed. No change in mass occurred.

Spiders were allowed at least 15 min to warm-up before being taken to the site of an undisturbed population of unmarked individuals. Web dimensions (the longest distance across the bowl and a line perpendicular to it) were measured prior to each interaction. The area of the sheet was later calculated by applying these measurements to the formula for the area of an ellipse (sensu Rypstra 1982). Marked spiders (intruders) were transferred from their vial to a syringe with the end snipped off. The plunger of the syringe was slowly depressed and the spider moved toward the open end, which was held above the knockdown structure of the web. The spider was allowed to crawl down into the webbing. During 1983, behavior was recorded *ad libitum* (Altmann 1974) until one spider left the web or until both spiders ceased movement for five minutes. If spiders had thus become inactive, the web site was marked with flagging tape bearing the intruder's number in waterproof ink. The web site was revisited from three to 24 h later to record the outcome of the encounter and to collect the original owner, if possible. I re-checked web sites until the interaction seemed to be over. The spider that occupied the preferred position at the center of the bowl was considered to be the winner. The loser was most often found high in the knockdown structure or clinging to adjacent vegetation. In 1984, *ad libitum* observations were not made, but additional encounters were initiated and sites were revisited to determine the outcome. The size relationship of the interacting spiders was determined when the original owner was collected and weighed.

In order to estimate if differences in prey availability existed at different web sites, 25 sticky traps were placed beside randomly chosen webs in the area where interactions were performed. These traps consisted of the bottom 6 cm of a

styrofoam cup coated on the outside with Stickem Special® (Seabright Enterprises, Emeryville, California). Traps were fastened (with a clothes-pin), upside-down, to the vegetation near a web. They were set out at 1630 hrs on 17 May 1984 and collected 24 h later. Insects were removed with forceps, identified to order or family, and measured (length in mm). Insects from each trap were wrapped in a piece of filter paper and dried in a drying oven for three days. The dried insects were weighed to the nearest thousandth of a mg on a Mettler H10/H20® analytical balance.

RESULTS

Twelve recognizable behaviors were obvious from *ad libitum* observations of 35 interactions. These were: taste tarsi, groom, search web, pull web, shake web, retreat, advance, lunge, raise legs/wave legs/touch legs, contact, chase, explore web. Most are self explanatory, and are similar to behaviors previously described from bowl-and-doily spiders (Suter and Renkes 1984; Suter and Keiley 1984). "Taste tarsi" was observed in every interaction. Upon introduction into the web, the intruder brought the tarsus of a leg to its mouthparts, and repeated this action with several legs. This was often directly followed by or combined with various grooming behaviors.

The average mass of owner spiders was 6.49 mg (SD = 2.15 mg; $N = 54$), and that of intruders was 6.39 mg (SD = 2.28 mg; $N = 54$). Where size asymmetries existed between opponents, the larger spider was on the average 35% heavier (SD = 15%). In 17 interactions performed, the owner was heavier. In 20, the spiders were of approximately equal size (less than 10% difference in weight). In 17 others, the intruder was heavier. A Chi-square test for independence supports the conclusion that winning was independent of size ($p > 0.50$) (Table 1). Although size does not significantly affect the interaction outcome, resident status does (Table 2). Regardless of what sort of size asymmetry existed, owners won significantly more disputes than did intruders ($x^2 = 6.231$; $p < 0.02$) (Table 2). However, closer examination of the data suggests that some size effect may have existed, but because of small sample sizes was not significant. For example, when owners and intruders were of equal size, intruders only won 25% of the interactons, whereas when intruders were heavier than owners they won 41% of the interactions (Table 1).

The average area of a sheet-web used in encounters was 557.43 cm² (SD = 288.08 cm²). There was no significant correlation between the area of the sheet-web and the mass of the owner ($r = 0.078$). No significant difference is apparent in web area between owners which won ($\bar{x} = 547.54$ cm², SD = 272.89 cm²) and owners which lost ($\bar{x} = 577.78$ cm², SD = 308.27 cm²) (Mann-Whitney U test, $p > 0.05$). This suggests that the area of the web had no correlation with the RHP assessment of owners. Though only a short-term estimate, there was some variability in the biomass of prey captured at different web sites (mean dry weight/trap = 0.284 mg, SD = 0.317 mg). The various types of insects captured were: homopterans and hemipterans (1 mm-4 mm), midges (1 mm-2 mm), flies (1 mm-4 mm), wasps (1 mm-3 mm), staphylinid beetles (1 mm), various other beetles (2 mm-6 mm), and thrips (1 mm).

Table 1.—Relationship between size asymmetry and interaction outcome.

| | Number of Wins | | |
Size Relationship	Owner	Intruder	Conclusion
Owner heavier	12 (71%)	5 (29%)	$\chi^2 = 1.164$
Equal weights (within 10% of each other)	15 (75%)	5 (25%)	df = 2, $p > 0.50$
Intruder heavier	10 (59%)	7 (41%)	Accept null hypothesis: winning is independent of spider size.

DISCUSSION

Austad (1983) demonstrated game-playing strategies in male *F. pyramitela*, but female behavior was not examined intensively. However, Suter and Keiley (1984) noted that all agonistic behaviors recorded for males have also been recorded from agonistic interactions between females. Observations of intruder grooming behaviors upon release into a conspecific web suggests that some chemical cue may exist. Since only two interactons were observed outside of contrived situations, perhaps such interactions are actually rare due to some chemical mechanism for detection and avoidance of conspecific webs. Suter and Hirscheimer (in press) have found multiple web-borne pheromones on the webs of *F. pyramitela* females which elicit both courtship and positive geotaxis from males. It may be possible that these chemicals are also detected by conspecific females.

The evidence presented here suggests that web ownership figures significantly in the determination of outcomes of agonistic encounters in female bowl-and-doily spiders. This is contrary to what is known of combat in other spider species. Other studies have found that relative weight, not resident status significantly influences the probability of winning in interactions between females over webs (Buskirk 1975; Ross 1977; Riechert 1978; Wise 1983). However, significant resident advantage was found in combats between male *F. pyramitela* which were closely matched in size (Suter and Keiley 1984). Two factors may explain the owner-biased outcomes observed in the present study. Sheet-webs of the type which *F. pyramitela* builds contain more silk than other types of spider webs (Rypstra 1982). These elaborate webs also have specific substrate requirements for their construction. Rypstra (1983) suggests that such specific substrate requirements may make web sites a limiting resource. In this study, the actual size of the

Table 2.—Effect of weight and resident status on interaction outcome.

| | Relative frequency | | | |
| | Winner is: | | | |
	Larger	Smaller	Test used	Conclusion
Weight (mg)	19 (56%)	15 (44%)	$\chi^2 = 0.4076$	Accept null hypothesis: weight
	(N = 34)		df = 1, $p > 0.50$	bears no significance on outcome.
	Winner is:			
	Owner	Intruder		
Resident status	37 (68%)	17 (31%)	$\chi^2 = 6.231$	Reject null hypothesis:
	(N = 54)		df = 2, $p < 0.02$	owner wins more often.

web had no effect on the interaction outcome; owners were more likely to win regardless of the size of their web. I propose that the apparent high value of webs in terms of energy investment and the possibility that web sites are a limiting resource may have selected for generally tenacious defense behavior by web owners in bowl-and-doily spiders. The web is also very important because it is the site of courtship and mating activity.

This study indicates that female bowl-and-doily spiders have little tolerance for conspecific females which invade their webs. However, the degree of tolerance may change under different environmental conditions. For example, observations of possible cohabitation of females in one web (Weger and Tietjen 1984) may have occurred under higher prey density conditions than existed in the present study. It is not yet clear, however, whether these were examples of tolerance of conspecifics or were agonistic interactions in progress. In contrast to these results, a study by Suter (1985) found that males often cohabit with females for long periods of time, but does not report any observations of females cohabiting. Male linyphiids are unusual among male spiders in that they feed frequently, and temporarily use female's webs for this purpose. A difference in the context of communication signals (reproductive rather than aggressive by the male) as well as potential benefits to the female by a reduced probability of death through predation by theridiid or mimetid spider predators (Suter 1985) accounts for this special case of temporary tolerance.

Though some variability in prey abundance existed between web sites in the present study, the significance of this variability is difficult to assess. It would seem that most of the owners were at sites that at least met their requirements, otherwise it would be predicted that they would abandon rather than defend the web. Linyphiids are known to abandon web sites in response to low prey levels, even without the added factor of web intrusion (Martyniuk 1983). It is also possible that the availability of web sites with respect to population density may affect spacing patterns and tolerance of conspecifics. Janetos (1984) found that an abundance of web sites at his study area made competitive interactions unprofitable. As in this study, he never observed female bowl-and-doily spiders cohabiting in webs.

Within-species variation in aggressive behaviors has also been seen in other spiders (Riechert, in press). Two populations of the spider *Agelenopsis aperta* have been shown to have differences in behavior with a genetic basis. These differences are associated with differences in microclimate and prey density between the different habitats occupied (Riechert 1978, 1979). Rypstra (1983) has shown that spider species which are normally solitary will increase tolerance of conspecifics when provided with high food levels and numerous web sites. Evidence provided by several different studies on bowl-and-doily spiders indicates that some variation exists in levels of tolerance for conspecifics and the occurrence of intraspecific interactions (Janetos 1984; Weger and Tiejen 1984; Suter 1985; present study). Additional studies of this variation under differing conditions of web site and prey availability may provide further evidence that some spiders are able to alter their defensive strategies as changes occur in the costs and benefits associated with engaging in an agonistic encounter.

ACKNOWLEDGMENTS

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SEASONAL AND LATITUDINAL VARIATION IN SPIDER PREY OF THE MUD DAUBER *CHALYBION CALIFORNICUM* (HYMENOPTERA, SPHECIDAE)

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ABSTRACT

Spider prey of the Blue Mud Dauber, *Chalybion californicum* (Saussure), in eastern Missouri included 15 species representing four families. Araneidae was the most diverse family (nine species), but Theridiidae were more numerous, with *Steatoda americana* (Emerton) outnumbering all other species combined. Temporal abundances of the nine spider taxa most commonly captured by the wasps in Missouri suggest that wasps collect spiders in numbers relative to their seasonal and relative abundances, accessibility as prey, or size suitability. Spider prey of the same wasp species in northern Florida included 31 species representing nine families. Araneidae was both the most diverse (19 species) and most numerous family and exhibited a pattern of seasonal increase in abundance as prey of *C. californicum*. Theridiidae constituted a majority of the total individuals in both the Missouri survey and a similar survey from Maryland, while a corresponding study in southern Oklahoma resembled the Florida survey in having high proportions and numbers of Araneidae.

INTRODUCTION

Mud dauber wasps of the genera *Chalybion, Sceliphron,* and *Trypargilum* (Sphecidae) are well known to provision their nests with spiders (Araneae)

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collected from surrounding habitats as food for developing young. The contents of these wasps' nests have been examined by several investigators (Adato-Barrion and Barrion 1981; Brown 1974; Dorris 1969, 1970; Horner and Klein 1979; Irving and Hinman 1935; Obin 1981; Muma and Jeffers 1945; Peckham and Peckham 1898; Rau 1935a, b; Rau and Rau 1916; Sychevskaya 1973; Ward 1970). The predatory behavior of *Chalybion californicum* (Saussure) is described by Coville (1976) and that of *Sceliphron caementarium* (Drury) by Eberhard (1970). Rau (1915) describes behavioral reactions of both *C. californicum* and *S. caementarium* to manipulations of the spider prey in their nests. Obin (1981) gives an interesting account of the relations between the wasps and spiders that live near their nests.

Chalybion californicum (= *caeruleum* of authors) is a common steel-blue wasp distributed from southern Canada into northern Mexico (Bohart and Menke 1963). The species is exclusively an inquiline of other mud dauber genera; that is, *C. californicum* females do not build their own nests but instead re-use nest cells of other mud dauber species (early natural history literature incorrectly ascribes nest construction to *Chalybion*). We present here taxonomic analyses of the spider prey of *Chalybion californicum* in eastern Missouri and northern Florida and compare the results with those of two previous studies, that of Muma and Jeffers (1945) and of Horner and Klein (1979). Temporal variation in both prey species and numbers taken by *C. californicum* suggests that the wasps capture spiders not only according to size and habitat but also to relative and seasonal abundances. Proportional representation of araneid and theridiid prey in the four surveys suggests a latitudinal patterning of prey collection by *C. californicum*

STUDY SITES AND METHODS

Study sites.—In Missouri, the study site was Washington University's Tyson Research Center, near Eureka in southwest St. Louis County. The Research Center is largely mature second-growth oak-hickory forest (described quantitatively by Hampe 1984) with clearings maintained as early successional oldfields by biennial mowing. Substantial populations of *Sceliphron caementarium* nest in old warehouses and on abandoned railroad loading platforms that are near both oldfield and forest habitats. *C. californicum* is a common inquiline of the *S. caementarium* nests.

In Florida, field studies were conducted on *C. californicum* at several sites in Alachua Co. Two of these, Lake Wauburg and "ABC", yielded data for the present study. The Lake Wauburg site consisted of two structures. One, a wooden crawl space with an unfinished pine ceiling and open sides, was within 5 m of the lakefront. The structure was surrounded on three sides by a frequently mowed lawn that was dotted with palms and turkey oaks. A stand of palmetto and hardwoods was located approximately 100 m away. Wasps also nested on the painted, exterior walls of a wooden garage situated 150 m from the lake shoreline immediately next to a small plot of palmetto-hardwood forest.

The "ABC" nesting site consisted of the underside of a wooden bridge spanning Rocky Creek, ca 1 km from State Road 121. The site is situated in the middle of a mesic hammock through which the creek runs. The hammock forest is replaced by cleared, agricultural plots and secondary growth within several hundred meters of the site.

Methods.—In Missouri, 11 spiders were taken in 1983 from *C. californicum* returning to their nests with prey. Three nests of *C. californicum* (with one active cell each) were also collected, opened, and their spider contents were evaluated. Sixty-six cells in 59 additional nests were collected and opened in May through September of 1984. Sampled nests were generally ones in which provisioning had been observed on the day of collection. Nests were collected intact, and individual cells were opened. The fresh spiders (the wasps sting and immobilize but do not kill their prey) were collected and preserved in 70% ethanol. Spiders mutilated by feeding larvae such that they could not be identified were not collected. Voucher specimens of all collected taxa are deposited in the Department of Biology's Museum of Natural History, University of Missouri—St. Louis.

In Florida, sixty-two nests cells in 55 nests were examined for spider contents in 1980 and 1981. As in Missouri, nests were collected intact and the cells opened. Spiders were removed and placed into 70% ethanol and held for identification. Voucher specimens of all taxa are housed in the collections of H. J. Brockmann and M. S. Obin, Department of Zoology, University of Florida, Gainesville.

RESULTS AND DISCUSSION

In Missouri, 56 of the 62 nests had only a single active *C. californicum* cell; five nests had two active cells, and one nest had three. Thirty-four cells were fully provisioned and sealed; 35 were only partially provisioned and were open. Sealed cells contained from 8 to 33 spiders; unsealed cells had from 2 to 22. The total of 860 spiders included 15 species representing four families (Table 1). Thirteen immature *Araneus* could not be identified to species. *Steatoda americana* (Emerton) (Theridiidae) represented 73% of the total collection.

In Florida, not all nest cells were completely provisioned. The number of spiders per cell ranged from one to 37. As in Missouri, full, sealed cells containing an egg or larva were considered completely provisioned. The total of 741 spiders included 31 species representing nine families (Table 1).

The nature and diversity of habits near the wasps' nests may have influenced the diversity and abundance of spiders collected as prey. The warehouse complex that was the Missouri study site is poorly maintained. Consequently, many cracks and crevices exist in the structures and their concrete foundations as well as in the abandoned railroad platforms. These fissues provided abundant web suspension sites favored by theridiid spiders (Kaston 1948) as well as some araneids (Muma and Jeffers 1945). Immediately adjacent oldfield habitats and foliage provided sites where other araneid spiders preferentially placed their webs. The abundance of theridiid and araneid spiders in the wasps' nests may thus reflect in part spider abundance in the habitats nearest the wasps' nesting area. Obin (1981) has observed that *C. californicum* and their spider prey in Florida have similar selections of particular habitats and structures.

Seasonal prey patterning.—Patterning of the monthly abundances of the nine major prey species found in *C. californicum* nests in Missouri is shown in Table 2. The range of dates across which any prey species was taken is in each case encompassed by known dates for seasonal activity as reported by such authors as Kaston (1948, 1970, 1976) and Levi (1973). The data of Table 2 may in some cases directly reflect such phenology. For example, the diminished number of *Steatoda americana* taken by wasps in August and September may reflect

Table 1.—Taxa and abundance of spider prey of *Chalybion californicum* (Saussure) at Tyson Research Center, St. Louis Co., Missouri (MO) in 1983 and 1984 and at the Lake Wauburg and "ABC" sites in Alachua Co., Florida (FL) in 1980 and 1981.

| FAMILY | SPECIES | *N* (individuals) | |
		MO	FL
ARANEIDAE	*Acanthepeira stellata* (Marx)		29
	Acacesia hamata (Hentz)		1
	Araneus cingulatus (Walckenaer)	18	
	Araneus marmoreus Clerck	24	
	Araneus miniatus (Walckenaer)		3
	Araneus pegnia (Walckenaer)		5
	Araneus sp.	13	2
	Araniella displicata (Hentz)	1	
	Arigope aurantia Lucas	26	122
	Argiope sp.		8
	Eustala anastera (Walckenaer)		21
	Gea heptagon (Hentz)	7	166
	Larinia borealis Banks		1
	Leucauge venusta (Walckenaer)		10
	Mangora gibberosa (Hentz)		11
	Mecynogea lemniscata (Walckenaer)		113
	Metazygia wittfeldae (McCook)		1
	Micrathena mitrata (Hentz)	1	
	Micrathena sagittata (Walckenaer)	3	8
	Neoscona arabesca (Walckenaer)	23	8
	Neoscona domiciliorum (Hentz)		2
	Neoscona hentzi (Keyserling)	3	
	Neoscona sp.		2
	Nephila clavipes (L.)		25
CLUBIONIDAE	*Clubionoides excepta* (L. Koch)		1
MIMETIDAE	*Mimetus* sp.		1
OXYOPIDAE	*Peucetia viridans* (Hentz)		3
PISAURIDAE	*Pisaurina undulata* (Keyserling)		1
SALTICIDAE	*Eris marginata* (Walckenaer)		1
	Metaphidippus protervus (Walckenaer)	1	
TETRAGNATHIDAE	*Tetragnatha guatemalensis* (Seeley)		1
THERIDIIDAE	*Argyrodes globosus* Keyserling		1
	Latrodectus mactans (Fabricius)		42
	Latrodectus variolus (Walckenaer)	48	2
	Steatoda americana (Emerton)	629	
	Steatoda borealis (Hentz)	9	
	Steatoda grossa (C. L. Koch)		18
	Theridion frondeum Hentz	53	
	Theridion pictipes Keyserling		113
	Tidarren sisyphoides (Walckenaer)		11
THOMISIDAE	*Misumenops asperatus* (Hentz)		6
	Misumenops oblongus (Keyserling)		2
	Philodromus washita Banks	1	
	TOTAL	860	741

diminished abundance in those months (Kaston 1948). The occurrence of *Latrodectus variolus* (Walckenaer) as prey only after mid summer does not accurately reflect the known April to November phenology of that species (Wilson 1967), however, and suggests that the wasps shifted to it as a prey item of lower preference as numbers of *S. americana* in the environment diminished. Analogous phenomena may explain the similar shift in frequency in nest cells

Table 2.—Monthly patterning of the numbers of individuals of the nine spider taxa most frequently collected from nest cells of *Chalybion californicum* (Saussure) in St. Louis Co., Missouri, in 1983 and 1984. Numbers in parentheses beneath the months indicate the number of nests and the number of cells sampled, respectively, for that month.

TAXA	MAY (1,1)	JUNE (13,15)	JULY (27,31)	AUG. (17,18)	SEP. (4,4)
THERIDIIDAE					
Steatoda americana	31	198	312	87	1
Theridion frondeum	—	35	18	—	—
Latrodectus variolus	—	—	3	22	23
Steatoda borealis	—	—	1	2	6
ARANEIDAE					
Araneus cingulatus	—	17	1	—	—
Neoscona arabesca	—	10	6	7	—
Araneus marmoreus	—	—	4	16	4
Argiope aurantia	—	—	22	4	—
Gea heptagon	—	—	3	4	—

from *Araneus cingulatus* (Walckenaer) to *A. marmoreus* Clerck (Table 2). The patterning for *Argiope aurantia* Lucas probably reflects size suitability; though the spiders are known to be active until October (Levi 1973), spiders in late summer and fall are too large to be placed into a mud dauber cell. Thus the data of Table 2 together with information on spider phenologies and growth patterns suggest that the number of individuals of any spider species in the nest cells reflects components of seasonal occurrence, seasonal size patterning, wasp preferenda, or combinations of these. Such phenomena may also explain the increased frequency of Araneidae between April and August as prey of *C. californicum* in Florida (Table 3), for Obin (1981) notes that small-sized araneid spiders (e.g., *Mecynogea lemniscata* (Walckenaer), *Gea heptagon* (Hentz)) are found in Florida throughout the summer.

Latitudinal differences.—The present survey from Missouri and one from Maryland (Muma and Jeffers 1945) had more than two thirds of the total number of individual spiders in the Theridiidae, while a survey in southern Oklahoma (Horner and Klein 1979) and the present survey from Florida had more than two thirds of the total number of individuals in the Araneidae (Table 4). Latitude is a correlate of this observed difference in nest contents. The present Missouri survey, at 38°31′N latitude, and the Maryland survey, at ca 39°0′N, are north of the Oklahoma and Florida surveys, at ca 34°30′N and ca 29°37′N, respectively. The number of species per family and their proportions of the total

Table 3.—Seasonal variation in prey capture by the mud dauber *Chalybion californicum* at two sites in Alachua County, Florida during 1980 and 1981. The relative frequency of capture for each spider family is given as a proportion of all spider prey during the period indicated. Numbers in parentheses beneath the sample dates indicate the number of nests and the number of cells sampled, respectively.

TAXA	APRIL 1-MAY 31 (10,15)	JUNE 1-JULY 1 (11,12)	JULY 16-OCTOBER 1 (34,35)
ARANEIDAE	136/245 (55.5%)	84/128 (65.6%)	318/368 (86.4%)
THERIDIIDAE	106/245 (43.3%)	34/128 (26.6%)	47/368 (12.8%)
Other	3/245 (1.2%)	10/128 (7.8%)	3/368 (0.8%)

Table 4.—Proportional representation by family of the numbers of individuals of Araneae in four surveys of the prey of *Chalybion californicum* (Saussure). MO = St. Louis Co., Missouri (*N* = 860; present study); MD = Maryland (*N* = 927; Muma and Jeffers 1945); OK = Comanche Co., Oklahoma (*N* = 446; Horner and Klein 1979); FL = Alachua Co., Florida (*N* = 741; present study). The latitudes of the study sites are given beneath the column headings. Totals do not equal 1.000 due to rounding error.

TAXA	MO 38°31'	MD 39°0'	OK 34°30'	FL 29°37'
Anyphaenidae	—	0.001	—	—
Araneidae	0.138	0.269	0.699	0.726
Clubionidae	—	—	—	0.001
Linyphiidae	—	0.001	—	—
Lycosidae	—	—	0.002	—
Mimetidae	—	0.001	—	0.001
Oxyopidae	—	0.016	—	0.004
Philodromidae	—	—	0.004	—
Pisauridae	—	—	—	0.001
Salticidae	0.001	0.016	—	0.001
Tetragnathidae	—	—	—	0.001
Theridiidae	0.859	0.677	0.294	0.252
Thomisidae	0.001	0.018	—	0.011
TOTALS	0.999	0.999	0.999	0.998

number of species captured at a site show a similar but not identical pattern; only the most northerly survey, in Maryland (Muma and Jeffers 1945), had Theridiidae with the largest number and proportion of species (Table 5).

At least two factors may underly these latitudinal differences in prey taxa of *C. californicum*. First, behavioral components of prey search and capture may vary between northern and southern wasp populations. Obin (1981) suggests that individual wasps may vary in their responses to spiders as a function of searching locale, which suggests that the wasps may form search images for specific spider taxa. Second, composition of the spider fauna may vary with latitude and/or specific features of the habitat surrounding each study site. Obin (1981) suggests that the lower percentage of *Latrodectus mactans* (Fabricius) taken by *C. californicum* in Florida than in Maryland (Muma and Jeffers 1945) reflects the availability of appropriately sized (i.e., small) araneid prey throughout the summer in Florida. The most southerly survey had the highest number of species, suggesting a latitudinal component of spider diversity, but the most northerly survey, which is based on the largest number of specimens, has the second highest species number suggesting that sampling intensity may also affect the data.

Our study demonstrates that the proportional representation of theridiid and araneid prey abundance can differ greatly between sites (Table 4, columns MO and OK) even though the number of available prey species and the number of species per family (= diversity) are similar (Table 5, columns MO and OK). We suggest, therefore, that surveys of wasp-collected spider taxa be implemented at two or more sites in conjunction with independent, parallel surveys of spider abundance and diversity. Such studies could reveal if *C. californicum* females consistently select a particular subset of the full araneid diversity available to them. If so, the relatively easy technique of sampling spiders from recently provisioned mud dauber nests could provide a useful diagnostic tool for

Table 5.—Number of species per family and their proportions of the total number of species per survey in four surveys of the spider prey of *Chalybion californicum* (Saussure). MO = St. Louis Co., Missouri (present study); MD = Maryland (Muma and Jeffers 1945); OK = Comanche Co., Oklahoma (Horner and Klein 1979); FL = Alachua Co., Florida (present study). The latitudes of the study sites are given beneath the column headings. Proportion totals do not equal 1.000 due to rounding error.

TAXA	MO 38°31'	MD 39°0'	OK 34°30'	FL 29°37'
Anyphaenidae	—	1/0.052	—	—
Araneidae[a]	9/0.600	[b]4/0.201	7/0.538	17/0.548
Clubionidae	—	—	—	1/0.032
Linyphiidae	—	1/0.052	—	—
Lycosidae	—	—	1/0.076	—
Mimetidae	—	1/0.052	—	1/0.032
Oxyopidae	—	[b]2/0.105	—	1/0.032
Philodromidae	—	—	2/0.153	—
Pisauridae	—	—	—	1/0.032
Salticidae	1/0.066	2/0.105	—	1/0.032
Tetragnathidae	—	—	—	1/0.032
Theridiidae	4/0.266	[b]7/0.368	3/0.230	6/0.193
Thomisidae	1/0.066	[b]1/0.052	—	2/0.064
TOTALS	15/0.998	[b]19/0.987	13/0.987	31/0.997

[a]Immature *Araneus* that could not be determined to species are not included.

[b]These are minimum estimates of the number of species; actual numbers may have been higher.

biogeographic analysis of spider diversity within the limits of wasp prey taxa and prey size preferenda.

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COURTSHIP AND COPULATORY BEHAVIOR
OF THE FUNNEL-WEB SPIDER,
HOLOLENA ADNEXA (ARANEAE, AGELENIDAE)

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ABSTRACT

Courtship and copulatory behavior were observed in the funnel-web spider, *Hololena adnexa* (Chamberlin and Gertsch). Overall these behaviors were similar to those reported for *Agelenopsis* species. However, behavioral differences were found in the precopulation stage.

An unusual pattern for male palpal insertion duration during copulation was discovered. Initial short duration insertions were followed by a peak of longer insertion durations; however, subsequent insertions decreased in duration. The peak in insertion duration was postulated to correspond to the maximum time of transfer of sperm.

INTRODUCTION

Basic life history data have yet to be gathered for many spider species, and this deficiency is particularly noticeable in the areas of courtship and mating behavior (see recent review by Robinson 1982). In the family Agelenidae there have been a few studies and these are briefly reviewed. Gering (1953) focused on courtship and copulation in three species of *Agelenopsis: A. aperta* Gertsch, *A. oklahoma* Gertsch, and *A. pennsylvanica* C. L. Koch. He also presented a detailed description of the mechanics of palpal insertion for these species. Krafft et al. (1978) recorded the frequency of vibratory signals produced by male *Tegenaria parietina* (Fourcroy) and *Coelotes terrestris* (Wider) during courtship. Leborgne et al. (1980) examined the possibility that males use chemical cues to recognize female webs and recorded the frequency of vibrations produced by males during courtship for *Tegenaria domestica* (Clerck) and *T. pagana* C. L. Koch. Using these same species and *Coelotes terrestris*, Roland (1984) found males orienting to draglines of conspecific females in T-maze experiments.

The current study focuses on the courtship and copulatory behavior of a western U.S. agelenid, *Hololena adnexa* (Chamberlin and Gertsch). *Hololena adnexa* is one of the most common urban garden spiders in the San Francisco Bay Area of California, yet like many spider species it has received no more than casual attention to date. It builds a typical horizontal agelenid non-sticky web with a funnel retreat on shrubs, trees and more rarely on the ground in plant duff. Often, large numbers of these spiders can be seen covering shrubbery with their dense webs. They become most noticeable in late summer, when one web can cover an area 20 cm or more in diameter. *Hololena adnexa* served as a good study animal since it was abundant and was maintained readily under laboratory conditions.

METHODS

Penultimate male and female *Hololena adnexa* were collected from landscape shrubs in Berkeley, California in the fall of 1980. They were kept in 97 mm × 27 mm glass vials plugged with cotton. House flies were provided as prey once a week, but no free water was given since previous rearings showed that it was unnecessary.

Virgin individuals were placed in separate plastic boxes (6.0 cm × 10.2 cm × 10.2 cm) 2 weeks prior to mating observations. For each mating, a male was placed on the edge of the female's web. Mating observations were made with and without the aid of a dissecting microscope. Insertions of each palpus were counted and timed. At the end of each mating the male was removed and the female was allowed to construct egg sacs within the box. Only those matings that resulted in fertile eggs were considered valid. Means are followed by standard deviations throughout this paper.

RESULTS

During the six-month period of study, seventeen complete matings were observed for 17 females and 14 males of *H. adnexa*. They constituted the basis for a five-step mating sequence (adopted from Gering (1953)) reported below.

Step 1-Courtship.—When placed on the female's web, the male responded by vigorously pumping his legs and abdomen in the vertical plane without palpal drumming. This produced one to six bouts of vibration, with each lasting from 3 to 90 sec. How often this behavior occurred was a function of the female's actions. In response to the male's movement on the web, the female usually went into cataleptic paralysis, characterized by drawing the legs close to the body and remaining immobile, as reported by Gering (1953). When the female became cataleptic after the initial vibrations, the male continued vibrating and searching until he found her. In two instances, she did not recognize the male after these first vibrations and attacked him as if he were prey. The male repelled such attacks with his longer legs, and a few additional vibrations caused the female to become cataleptic.

Step 2-Precopulation.—When the male found the female, usually in the funnel portion of the web, he grasped her last two pairs of legs in his chelicerae, near the patellae, facing the female's caudal end. He then lifted and dragged her to a different portion of the funnel. The time interval between male placement on a web and location of the female averaged 32.8 ± 20.3 min. This step ended when the male stopped moving, momentarily released the female, and turned her on her side in preparation for copulation. The length of time from first contact with the female to initiation of copulation averaged 9.8 ± 11.8 min.

Step 3-Copulation.—The male began copulation by moistening both palpi, drawing them one at a time through his chelicerae. He then applied either the right or left palpus to the female's epigynum, depending on which side she lay. If on her right side, he applied the right palpus; if on her left side, the left palpus (Fig. 1). Successful insertion of the embolus was outwardly evidenced by a noticeable swelling of the hematochae of that palpus. The number of repeated insertions of one palpus was variable among the test spiders, averaging 81.8 ± 25.6. However, duration of insertions followed a regular pattern (Fig. 2). For

Fig. 1.—Male and female in mating position.

approximately the first 20 insertions the hematochae became inflated for several seconds; subsequent insertions lasted 1 to 2 min. These longer insertion times continued for several palpal applications, but gradually diminished. After the male finished inserting one palpus he grasped the female and moved her to a new location before proceeding with the unused palpus. Only infrequently did the male turn the female on her other side and begin applying the other palpus. Occasionally a male experienced difficulty in keeping the embolus inserted when inflating the genital bulb. If this occurred, he cleaned the embolus and attempted the insertion again, sometimes up to 10 to 15 times. If still unsuccessful, he turned the female on her sternum and moved her to a new location or just turned her on her side and tried again, either with the same or the other palpus. During most matings each palpus was used in a single long series of insertions. However, in three cases, in which both palpi had already been used in a mating, the males reverted back to using the original palpus. The timing of these insertions did not follow the pattern for the initial insertion series, since no distinct maximum insertion time occurred (Fig. 3).

   Step 4-Postcopulation.—Following copulation, the male groomed his palpi and walked off and away from the female, leaving her in a cataleptic state for several seconds. Only twice when the male walked away did the female quickly recover and chase him off the web. Time from male placement on the web to departure from the mated female averaged 166.1 ± 43.1 min.

   Step 5-Sperm induction.—After each mating, the male was placed in a vial, where he soon refilled his palpi with sperm. I saw this behavior only three times
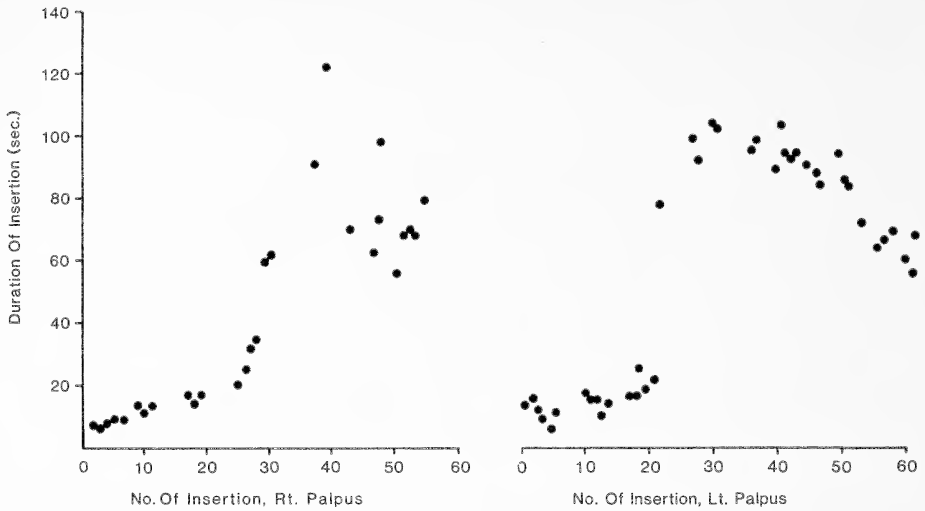
Fig. 2.—Relationship between duration and sequence of insertions of the right and left palpi of a single representative mating of *Hololena adnexa.*

and never completely for one spider; however, a general summary of the activity is offered. Sperm induction begins with the male spinning a small rectangular "sperm" web, which is broader at the ends than the middle. A drop of sperm from the genital aperture is placed on the center of the web. The male centers his cephalothorax over the web, moistens his palpi, and alternately applies each palpus to the sperm droplet by reaching beneath the web. During this procedure no evidence of hematochal swelling can be observed. The entire process of web building to charging of palpi lasts 25 to 30 min.

DISCUSSION

Male chemotactile perception of a pheromone on conspecific female silk has been demonstrated in at least four web-building spider families; Araneidae, Linyphiidae, Theridiidae, and Agelenidae (Meyer 1928; Suter and Renkes 1982; Ross and Smith 1979; Leborgne et al. 1980). Initiation of mating behavior in *H. adnexa* males occurred when the male touched female silk. This suggests either a chemotactic or tactile stimulus. Visual cues were unlikely, for when courtship was initiated the female was in the funnel of the web and not visible. Chemical, tactile, or both types of cues from the webs of *H. adnexa* females probably trigger courtship behavior in males. Chemotactic reception during courtship has been implicated previously in three other agelenids: *Tegenaria domestica, T. pagana* and *Coeletes terrestris* (Leborgne et al. 1980; Roland 1984).

Successful copulation is dependent on the coupling of the male palpus to the female's epigynum. Gering (1953) provides great detail on how the male palpus of *Agelenopsis* mechanically fits into the female epigynum. Probably the most critical structure is the conductor of the palpus, which locks into a coupling cavity anchoring the palpus onto the epigynum. This allows the genital bulb to twist the embolus into the female's bursa. Gering examined male and female structures of an unidentified species of *Hololena* and found them capable of the same procedures described for *Agelenopsis* mating.
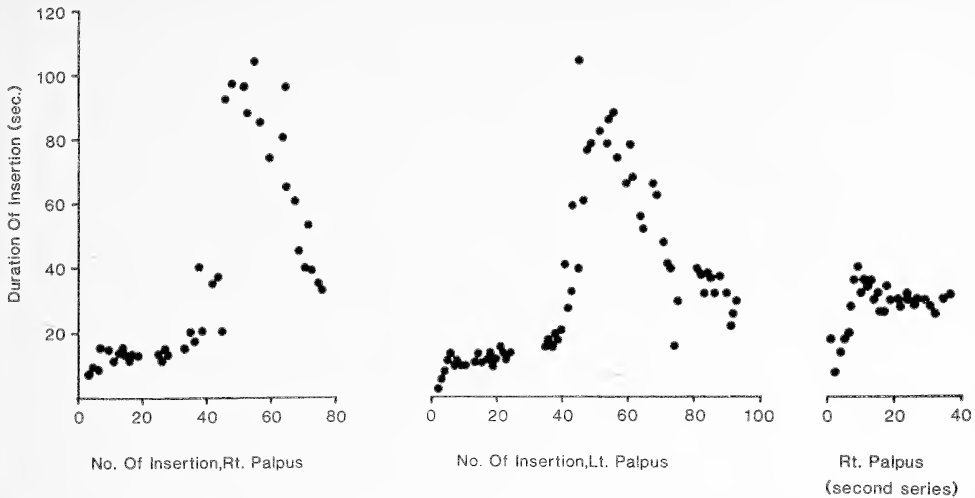
Fig. 3.—Relationship between duration and sequence of insertions of the right and left palpi of a single representative mating of *Hololena adnexa* with a second series for the right palpus.

Positioning of the female by the male is critical for successful copulation, aligning male and female structures for a proper fit. Alignment of male to female takes place during the precopulation stage. Gering (1953) divided this stage into four substages: contact, reversal, positioning, and cleaning. Differences were observed in the first three substages between *H. adnexa* and *Agelenopsis*. Gering described the contact stage as a lunge and quick seizure of the female, a behavior not observed in the male of *H. adnexa*, which slowly touched and grasped the female. After grasping her, the male usually moved her to another location in the funnel, a behavior not reported for *Agelenopsis*. Gering stated that mounting the female usually occurred from the rear, making reversal necessary. In all but a few of the *H. adnexa* matings, mountings were from the front, thereby eliminating the need to reverse position. The positioning substage in *Agelenopsis* and *H. adnexa* was quite different. In *Agelenopsis*, the male is draped across the female at an angle of 45⁰, while the male *H. adnexa* stood parallel alongside the female. The differences found in the mating stance between *H. adnexa* and *Agelenopsis* may relate to differences in structure of the male palpi.

A pattern for palpal insertion duration was found for *H. adnexa* that has not yet been described in agelenids. Gering did not follow a complete mating between male and female *Agelenopsis*, since he interrupted mating after six insertions and concentrated on the timing and mechanics of individual insertions. Therefore, Gering could not have observed how insertion times may have changed during a mating. In *H. adnexa* insertion durations were found to be shorter at the beginning and end of a series than halfway through it (Figs. 2 and 3). The longest insertion lasted about 100 sec. I hypothesized that all short interval insertions (20 sec or less) previous to this peak probably resulted in no sperm transfer. Maximum distension of the hematodocha for *Agelenopsis* species was equated with transfer of sperm, and this required an average of 72 sec and a minimum of 16 sec. Although the amount of time required for maximum distension in *H. adnexa* is unknown, it may be that an insertion lasting 20 sec or less would not allow enough time to totally insert the embolus, based on the similarity of palpal morphology to *Agelenopsis* species.

The duration of insertion at maximum distension may be determined by the quantity of sperm transferred. Maximum insertion time would then represent the period when maximum transfer of sperm occurred. Insertions immediately following the insertion time peak could serve to deplete what sperm remained in the fundus. When males were observed reinserting a palpus in a second series, this could also be for emptying any remaining sperm. Depleting the fundus may account for there not being a peak for the second series, but just a number of insertions for approximately equal time intervals (all longer than 20 sec) (Fig. 3).

An alternate interpretation presented first by Helsdingen (1965) for *Lepthyphantes leprosus* (Ohlert) and subsequently tested by Rovner (1975) on *Schizocosa saltatrix* (Hentz) and *S. avida* (Walckenaer) states that a structure associated with haematodochal inflation, for instance a valve within the palp, becomes fatigued with repeated use during copulation. Thus, insertion durations increase during copulation.

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RESEARCH NOTES

WEB ORIENTATION IN THE SPIDER
MANGORA GIBBEROSA (HENTZ) (ARANEAE, ARANEIDAE)

Diurnal orb-weaving spiders which maintain a position at the web-hub may be exposed to direct sunlight. Many orb-weavers use a variety of adaptations to control insolation while on or near the web, including reflective body colors (Robinson and Robinson 1978; Tolbert 1979), body orientations (Coventry 1967; Krakauer 1972; Robinson and Robinson 1974, 1978; Moore 1978; Carrel 1978; Tolbert 1979), and web orientations (Coventry 1967; Carrel 1978; Tolbert 1979; Biere and Uetz 1981). Apparently light is the cue used to direct these thermoregulatory behaviors (Robinson and Robinson 1973).

This study examines the compass orientation of webs of the orb-weaver *Mangora gibberosa* in young pine plantations in Northern Florida in October. This habitat is relatively open and spiders utilizing it may be exposed to high levels of insolation for all or part of the day.

Data were collected on October 2nd and 7th. On both days, the compass angle of the sun at sunrise was recorded and then the pine plantation was traversed and orientations taken of the first 25 *Mangora* webs encountered. On October 7th, 10 of the webs were checked again at noon to determine if *Mangora* rebuilds its web or remains at the web-hub when the sun is at its zenith. Web orientation was defined as the compass direction that the side of the web, on which the spider was sitting, faced. The web orientations were determined by projecting a hypothetical line through the middle of the spider and the web-hub with a compass and recording the resulting angle. For data collection and analysis, north was arbitrarily set at 0°.

The compass orientations of the webs on both days were unimodally distributed (Rayleigh's Test; both $p < 0.01$), with mean orientations of 116 ± 7° and 128 ± 32°, respectively (Fig. 1). These orientations were not significantly different from each other (Wheeler and Watson Test), and not significantly different from the compass direction of the sun (110°) at sunrise (Stephan's Test). There were no changes in the observed web orientations when the webs were checked at noon, and the spiders were found at the hubs of their webs. This suggests that *M. gibberosa* does not rebuild its web over the course of the day with respect to light, and does not use a retreat to control insolation.

We suggest *Mangora gibberosa*, like other orb-weavers, uses early morning light as a cue to orient its web. Such orientations to sunrise would maximize the surface area of the body exposed to insolation and allow the spiders to warm quickly during the coolest part of the day (Fig. 2). A quick warmup in the morning may be advantageous to prey capture, particularly during the cooler months of the year such as October. Nothing is known about the web orientation of *M. gibberosa* during other months of the year. However, a web orientation toward early morning light, in conjunction with the vertical position of the spider
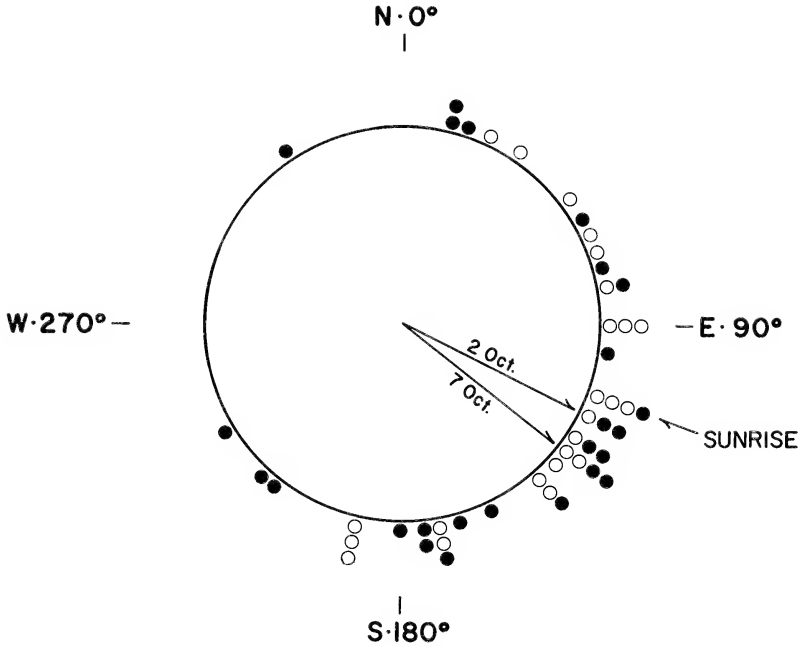
Fig. 1.—Web orientation by the spider *M. gibberosa*. The mean compass orientation (± circular deviation) of *M. gibberosa* webs for Oct. 2 (white circles) was 116 ± 7° (*n* = 25 webs); for Oct. 7 (black circles) it was 128 ± 32° (*n* = 25 webs). Sunrise was at 110° both days.
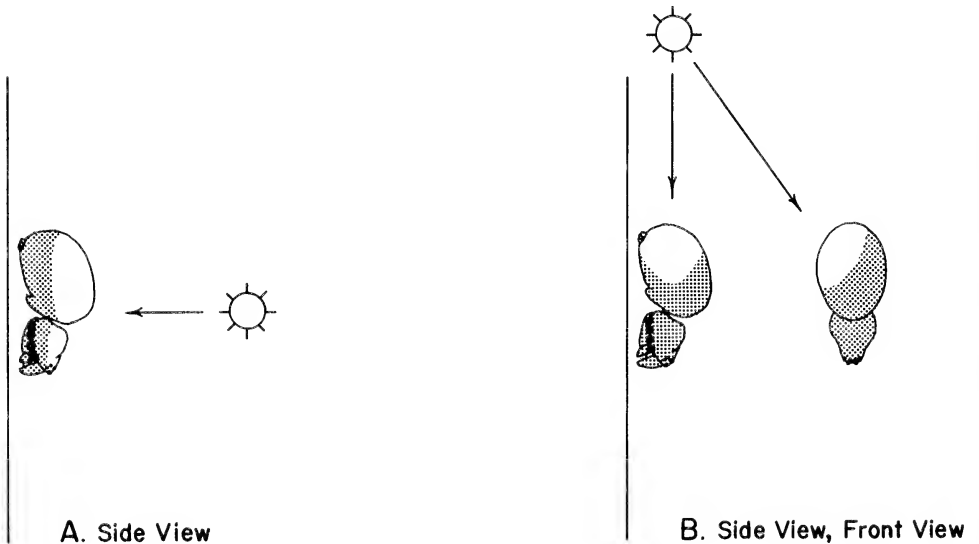
Fig. 2.—A side view of the web of *M. gibberosa* oriented to early morning light showing the surface area of the spider exposed to insolation (A), and in the same orientation showing a side and front view of the surface area of the spider exposed to insolation when the sun is at or near its zenith (B). Non-stippled areas represent exposed body surface. The spider drawings are modified from Kaston (1981).

on the web, would present the side of the spider to the sun, thereby minimizing the surface area of the spider exposed to insolation when the sun is overhead (Fig. 2). In open habitats, such as pine woods, where this spider is commonly found (Gaddy and Morse 1985), such an orientation would be advantageous during the summer months when temperature and insolation are high (Biere and Uetz 1981). The orientation to light demonstrated by *M. gibberosa* is consistent with those observed for other diurnal orb-weavers using open habitats (*Nephila*: Krakauer 1972; Robinson and Robinson 1973, 1974, 1978; Carrel 1978; *Argiope*: Coventry 1967; Tolbert 1979; *Micrathena*: Biere and Uetz 1981).

We would like to thank J. Reiskind for identification of *M. gibberosa* and for his interest in the project. All statistical tests are from Batschelet (1965).

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SUSCEPTIBILITY OF SPIDER SPECIES
TO THE FUNGUS *NOMURAEA ATYPICOLA*

One of the most common pathogenic fungi attacking spiders is the hyphomycete *Nomuraea atypicola* (Yasuda) Samson (see Nentwig, W. 1985. J. Arachnol., 13:272-274, for review of literature). There are three known species in the genus *Nomuraea*. The best known, *N. rileyi* (Yasuda) Samson (Samson, R. A. 1974. Studies in Mycol., 6:80-85), is primarily a pathogen of insects and the causative agent for natural epizootics in populations of many lepidopteran larvae (Ignoffo, C. M. 1981. In Microbial Control of Pests and Plant Diseases, 1970-1980. ed. H. D. Burges, Acad. Press. 914 pp). *N. atypicola* has been primarily isolated from spiders; Petch (1939. Trans. Br. Mycol. Soc., 23:139-140) reported its isolation from the ctenizid *Kishinoyeus typicus* Kisida (since renamed *Latouchia typica*). The third species, *N. anemonoides* Hocking, has been isolated only from soil (Hocking, A. D. 1977. Trans. Br. Mycol. Soc., 69:511-513).

N. atypicola was named and described as a species of *Spicaria* on the basis of herbarium specimens and living cultures, and combined by Samson (loc. cit.) in

Table 1.—Relative susceptibility of spiders to topical applications of conidia of *Nomuraea atypicola*. * Diagnosed as positive mycosis.

Species	No. Tested	No. Positive	Minimum Time (Days) to Death*
Loxoscelidae			
Loxosceles reclusa Gertsch & Mulaik	7	2	2
Theridiidae			
Achaearanea tepidariorum (C. L. Koch)	2	2	6
Linyphiidae			
Frontinella pyramitella (Walckenaer)	1	1	3
Araneidae			
Argiope aurantia Lucas	2	2	12
Acanthepeira stellata (Marx)	2	2	20
Cyclosa sp.	1	0	—
Neoscona sp.	2	1	31
Tetragnathidae			
Tetragnatha laboriosa Hentz	7	7	3
Agelenidae			
Agelenopsis sp.	3	2	11
Lycosidae			
Lycosa rabida Walckenaer	1	1	21
Lycosa sp.	1	0	—
Pardosa sp.	2	0	—
Anyphaenidae			
Anyphaena sp.	1	1	9
Thomisidae			
Misumenops sp.	1	1	15
Xysticus sp.	4	1	27
Salticidae			
Henizia ambigua (Walckenaer)	1	1	3
Phidippus audax (Hentz)	7	4	10
P. clarus Keyserling	6	6	2
Phidippus sp.	11	8	1
Metaphidippus galathea (Walckenaer)	1	1	13

Fig. 1.—Mycelial outgrowth of *N. atypicola* from an adult of *Lycosa rabida*.

Nomuraea. It is considered to be the anamorph of *Cordyceps cylindrica* Petch (Petch, T. 1938. Trans. Br. Mycol. Soc., 21:34-67). In a recent observation (Nentwig, loc. cit.) natural mycoses of *N. atypicola* were reported from the araneids *Argiope argentata* (Fabricius), *A. savignyi* Levi and *Nephila clavipes* (Linnaeus). The objective of the present study was to determine the susceptibility of a taxonomically and ecologically diverse range of spider species to *N. atypicola*.

We used *Nomuraea atypicola* (Yasuda) Samson isolate #CBS, R-01000, from the laboratory of the third author. The isolate was obtained by culturing ascospores of the fungus parasitizing an unidentified trap door spider and found in forest soil in Guamá, Pará, Brazil. Inoculum from this isolate was transferred to petri dishes and *N. atypicola* was then cultured and propagated on malt-ager at 25 ± 1°C. Conidia were harvested after incubation of the cultures for at least 7 days. Adult and subadult spiders were collected between September 6 and October 18, 1985, in buildings, backyards, an alfalfa field and a native tall grass prairie in Boone and Callaway counties, Missouri, U.S.A.

All spiders were exposed to the fungus within 24 h of collection. They were first immobilized with CO_2 (flow rate of 30 cm^3/min, Lab-Crest Mark III Flowmeter®, Fisher and Porter, Chicago, Ill. 60651) and then conidia were topically applied to the ventral and dorsal surfaces of the cephalothorax and abdomen. Approximately 50 μl of a conidial suspension, containing 3 X 10^5 conidia per ml in 0.03% of the detergent Tween-80®, was used for each spider. Treated spiders were individually placed in either a standard 100 X 15mm petri dish (with wet filter paper) or, for larger individuals, a 1/2 pint ice-cream container (with a wet, 4 cm-long dental wick) that was covered with a petri plate lid. The treated spiders were incubated at 25 ± 1°C and checked daily for mortality. After three days, all surviving animals were fed appropriate sized cabbage looper larvae, *Trichoplusia ni*, twice weekly until they died or the experiment was terminated (a maximum of 78 days). Spiders appeared to remain

healthy, consuming the offered *T. ni* larvae and producing silk, until the time of death. All dead spiders were microscopically examined for the presence of *N. atypicola* mycosis.

Our experiments with *N. atypicola* satisfy Koch's postulates. Seventeen of the 20 species that were treated developed *N. atypicola* mycosis (Table 1 and Fig. 1). The three nonsusceptible species, representing four specimens from two families (Araneidae and Lycosidae), were in the genera *Cyclosa, Lycosa,* and *Pardosa.* We also subjected an opilionid, *Leiobunum vittatum* Say (Phalangiidae), to the same protocol. All three individuals tested developed the mycosis, the earliest in two days following application of conidia.

There are no obvious trends in our results. The tested species represent a reasonably broad spectrum of taxonomic and ecological diversity within the spider suborder Labidognatha, as well as a member of one other arachnid order. If the results on *L. vittatum* are any indication, *N. atypicola* may attack not just spiders but arachnids generally.

All previous references to host range of this fungus have been anecdotal. Our results indicate that *N. atypicola* has a broad potential host range; determination of its importance as a mortality agent will require increased awareness on the part of collectors and field ecologists.

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NOTES ON SPIDER NATURAL HISTORY:
THE WEBS AND HABITS OF *ARANEUS NIVEUS* AND *A. CINGULATUS* (ARANEAE, ARANEIDAE)

In his revision of the *Araneus pegnia* (Walckenaer) species group of North America, H. W. Levi (1973. Bull. Mus. Comp. Zool., 145:473-552) acknowledged the help of specid wasps that had collected a critical portion of the material forming the basis of his revision. Several new or rare species appeared in the otherwise well-known New England fauna, and Levi attributed their rarity to the habit of living in tree-tops, where the wasps foraged. This note reports several observations suggesting that Levi was correct, and includes for the first time photographs of the webs of *Araneus niveus* (Hentz) (Figs. 1-3), and *A. cingulatus* (Walckenaer) (Figs. 4-5).
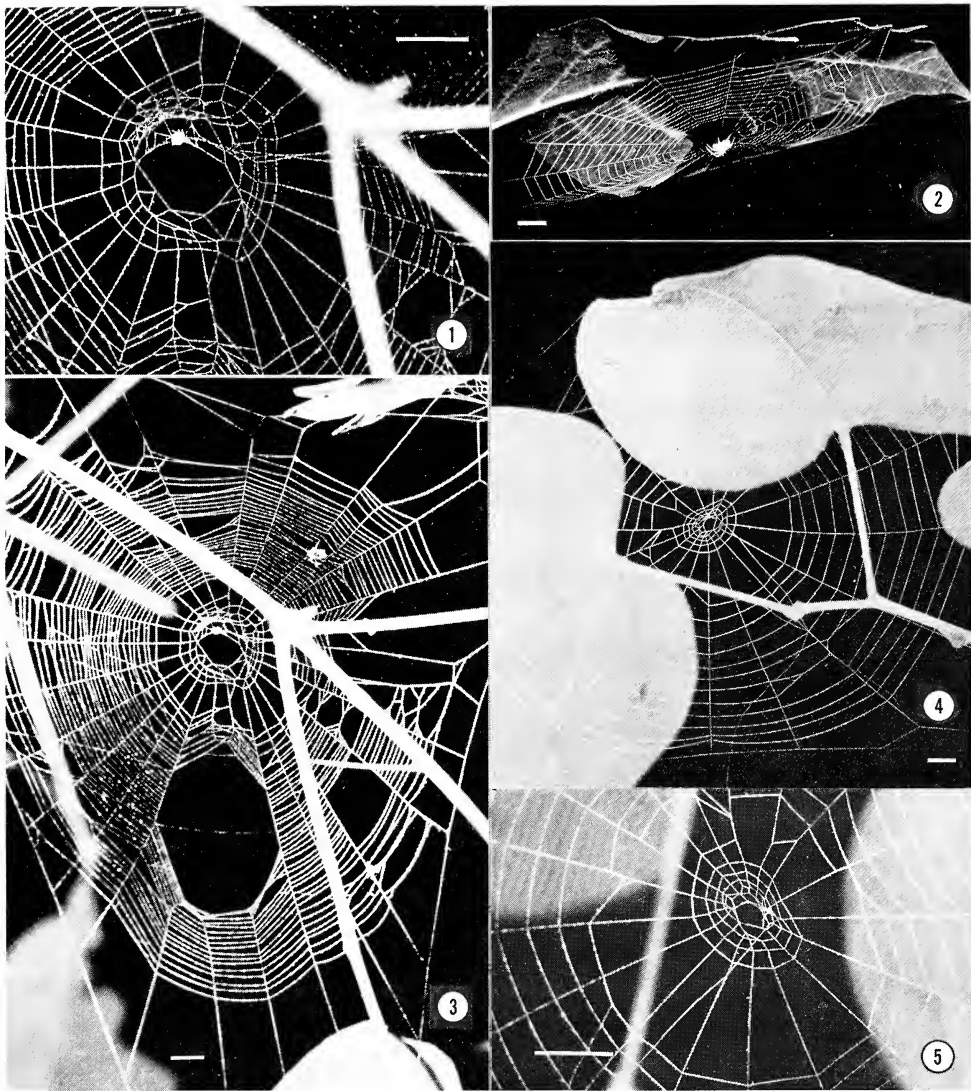
Figs. 1-3.—*Araneus niveus*: 1, close-up of open hub, showing loose non-sticky spiral; 2, adult female web; 3, different adult female web spanning several leaves. Figs. 4-5.—*A. cingulatus*: 4, adult female web spanning two leaves; 5, close-up of open hub and loose spiral. Scale lines = 1 cm.

These nocturnally active species were all taken about 1 h after sundown during July 9-16, 1985 from newly constructed webs in the crown of a wind-thrown oak (*Quercus alba*, estimated height 15 m), in mesic hardwood forest of Rock Creek Park, Washington, DC. The tree had fallen a few days before during a thunder storm. About 20 animals had built webs in the crown, and a few more in the shrub layer immediately surrounding the fallen crown. None were found far from the fallen tree. All evidence suggested that the spiders resided in the standing tree canopy and had "ridden" it to the ground when it fell. Despite a wide diversity of potential web sites, many webs of both species spanned the lobes of single oak leaves (Fig. 2), or a few parallel leaves (Fig. 4). The web planes were parallel to the lower leaf surface (Fig. 2), suggesting that these webs were placed to intercept insects landing or taking off from the underside of the leaf. Thus a guild of

canopy-dwelling orb weavers may exist, which spins webs across the undersurface of leaves to capture aerial prey.

The web architectures of all three species are similar to other published photos of *Araneus* webs (e.g., Levi, H. W. 1971. Bull. Mus. Comp. Zool., 141:131-179; Levi, 1973, cited above; Witt, P. N., & R. Baum. 1960. Behaviour, 16:309-318): a slightly elliptical form, a messy, open hub surrounded by an irregular, loosely spiralled remnant of the non-sticky spiral; moderate numbers of radii (R) and sticky spirals (SS) (*niveus*: 17-26R, 13-43SS, *n* = 4; *cingulatus*: 16-20R, 12-23SS, *n* = 3) no signal line, and spider at the hub. These web features may characterize the genus *Araneus*, or at least, a monophyletic group including *Araneus*. The description of *A. cingulatus* by Levi (1973) agreed well with the living animals, but live *A. niveus* had a salmon or pink dorsal patch on a greenish-white abdomen, whereas Levi mentioned a black patch in a similar position. He did not see live animals.

The ability to identify species by field characters or habits has been a crucial step in the development of many disciplines in natural history. Our knowledge of spider natural history would prosper more quickly if specialist knowledge, equipment, and preserved specimens were not a prerequisite. Much information is already available on web architecture, and it seems better to share it now rather than to hoard it in anticipation of some larger project, such as a comprehensive field guide. I would like to thank Claudia Sobrevila for help in the field, and H. W. levi for suggesting improvements to the manuscript.

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OBSERVATIONS ON COMMENSAL DIPTERA (MILICIIDAE AND CHLOROPIDAE) ASSOCIATED WITH SPIDERS IN ALABAMA

A number of commensal Diptera feed simultaneously with spiders on fluids coating the exterior of spider prey (Robinson, M. H. and B. Robinson. 1977. Psyche, 84:150-157; Sivinski, J. and M. Stowe. 1980. Psyche, 87:337-348). Some of these Diptera were observed on prey of three species of spiders in Lee Co., Alabama during 1979-1983 (Table 1). On 18 October 1979 an adult green lynx spider, *Peucetia viridans* (Hentz), was found feeding on a honey bee, *Apis mellifera* L., in an old field near Auburn, Alabama. A single *Desmometopa m-niqrum* (Zetterstedt) was feeding on fluids on the bee. On 12 November 1979, in the same location, four *D. m-niqrum* were found feeding on another honey bee captured by a green lynx spider. These two prey with commensals were among 20 prey of green lynx spiders collected in the old field habitat in 1979, a 10% incidence of commensalism. These two instances were the only observations of

Table 1.—Commensal Diptera associated with spiders and their prey in Lee Co., Alabama, 1979-1983.

Commensal Diptera			
Taxon	Total	Prey species	Spider species
Milichiidae:			
Desmometopa m-niqrum	5	*Apis mellifera* (Hymenoptera, Apidae)	*Peucetia viridans* (Oxyopidae)
D. m-niqrum	2	*A. mellifera*	*Phidippus audax* (Salticidae)
Neophyllomyza sp.	2	*Leptoglossus phyllopus* (Hemiptera, Coreidae)	*Xysticus elegans* (Thomisidae)
Milichiella lacteipennis	4	*Brochymena quadripustulata* (Hemiptera, Pentatomidae)	*P. viridans*
M. lacteipennis	13	*L. phyllopus*	*P. viridans*
Neophyllomyza sp.	4	*L. phyllopus*	*P. viridans*
Paramyia nitens	1	*L. phyllopus*	*P. viridans*
Chloropidae:			
Olcella cinerea	17	*L. phyllopus*	*P. viridans*
Olcella sp.	1	*L. phyllopus*	*P. viridans*

green lynx spiders feeding on honey bees in this field. The only other instance of *D. m-nigrum* feeding as a commensal was observed on 15 May 1983, when an adult female jumping spider, *Phidippus audax* (Hentz), was found feeding on a honey bee in a fencerow near Auburn. Two *D. m-niqrum* were collected from this prey item.

On 9 June 1983 an adult female crab spider, *Xysticus elegans* Keyserling, was observed feeding on a leaf-footed bug, *Leptoglossus phyllopus* (L.), in the fencerow. Two *Neophyllomyza* sp. were feeding on this prey item. On 4 September 1983 an adult green lynx spider was found on a sapling tree growing on a lawn ca. 20 m from the fencerow. It had captured a stink bug, *Brochymena quadripustulata* (F.). Four *Milichiella lacteipennis* (Loew) also were feeding on this bug.

Only one of 74 prey (1.4%) of green lynx spiders collected in cotton fields in Lee Co., Alabama from 1979-1981 was found with commensals. On 31 August 1981, 36 commensal flies were found feeding simultaneously on a *L. phyllopus* captured by a green lynx spider in a cotton field. Three species of Milichiidae and two species of Chloropidae were collected from this prey item (see Table 1). The specimens of *L. phyllopus* and *B. quadripustulata* with commensals were the only representatives of these hemipteran species captured by spiders in this study.

Sivinski and Stowe (1980) suggested that hymenopterans may be more attractive to Milichiidae than are other prey. This is supported in the case of *D. m-niqrum* by our observations that this species was found feeding as a commensal only on honey bees. The other commensal dipterans, however, were apparently attracted to the two hemipteran prey species. Prey preference studies are needed to determine the range of prey which are attractive to the various commensal species.

Commensal associations with spiders by *M. lacteipennis*, *O. cinerea*, and *Olcella* sp. have not been reported previously.

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FIRST RECORD OF THE SCORPION *PARAIURUS NORDMANNI* (BIRULA, 1899) (SCORPIONES, IURIDAE) IN GREECE

For over 80 years, the iurid scorpion *Paraiurus* (= *Calchas*) *nordmanni* (Birula) was known only from several localities in the Coruh River Valley in northeastern Turkey. Recently, (Kinzelbach, R. 1980. Verh. naturwiss. Ver. Hamburg NF, 23:169-174) two additional records for the species in Turkey were reported: from Siirt in northeastern Turkey and from Antalya along the southern coast. To date, the species is known only from the asbove locatities.

While sorting through undetermined scorpion material in the collection of the Field Museum of Natural History (Chicago, U.S.A.), I identified a subadult male specimen of *P. nordmanni* from Samos Island, Greece (off the western coast of Turkey). The specimen was taken on 23 April 1979 by A. Riedel on the south slope of Mt. Spiliani, 2 km N of Pithagorion. Habitat information on the label indicates that the specimen was collected in an oak forest among limestone rocks. Two specimens of *Euscorpius carpathicus* were also collected on that island by the same collector, but neither were from the slopes of Mt. Spiliani.

This record is significant because of our very limited knowledge of the distribution of this scorpion. It is the first record for *P. nordmanni* outside Turkey, extending the range westward by more than 400 km and represents the first island record. This indicates that the scorpion has a much wider distribution than previously suspected. Its apparent rarity may be due to the fact that its populations have not been sampled with ultraviolet light detection techniques.

I am grateful to Dr. Daniel A. Summers of the Field Museum of Natural History, Chicago, for the loan of material from that institution.

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ORB-WEAVER ABUNDANCE IN
THREE FORESTED COMMUNITIES IN THE
SOUTHERN APPALACHIAN MOUNTAINS OF SOUTH CAROLINA

Very little quantitative information exists on the relationship between spider abundance and plant community. In reviewing the literature on the variability of spider abundance from place to place, Rypstra (Rypstra, A. L. 1986. Amer. Midland Nat., 115:42-51) listed three general factors as "determinants" of the number and distribution of spiders: (1) vegetation (as structure), (2) abundance of insects, and (3) the physical environment (primarily temperature and humidity). Some workers have documented a close association between abstract vegetation communities and spider communities (Barnes, R. D. and B. M. Barnes. 1955. Ecology, 36:658-66; Luczak, J. 1963. Ekol. Polska A., 11:159-221). Luczak (op. cit.) went as far as to point out that a given "biotope" will harbor a specific association of spider species. Although Rypstra (op. cit.) was concerned with relative abundance of web spiders in general and not with the relative abundance of various species in different communities, her conclusions seem to be compatible with those of Barnes and Barnes (op. cit.) and Luczak (op. cit.). Here, I present data indicating that the abundance of several species of orb-weavers is significantly different in three forested communities in the mountains of South Carolina.

While sampling vegetation in a mesic cove forest community and in a nearby xeric oak-hickory community in the southern Appalachians of South Carolina, I noticed a marked difference in the abundance of *Leucauge venusta* (Walckenaer). This orb-weaver was much more abundant in the mesic cove forest (Station Cove) than in the drier oak-hickory woods (Walhalla). In 1984, I initiated a procedure to quantify the abundance of several orb-weavers in the two communities, and in 1985, I followed the same procedure in a hemlock ravine community (Battle Creek). Two permanent strip transects 40 m x 1.5 m were established in each of the three communities. The transects were walked monthly (about mid-month) between 1000 and 1400 hours and all adult orb-weavers seen in webs were counted. Representative specimens of each species encountered were collected and deposited in the Clemson University Arthropod Collection, Department of Entomology, Clemson University, Clemson, South Carolina.

All three study areas are found in Oconee County, South Carolina along the eastern edge of the Blue Ridge physiographic province. Station Cove, the mesic cove community, is approximately 8 kilometers north of Walhalla, South Carolina (34°46′N 83°04′W). The oak-hickory community (Walhalla) is 2 kilometers south of Walhalla, and the hemlock ravine (Battle Creek) is approximately 20 kilometers southwest of Walhalla. Station Cove is dominated by tulip poplar (*Liriodendron tulipifera*), beech (*Fagus grandifolia*), basswood (*Tilia heterophylla*), and white ash (*Fraxinus americana*). The Walhalla oak-hickory site is dominated by white oak (*Quercus alba*), scarlet oak (*Quercus coccinea*), and mockernut hickory (*Carya tomentosa*). The dominant canopy trees at Battle Creek hemlock ravine are eastern hemlock (*Tsuga canadensis*), beech, and tulip poplar. A dense shrub layer of evergreen *Rhododendron* spp. is present at Battle Creek, a less dense layer of *Lindera benzoin* and *Asimina triloba* is

Table 1.—Orb-weaver abundance in three forested communities in the southern Appalachians. Study sites: SC-Station Cove; BC-Battle Creek; WA-Walhalla. Data were collected from Station Cove in 1984 and 1985 and from Walhalla and Battle Creek in 1985 and 1986. Numbers indicate adult orb weavers encountered on two 40 m x 1.5 m transects walked at each site.

SPECIES	JUNE			JULY			AUG			SEPT		
	SC	BC	WA	SC	BC	WA	SC	BC	WA	SC	BC	WA
Araneus bicentenarius	0/0	1/0	1/0	0/0	2/0	1/0	0/0	1/0	1/0	0/0	0/0	0/0
Eustala anastera	0/0	0/0	0/1	0/0	0/1	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Leucauge venusta	112/80	40/52	1/2	18/22	8/12	2/1	6/8	0/0	0/0	0/0	0/0	0/0
Mangora maculata	0/0	0/0	0/0	0/0	0/0	0/0	23/28	6/10	1/3	20/25	15/18	5/5
Mecynogea lemniscata	0/0	0/0	10/12	0/0	0/0	8/10	0/0	0/0	6/10	0/0	0/0	0/0
Metepeira labyrinthea	0/0	0/0	2/2	0/0	0/0	2/3	0/0	0/0	2/3	0/0	0/0	1/1
Micrathena gracilis	0/0	0/0	0/1	0/0	1/0	4/6	0/0	0/0	6/8	0/0	0/0	1/1
Micrathena mitrata	0/0	0/0	0/0	4/5	2/2	0/0	8/10	5/6	6/8	2/4	4/6	12/18
Neoscona domiciliorum	0/0	0/0	0/0	0/0	0/0	0/0	8/6	10/6	1/1	10/8	15/20	0/1
Verrucosa arenata	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	7/10	0/0	0/0	6/11

present at Station Cove, and a sparse layer of saplings and mixed shrubs is present at the Walhalla oak-hickory site. Relative site moisture was calculated for each site using Parker's (Parker, A. J. 1982. Phys. Geogr., 3:160-68) Topographic Relative Moisture Index (an index ranging from 0-100 using slope angle, aspect, and other microsite variables). According to the index, Station Cove is the most mesic site with a 56, Battle Creek is mid-mesic with 45, and the Walhalla site falls near the xeric end of the index at 24.

The results here indicate that a marked difference exists in orb-weaver abundance between the mesic and xeric sites (Table 1). At Station Cove and Battle Creek, *Leucauge venusta* (Walckenaer) was the dominant early summer spider, being especially abundant at Station Cove; however, at the more xeric Walhalla site *Mecynogea lemniscata* (Walckenaer) was the dominant orb-weaver in June and July, with *Leucauge venusta* rare. *Mangora maculata* (Keyserling) was the dominant late summer (August and September) orb-weaver at Station Cove and shared dominance with *Neoscona domiciliorum* (Hentz) and *Verrucosa arenata* (Walckenaer) at Battle Creek (Table 1). In August at the Walhalla site, *Mecynogea lemniscata*, *Micrathena gracilis* (Walckenaer), and *Micrathena mitrata* (Walckenaer) were all abundant, while in September *Micrathena mitrata* was dominant.

The data from the three sites seem to indicate that, at least in the southern Appalachians, *Leucauge venusta*, *Mangora maculata*, *Neoscona domiciliorum*, and *Verrucosa arenata* are primarily species of densely-shaded mesic sites. (Gaddy and Morse (Gaddy, L. L. and J. C. Morse, 1985. South Carolina Agr. Exp. Stat. Bull., p. 1094) noted that in South Carolina *Neoscona domiciliorum* is abundant in Coastal Plain swamps.) Conversely, *Mecynogea lemniscata* and *Metepeira labyrinthea*, neither of which was observed along transects in Station Cove and Battle Creek, appear to be spiders of more open, xeric sites. The site preference of *Micrathena mitrata*, which was common at all three sites in August and September, is unclear. *Araneus bicentenarius* McCook and *Eustala anastera* (Walckenaer) were found at both the Walhalla site and at Battle Creek; however, because of their rarity at the two sites, no conclusions concerning site preference can be reached (Table 1).

The relationship between site moisture, canopy coverage, and species composition has not been adequately studied. Because quantitative analyses of the physical parameters (light intensity, soil moisture, absolute humidity, etc.) or the measurement of relative abundances of insects were not undertaken at the three sites, it is impossible to pinpoint the factors that regulate species dominance and distribution. Light intensity, for example, is obviously an important factor in orb-weaver site selection. The data presented here, however, indicate that some orb-weavers respond to moisture gradients. Furthermore, the data support the general conclusions of Barnes and Barnes (op. cit.) and Luczak (op. cit.) concerning associations between spider and plant communities and strongly infer that, like other organisms, orb-weavers probably have optimal environmental conditions under which they are most abundant.

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CROSSOPRIZA (LYONI?) (ARANEAE, PHOLCIDAE)
EATS HER OWN EGGS

Pholcids are ideal subjects for the study of development from oviposition to emergence from the egg sac, because the eggs can be observed without the need to interfere with the intact sac. In the course of such a study, on *Crossopriza (lyoni?)* (Blackwall 1867), it became apparent that females often ate one or more of their eggs.

The egg sac is normally grasped by the female's chelicerae at a point where the 'string-bag' arrangement of silken threads is replaced by a substantial sheet of silk about three egg-diameters in extent. Not infrequently the female will change the position of her grip.

Most of the females under study would eat one or more of their own eggs at irregular intervals. Figs. 1-2 show the drained chorions of two eggs lying on the periphery of the egg mass of a female *C. (lyoni?)*. Necessarily, the position of the consumed eggs shows the extent to which the female changes the position of her grip. Whether the eggs consumed are infertile and, if so, whether the female can
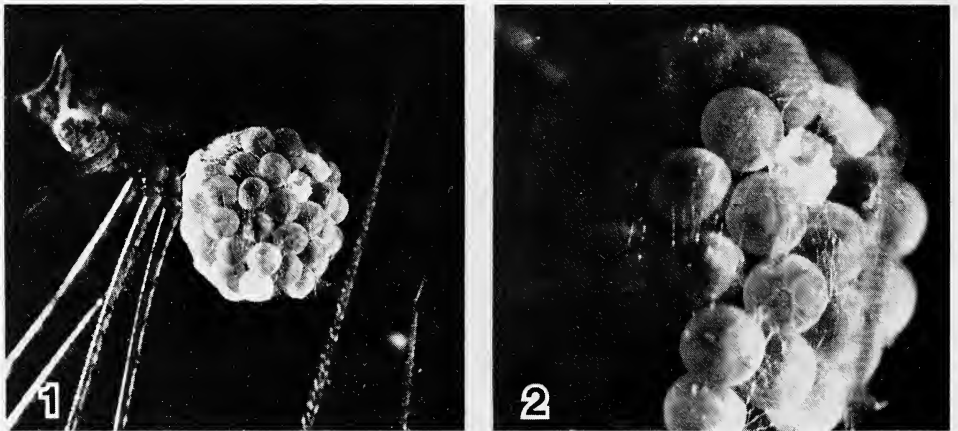
Figs. 1-2.—*Crossopriza (lyoni?)*: 1, female with egg sac; two consumed eggs are visible at the upper right of the egg mass; 2, closeup of the consumed eggs on the periphery of the egg mass.

detect this, is unknown. In a previous paper, the benefits of an infertile egg resource for developing spiderlings of *Theridion rufipes* Lucas was considered (Downes, M. F. 1987. J. Australian Entomol. Soc., in press). As a general observation, the proportion of infertile eggs in egg sacs of *C. (lyoni?)* seems markedly high, but to what extent the spiderlings feed on these, when they are able to do so, is unclear. The female, however, normally eats a few or many before hatching commences.

Robert Raven made the identification, and in doing so noted a discrepancy in a diagnostic character (a lack of thorns on ventral femur I of males) in specimens from Townsville. This explains the question mark after the specific epithet.

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PREDATION BY SPIDERS ON PERIODICAL CICADAS
(HOMOPTERA, *MAGICICADA*)

Periodical cicadas (Homoptera, Cicadidae, *Magicicada* spp.) are noted for massive emergences of adults that occur on either 17-year or 13-year cycles in eastern United States (Simon 1979). Such emergences present veritable cornucopias to insectivorous predators and represent the classic example of predator swamping or satiation (Lloyd and Dybas 1966a, b). Periodical cicadas apparently contain no noxious compounds (Brown and Chippendale 1973) and a wide variety of vertebrate predators, particularly birds, have been reported feasting on periodical cicadas. Little attention has been given to arthropod predation on periodical cicadas. Since emergences occur in early summer, adults have died when arthropod predators (e.g., cicada killer wasps (Sphecidae)) that specialize on dog-day cicadas (*Tibicen* sp.) become active in late summer. However, we noted several arthropod predators, e.g., spiders, dragonflies, and juvenile reduviids, eating adult periodical cicidas during an emergence of 13-year periodical cicadas in May and June of 1985 in northwestern Arkansas. Spiders were the most commonly observed arthropod predators eating periodical cicadas. In this report, we document several instances of spiders eating periodical cicadas and discuss reasons why periodical cicadas may be vulnerable prey for certain kinds of spiders.

***Latrodectus mactans* (Fabricius)**.—At 0900 on 10 May 1985 at Durham, Washington Co., an immature black widow was observed preying on an adult periodical cicada. The spider had belayed the cicada and was hoisting it up into foliage about 12 cm off the ground, in a manner similar to that depicted in Gertsch (1979). Neither spider or cicada was collected; spider identification by J. Heiss was based on detailed field notes.

***Agelenopsis naevia* (Walckenaer)**.—Funnel web spiders, which were common at our study site at Durham, were observed eating periodical cicadas on several occasions. On 9 June 1985, six of 26 (23%) funnel webs with spiders present contained remains of at least one adult periodical cicada; six cicada exoskeletons were found in one web (C. Kellner pers. obs.). An immature female *A. naevia* collected in late May weighed 336 mg (fresh weight); the female *M. cassini* she was eating weighed 333 mg.

***Xysticus* spp.**—On five occasions between 6-25 May at Durham, *Xysticus* crab spiders were found feeding on adult cicadas in plastic mesh emergence traps. The cone-shaped traps sampled 0.5 m^2 of ground surface (see Steward 1986). Crab spiders were found feeding on cicadas that had become tangled in the mesh at the top of the cone. Additionally, a crab spider was observed feeding on a periodical cicada on the ground at 0930 on 6 May; another was observed feeding on a cicada 0.3 m off the ground at 0900 on 10 May. Although several crab spiders were photographed in the act of feeding, positive species determinations could not be made from photographs (J. Heiss, pers. comm.). Two nearly-identical species, *X. elegans* Keyserling and *X. fraternus* Banks, commonly occur in northwestern Arkansas (Heiss 1977).

Phidippus audax (Hentz).—At 1200 on 9 May at Durham, a 326 mg female *P. audax* was collected while dragging a 443 mg male periodical cicada (*M. cassini*) by the head through tall grass. C. Simon (pers. comm.) also has observed this jumping spider eating periodical cicadas.

Phidippus whitmani Peckham and Peckham.—In late May at Durham, a 97 mg female *P. whitmani* was collected in tall grass while feeding on a 425 mg female cicada (*M. cassini*). The spider had grasped its prey just posterior to the head.

Phidippus sp.—At 0930 on 15 June at Leatherwood Reservoir, Carroll Co., a salticid was collected in a woody shrub while feeding on a cicada. The spider was similar in size and exhibited a similar feeding behavior to *P. whitmani*, but probably was not that species (J. Heiss, pers. comm.). The specimen was lost in the mail before it could be positively identified.

Two other observations of unidentified salticids were made: a salticid was found feeding on a periodical cicada on the ground at Durham at 1100 on 9 June; another salticid was observed feeding on a cicada on the ground at 0800 on 25 June at Lake Wilson, Washington Co.

Several species of diurnally-active jumping spiders captured periodical cicadas, despite the larger size and mass of cicadas. Other researchers have also found that salticids commonly (Robinson and Valerio 1977) or occasionally (Jackson 1977) eat large prey. *Xysticus* also has been reported to capture large prey (Morse 1983). Although limited, our observations are consistent with those of Freed (1984), i.e., female jumping spiders tend to attack larger prey than do male jumping spiders. Also, jumping spiders tended to attack large prey along the suture between the head and prothorax.

Webless spiders usually do not capture large hard-bodied prey (see Enders 1975); however, events associated with cicada eclosion may make periodical cicadas particularly vulnerable to hunting spiders. After digging out of the ground, periodical cicada nymphs climb vegetation, undergo the last molt, and emerge as adults. Adults hang motionless for about two hours while the exoskeleton hardens. Most periodical cicadas emerge during night, but we commonly found freshly eclosed cicadas hanging in vegetation after dawn until mid-morning. Most of our observations of predation by hunting spiders were during morning hours, suggesting that spiders were capturing cicadas in the act of hardening.

Periodical cicadas probably dropped from the canopy into funnel webs of *Agelenopsis naevia*, which orient their webs parallel to the ground. Adult periodical cicadas spend much of their time in the forest canopy, where males form chorus centers that attract females. Females oviposit in the canopy after mating. Orb-weaving spiders that oriented webs perpendicular to the ground apparently did not capture cicadas: daily checks of webs of two common orb-weavers, *Neoscona arabesca* (Walckenaer) and *Micrathena gracilis* (Walckenaer), throughout the cicada emergence failed to produce any cicada prey.

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BOOK REVIEWS

Nentwig, W. (Ed.) 1987. Ecophysiology of Spiders. Springer-Verlag; Berlin, Heidelberg, New York and Tokyo. 448 pp. 133 figs. (price $149.00).

In compiling this book consisting of 28 chapters focusing on specific aspects of physiology and ecophysiology in spiders, Nentwig has done a valuable service for those interested in the biology of this remarkable taxon. There has been explosive growth in these areas over the past 20 years, thus creating the need to take stock of what has been done as-well-as to point out problems for future study. Such discourse is also important in that a much more complete interpretation of the data and hypotheses can be provided than is possible in primary reports. Arachnologists and other biologists will find that *Ecophysiology of Spiders* admirably meets these goals. This text is a welcome and valuable complement to other recent books devoted to specialized areas of spider biology (Witt and Rovner 1982; Barth 1985; Shear 1986).

The book is organized into five sections, each containing from three to eight chapters. Each chapter is authored by a specialist. The list of authors is international and thus represents the cosmopolitan nature of research in arachnid biology. The text, in English, does not suffer from this international flavor.

The main divisions are diverse which is consistent with the editor's rather broad definition of ecophysiology. They include "Cuticle, Temperature and Respiration"; "Glands, Silk and Webs"; "Feeding Ecology"; "Parasites"; and "Environment and Life History". Although the scope of individual chapters varies, ranging from the short but elegant and insightful discourse by Nakamura on hunger and starvation (9 pp.) to Putz's extended and comprehensive discussion of thermal and water relationships (30 pp.), each provides a fairly complete account of the subject in question.

Despite the focus on autecology, this text is the most authorative treatise available concerning cuticle morphology and the physiology of silk production, excretion, circulation, digestion, respiration, and molting hormones. The chapters dealing with these and other subjects are put in perspective by comparison with other chelicerates, insects, and in some cases, other taxa. As such, the book's value is extended to a wider audience of biologists. Workers who concentrate their efforts in the laboratory will be impressed by the rich diversity of behaviors and other elements of the natural history of spiders described in various chapters. This feature is of inestimable value in providing a more valid consideration of the significance of their findings relative to the ecology of this complex group.

The three chapters devoted to parasites of spiders present an intriguing picture of an often overlooked aspect of spider biology. Their scope is somewhat more limited than in other chapters, given the limitations of available information, yet they provide valuable and stimulating insights as to the potential value of future research in this area *vis-à-vis* spider evolution and population biology.

One can always take issue with the choice of subjects treated in such a text. One might argue, for example, that the chapter "Spider Venoms and their Effects" by Maretic is too clinical to be included in this volume, given its stated purpose. Be that as it may, this specific chapter contains a wealth of information

that can be of value to practicing araneologists in providing answers to questions often asked by the general public. As such, I welcome its inclusion in what will prove to be a landmark publication on spiders. One can also argue that this text does not cover all areas of spider physiology: this is not a serious limitation given the subject matter discussed in other recent texts cited earlier in this review.

References are listed at the end of the text, as is usual in books of this type instead of at the end of each chapter. This method will frustrate some who need to credit specific citations but is very convenient for those who use the list for general reference. This list is comprehensive and up-to-date, with the latest publications listed from 1986. Important papers and review articles are specially marked. An annotated appendix is provided, with citations, to give a brief summary of spider systematics, a feature of value for those with a non-taxonomic background. The index is extensive and workable. The figures are of excellent quality and are provided with clearly written figure legends. The text is well edited, with few noticeable errors. Most are typographical and not likely to cause problems. Others are minor but irritating: the inconsistent use of both a comma and period as a radix mark (p. 147); the ambiguous use of more than one solidus, (/), to represent products or quotients of two or more physiological dimensions. A slightly more serious error appears on page 71: in the context of the sentence, *Mitopus morio* would be considered an insect or a mite by one not familar with arachnids when in fact it is a daddy-long-legs in the order Opiliones.

The high price will probably force many to use a library to gain access to this fine text; one hopes a lower priced (soft-cover) edition will become available.

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Griswold, C. E.   1987.   A Revision of the Jumping Spider Genus *Habronattus* F. O. P.-Cambridge (Araneae: Salticidae), with Phenetic and Cladistic Analyses. University of California Publications in Entomology 107, ix + 344 pp. (price $34.00). Available from University of California Press, 2120 Berkeley, California 94720, USA.

This is the first major revision published of a predominantly North American salticid genus to appear since the Peckhams' works of the late 1800's and early 1900's. Three-quarters of a century is far too long to wait; the simple structure of the genitalia being the main deterrent to taxonomic work in the family. Fortunately, Griswold's monograph shows what can be done within these constraints. It comes at an appropriate time with the rise of interest in salticid biology, especially in behavioral studies. This paper is a significant contribution to salticid taxonomy on several levels.

Habronattus is the largest primarily North American jumping spider genus, comprising 94 species in nine species groups, and a number of species unplaced as to group. It is, along with *Phidippus*, the genus that contains some of the most flamboyant males and the most strikingly sexually dimorphic species. Because of the very similar genitalia in many of the species, reliance is placed on somatic characters to an unusual extent to define species and in the key. That he has been

successful in this approach is in part due to his exhaustive character search; 172 were studied! The key is for males only and works well. As in any long key, there are numerous opportunities to go astray; read *both* parts of the couplet before you make your choice. In couplet 1 the first part leads to couplet 2, *not 12* as written. Couplet 52 will probably appear puzzling because the first line of the second part has been accidentally omitted. It most likely reads: "Tibia I with anteroventral spines. . . . " Females are not keyed and some males and females are not illustrated. To determine females one must resort to the Peckhams' 1909 revision in conjunction with this monograph. The range maps provide clues in sorting out possible choices. It would have been helpful to have more illustrations, particularly in regard to females and to some inadequately illustrated males.

Griswold's setting of *Habronattus* in relation to the other salticid genera, and to *Pellenes* in particular, is felicitous. He has done an excellent analysis of this vexatious complex of genera. Also worthy of note is his discussion of apomorphic and plesiomorphic character states.

There are several minor misspellings, none of which are confusing. *Maevia* has been sporadically misspelled as *Meavia* in several places; sometimes both spellings occur on the same page. One important omission is the lack of a species index; I constructed my own, which saves much page flipping. Despite the minor shortcomings, this is a major contribution and one that I will refer to for many years, not only for identification, but for the methodology and approach to taxonomic problems.

Bruce Cutler, 1966 Eustis Street, Lauderdale, Minnesota 55113.

NOMENCLATURE NOTES

The International Commission on Zoological Nomenclature has made the following rulings under its plenary powers:

Opinion 1421.—*Erigone* Audouin, 1826 (Arachnida, Araneae): *Erigone longipalpis* Sundevall, 1830, designated as type species.

Opinion 1432.—*Olpium* Koch, 1873 (Arachnida, Pseudoscorpionida): *Obisium pallipes* Lucas, 1846 designated as type species; interpretation of the nominal species *Olpium kochi* Simon, 1881.

Opinion 1426.—*Argyrodes* Simon, 1864 and *Robertus* O. Pickard-Cambridge, 1879 (Arachnida, Araneae): conserved.

THE AMERICAN ARACHNOLOGICAL SOCIETY

The American Arachnological Society was founded in August, 1972, to promote the study of Arachnida, to achieve closer cooperation between amateur and professional arachnologists, and to publish *The Journal of Arachnology.*

Membership in the Society is open to all persons interested in the Arachnida. Annual dues are $25.00 for regular members, $15.00 for student members. Correspondence concerning membership in the Society must be addressed to the Membership Secretary. Members of the Society receive a subscription to *The Journal of Arachnology.* In addition, members receive the bi-annual newsletter of the Society, *American Arachnology.*

American Arachnology, edited by the Secretary, contains arachnological news and comments, requests for specimens and hard-to-find literature, information about arachnology courses and professional meetings, abstracts of papers presented at the Society's meetings, address changes and new listings of subscribers, and many other items intended to keep arachnologists informed about recent events and developments in arachnology. Contributions for *American Arachnology* must be sent directly to the Secretary of the Society.

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REVISION DE LOS GENEROS DEL GRUPO HURIEAE (ARANEAE, SALTICIDAE)

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ABSTRACT

Hurieae is a group of five genera defined by the combined presence of the following characters: small chelicerae with three to five teeth on promargin and one tooth on retromargin; fourth leg much longer than third; third ocular row wider or at least equal to first row; narrow clypeus; two or three tibial retrolateral apophyses.

Revised diagnosis of *Scoturius* Simon and *Atelurius* Simon and the redescription of *Atelurius segmentatus* Simon are given. The male of *S. tigris* is described for the first time. *Atelurius incertus* Banks is transferred to *Zygoballus* as a new combination. Two new genera are described: (1) *Admesturius* n. gen. with two species, *A. schajovskoyi* n. sp. and *A. bitaeniatus* (Simon) n. comb., the female of which is described for the first time, (2) *Simonurius* n. gen. with four species: *Simonurius gladiferus* (Simon) n. comb., *S. campestratus* (Simon) n. comb., *S. quadratarius* (Simon) n. comb. and *S. expers* n. sp.

ABSTRACTO

Hurieae es un grupo de cinco géneros, definido por la presencia combinada de los siguientes caracteres: quelíceros pequeños con tres a cinco dientes en promargen y un diente en retromargen; cuarta pata más larga que la tercera; tercera hilera ocular más ancha o al menos igual a la primera hilera; clípeo angosto; dos o tres apófisis tibiales retrolaterales.

Se dan las diagnosis revisadas de *Scoturius* Simon y *Atelurius* Simon, y la redescripción de *Atelurius segmentatus* Simon. El macho de *S. tigris* se describe por primera vez. *Atelurius incertus* Banks se transfiere a *Zygoballus* como nueva combinación. Se describen dos géneros nuevos: (1) *Admesturius* n. gen. con dos especies, *A. schajovskoyi* n. sp. y *A. bitaeniatus* (Simon) n. comb. de la cual se describe la hembra por primera vez, (2) *Simonurius* n. gen. con cuatro especies: *Simonurius gladiferus* (Simon) n. comb., *S. campestratus* (Simon) n. comb., *S. quadratarius* (Simon) n. comb. y *S. expers* n. sp.

INTRODUCCION

En el presente trabajo se estudian los géneros del grupo Hurieae, tal como fuera definido por Simon (1901a: 583). Comprende los géneros *Hurius, Scoturius, Atelurius, Simonurius* gen. n. y *Admesturius* gen. n., que se caracterizan por la presencia combinada de los siguientes caracteres: quelíceros pequeños, verticales, paralelos, con surco ungueal breve, el promargen con tres a cinco dientes y el retromargen con uno, cercano a la base de la uña; pata IV mucho más larga que pata III; área ocular más ancha atrás (por excepción paralela); clípeo angosto; palpo del macho con dos o tres grandes apófisis tibiales.

Esta combinación de caracteres parece ser única en Salticidae, en especial la existencia simultánea de un diente en retromargen y tres o más en promargen. Los géneros más cercanos son los de los grupos Sitticeae y Chalcoscirteae (*sensu* Simon 1901a: 572, 577) que se diferencian de Hurieae por la estructura palpal y por carecer de dientes en retromargen.

MATERIAL Y MÉTODOS

Las medidas se expresan en milímetros y han sido tomadas según se explica en una publicación anterior (Galiano 1963). La quetotaxia se describe según Platnick y Shadab (1975) con ligeras modificaciones. Las abreviaturas son las siguientes: OLA, OMA, OMP, OLP, ojos laterales anteriores, medios anteriores, medios posteriores y laterales posteriores, respectivamente; p, prolateral, r, retrolateral, d, dorsal, v, ventral, ap, apical; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MCZ, Museum of Comparative Zoology, Harvard; MZSP, Museo de Zoología de la Universidade de São Paulo, Brasil; MPM, Milwaukee Public Museum; MLP, Museo de La Plata, Buenos Aires; IDPN, Instituto de Defesa do Patrimonio Natural, Curitiba, Brasil; MNHNP, Muséum National D'Histoire Naturelle, Paris.

CLAVE PARA LOS GÉNEROS DEL GRUPO HURIEAE

Machos

1. Palpo con dos apófisis tibiales... 2
   Palpo con tres apófisis tibiales.. *Scoturius*

2. Bulbo con apófisis media..................................... *Simonurius* gen. n.
   Bulbo sin apófisis media.. 3

3. Embolo muy largo, circundando el bulbo en más de una vuelta....... *Atelurius*
   Ëmbolo corto.. 4

4. Prosoma bajo y largo; pata I muy engrosada; patas posteriores con muy pocas espinas; émbolo con dentículos basales..................... *Admesturius* gen. n.
   Prosoma más alto y corto; pata I delgada; patas posteriores con espinas fuertes y abundantes; émbolo sin dentículos basales............................. *Hurius*

Hembras
(No se conoce la hembra de *Atelurius*)

1. Epigino con un gran orificio elíptico anterior........................ *Scoturius*
   Epigino con dos orificios... 2

2. Espermatecas grandes, reniformes; conductos cortos, angostos, levemente curvos.. *Simonurius* gen. n.
   Espermatecas pequeñas, esféricas; conductos largos, anchos, en parte espiralados... 3

3. Epigino con bolsillos de anclaje.. *Hurius*

    Epigino sin bolsillos de anclaje............................. *Admesturius* gen. n.

Género *Scoturius* Simon

Scoturius Simon 1901a:584, 585 (n. gen.); Petrunkevitch 1928:203; Roewer 1954:1184; Bonnet 1958:3976; Brignoli 1983:628.

Diagnosis (revisada).—Se diferencia de los otros géneros del grupo Hurieae por tener tres apófisis tibiales en el palpo y por la ausencia de apófisis media en el bulbo. Se distingue de *Semiopyla*, cuyo palpo es semejante, por tener un diente en retromargen.

Descripción.—Prosoma ancho y alto (ancho 77-81% del largo, alto 45-51% del largo). Mitad anterior de la región torácica en el mismo nivel que la cefálica; declive posterior muy abrupto. Estría poco marcada. Clípeo angosto. Promargen con cinco dientes, cuatro de ellos sobre una base común; retromargen con un diente. Area ocular ocupando la mitad de la longitud del prosoma; más ancha atrás que adelante, con OMP más cerca de OLA. Patas largas y delgadas, con abundantes espinas. Machos I-IV-III-II; hembras IV-I-III-II. Tibia del palpo con tres apófisis de las cuales la ventral es la más larga y tiene la superficie finamente espiculada. Embolo largo, con ancha *pars pendula*. Epigino con orificio de entrada impar y medio; primera porción de los conductos dilatada en una amplia cámara.

Especie tipo.—*Scoturius tigris* Simon 1901b.

Scoturius tigris Simon
Figs. 4, 7, 8, 13-15

Scoturius tigris Simon 1901b:154 (hembra Lectotypus, de Paraguay, col. Gounelle, en MNHNP, examinada); 1901a:585, figs. 705-707; Petrunkevitch 1911:705; 1928:203; Mello-Leitão 1946:49; Roewer 1954:1185; Bonnet 1958:3977; Galiano 1962a:68; 1963:441, lám. 34, fig. 5, lám. 38, fig. 8 (redescripción); Brignoli 1983:628.

Macho.—Largo total 4.30. Prosoma: largo 2.03, ancho 1.57, alto 0.93. Clípeo, alto 0.08. Area ocular: largo 0.97; ancho de hilera anterior 1.47; de hilera posterior 1.48; distancia OLA-OMP 0.22; OMP-OLP 0.30; diámetro OMA 0.53. Estría torácica 0.12 más atrás de OLP. Láminas maxilares con ángulo redondeado. Esternón tan ancho como la base del labio; algo rebordeado en escotadura de coxa I. Quelíceros pequeños, verticales; surco ungueal breve; promargen con cinco dientes; retromargen con uno (Fig. 15).

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	1.22	0.82	1.08	0.87	0.45	4.44
II	0.98	0.67	0.68	0.62	0.38	3.33
III	0.95	0.47	0.53	0.67	0.40	3.02
IV	1.20	0.57	0.75	0.70	0.50	3.72

Quetotaxia: Fémures I d 1-1-1, p ap 1; II d 1-1-1, p ap 1, r ap 1; III d 1-1-1, p 1-2, r ap 2; IV d 1-1-1, p ap 2, r ap 1. Patellas II p 1; III, IV r 1. Tibias I, II v 2-2-2; III v 1-2, p 1-1, r 1-1-1; IV v 2-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v 1-2, p 1-2, r 1-2; IV v 1-2, p 1-2; r 1-1-2. Palpos: Figs. 13, 14.
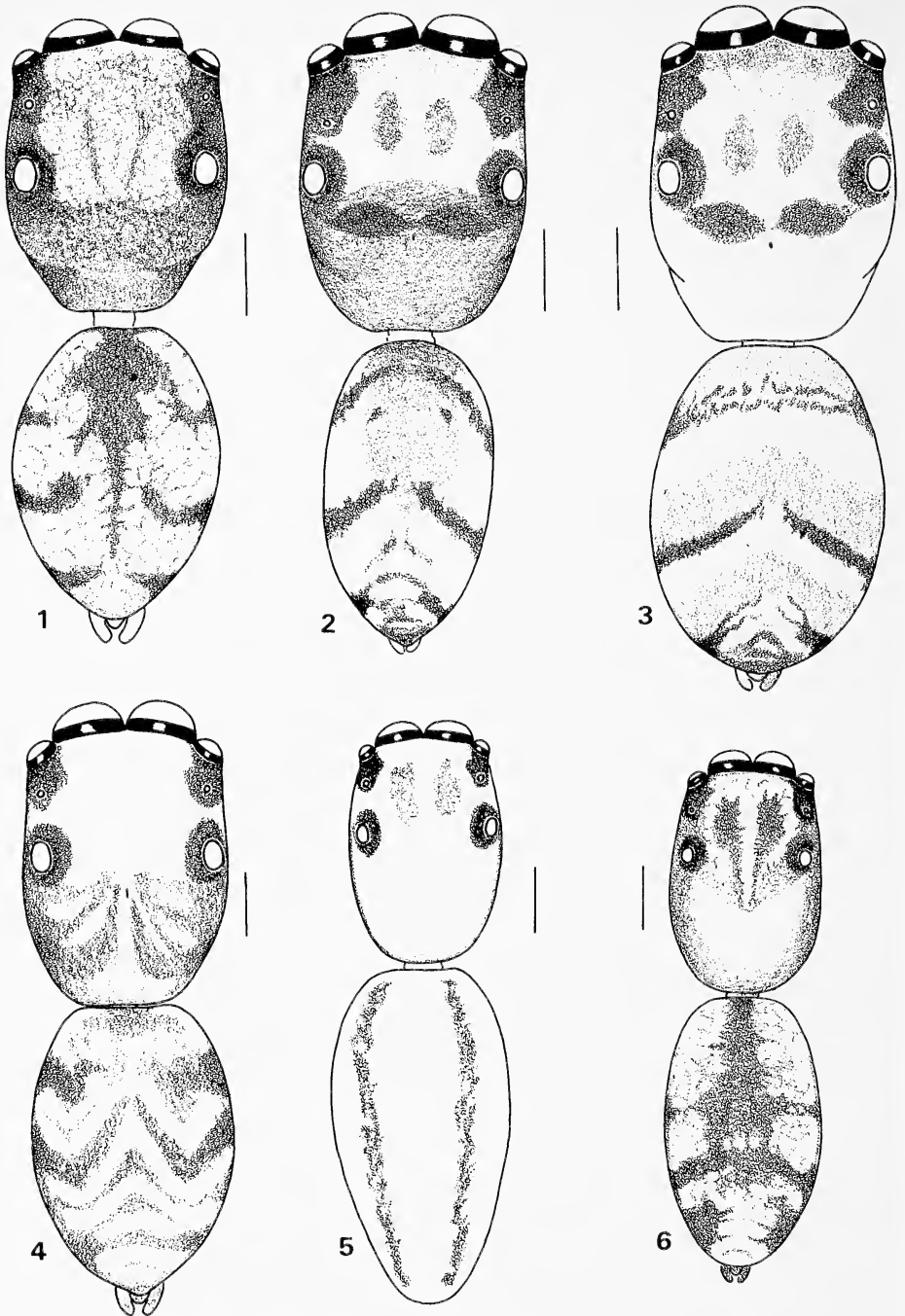
Figs. 1-6.—Cuerpos, vista dorsal: 1, *Atelurius segmentatus*, macho; 2-3, *Simonurius gladiferus*, 2, macho; 3, hembra; 4, *Scoturius tigris*, macho; 5, *Admesturius bitaeniatus*, hembra; 6, *Admesturius schajovskoyi*, macho. Escala 0.5 mm.

Aspecto y color en alcohol.—Prosoma anaranjado, con la región cefálica amarilla y grandes manchas oculares negras. Parece haber tenido pelos rojos sobre la región cefálica y blancos en la torácica y en el declive. Clípeo sin barba, con algunos pelos rojizos cerca del borde; pelos blancos bajo los OLA. Cara
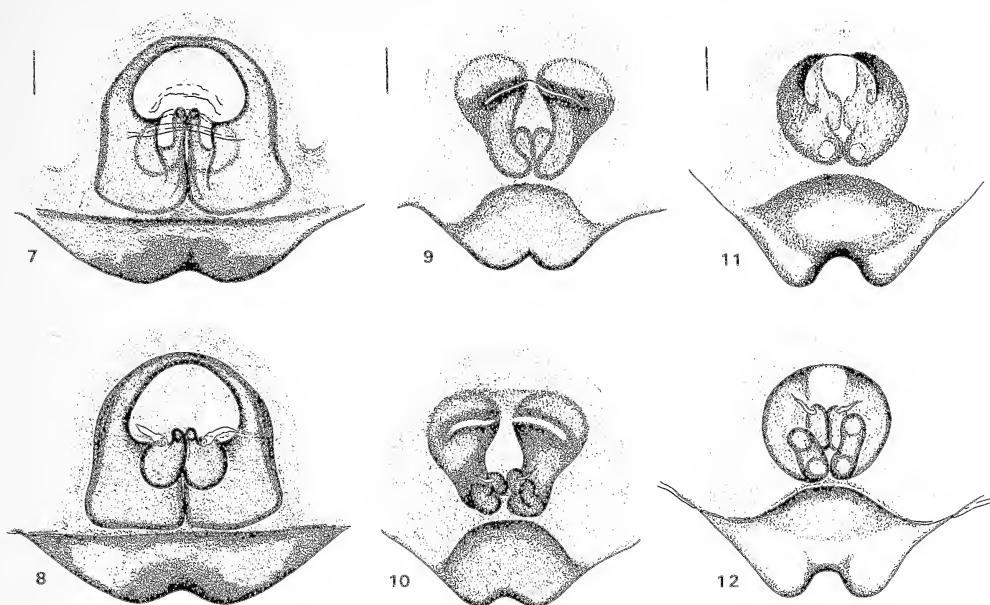
Figs. 7-12.—Epiginos: 7-8, *Scoturius tigris*, 7, ventral; 8, dorsal; 9-10, *Admesturius bitaeniatus*, 9, ventral; 10, dorsal; 11-12, *Admesturius schajovskoyi*, Holotipo; 11, ventral; 12, dorsal. Escala 100 μ.

anterior de los quelíceros con pelos rojizos. Piezas bucales y esternón, pardo claro; labio pardo oscuro. Opistosoma amarillo pálido, con tres bandas pardo negruzco, transversales, en forma de V invertida. (Fig. 4). Costados con manchas pardas; vientre amarillo. Patas amarillas, con manchas oscuras en fémur, tibia y metatarso. (El espécimen está bastante decolorado y depilado).

Nota.—Aunque Simon (1901b) menciona la especie para Brasil (Minas y Mato Grosso), no se halló material de esa procedencia en el MNHNP.

La descripción del Lectotypus hembra se dio en una publicación anterior (Galiano 1963). Se agrega aquí la ilustración del epigino clarificado. (Figs. 7, 8).

Material estudiado.—ARGENTINA: Misiones; Santa María, noviembre 1954 (Schiapelli y Galiano), 1 hembra No 5571 (MACN). PARAGUAY: Asunción, (Peckham & Peckham), 1 macho, 1 hembra (MPM).

Scoturius taeniatus Mello-Leitão

Scoturius taeniatus Mello-Leitão 1917:145 (hembra de Brasil, Pinheiro, no examinado); Roewer 1954:1184; Bonnet 1958:3977 (*bitaeniatus*); Galiano 1981:14.

Nota.—El tipo de esta especie debe considerarse perdido. La descripción es insuficiente para reconocerla, aunque parece acercarse a Dendryphantinae. Se la considera *species inquirendae*.

Género *Atelurius* Simon

Atelurius Simon 1901a:584, 585 (n. gen.); Petrunkevitch 1928:202; Roewer 1954:1184; Bonnet 1955:770; Brignoli 1983:626.

Diagnosis (revisada).—Se diferencia de *Scoturius* por tener solo dos apófisis en tibia del palpo; de *Hurius* por tener un émbolo larguísimo; de *Simonurius* gen. n. por carecer de apófisis media en el bulbo y de *Admesturius* gen. n. por tener las patas I delgadas.

Descripción.—Prosoma muy ancho y alto (ancho 86-90% del largo, alto 58-62% del largo). Area ocular ocupando la mitad del largo del prosoma; más ancha atrás que adelante; OMP mucho más cerca de OLA. Clípeo bajo, apenas la mitad del radio de los OMA; con barba. Sin estría torácica. Cutícula del prosoma granulada. Esternón algo más ancho que la base del labio; ligeramente rebordeado en las escotaduras de coxas I. Quelíceros pequeños, verticales, paralelos, ligeramente excavados en la cara interna; surco ungueal breve; promargen con cinco dientes; retromargen con uno. Patas I-IV-II-III; delgadas, moderadamente largas, con pocas espinas. Tibia I sin espinas o con una o dos ventrales; tibias III y IV sin espinas o con solo una. Palpos pequeños, tibia con dos apófisis retrolaterales cortas; la ventral membranosa. Bulbo pequeño, disciforme, circundado por el largo émbolo que da una vuelta y media a su alrededor.

Especie tipo.—*Atelurius segmentatus* Simon 1901b.

Atelurius segmentatus Simon
Figs. 1, 16, 17

Atelurius segmentatus Simon 1901b:154 (macho Holotypus de Venezuela, Caracas, col. Simon, en MNHNP, examinado); 1901a:584, 585, fig. 709; Petrunkevitch 1911:595; 1928:202; Roewer 1954:1184; Bonnet 1955:770; Galiano 1963:303, lám 10, figs. 9 y 10 (redescripción).

Nota.—En una publicación anterior (Galiano 1963) se redescribió la especie. Creo necesario brindar una mejor ilustración del palpo (Figs. 16, 17). Se amplía la distribución georgráfica a Brasil. La hembra es desconocida.

Material estudiado.—BRASIL: São Paulo, Faz. Pau d'Alto Itú, agosto 1960 (Pereira, Martins), 1 macho E 1329 (MZSP); São Roque, junio 1944 (F. Lane), 1 macho 8269 (MACN).

Atelurius incertus Banks
Fig. 18

Atelurius incertus Banks 1929:71, fig. 61 (una hembra Lectotypus, aquí designada y una hembra Paralectotypus, de Panamá, Barro Colorado Is., C.Z., col. Banks, en MCZ, examinadas); Chickering 1946:253, figs. 214-218 (macho); Roewer 1954:1184; Bonnet 1955:770.

Nota.—Los ejemplares típicos presentan dos dientes en promargen y una carena bidentada en retromargen. El macho descripto por Chickering como Allotypus pertenece al grupo de especies clasificadas en *Sassacus* por Simon. Chickering encontró a esta especie próxima a *Zygoballus*. Sin duda es una fissidentada que debe ser excluida del género. Se establece *Zygoballus incertus* n. comb. Se ilustra el epigino (Fig. 18).

Género *Hurius* Simon

Hurius Simon 1901a:583, 585 (n. gen.); Petrunkevitch 1928:202; Roewer 1954:1184; Bonnet 1957:2237; Brignoli 1983:627; Galiano 1985:10 (revisión).
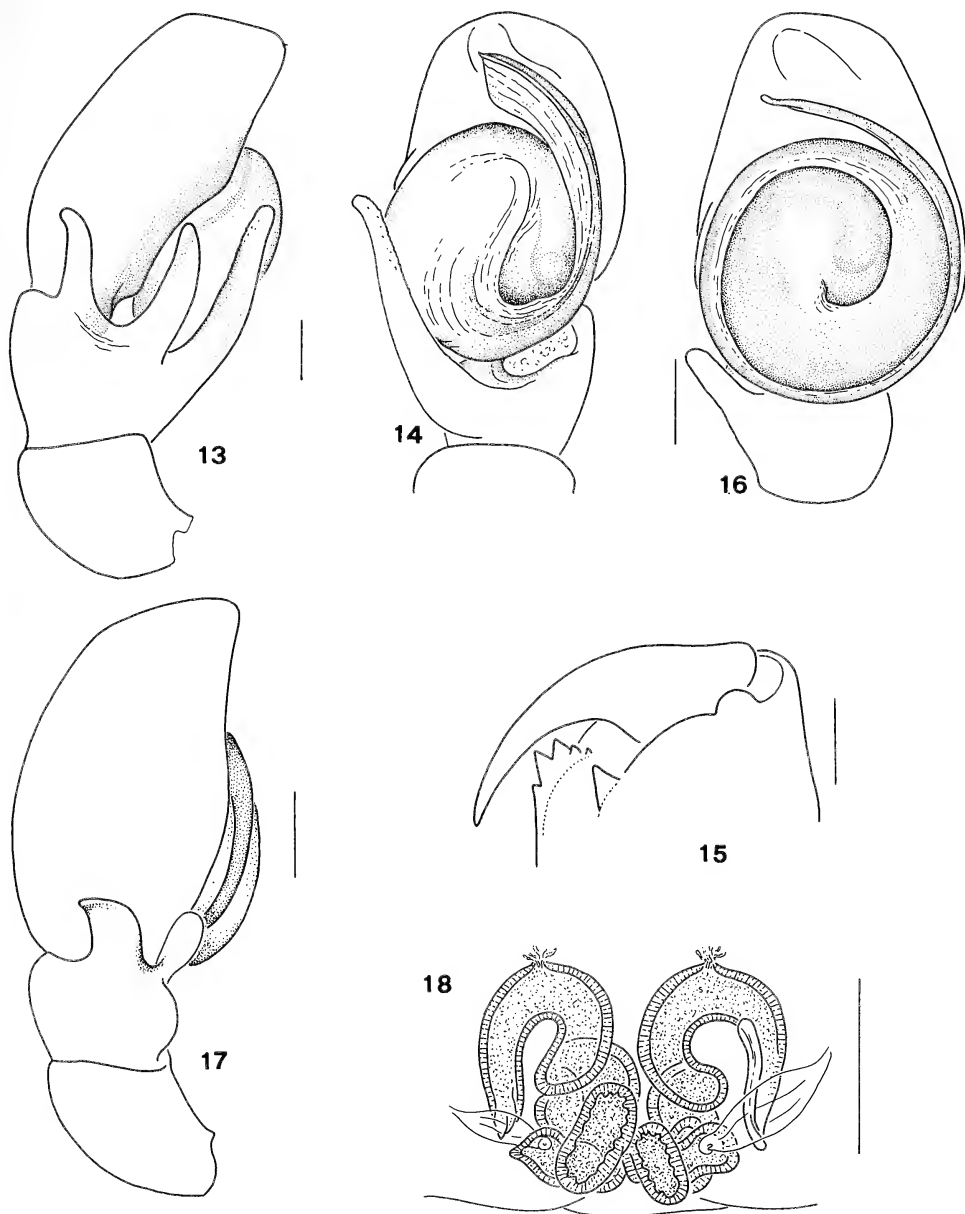
Figs. 13-18.—13-15, *Scoturius tigris*, macho; 13-14, palpo; 13, retrolateral; 14, ventral; 15, quelícero, ventral; 16-17, *Atelurius segmentatus*, palpo; 16, ventral; 17, retrolateral; 18, *Zygoballus incertus* (Lectotipo de *Atelurius incertus*), epigino, dorsal. Escala 100 μ.

Spinurius Mello-Leitão 1941:187 (n. gen.); Roewer 1954:1185; Brignoli 1983:628, 749 (*Spinutius, lapsus*).

Especie tipo.—*Hurius vulpinus* Simon 1901.

Nota.—En una publicación anterior (Galiano 1985) se realizó la revisión del género, que comprende las siguientes especies: *H. vulpinus, H. petrohue* Galiano, *H. pisac* Galiano y *H. aeneus* (Mello-Leitão 1941).

Admesturius, nuevo género

Etimología.—Combinación arbitraria de los nombres *Admestina* y *Hurius*. Masculino.

Diagnosis.—Se diferencia de *Hurius* por el cuerpo más alargado y aplanado y por el primer par de patas muy engrosado, con escasas espinas. Se diferencia de *Admestina* por la dentición de los quelíceros y la presencia de dos grandes apófisis tibiales en el palpo.

Descripción.—Prosoma bajo y largo (ancho 65-78% del largo, alto 33-39% del largo); la región torácica en el mismo nivel que la cefálica, con el declive breve y muy atrás. Sin estría torácica. Area ocular ocupando 39-44% del largo del prosoma; más ancha atrás que adelante; OMP mucho más cerca de OLA. Clípeo angosto (igual o menor que el radio de OMA), desnudo en los machos y con barba en las hembras. Quelíceros pequeños, verticales, paralelos; surco ungueal breve; promargen con tres a cinco dientes (los angulares sobre una base común); retromargen con un diente, cercano a la base de la uña. Láminas maxilares redondeadas. Esternón igual o apenas más ancho que la base del labio. Patas I-IV-II-III en machos y IV-I-II-III en hembras. Pata I mucho más gruesa que las demás, con fémur claviforme y tibia cilíndrica. Espinas escasas. Palpo con dos grandes apófisis tibiales retrolaterales; émbolo breve en posición prolateral apical; base con dientecitos esclerosados. Epigino grande, con borde posterior bilobado; dos aberturas en forma de surco en la mitad anterior; conductos gruesos, espermatecas centrales, mediocres.

Especie tipo.—*Admesturius schajovskoyi*, nueva especie.

Admesturius schajovskoyi, nueva especie
Figs. 6, 11, 12, 20-26

Admestina bitaeniata Galiano 1962b:184 (no Simon 1902).

Etimología.—El nombre específico es un patronímico en homenaje al fallecido Ing. Sergio Schajovskoy.

Diagnosis.—Se diferencia de *A. bitaeniatus* por el colorido del opistosoma y porque las hendiduras que sirven de entrada al epigino se orientan longitudinalmente.

Descripción.—Holotypus hembra. Largo total 4.80. Prosoma: largo 2.20, ancho 1.43, alto 0.80. Clípeo, alto 0.08. Area ocular: largo 0.87; ancho de hilera anterior 1.12; de hilera posterior 1.24; distancia OLA-OMP 0.17; OMP-OLP 0.37; diámetro OMA 0.42. Quelíceros: promargen con cinco dientes; retromargen con uno.

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	1.08	0.68	0.62	0.45	0.30	3.13
II	0.87	0.38	0.47	0.40	0.30	2.42
III	0.75	0.38	0.40	0.47	0.33	2.33
IV	1.17	0.60	0.70	0.67	0.42	3.56

Quetotaxia: Fémures I d 1; II d 1-1; III d 1-1, p ap 1; IV d 1-1-1. Tibias I v 2; II v lr; IV v lp-lp. Metatarsos I, II v 2-2; III ap 5; IV ap 5, v lp. Epigino: Figs. 11, 12. Placa de gran tamaño, con borde posterior bilobado, sobrepasando el pliegue

epigástrico. En la mitad anterior, un surco en forma de U invertida, en cuyos brazos se encuentran las hendiduras de entrada a los conductos de las espermatecas. Primera parte de los conductos muy ancha; espermatecas centrales,˙ pequeñas.

Aspecto y color en alcohol.—Prosoma pardo rojizo oscuro, con la región cefálica amarilla y grandes manchas oculares negras. La cutícula de la región cefálica deja ver por trasparencia manchas blancas marmoradas, que se prolongan detrás de los ojos posteriores formando un triángulo cuyo vértice llega al punto donde debería estar la estría. En los costados del prosoma, una banda marginal rojiza, que se amplía hacia atrás; por sobre ella, una banda amarilla con pelos blancos, que también cubren la superficie dorsal, ocupan el espacio bajo los OLA y forman la barba del clípeo. Esternón y piezas bucales pardo oscuro. Quelíceros pardo rojizo. Opistosoma blanquecino, con manchas blancas marmoradas que se ven por trasparencia de la cutícula. Una banda media longitudinal basal y dos a tres pares de bandas trasversas, laterales, algo oblicuas, apicales, de color grisáceo. En el extremo apical, dos o tres banditas en V invertida, grisáceas. Costados blanquecinos, con manchitas negruzcas, vientre blanquecino, marmorado con una gran mancha negra apical que bordea la base de las hileras y se prolonga hacia adelante por dos finas líneas negruzcas que alcanzan la mitad del vientre. Palpos blanquecinos. Pata I blanquecina, con mitad apical de fémur, patella y tibia parda, con caras laterales negruzcas. Pata II blanquecina, con una banda negruzca ventral apical en fémur; ápice de patella y tibia oscurecidos. Pata III como II; IV con ancho anillo apical negruzco en fémur; patella y ápice de tibia con anillos grisáceos; ápice de metatarso negruzco.

Macho Paratypus No. 8275 MACN.—Largo total 4.07. Prosoma: largo 1.90, ancho 1.37, alto 0.73. Clípeo, alto 0.08. Area ocular: largo 0.82; ancho de hilera anterior 1.06; de hilera posterior 1.12; distancia OLA-OMP 0.13; OMP-OLP 0.30; diámetro OMA 0.40. Láminas maxilares redondeadas. Esternón apenas más angosto que la base del labio. Quelíceros: paralelos, verticales, levemente excavados en la cara interna. Surco ungueal breve; promargen con tres dientes en un quelícero y cuatro en el otro; retromargen con uno.

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	1.15	0.72	0.82	0.53	0.37	3.59
II	0.83	0.52	0.48	0.42	0.32	2.57
III	0.78	0.37	0.42	0.47	0.33	2.37
IV	1.12	0.52	0.67	0.60	0.37	3.28

Quetotaxia: Fémures I d 1-1, p ap 1; II d 1-1-1, p ap 2; III d 1-1-1, p 1-2, r ap 1; IV d 1-1-1, p 1, r 1. Tibias I v 2; II v 1r; III v ap 1; IV v 1p-1p, p 1, r 1. Metatarsos I, II v 2-2; III ap 5; IV ap 5, r 1. Palpos: Figs. 20-23. Tibia con dos grandes apófisis, la ventral menos esclerosada. Embolo prolateral apical, con dentículos basales.

Aspecto y color en alcohol.—Esencialmente como la hembra, pero con las bandas laterales de pelos blancos del prosoma más evidentes. Bajo los OLA pelos blancos, pero bajo los OMA el clípeo es desnudo. Pata I engrosada, más larga que en la hembra (Fig. 26).

Variaciones.—En los machos las relaciones entre el largo, ancho y alto del prosoma pueden ser las siguientes: ancho 68-72% del largo, alto 36-39% del largo. Area ocular ocupando 39-43% del largo del prosoma. Los dientes promarginales
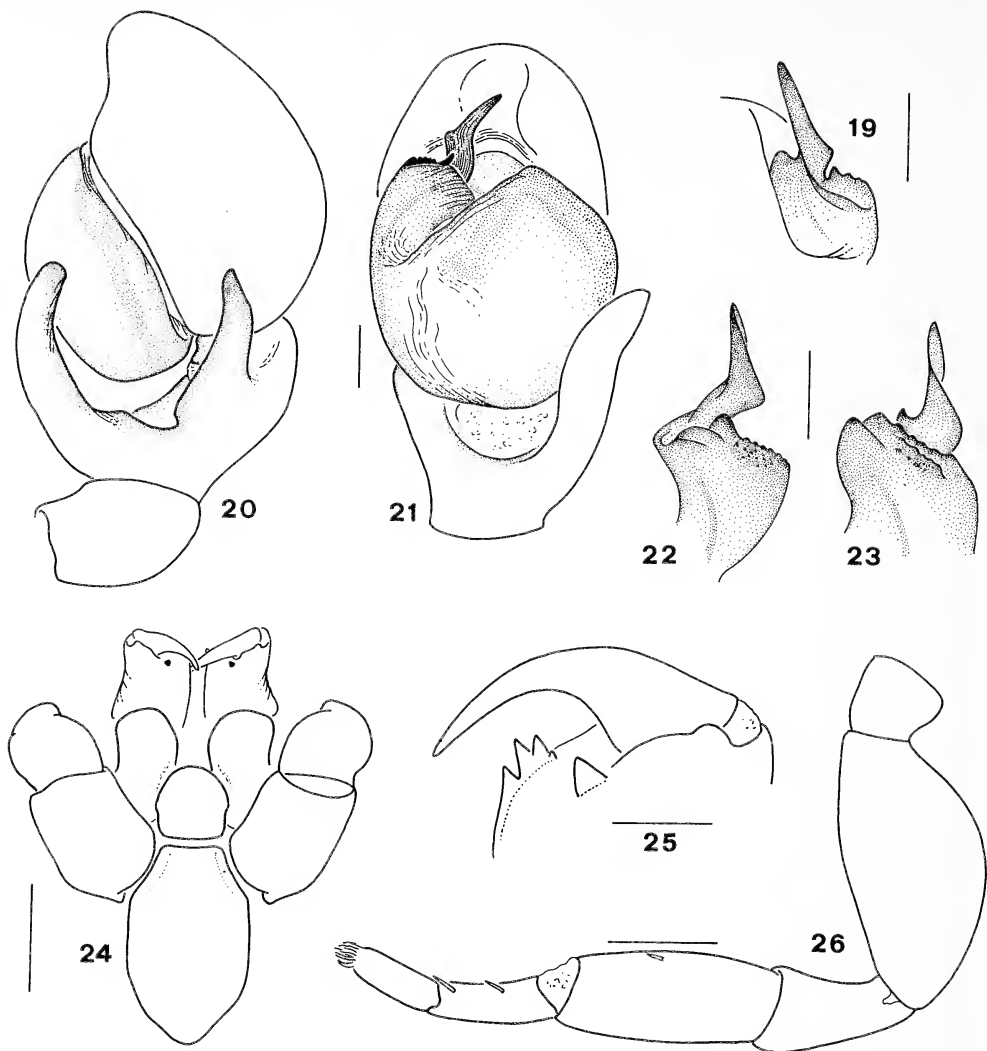
Figs. 19-26.—19, *Admesturius bitaeniatus*, macho, extremo del émbolo, ventral; 20-26, *Admesturius schajovskoyi*, macho; 20-21, palpo; 20, retrolateral; 21, ventral; 22-23, extremo del émbolo; 22, ventral; 23, prolateral; 24, prosoma, ventral; 25, quelícero, ventral; 26, pata I, retrolateral. Escala 100 μ, salvo indicación.

pueden ser de tres a cinco. Quetotaxia: Fémur III p ap 2; Tibia IV v 1p-1p, p 1, r 1. En las hembras las proporciones pueden ser: ancho 65-73% del largo, alto 37-39% del largo, área ocular ocupando 39-43% del largo del prosoma. Promargen del quelícero con cuatro a cinco dientes. Quetotaxia: Tibia I v 1r-2; II v 1r-1r; III p 1. Metatarso IV p 1, r 1.

Material estudiado.—ARGENTINA: Neuquén; Parque Nacional Lanín, Pucará, diciembre 1972 (S. Schajovskoy), 1 hembra Holotypus No. 8271 (MACN), 1 hembra Paratypus No. 8272 (MACN); Chubut; Parque Nacional Los Alerces, marzo 1974 (Bordón), 1 hembra Paratypus No. 8273 (MACN); febrero 1985 (M. Ramírez), 1 hembra Paratypus No. 8274 (MACN); febrero 1986 (M. Ramírez), 2 machos, 2 hembras Paratypi No. 8307 (MACN); Río Negro; Parque Nacional Nahuel Huapi, diciembre 1960 (Havrylenko), 1 macho Paratypus No. 5452 (MACN); El Bolsón, febrero 1965 (M. Birabén), 1 macho, 1 hembra Paratypi No. 8275 (MACN). CHILE: Llanquihue; Ensenada, 17 marzo 1965 (H. W. Levi), 1 macho Paratypus (MCZ).

Admesturius bitaeniatus (Simon), nueva combinación
Figs. 5, 9, 10, 19

Admestina bitaeniata Simon 1902:28 (macho Holotypus de Chile, Sierra de Chillán, col. Gounelle, en
    MNHNP, examinado); 1901a:615, 624; 1904:113; Petrunkevitch 1911:588; Roewer 1954:1185;
    Bonnet 1955:159; Galiano 1963:283, lám. 3, figs. 1-3, 9 (redescripción).

Hembra.—Largo total 4.23. Prosoma: largo 1.70, ancho 1.17, alto 0.63. Clípeo,
alto 0.06. Area ocular: largo 0.72; ancho de hilera anterior 0.97; de hilera
posterior 1.07; distancia OLA-OMP 0.13; OMP-OLP 0.25; diámetro OMA 0.37.
Quelíceros pequeños, paralelos, verticales; promargen con cuatro dientes, los del
medio sobre una base común; retromargen con uno.

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	0.83	0.53	0.55	0.40	0.28	2.59
II	0.67	0.40	0.38	0.33	0.25	2.03
III	0.57	0.30	0.37	0.37	0.30	1.91
IV	0.93	0.47	0.63	0.50	0.35	2.88

Quetotaxia: Fémures II d 1; III d 1; p ap 1, r ap 1; IV d 1-1, p ap 1, r ap 1.
Tibias I v 1p-2; II v 1r; IV v 1p. Metatarsos I, II v 2-2; III ap 4; IV v 1-1, p ap 1,
r 1-1. Epigino: Figs. 9, 10. Entrada a los conductos de las espermatecas por un
par de hendiduras transversales.

Aspecto y color en alcohol.—Cuerpo alargado y aplanado (Fig. 5). Prosoma
anaranjado, con la región cefálica amarilla y dos manchas grisáceas en el medio
del área ocular. Bajo la cutícula se trasparentan manchas blancas marmoradas.
Toda la superficie cubierta por pelitos blancos acostados, que forman una banda
longitudinal desde el margen anterior hasta la estría y dos anchas bandas laterales
submarginales, que pasan bajo los OLA y forman la barba del clípeo.
Opistosoma blanquecino, con manchas blancas que se ven por trasparencia; en el
dorso, dos anchas bandas pardas paralelas, bien separadas entre si. Esternón y
piezas bucales pardo claro. Patas y palpos amarillos.

Macho.—Largo total 2.77. Prosoma: largo 1.50, ancho 1.00, alto 0.50. Clípeo,
alto 0.07. Area ocular: largo 0.62; ancho de hilera anterior 0.87; de hilera
posterior 0.92; distancia OLA-OMP 0.13; OMP-OLP 0.21; diámetro OMA 0.32.
Quelíceros con cara interna levemente excavada; promargen con cuatro dientes;
retromargen con uno.

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	0.87	0.50	0.63	0.40	0.28	2.68
II	0.60	0.33	0.33	0.32	0.30	1.88
III	0.60	0.25	0.33	0.32	0.22	1.72
IV	0.80	0.40	0.47	0.42	0.32	2.41

Quetotaxia: Fémures I d 1, p ap 1; II d 1-1, p ap 1; III d 1-1, p ap 1, r ap 1; IV d
1-1-1, p ap 1, r ap 1. Tibias I, II v 2; IV v 1p-1p, p 1. Metatarsos I v 2-2; II v 2-
1p; III ap 4; IV v 1r, ap 5. Palpos: difiere de *A. schajovskoyi* por la forma del
émbolo (Fig. 19).

Aspecto y color en alcohol.—Como la hembra.

Nota.—Hasta ahora no se ha hallado esta especie en la Argentina. La cita de
Galiano (1962) corresponde a *A. schajovskoyi*.

Material estudiado.—CHILE: Cautin, NE de Villarrica, 16-31 diciembre 1964 (L. Peña), 1 hembra (MCZ); Llanquihue, 2-3 km NW Ensenada, 18 marzo 1965 (H. W. Levi), 1 macho (MCZ); Talca, Alto de Vilches, 17-24 octubre 1964 (L. Peña), 1 hembra (MCZ); Linares, enero 1947 (L. Peña), 1 macho, 1 hembra No. 6008 (MACN).

Simonurius, nuevo género

Akela (part) Simon 1901a:568, 571; 1901b:145, 146; Mello-Leitão 1933:61; 1941:182; 1944:319; Galiano 1963:285-287.

Diagnosis.—Se diferencia de los otros géneros de Hurieae por presentar una apófisis media en el bulbo. Se distingue de *Akela* Peckham y Peckham 1896, por los siguientes caracteres: en *Akela* los quelíceros son robustos con la mitad distal divergente, la cara anterior convexa y el surco ungueal largo, con dos dientes en promargen y uno en retromargen, bien alejado de la base de la uña. El esternón es cordiforme y las láminas maxilares tienen el borde superior recto y el ángulo externo saliente. En *Simonurius* los quelíceros son pequeños, paralelos, verticales, con la cara anterior aplanada y el surco ungueal breve, con tres a cinco dientes en promargen y uno en retromargen, muy cerca de la base de la uña. El esternón es alargado y las láminas maxilares son redondeadas. En *Akela* el área ocular es paralela, con OMP en el medio o más cerca de OLP; en *Simonurius* el área ocular es más ancha atrás, con OMP más cerca de OLA. El palpo de *Akela* tiene una pequeña apófisis retrolateral tibial y el bulbo sin apófisis mediana, mientras que en *Simonurius* la tibia palpal lleva dos grandes apófisis retrolaterales y el bulbo presenta una apófisis mediana muy desarrollada. En *Akela* la tibia I tiene v 2-2-2 espinas y en *Simonurius*, v 2-2.

Descripción.—Prosoma ancho y alto (ancho 70-83% del largo, alto 45-57% del largo). Area ocular ocupando 43-57% del largo del prosoma; más ancha que larga, más ancha atrás que adelante; OMP más cerca de OLA. Estría torácica puntiforme o ausente. Clípeo angosto, menor que el radio de OMA, desnudo en machos y con barba rala en hembras. Esternón alargado, de igual ancho que la base del labio, ligeramente rebordeado en escotaduras de coxas I. Láminas maxilares redondeadas. Quelíceros pequeños, paralelos, verticales; surco ungueal breve; promargen con tres a cinco dientes, algunos sobre una base común; retromargen con un diente. Pata IV siempre mucho más larga que III. Espinas abundantes; tibia y metatarso I con 2 pares de espinas ventrales; patas posteriores muy espinosas. Palpo con dos grandes apófisis tibiales retrolaterales; émbolo breve; bulbo con apófisis media espiniforme.

Especie tipo.—*Akela gladifera* Simon 1901.

Simonurius gladiferus (Simon), nueva combinación
Figs. 2, 3, 27-32

Akela gladifera Simon 1901b:146 (macho Holotypus de Argentina, Buenos Aires, col. C. Berg, en MNHNP, examinado); 1901a:568, 569, 571, fig. 688; Mello-Leitão 1933:61; 1944:319; Roewer 1954:1171; Bonnet 1955:222; Galiano 1963:286, lám. 4, figs. 1, 2 (redescripción).

Akela trilineata Mello-Leitão 1941:182, fig. 76 (hembra Holotypus de Argentina, La Rioja, Chilecito, Bajo de Doria, No. 14972 en MLP, examinado); Roewer 1954:1172; Galiano 1980:34. NUEVA SINONIMIA.
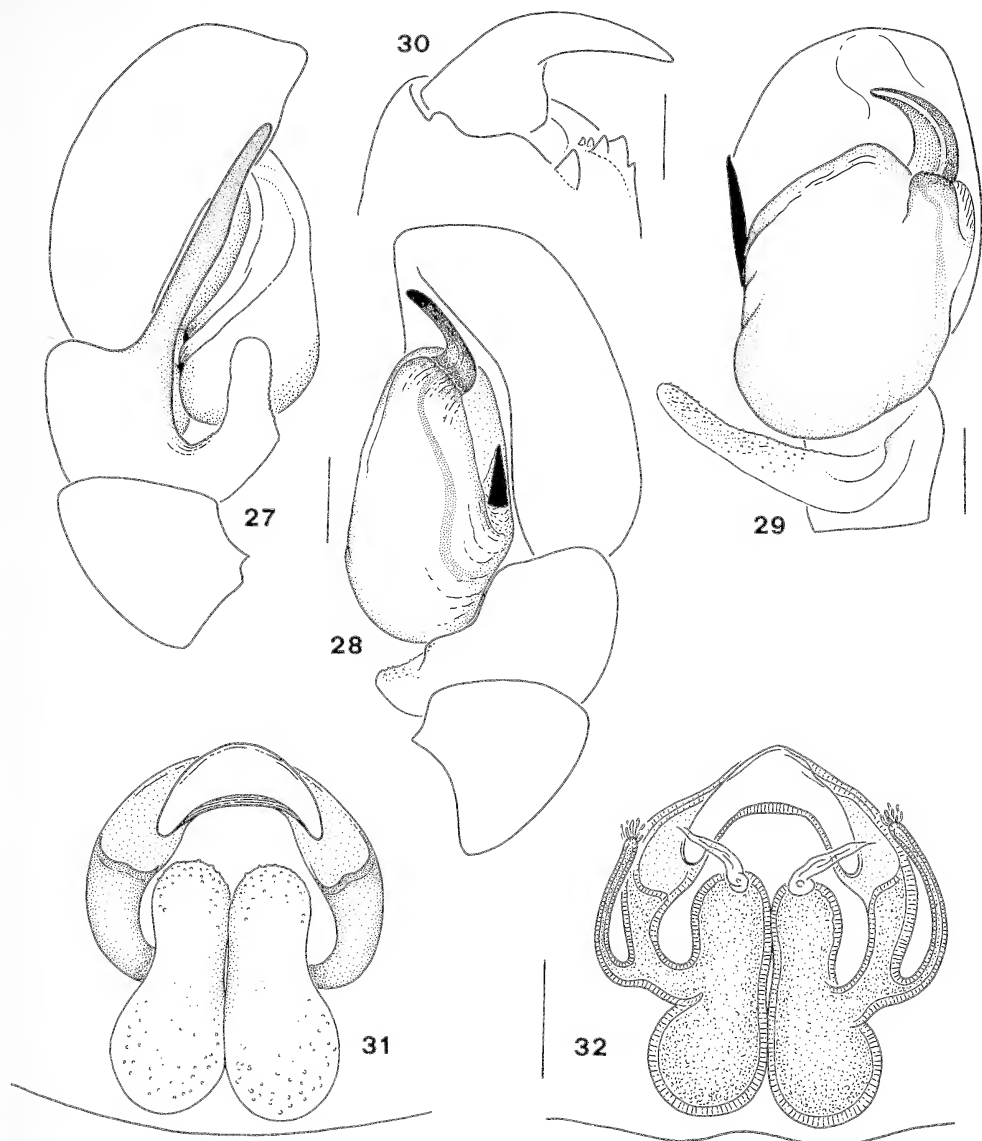
Figs. 27-32.—*Simonurius gladiferus*; 27-29, palpo; 27, retrolateral; 28, prolateral; 29, ventral; 30-32, hembra; 30, quelícero, ventral; 31-32, epigino; 31, ventral; 32, dorsal. Escala 100 μ.

Macho.—Largo total 3.27. Prosoma: largo 1.63, ancho 1.30, alto 0.87. Clípeo, alto 0.06. Area ocular: largo 0.80; ancho de hilera anterior 1.20; de hilera posterior 1.25; distancia OLA-OMP 0.18; OMP-OLP 0.22; diámetro OMA 0.40. Estría torácica puntiforme, 0.23 más atrás de OLP. Quelíceros: promargen con cuatro dientes; retromargen con uno. Quetotaxia: Fémures I, II d 1-1-1, p ap 2; III, IV d 1-1-1, p ap 2, r ap 1. Patellas I, II p 1; III, IV r 1. Tibias I v 2-2, p 1-1-1; II p 1-1, r 1-1; III p 1-1, r 1-1-1; IV d 1, v 1p-1p, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2, p ap 1; III v 1-2, p 1-2, r 1-2; IV v 1-2, p 1-1-2, r 1-1-2. Palpos: Figs. 27-29.

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	1.00	0.58	0.78	0.68	0.38	3.42
II	0.42	0.48	0.52	0.47	0.32	2.21
III	0.78	0.40	0.38	0.50	0.33	2.39
IV	1.17	0.52	0.58	0.67	0.33	3.27

Aspecto y color en alcohol.—Prosoma anaranjado, con la región cefálica amarilla; grandes manchas oculares negras, dos manchas grisáceas en el medio del área ocular y dos manchas negras con pelos negros, alargadas transversalmente, limitando por detrás la región cefálica. Región torácica negruzca. Lados del prosoma anaranjados, limitando con la zona negruzca por una línea irregular. Clípeo anaranjado, solo con algunos pelos negros. Todas las zonas amarillo naranja, cubiertas por pelitos blancos. Quelíceros anaranjado pálido, con ápice amarillo. Opistosoma armarillo blanquecino, con un área basal dorsal grisácea. Tres bandas negruzcas en forma de V invertida (a veces interrumpidas en el medio), una sub-basal, una media y otra subapical, seguidas por dos o tres cortas banditas transversas sobre el tubérculo anal. Detrás de cada banda negruzca, una ancha banda amarilla con pelos blancos y luego una banda amarilla con pelos anaranjados (Fig. 3). Patas blanquecinas, traslúcidas, ligeramente oscurecidas en los fémures; pata I con una banda negra prolateral en patela, tibia y base de metatarso. Palpos blanquecinos, algo amarillentos en tarso. La apófisis tibial ventral es traslúcida, con la superficie cubierta de dentículos.

Hembra.—Largo total 3.46. Prosoma: largo 1.87, ancho 1.50, alto 0.90. Clípeo, alto 0.06. Area ocular: largo 0.85; ancho de hilera anterior 1.32; de hilera posterior 1.40; distancia OLA-OMP 0.20; OMP-OLP 0.27; diámetro OMA 0.45. Estría torácica puntiforme, 0.25 más atrás de OLP. Quelíceros: promargen con cinco dientes, tres de ellos sobre una base común. (Fig. 30).

| Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	0.85	0.63	0.53	0.45	0.30	2.76
II	0.77	0.53	0.47	0.43	0.27	2.47
III	0.78	0.40	0.42	0.45	0.30	2.35
IV	1.17	0.62	0.65	0.67	0.35	3.46

Quetotaxia: Fémures I, II d 1-1-1, p ap 1; III d 1-1-1, p ap 2, r ap 1; IV d 1-1-1, p ap 1, r ap 1. Patellas III, IV r 1. Tibias I v 2-2-1p; II p 1-1, r 1-1; III p 1-1-1, r 1-1-1; IV v 1p-1p, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v 1-2, p 1-2, r 1-2; IV v 1-2, p 1-1-2, r 1-1-2. Epigino: Figs. 31, 32.

Aspecto y color en alcohol.—Como en el macho, excepto que la región torácica es amarilla y falta la zona grisácea dorsal en opistosoma. (Fig. 3).

Variaciones.—Machos, Fémur I p ap 1; II, III, IV p ap 1, r ap 1. Patellas II p 1, r 1; III, IV p 1, r 1. Tibias I p 1-1; III d 1. Metatarsos III v ap 1; IV v 1p-1p. Hembras, Tibias I v 2-2; II v 1 r; IV d 1, v 1p.

Nota.—Todos los especímenes provienen de áreas serranas. Los ejemplares del lote 8277 se hallaron en las sierras, en zonas relativamente húmedas a la orilla de corrientes de agua, sobre follaje, nunca bajo piedra.

Material estudiado.—ARGENTINA: Buenos Aires; Tandil, 2 noviembre 1969 (C. Rebollo), 2 machos No. 8276 (MACN); Córdoba; Cura Brochero, La Aguadita, noviembre 1985 (Galiano, Miranda), 3 machos, 4 hembras No. 8277 (MACN); Santa Rosa de Calamuchita, febrero 1952 (M. J. Viana), 1 hembra No. 8280 (MACN); diciembre 1941, 2 hembras No. 8279 (MACN); diciembre 1940, 1 hembra No. 8278 (MACN).
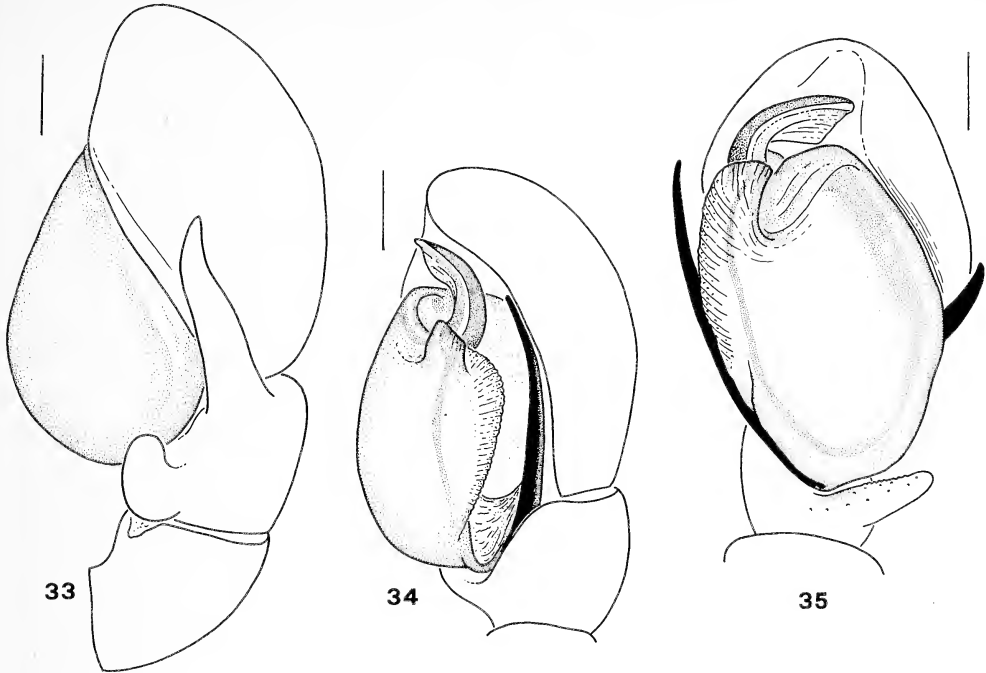
Figs. 33-35.—*Simonurius expers* palpos; 33, 35, Holotipo; 33, retrolateral; 35, ventral; 34, Paratipo, prolateral. Escala 100 μ.

Simonurius expers, nueva especie
Figs. 33-35

Etimología.—Del latín *expers*, que no tiene o está desprovisto. Se refiere a que no se conoce la hembra.

Diagnosis.—Se diferencia de *S. gladiferus* y de *S. quadratarius* por la gran longitud de la apófisis media del bulbo, que sobrepasa la base del émbolo.

Descripción.—Holotypus macho. Largo total 3.53. Prosoma: largo 1.60, ancho 1.32, alto 0.87. Clípeo, alto 0.08. Area ocular: largo 0.67; ancho de hilera anterior 1.23; de hilera posterior 1.28; distancia OLA-OMP 0.20; OMP-OLP 0.22; diámetro OMA 0.42. Sin estría torácica. Quelíceros: pequeños, paralelos, verticales, algo más delgados en el ápice; promargen con cuatro dientes; retromargen con uno.

Pata	Fémur	Patella	Tibia	Metatarso	Tarso	Total
I	1.03	0.68	0.93	0.75	0.42	3.81
II	0.80	0.50	0.55	0.50	0.32	2.67
III	0.82	0.33	0.42	0.48	0.32	2.37
IV	1.02	0.43	0.60	0.60	0.33	2.98

Quetotaxia: Fémures I d 1-1-1, p ap 1; II, III d 1-1-1, p ap 1, r ap 1; IV d 1-1-1, p ap 2, r ap 1. Patellas I, II p 1; III r 1; IV p 1, r 1. Tibias I v 2-2, p 1; II v 1r-1r, p 1-1-1; III v 1p, p 1-1, r 1-1; IV d 1, v 1p-1p, p 1-1-1, r 1-1-1. Metatarsos I v 2-2; II v 2-2, p 1-1; III v 1p, p 1-2, r 1-1; IV v 1p-1p, p 1-1, r 1-1-2.
Palpos: Figs. 33-35.

Aspecto y color en alcohol.—Como *S. gladiferus*.

Hembra.—Desconocida.

Nota.—Según la indicación del colector, el ejemplar se halló sobre *Eryngyum pandanifolium.*

Material estudiado.—ARGENTINA: Buenos Aires; Delta del Paraná, Arroyo Correa, diciembre 1951 (A. O. Bachmann), macho Holotypus No. 8281 (MACN); 1 macho Paratypus No. 8282 (MACN), sin localidad ni colector.

Simonurius campestratus (Simon), nueva combinación

Akela campestrata Simon 1901b:145 (macho Holotypus de Venezuela, Colonia Tovar, col. E. Simon, en MNHNP, examinado); 1901a:571; Petrunkevitch 1911:590; Mello-Leitão 1949:19; Roewer 1954:1171; Bonnet 1955:222; Galiano 1963:285.

Nota.—Es probable que se trate de un sinónimo de *S. quadratarius* del cual se diferencia apenas por el prosoma algo más elevado y el color más oscuro. Mello-Leitão citó esta especie para Brasil, Foz do Koluene.

Simonurius quadratarius (Simon), nueva combinación

Akela quadrataria Simon 1901b:145 (macho Holotypus de Venezuela, Colonia Tovar, col. E. Simon, en MNHNP, examinado); 1901a:569, 571; Petrunkevitch 1911:590; Roewer 1954:1172; Bonnet 1955:222; Galiano 1963:287, lám. 4, figs. 3-5 (redescripción).

Nota.—La apófisis media del bulbo es más larga que en *gladiferus* pero más corta que en *S. expers* sp. n.

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EFFECTS OF DIET ON THE DEVELOPMENT OF *LOXOSCELES LAETA* (NICOLET) (ARANEAE, LOXOSCELIDAE)

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ABSTRACT

Spiderlings of *Loxosceles laeta* from a single egg sac were fed on two different diets: a varied one of fruit flies, mealworms and about ten meals of miscellaneous insects, and a limited one of fruit flies and mealworms only. About three times as many of those on the limited diet died before maturity (61%) as those on a varied diet (21%). Those on a varied diet had fewer molts to maturity, reached adulthood sooner, but lived longer as adults and had a longer total life span than those on the limited diet. They also grew to a larger size than ones on the limited diet. Both populations showed similar survivorship curves, except for the limited diet group in which initial deaths during molting, before adulthood, showed 50% deaths in the first year. After that the survivorship curve was an A type like the other group. It is concluded that the diet of this spider and probably all spiders should include a variety of insects to approximate the best growing conditions.

INTRODUCTION

This study was undertaken to determine whether features of the life cycle of this spider, fed a limited diet of fruit flies and mealworm larvae, often fed to spiders in rearing studies, was adequate. Although the range of these spiders, *Loxosceles laeta*, is in South America, this study was done on individuals from a population which has lived in the Southern California area for an unknown length of time, certainly for many years. They are well established there and elsewhere in the world (Gertsch and Ennik 1983).

METHODS

About 130 spiderlings from one egg sac were reared and maintained until death. The female from which the spiderlings were obtained was collected in Sierra Madre, in the San Gabriel Valley of the Los Angeles area in June 1969. She was immature and molted on 12 July and again, to become mature, on 1 November. She was mated to a male which was captured as an immature in July 1969. He became adult on 8 October. On May 1st 1970 a successful mating occurred and an egg sac was laid on 4 June 1970. Young spiderlings emerged on

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27 July. They were placed separately in plastic vials (about 40 cm^3 for spiderlings and 80 cm^3 for late instars and adults) with tight snap caps. None of them was given water, and seldom, except during feeding, was the cap removed. There was probably little water vapor in the vial (it was not tested) because room humidity was low, usually around 10% to 20%, and scarcely ever exceeded 30%. The spiders were kept at room temperature, ranging from 15° to 20°C, probably similar to the habitats in houses where they lived. The vials in which the spiders lived were stored on the same shelves in a cabinet at the lab or later, when I moved to Santa Fe, in my house where environmental conditions were not significantly different. Each spider in both groups was fed equal amounts of food at the same time irregularly every two to three weeks.

The group of 50 specimens reared on a varied diet was fed fruit flies, *Drosophila melanogaster* (mostly vestigial-winged mutants) when they were small, and larvae of the mealworm beetle, *Tenebrio molitor*, when they were larger. In addition, about ten meals during their lives consisted of miscellaneous insects (a mixture of insects from sweeping vegetation outside—one that consisted of flies, bugs and insects of a few other orders).

Another group of 80 spiders were fed *only* fruit flies and mealworms. Three spiders were accidentally killed while being fed so the total number in each group at the end was 48 and 79 respectively. The reason for the unequal numbers in the two groups is unimportant to the result, as the numbers were sufficient to document differences between spiders. Sex, size and any other variables were randomly distributed in the two samples. Individual records of when spiders were fed, when they molted, when they became mature and what each carapace width was each time were made. Summaries are shown in the tables.

Somewhat over a year after those that lived had reached maturity (two to three years), rather than preserving them, I ceased feeding them as I had been doing. Although this last part of the study was not in my original plans, it transpired that they became a significant part of the results. For two and a half years (December 1973 until 22 July 1976) they were all fed one mealworm each on four different occasions at irregular intervals (three to ten months). After 22 July I ceased feeding them entirely. By that time only 23 females and no males were still alive. Some of the results of the starvation of the 14 females on a varied diet have already been published (Lowrie 1980). This report adds the results of the growth of the nine starved females on a limited diet.

RESULTS AND DISCUSSION

Longevity and development.—Of the total of 127 spiderlings that were studied until their death, on the varied diet 21% (10 of 48) died at various times, usually while molting, before reaching maturity. This whole group had a mean life span of 236 days, a range of 166.5 to 306.3 days (95% confidence level). Of the 79 on a limited diet, 61% (48 of 79) died before adulthood. Only two meals of miscellaneous insects had been fed those on a varied died during their growth as immatures out of about 75 total meals. Those on a limited diet had a mean life duration of 324 days, a range from 297 to 351 days (95% confidence level), nearly 50% longer than those on a varied diet. Of the two populations, those on a restricted diet showed a significantly greater number of deaths than those on a varied diet ($P < 0.01$).

Table 1.—Longevity of male *Loxosceles laeta*. Twenty-two were fed on a varied diet (V), while 14 were fed on a limited diet (L). Asterisk refers to the number of molts *after* emergence from egg sac. *N* = 36.

	No. of Molts*		Days to Adulthood		Days as Adult		Total Days of Life		Carapace Width	
	V	L	V	L	V	L	V	L	V	L
Mean	7.3	8.0	819	930	598	200	1417	1132	3.5	3.3
SD	0.77	0.78	194	213	197	167	97	295	0.17	0.23
SE	0.16	0.21	41	57	42	45	21	79	0.04	0.06
95%	6.9	7.5	733	807	511	104	1374	961	3.4	3.2
confidence	to	to	to	to	to	to	to	to	to	to
interval	7.6	8.4	905	1053	685	297	1460	1303	3.6	3.5
Sample	6	7	547	714	227	24	1101	817	3.2	3.0
range	to	to	to	to	to	to	to	to	to	to
	9	9	1200	1227	912	635	1494	1500	3.8	3.7
t-test (34 degrees of freedom)	2.682		1.615		6.260		4.200		2.701	
Significance level	< 0.02		< 0.11		< 0.001		< 0.001		< 0.02	

Longevity of adults.—Males (Table 1) are significantly shorter lived than the females (Table 2). Both feeding regimes resulted in virtually all males being dead by the time the first female died. Tables 1 and 2 show (95% confidence level) that males on a limited diet died in a shorter time (mean of 1132 days) than those on a varied diet (mean of 1417 days). Females on limited diets lived a shorter time (mean of 1844 days) than those on varied diets (mean of 2507 days). Student's t-test corroborates the significance of the differences (Tables 1 and 2).

Although females take only a slightly shorter time to reach adulthood (762 days with varied diets; 819 days for males) they lived as adults almost three times as long as the males (males 598 days; females 1745 days). Galiano (1967) reared *Loxosceles* to maturity in an average of 316 days for females and 406.5 days for males. Further life cycle work by Galiano and Hall (1973) indicates a slightly longer time to maturity than in her 1967 study: 328.5 days to maturity for females and 454.7 days for males. Likewise for the number of days as an adult and total life span. Their figures for females indicate 1547.4 days as adults for virgin females and a total of 1893.8 total days of life, while males who had not copulated lived for 640.9 and 1155.4 days respectively. These data show lengths of life consistently shorter than mine and probably significantly so.

I have no explanation for this shorter maturing time for the Argentinian specimens in contrast with the Californian. Possible explanations are that this California group was a different population which has been living in a different locality for an unknown time and that it may have evolved different growth characteristics. Rearing conditions (temperature, humidity, frequency of feeding and type of prey, etc.) were also somewhat different and could be responsible for the differences.

During the period of starvation the females on a limited diet lived only half as long as those on a varied diet (244 days versus 453 days). The two samples indicate that the differences between the two populations were highly significant ($P < 0.01$). The survivorship curve (Fig. 1) shows the growth curve of those on a

Table 2.—Longevity of female *Loxosceles laeta*. Sixteen were fed on a varied diet (V), while 17 were fed on a limited diet (L). Asterisk refers to the number of molts *after* emergence from egg sac. $N = 33$.

	No. of Molts*		Days to Adulthood		Days as Adult		Total Days of Life		Carapace Width		No. Days Life (Starvation)	
	V	L	V	L	V	L	V	L	V	L	V	L
Mean	7.5	8.1	762	900	1745	1074	2507	1844	4.0	3.65	453	244
SD	0.52	0.70	104	211	327	641	300	720	0.37	0.55	171	148
SE	0.13	0.17	26.5	54	82	166	75	175	0.09	0.13	46	49
95%	7.2	7.8	707	784	1571	908	2348	1474	3.8	3.4	354	130
confidence	to	to	to	to	to	to	to	to	to	to	to	to
interval	7.8	8.5	818	1017	1919	1240	2667	2215	4.2	3.9	551	357
Sample	7	7	669	700	1028	38	1746	815	3.3	2.95	219	7
range	to	to	to	to	to	to	to	to	to	to	to	to
	8	9	973	1431	2108	1836	2872	2646	4.45	4.4	755	499
t-test (34 degrees of freedom)	2.797		2.320		3.755		3.413		2.207		3.482	
Significance level	< 0.01		< 0.05		< 0.001		< 0.01		< 0.05		< 0.01	

varied diet to be the type A curve of Allee et al. (1949, p. 300); those that live with a minimum of mortality in the first part of their life cycle and then die within a short time at the end of their life cycle. The initial death rate of those on a limited diet, however, fits the type C curve better with the initial death rate high, in the first part of the curve. However, after maturity it fits the type A curve quite well. It might be noted that longevity in this study is probably longer than it would be in a wild population because predation and parasitism were non-existent because the spiders were in enclosed vials where these processes could not affect them. Also, food was readily available and probably more than it would have been in the wild.

Number of molts to adulthood and size (Carapace Width) differences.—Those spiders living on a limited diet showed a slightly, but significantly, greater mean number of molts necessary to reach adulthood. Although the actual number of molts after emergence from the egg sac is similar for males and females, statistically their differences are significant ($P < 0.02$). The conclusions are that those on restricted diets are slower to attain maturity, averaging nearly one more molt to adulthood. Galiano's (1967) specimens showed the same range of number of molts.

Carapace width as a measure of size is used because Hagstrum (1971) has shown that this structure does not vary in measurements significantly even if taken at various times between molts. The average female on a varied diet had a carapace width about 10% larger than the female on the limited diet. In the male the increase is only a little over 5%. The differences between carapace widths of those on a restricted diet versus limited diet is significant (female $P < 0.05$, male $P < 0.02$). The "well-fed" varied-diet individuals consistently grow to a significantly larger size. This might be expected since with better nutrition better growth is typically the case in animals.
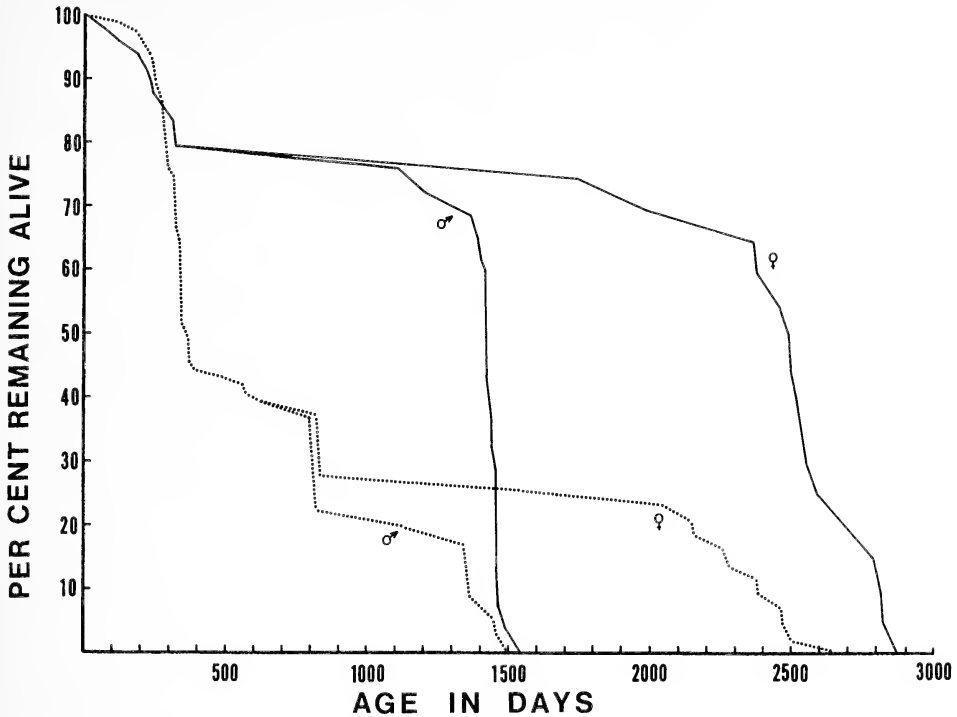
Fig. 1.—Survivorship curve of *Loxosceles laeta*. Dotted line = spiders on a restricted diet. Solid line = spiders on a varied diet.

CONCLUSIONS

Why those on a varied diet died sooner than the immatures on a restricted diet was not determined. It probably is related to the longer life as immatures with more molts which are critical periods when death usually occurs. This effect resulted in spite of the varied diet spiderlings having had only two meals of miscellaneous insects out of 50 to 75 meals during this period. Similarly those on a more varied diet had fewer molts, reached maturity sooner, lived longer as adults and had a longer life span than those on a restricted diet. The adult size of those on a varied diet was greater and starved adults on a varied diet lived nearly twice as long as those on a limited diet.

The basic conclusions seem clear that in this species a varied diet, even though it varies by only a few meals of miscellaneous insects, is a better, more healthy, probably more adequate diet than only mealworms and fruit flies. In any experiment involving rearing or maintaining *Loxosceles laeta* and probably other species of *Loxosceles*, and possibly any species of spiders, a varied diet should be provided to ensure that all necessary nutrients are present. According to Brues (1946), Patton (1963) and Wigglesworth (1947), these results would seem to fit expectations in diets in that most diets of insects must contain a certain spectrum (varying with the insect) of carbohydrates, fats, proteins, vitamins, minerals, etc. Spiders would not be expected to differ in this general regard.

ACKNOWLEDGMENTS

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NOTES ON THE LIFE HISTORY AND BEHAVIOR OF THE COMMUNAL SPIDER *CYRTOPHORA MOLUCCENSIS* (DOLESCHALL) (ARANEAE, ARANEIDAE) IN YAP, CAROLINE ISLANDS

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ABSTRACT

Cyrtophora moluccensis is a semi-social tropical spider that builds colonies that may contain hundreds of individuals of that species plus several other species. Studies in Yap were undertaken to determine the time required for development from egg to sexual maturity. The smaller instars were cage reared; and in the field, the larger instars were marked for observation. Although the duration of different instars is similar, there is considerable variation among individuals. Each instar lasts about 11 days. After emerging from the cocoon, males mature in about two months, and females in about four months. Mating occurs only near mid-day, and females may mate more than once. Each cocoon averages 1250 eggs, and nearly all the eggs hatch and emerge from the cocoon. The time between production of the cocoon and emergence of the young is about 25 days. Although one female produced seven cocoons, females typically produce three or four cocoons at 10-23 day intervals.

INTRODUCTION

Of the 30,000 known species of spiders, only about 33 show good evidence of group living (Burgess 1978). One of these species is *Cyrtophora moluccensis* (Doleschall), a semi-social spider found in the tropical Pacific, India, Malaysia and Southern Japan. The species is usually found in large colonies containing hundreds of individuals in all stages of the life cycle. The webs are most abundant in areas where the natural vegetation has been disturbed, such as gardens, near roadsides, or in scrub vegetation. In gardens the colonies may become large enough to be plant pests. Sometimes gasoline-soaked coconut fronds are thrown on them and burned. Colonies are present year-round, and in New Guinea one colony was known to have occupied the same site for 12 years (Lubin 1980). The communal webs have been illustrated by Lubin (1973, 1980) and Sabath, et al., (1974).

Relatively few spiders have been investigated to determine longevity and time to maturity. Levy (1970) determined the life cycle of *Thomisus onustus* and summarized the life cycles of 31 other species that have been studied. He noted that the duration of the developmental period has been shown to be wide range—from a quick developmental time where there are two generations per year in the lycosid *Pirata piraticus* to as much as ten years for attaining maturity in species of Theraphosids. In temperate zones, where spiders are limited by cold weather,

some species overwinter as adults; but in many species, the spiderlings hatch in the fall and stay in the cocoon through the winter. Although there are reports of spiders living several years, most spiders in the temperate zone live only 12-18 months (Bonnet 1935). Compared to those in the temperate zones, the life-cycles of tropical spiders are not well-known. Robinson and Robinson (1973) found in New Guinea that adult and immature *Nephila maculata* (Fabricius) were present throughout the year but were more abundant during the wetter seasons. Egg laying occurred throughout the year. However, Thakur and Tembe (1956) found that *N. maculata* near Bombay is markedly seasonal. Lubin (1972) provided data on the life history of *Cyrtophora moluccensis* in New Guinea. The *Cyrtophora* web, a high cost, relatively inefficient trap for flying insects, has increased durability and strength with a low frequency of renewal (Lubin 1973, 1974). Sabath, et al., (1974) studied *C. moluccensis* on Guam and described the cocoon, number of eggs per cocoon, and the inquilines of the web. I will discuss here the length of time required to reach maturity, number of cocoons, interval between production of cocoons and other aspects of reproduction.

METHODS

Observations on *Cyrtophora moluccensis* (Doleschall) were made in the natural habitat from January 1980 to June 1980 on the island of Yap in the Caroline Islands. The Yap Islands lie in the western part of the Caroline Island group about 1000 km southwest of Guam, cover a total area of about 200 km^2, and were formed by land upheaval. The warmest and coolest months differ by only 1^0C in average temperature, with the daily maximum and minimum averaging 30^0 and 24^0C. Normal annual rainfall is over 300 cm: the drier season (December through April) averages 13-20 cm monthly, and the wetter season (May through November) averages 25-38 cm monthly. Relative humidity (RH) rarely falls below 75%. Daily observations of the spiders were made in the village of Fedor, where the communal webs were very abundant in and around the garden patches of taro (*Cyrtosperma chamissonis*). Largely because of the size of the communal web, it was not possible to rear the female spiders in an enclosure. This made it necessary to use several different methods of observation and measurement.

Early development.—Newly formed cocoons were removed from the web, opened, placed in stoppered glass vials that had a strip of paper to admit air inserted between the stopper and vial, and observed each day with a dissecting microscope.

Early instars.—Because there was no way to mark the early instars without damaging them, individuals had to be identified by location in the web. This was not entirely satisfactory because the early instars move from one location to another, even occasionally moving into another's orb-web and displacing the original habitant. Data on the early instars were collected in three ways: (1) direct observation in the field, (2) placing hatching cocoons in a screen enclosure ($1 \times 2 \times 0.5$ meters) in Yap, and (3) placing cocoons from Yap in screen enclosures in controlled temperature and humidity chambers (25-30^0C and 80% RH) in Indianapolis, Indiana. Because these young individuals usually would not build normal webs when alone in experimental chambers, it was necessary to have large numbers of them together. This made it difficult to be certain of the identity of a particular individual on successive days. *Drosophila melanogaster* colonies were

satisfactory food sources for instars II and III but not for the later instars. No good food supply was found for the intermediate instars. *Drosophila* seemed too small for them, and the spiders were unable to capture larger dipterans.

Later instars.— All observations on the later female instars (instar V-X) were made in the field. Newly molted individuals could be recognized by their pale grey-green color which remained for about a day following ecdysis. Newly molted individuals were marked on a leg or the abdomen with a spot of model airplane paint which did not seem to interfere with their normal activity, and were observed each day in their natural habitat. Attempts to move individuals to start a new colony were not successful, largely because of the high predation by the very abundant skink populations (*Emoia callisticta* and *Emoia caeruleocauda*). When investigators tore down a communal web, several skinks appeared and quickly devoured all the displaced spiders.

RESULTS AND DISCUSSION

Colony size.—Although solitary individuals are occasionally found, the species characteristically lives in colonies composed of hundreds of individuals of *Cyrtophora moluccensis* and fewer numbers of several other species. All the members in one average size colony (about 15 m^2) were collected and identified: the colony contained 447 specimens of *Cyrtophora* and 236 specimens divided among six other species (Table 1). This averaged 30 *Cyrtophora* and 45 spiders of all species per m^2. One doughnut-shaped colony was 28 meters in circumference. Wheeler (1926), reporting that colonies of *Cyrtophora citricola* can be immense, described one colony of over 1000 ft^2.

Number and size of instars.—Because it was not possible to feed the larger instars properly, no females were reared in the laboratory from egg to maturity. From marked individuals in the field and the specimens kept in the laboratory, it was possible to determine the amount of time in each stage of development. By daily observations, some females were followed through three instars. Excluding the deutovum, the duration of the various instars was 6-22 days, with the mean being 11 days ($N = 59$). Although the time in each instar varied within instars and among instars, the overall picture shows a regular progression in development with no instars developing particularly fast or slow relative to the others. Other investigators who have reared spiders under controlled conditions have reported a problem with constancy in the number of developmental instars. Deevey (1949) found that *Lactrodectus mactans* females that were fed maximally matured at the seventh molt while those fed only every fourth day required 8-9 molts. Whitcomb, Hite and Eason (1966) found great variations in the number of instars in *Peucetia viridans* even when all spiderlings were reared under identical conditions. Miyashita (1968) noted that the number of instars in *Lycosa T-insignita* increased as the interval of food supply was prolonged. Conversely, Turnbull (1965) found that *Agelenopsis potteri* matured in seven instars regardless of the feeding rate. Robinson and Robinson (1978) concluded that the number of molts that spiders of the same sex undergo before maturity is variable, and that the greater the number of molts, the larger was the adult spider. Working with *Argiope argentata* and *A. aemula*, they found that the females had up to 15 instars, although some females matured at the thirteenth or fourteenth instar; and the males at either the seventh or eighth instar.

Table 1.—Number of specimens present in one average size colony of *Cyrtophora*. The longest dimensions of the web were 5 meters by 4 meters; the lowest point about 0.5 meter above the ground, the top about 1.0 meter high. Total surface area was 15 m^2 and the volume was 12.5 m^3. All specimens were taken from the same web on the same day (March 7, 1980).

Species	Male	Female	Immature	Total
Cyrtophora moluccensis	49	10	390	447
Argyrodes argentatus	4	40	136	217
Argyrodes sp. C	15	12	42	69
Argyrodes sp. D	19	17	14	50
Neoscona sp. D	—	—	1	1
Argiope appensa	—	—	1	1
			Total for colony—	785

Since limited field study made it impossible to determine the number of instars and, therefore, the total time to maturity for any single female, an analysis of the size classes of *Cyrtophora* from the censused colony (Table 1) was undertaken. Several studies have shown that determination of instar usually cannot be accomplished by carapace measurements (Edmunds 1982; Kaston 1970) because the size ranges of the different instars overlap. Measurements of the *Cyrtophora* carapace length and width indicated that there were distinct size classes, but they did not provide a clear separation of the various instars (Table 2). However, the total number of dorsal spines on both the left and right leg III, together with the length of leg I (patella through tarsus) did show a significant separation (Fig. 1). The other segments of leg I could not be measured without damage to the small specimens. Dorsal spines on both left and right leg III were counted because the number of spines on both legs was not consistent for many individuals. For example, the presumed instar VII never had more than two dorsal spines on leg III, but the count on 40 individuals showed left and right combinations of 2-2, 2-1, 2-0, and 1-2. The combination of 2-2 appeared in 33 of the 40 individuals examined. Although it is likely that some specimens have been incorrectly assigned to a certain instar, I feel confident that the separation by instar is generally accurate and that many females have 11 instars to reach maturity.

The first four instars could be distinguished by size with relative ease. Instars IV and V overlapped in size but most of the specimens were clearly of two different age groups. Some individuals of instars V and VI also overlapped in leg length ($\bar{x}$ = 3.40 mm and 4.79 mm, respectively), but all those specimens assigned to instar VI had at least one dorsal spine on leg III. It appears that they usually add a spine to leg III at each instar from instars VI-IX, but this is not always true. One specimen, assigned to instar VIII, had the same number of spines before and after molting. This probably explains the difference in number of spines on the left and right legs. Although this method of establishing the number of instars is inherently imprecise, it does provide a reasonable estimate of the number of instars in this colonial species. The variation in the number of instars cannot be determined from the data available.

Two males were reared successfully in the laboratory: the times from hatching to sexual maturity were 56 days and 66 days. The number of instars could not be accurately determined, and both specimens died while completing the last ecdysis.

Analysis of male specimens from the censused web indicated that there were six instars to sexual maturity. Several investigators have noted that there is a

Table 2.—Measurements of carapace, number of dorsal leg spines of leg III and leg length for the different instars.

	Carapace width (mm)	Carapace length (mm)	No. of Leg III dorsal spines			Patella—tarsus length (mm)	
			Left	Right	Total	Leg I	Leg IV
Instar I (deutovum); *N* = 5							
Mean	0.47	0.6	0	0	0	0.76	0.75
Range	0.4-0.5	0.0				0.76-0.78	0.75-0.76
SD	0.04	—				0.01	0.01
Instar II; *N* = 11							
Mean	0.52	0.67	0	0	0	1.22	1.09
Range	0.50-0.53	0.60-0.70				1.13-1.30	1.03-1.13
SD	0.01	0.03				0.05	0.04
Instar III; *N* = 14							
Mean	0.62	0.81	0	0	0	1.78	1.49
Range	0.58-0.70	0.71-0.90				1.63-1.96	1.46-1.66
SD	0.03	0.05				0.09	0.16
Instar IV; *N* = 24							
Mean	0.74	0.99	0	0	0	2.5	2.1
Range	0.7-0.8	0.8-1.1				2.2-2.7	1.8-2.2
SD	0.04	0.06				0.1	0.1
Instar V; *N* = 36							
Mean	0.94	1.22	0	0	0	3.40	2.77
Range	0.8-1.2	1.0-1.5				2.7-4.6	2.1-3.7
SD	0.09	0.10				0.37	0.31
Instar VI; *N* = 40							
Mean	1.23	1.66	0.93	0.93	1.85	4.79	3.82
Range	0.90-1.45	1.25-1.90	0-1	0-1	1-2	3.4-5.9	2.9-4.7
SD	0.12	0.15	0.26	0.26	0.35	0.48	0.36
Instar VII; *N* = 40							
Mean	1.69	2.29	1.95	1.8	3.8	6.79	5.50
Range	1.4-2.0	1.9-2.9	1-2	0-2	2-4	5.0-9.0	4.2-7.1
SD	0.18	0.25	0.22	0.56	0.49	0.85	0.73
Instar VIII; *N* = 37							
Mean	2.3	3.0	2.8	2.9	5.6	9.1	7.4
Range	1.8-3.0	2.3-3.4	2-4	2-4	5-7	7.3-11.7	5.9-8.9
SD	0.25	0.29	0.6	0.6	0.7	1.0	0.9
Instar IX; *N* = 32							
Mean	3.0	4.0	4.2	4.0	8.2	12.5	10.3
Range	2.1-3.9	3.2-4.9	3-5	3-5	7-10	9.8-15.6	8.0-12.4
SD	0.4	0.4	0.5	0.5	0.8	1.4	1.3
Instar X; *N* = 10							
Mean	4.8	6.3	6.2	6.0	12.2	19.0	16.4
Range	4.2-5.2	5.8-7.2	5-7	5-7	11-14	16.7-20.9	14.6-17.7
SD	0.3	0.4	0.6	0.6	0.9	1.4	1.0
Instar XI; *N* = 8							
Mean	6.5	7.9	6.2	7.1	13.3	24.5	20.7
Range	6.1-7.2	6.8-8.5	6-7	6-9	12-16	22.7-26.2	18.8-22.9
SD	0.3	0.6	0.4	1.0	1.2	1.1	1.2

tendency for the males of species with strong sexual size dimorphism to mature in fewer instars than the females (Levy 1970; Robinson and Robinson 1976, 1978). The sex of instars I (deutovum) and II could not be determined but at instar III the pedipalps of the males have a greater diameter than do the pedipalps of the females (male $\bar{x}$ = 0.10 mm, SD = 0.01, *N* = 10; and female, $\bar{x}$ = 0.07 mm, SD =
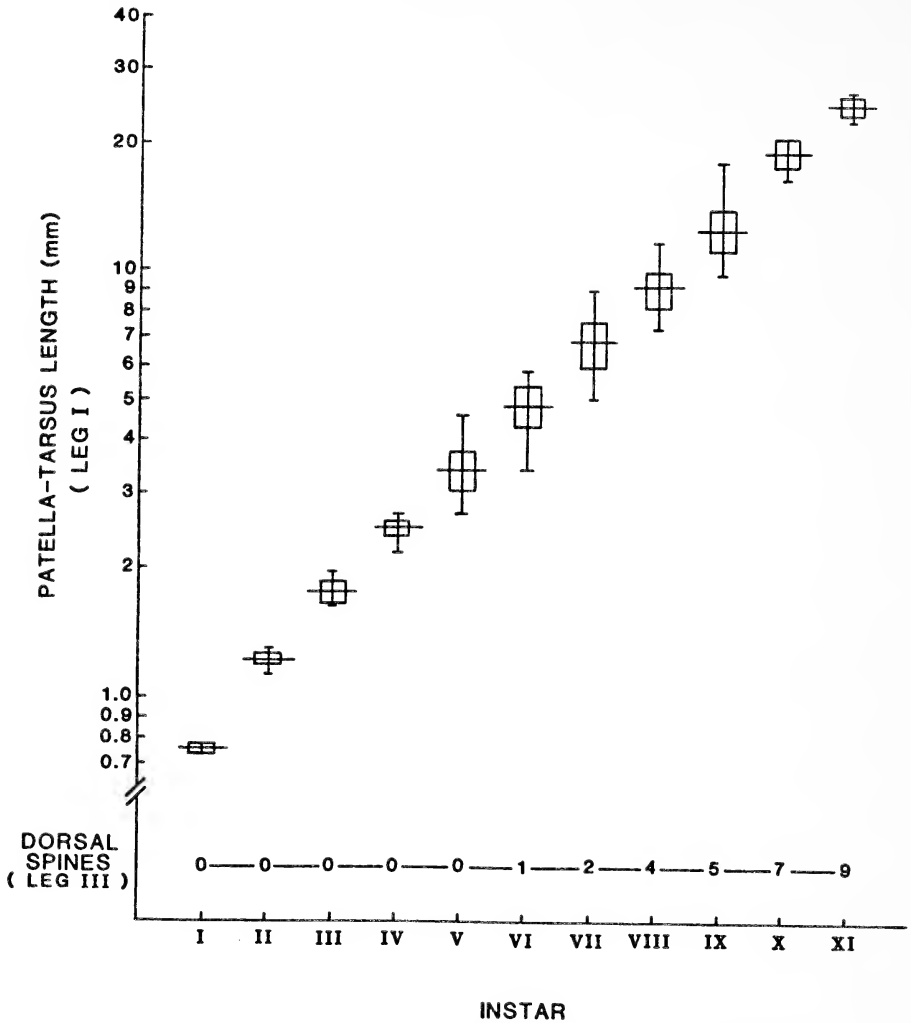
INSTAR

Fig. 1.—Comparison of the various size classes of *Cyrtophora moluccensis* females based on length of leg I and the number of dorsal spines on leg III. The vertical line represents the range, the horizontal line represents the mean, and the box indicates one standard deviation above and below the mean. The dorsal spine count indicates the maximum number of dorsal spines on either the left or right leg III.

0.003, N = 11). The male instar IV pedipalp tarsi are more enlarged ($\bar{x}$ = 0.18 mm, SD = 0.02, N = 14), being about three times the diameter of their leg I tarsi ($\bar{x}$ = 0.07 mm; SD = 0.003). At instar V the specimens are subadult, with greatly enlarged pedipalps ($\bar{x}$ = 0.57 mm, SD = 0.02, N = 12). Instar VI (49 specimens) were mature males. The carapace width of mature females was almost five times that of mature males (females = 6.5 mm, SD = 0.3; males = 1.3 mm, SD = 0.06).

Age at maturity.—Assuming that the female *C. moluccensis* has 11 instars, it is possible to estimate the age at maturity. Table 3 gives the times of embryonic development and the duration of each instar as determined in the laboratory and in the field. From the time the egg is laid until the female reaches sexual maturity is about four months. Adding the mean time spent in the cocoon (25.4 days) to the 56 and 66 days required for laboratory *C. moluccensis* males to reach

Table 3.—Length of time (days) for each developmental stage of immature females. Lab numbers for the egg indicate days until egg hatches to deutovum. Numbers for field conditions indicate time interval between when the egg was laid and when the instar II spiderlings emerge from the cocoon. Instar I (deutovum) data are from 11 cocoons, representing thousands of hatchlings.

						INSTAR					
	EGG	I	II	III	IV	V	VI	VII	VIII	IX	X
LAB											
Range	9-13	0	9-12	9-14	7-20	8-12	—				
Mean	11.8	3.5	10.5	13.2	13.2	10	20				
SD	1.3	0.7	1.7	1.8	4.6	1.6	0				
N	11	11	4	6	4	3	1				
FIELD											
Range	(← 24-28 →)					8-13	8-14	9-11	8-12	10-16	13-17
Mean	25.4					10.5	12.0	9.2	10.1	13.3	15.2
SD	1.5					2.5	2.2	1.8	1.4	1.9	1.6
N	8	0	0	0	0	2	5	5	12	13	15
ALL											
Mean						10.2	13.3	9.2	10.1	13.3	15.2
SD						2.0	3.6	1.8	1.4	1.9	1.6

maturity yields a value for males from egg to sexual maturity of about three months. Many spiders were followed through the five months of field study, but most of them died or disappeared during the period of observation. This agrees with Lubin (1980) who calculated that the adult female life span was about 3.5 months. Since it appears that the adults of this tropical araneid survive for about one-half year or less, in this respect they do not differ greatly from araneids of the temperate zones. Buskirk (1975) noted that the tropical araneid *Metabus gravidus* (Cambridge) became mature after five-seven months and that very few individuals survive longer than a year. Levy (1980) proposed two categories for spider life cycles: those in which both sexes undergo the same number of molts and mature at approximately the same time, and those where the male has fewer molts and completes his life cycle in a much shorter time than the female. Clearly, *Cyrtophora moluccensis* falls into this second category. Mating between spiders from the same cocoon is unlikely. This makes it necessary for males to mate with females from earlier cocoons, a situation usually possible only in the tropics. Reliable local informants in Yap indicated that the spiders are abundant throughout the year, as they are in New Guinea (Lubin 1980).

Mating.—Although the spiders were observed both day and night, no mating activity was seen earlier than 1100 hours nor later than 1400 hours. Of the 15 different matings seen, the median starting time was 1203 hours and the duration of courtship was 5-90 minutes. On one occasion, 21 males were active around a single female, but only two or three of them attempted to copulate. Usually only one male courted each female. Lubin (1980) reported that males spent more time on the webs of adult females that had just reached maturity than on webs of either last instar females or adult females that had already produced a cocoon, suggesting that females are most attractive during the period just after maturation and before laying the first egg.

Males usually live in a small orb built in the tangle of silk above or near the female's horizontal orb. The first evidence of mating seen is when a male leaves the tangle and moves toward the female's orb-web, entering around the outside

edge or through the orb's mesh and moving onto the lower surface. The male then advances toward the female which is normally in the center of her orb. After a short time (seconds to minutes) of walking about on the underside of the web, he attaches a mating thread (see Robinson and Robinson 1980) which is about 8-10 cm long to the orb and climbs on it. Holding on with legs II and IV, he moves his legs I dorsally until they are below his cephalothorax. He then begins rapidly vibrating the thread with legs III. Blanke (1972) observed similar mating behavior in *Cyrtophora citricola* and determined that the strumming rate was not constant but varied from 10-18 strokes per second. In *C. moluccensis* "strumming" may continue as long as 30-40 seconds. If the female doesn't respond he may move to another position, construct another mating thread, and begin vibrating the new thread. Up to this point the spiders have not touched each other. The female may respond by turning toward him, holding onto the web with her legs III and IV, and make a "beckoning" motion with her legs I and II, and sometimes her legs III. Sometimes the female's legs III touch each other midventrally. If the female responds to the male, he may drop (with a drag line) onto the female, copulate, remain in the mating position for perhaps 10 seconds and then rapidly drop away and land a few cm below her on his dragline. He then leaves the orb and returns to the tangle above the web. Occasionally the female will hold the male in position with her legs III; and after mating, she may wrap him in silk and eat him. On two occasions a female wrapped the male in silk and then threw him to the ground. One of these males was recovered; and after the silk was removed, he then scurried away apparently unharmed. The outcomes of 15 attempted matings were as follows: the male mated and was eaten (5); mated and escaped (4); mated and was thrown to the ground (1); did not copulate but was thrown to the ground (1); or female did not respond to male (4). The movements of the male appeared to be similar to those described by Blanke (1972) and by Robinson and Robinson (1980) for other species of *Cytrophora*.

Egg production.—*Cyrtophora moluccensis* females may mate several times before producing a cocoon. During a 6-day period one female responded several times to a male's courtship behavior, but only on day one of this period did mating appear to be successful. At that time she mated with two males. On day four a male attempted three times to mate with her, but each time he probably was not in the mating position long enough to copulate, although the female seemed receptive. On day five, a male attempted to copulate, and the female responded to his vibration of the mating thread (see Robinson and Robinson 1980); but each time the male dropped away from the female without mating. On day six a male again vibrated a mating thread three separate times, but the female did not respond. On the night following day six, she produced a cocoon.

The time interval between mating and production of a cocoon was observed in five females. The mean time between observed mating and the appearance of a cocoon was 4.4 days (range = 2-8; SD = 2.0), but there was no way to ascertain that the mating observed was the only source of the sperm that fertilized the eggs that were subsequently produced. Lubin (1972) observed one female for which the time between copulation and production of the cocoon was 15 days, but the present study indicated that the time period is somewhat shorter. Although *C. moluccensis* females add cocoons one below another in a string with the newest one at the bottom, the cocoons in a given string may not all be produced by the same female. At night the females frequently roam about through the communal

Table 4.—Time interval between production of successive cocoons for three *Cyrtophora* females.

	#1-2	#2-3	#3-4	#4-5	#5-6	#6-7	Median Interval
	Interval (days) Between Successive Cocoons						
Female A	11	12	14	18	12	25	15.3
Female B	18	22	13	—	—	—	17.6
Female C	17	14	18	—	—	—	16.3
Mean	15.3	16	15	18	12	25	
Range	11-18	12-22	13-18				
SD	3.1	4.3	2.2				

web, displace other females, and may or may not return to their original orb. On one occasion, two marked females, each having made a cocoon that later produced live spiderlings, switched orbs. Several days later each female produced a second cocoon which was attached to the first cocoon produced by the other female. On another occasion, a female moved her cocoon from its original location to another orb at least two meters away. Subrahmanyam (1968) reported that the cocoons suspended in the dome of *C. cicatrosa* did not all belong to the same spider, and only the lowest one was the property of the spider living in the web. Since this phenomenon has now been reported for two species of *Cyrtophora*, perhaps more studies with marked females will show that this practice is widespread.

Six females were observed daily from the time they produced one cocoon until they produced another cocoon. Of these, two were followed from the beginning of their maturity until they had produced their second cocoon. The mean time between first and second cocoons was 14.6 days (range = 10-23; SD = 4.2). One marked female was followed through the production of seven cocoons before she died: the mean time between successive cocoons was 15.3 days (Table 4). Lubin (1980) found that in New Guinea the average interval between successive cocoons was 27.0 days, almost twice the average time found for the Yap females. Whether this difference is environmental or genetic is not known.

Production of the cocoon began at about 2200-2400 hours and usually took about four hours. The female first formed in the center of her orb an inverted shallow disc of silk (in the shape of a "Frisbee"), filled it with eggs, and then covered it with silk, first with white silk and then with green silk. The cocoon was then cut free from the orb and attached by a silk "stalk" to the network of threads of the dense snare web above the orb. The female remained with the cocoon, usually with her legs III and IV touching it, until it hatched or until another cocoon was added below the first one.

On Guam, Sabath et al. (1974) found that two cocoons contained 1400 and 1850 developing eggs. A count of 11 cocoons from Yap showed a mean number of 1250 eggs per clutch (range 846-1834). In New Guinea, Lubin (1980) found cocoons containing 877 ± 299 eggs. As with the average time interval between successive cocoons, these differences in number of eggs per cocoon could result from either environmental or genetic causes. Although I made no detailed study of the number of eggs in sequential cocoons from the same female, later cocoons, appeared to contain as many eggs as earlier cocoons. In undamaged cocoons, virtually 100% of the eggs hatched, completed the molting from deutovum to instar II, and the spiderlings left the cocoon.

Hatching.—The eggs from the 11 opened cocoons in glass vials hatched into the deutovum in 9-13 days (Table 3). At this instar, lasting 3-5 days ($\bar{x}$ = 3.5, SD = 0.7, N = 11), the spiderlings have no functional mouthparts or setae. The deutovum (instar I) molts into the characteristic spider form, instar II. Under field conditions the mean time from egg laying to emergence from the cocoon was 25.4 days (range = 24-28; N = 8). This means the spiderlings had been at instar II for about 10 days when they left the cocoon. Only once were spiderlings observed leaving an undisturbed cocoon. At 1345 hours they were exiting, one after another, through a small rent in the cocoon.

"Nursery web".—After leaving the cocoon, the spiderlings form a tangle of threads or "nursery web" approximately 0.5 meters above the ground and remain there for an average of six days (field = 4-6, N = 7; lab = 5-7, N = 4). They do not capture prey while in the nursery web. These tangled webs are known for many species of spiders, but little has been written about their possible function. Gertsch (1949) shows a cluster of spiderling orb weavers preparing to disperse. In a controlled environment room at high humidity, the spiderlings had a very high mortality unless misted daily with an atomizer, yet in the natural environment they survive without either rain or dew. In the laboratory they were seen to move toward and drink small droplets of water caught in the tangled threads of the nursery web.

When disturbed these spiderlings exhibited a synchronous twitching activity which was observed both in the field and in the laboratory. It appeared that a large percentage of the individuals in the web plucked simultaneously at the web at intervals of about 1-5 seconds and continued for up to 12 seconds. Further studies on the behavioral ecology of spiderlings in the nursery web would be valuable. In view of the report by Smith and Mommsen (1984) of pollen feeding in spiderlings, it would be worth investigating the possible function of the nursery web as a pollen collecting structure.

After leaving the nursery web, the spiderlings move up into the communal web and build their own dome-shaped orbs within the tangle of threads supporting the orbs of the larger individuals. Again, only once was an undisturbed cluster of spiders seen leaving a nursery web. At 1930 hours the nursery web seemed to be full, but a few individuals were seen moving out of the nursery web and into the communal web above. By 2145 hours the nursery web was nearly empty, and small spiders were seen attached to twigs and threads of the communal web. The next day there was a noticable increase in the number of small orbs, each about 6 cm in diameter, around the large female web (about 1 meter in diameter) above the former nursery web. Although I observed no ballooning in *C. moluccensis*, Blanke (1972) found *C. citricola* spiderlings over 100 meters from the nearest colony, indicating that ballooning may have occurred.

ACKNOWLEDGMENTS

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A REVISION OF THE AMERICAN SPECIES OF THE ANTLIKE JUMPING SPIDER GENUS *SYNAGELES* (ARANEAE, SALTICIDAE)

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ABSTRACT

The American members of the antlike salticid genus *Synageles* are revised. *Synageles* species may be distinguished from other antlike salticids by the unique configuration of the genitalia. Other distinguishing characteristics are the spination of the tibia of the first legs, small size, flat appearance, waving of the second pair of legs, and the ultrastructure of the white body scales. In the New World this genus ranges from Canada to southern Mexico and the Bahamas. It is the only genus of antlike salticids restricted to the holarctic. The status of *Gertschia* is changed to that of a subgenus. The seven New World species are: *Synageles* (*Gertschia*) *bishopi* new species, *S.* (*G.*) *mexicanus* new species, *S.* (*G.*) *noxiosa* (Hentz). *Synageles* (*Synageles*) *canadensis* new species, *S.* (*S.*) *idahoanus* (Gertsch), *S.* (*S.*) *leechi* new species, and *S.* (*S.*) *occidentalis* new species.

INTRODUCTION

The genus *Synageles* was established by Simon for the Palearctic *Attus venator* Lucas (Simon 1876). Various American antlike salticids have been placed in the genus at various times and in 1945 Kaston established *Gertschia* for Hentz's *Synemosyna noxiosa*. Cutler (1970) further compounded the confusion in an unpublished doctoral thesis by lumping *Synageles* with *Peckhamia* in the genus *Consingis*. Since that time I have seen more specimens from North America and Europe. Thaler (1983) published a review of middle European *Synageles* with excellent illustrations, which helped clear up ambiguities concerning some European species not available to me.

The relationships of *Synageles* to other salticid genera are obscure. This is a recurring problem in the Salticidae. It is clear that the genus *Synagelides* bears at best only a superficial resemblance to *Synageles*, as judged by the illustrations in Bohdanowicz (1978, 1979), Bohdanowicz and Heciak (1980) and Proszynski (1979). Possible candidates for related genera are the New World antlike salticids *Peckhamia, Semora* and *Semorina* based on morphological and behavioral characteristics, but a firm relationship is premature at this time.

In the search for additional characters for use in inferring relationships among salticids, several authors (Cutler 1981b, 1982; Galiano 1975; Wanless 1978a,c) have examined the ultrastructure of the modified setae called scales. The most comprehensive study of salticid scales was done by Hill (1979), but only one species of antlike salticid was included in his study. The scales in *Synageles*, as in all antlike salticids I have examined (12+ genera), are pale colored in life or in

alcohol, and confined to three body areas. They occur as a band or patches between the row three eyes, as a narrow band or patch below the row three eyes on the side of the prosoma, and as paired patches on the anterior portion of the opisthosoma (rarely as a continuous band) where the opisthosoma is narrowed. Not all species examined have these scales, but in the genera examined, scales are present in at least one member of each genus. In this regard, the scales may become a useful character for comparative analysis. The presumed function of the scales is to act as an accentuating feature of the illusion in creating a narrow "wasp waist" (more exactly an "ant waist"), contributing to the antlike appearance of the spider.

I examined the scales of both sexes of *Synageles*; *(G.) bishopi*, *S. (G.) mexicanus*, *S. (G.) noxiosus*, *S. (S.) occidentalis* and *S. (S.) venator*. Scales of *S. (G.) mexicanus* are illustrated; prosomal (Fig. 2) and opisthosomal (Fig. 3). Similar scale morphology occurs in the American antlike salticid genera *Erica, Peckhamia* and *Synemosyna* (Cutler 1985). *Maevia* and *Marpissa* have scales which resemble these (Hill 1979, fig. 15), but the genitalia in these two genera are very different from those of the antlike salticids mentioned.

BEHAVIOR

Most antlike salticids elevate the first pair of legs in a convincing imitation of ant antennae (Reiskind 1977), but *Synageles* and *Peckhamia* utilize the second pair for this purpose. I have observed this in *S. (G.) noxiosus* and *S. (S.) occidentalis* in both sexes, and Engelhardt (1970) observed it in *S. (S.) venator*. Second leg elevation has been observed in species of other antlike salticid genera, but is rare. It occurs in a species of *Sarinda* (Jackson and Drummond III 1974), and E. Peckham (1889) noted the same for *Synemosyna formica* (Hentz). However, I have watched many *Synemosyna formica* of both sexes from Minnesota, New Jersey and New York, and in all cases the first pair of legs was used. Thus, except for sporadic occurrences in other genera, this behavior appears to be characteristic of *Synageles* and *Peckhamia*. Mating behavior has been noted in a few species of both subgenera and is similar in all species (Crane 1949; Cutler 1970; Engelhardt 1970; Richman 1982). Males display before females by lowering the front legs to the side or in front of the body, and the opisthosoma is lowered and elevated, or elevated and waved from side to side.

ANT RESEMBLANCE

There are many species of ants that occur in the same habitat as *Synageles*. However, the greatest similarities in size and coloration between adult *Synageles* appear to be with worker ants of the genera *Crematogaster* (G. B. Edwards *in litt.*), *Lasius* (Engelhardt 1970) and *Myrmica* (Cutler 1970). Ants are well known as unpalatable prey for many predators and have many supposed mimics (Wickler 1968). Few of these supposed spider—ant mimicry associations have been tested. I found that *S. (S.) occidentalis* appears to be protected to a certain extent from predation (Cutler 1970, to be published elsewhere), and Reiskind (1977) gives detailed behavioral and morphological reasons for considering certain antlike spiders in Panama as being mimics. It should be noted that there are

specialized ant predators among both the vertebrates and the invertebrates, so ant mimesis is not completely protective. *Synageles* have very small egg sacs, three or four eggs per sac (Cutler 1970; Engelhardt 1970). This has been generally cited as a result of the protective nature of ant mimesis. However, Wayne Maddison (*in litt.*) noted serial egg sacs in *S. (G.) noxiosus* from Ontario. One female made seven sacs, and the other possibly eight, certainly seven. I have observed in the small salticid *Talavera minuta* (Banks) egg sacs with two or three eggs, and this species is not antlike. The small number of eggs per sac probably results from the small size of the spider, and the necessity for the egg to be a certain size. The number of serial egg sacs functions to increase the total egg numbers per female.

GENITALIC MORPHOLOGY

The Salticidae are notorious for having simplified male external genitalia, and male *Synageles* have a simple palpus compared to most other members of the family. As may be seen by the illustrations in this paper and those of Thaler (1983), the only clear characteristics are the form of the tube-like embolus, and the shape of the tibial apophysis. The internal embolic tubes of the bulb are not visible, as they are in many salticids.

Females have a typical epigynal structure for the family. Distinguishing North American species of the genus ultimately depends on the shape of the internal ducts, although the posterior margin of the epigynum and the position of the external openings provide important clues.

Male *Synageles* have a large modified seta at the distal end of the cymbium (Fig. 4). Similar setae are found in other salticid genera, and the function is not known.

SUBGENERA

Three New World species form a compact group, *S. bishopi, S. mexicanus* and *S. noxiosus*. While they are clearly *Synageles*, they are obviously closely related and differ from the other members of the genus in genitalic features. There exists the name *Gertschia* for this group, and two subgenera are erected in this paper, *Gertschia* for these species, and *Synageles* for all other species. Details are given later in this paper.

POSSIBLE ALLOMETRIC CHARACTERS

One of the classic criteria used by Simon (1901) in his higher classification of salticids was the number and type of retromarginal cheliceral teeth. Many authors have subsequently commented on the variability of this feature in genera and species. Kaston (1945) discussed this in regard to *Synageles* (as *Gertschia*). In the American members of the subgenus *Synageles* this retromarginal tooth is most often single and simple, but sometimes single and bicuspid (fissident). However, in the subgenus *Gertschia* there may be one, one bicuspid, or two or three teeth. Smaller specimens of *S. (G.) noxiosus* including most males, usually have a single simple tooth on each chelicera, females often have a single bicuspid tooth. In *S. (G.) bishopi* both sexes usually have a single bicuspid tooth. The largest species of
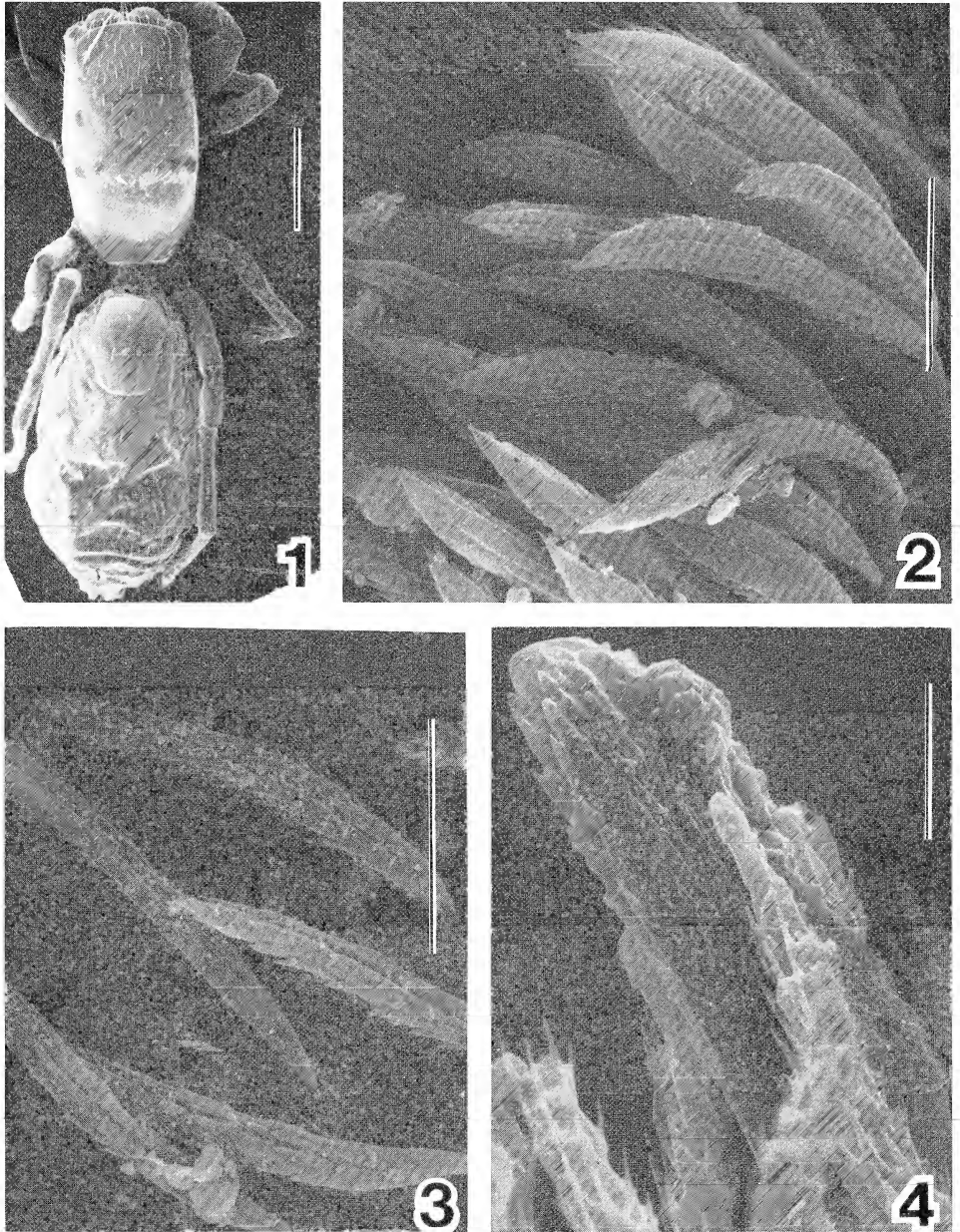
Figs. 1-4.—*Synageles* dorsal view and seta morphology: 1, dorsal view, female *S. (S.) noxiosus* 2-4; 2, *S. (G.) mexicanus* prosomal white scales, female; 3, opisthosomal white scales, female; 4, enlarged seta at distal tip of cymbium (large dark seta in center of micrograph), male. Scale lines: fig. 1=500 μm; figs. 2,3 = 25 μm; fig. 4 = 5 μm.

the genus *S. (G.) mexicanus*, often has two or three teeth on each chelicera. Another size trend in *Gertschia* concerns features of the male palpus. In small male *S. (G.) noxiosus* the embolus is relatively short and moderately curved and the cusps of the tibial apophysis are relatively short (Figs. 20 & 21). In the large male *S. (G.) mexicanus* the embolus is relatively longer with a sweeping curve, and the cusps of the tibial apophysis are long (Figs. 14 & 15). Also *S. (G.)*
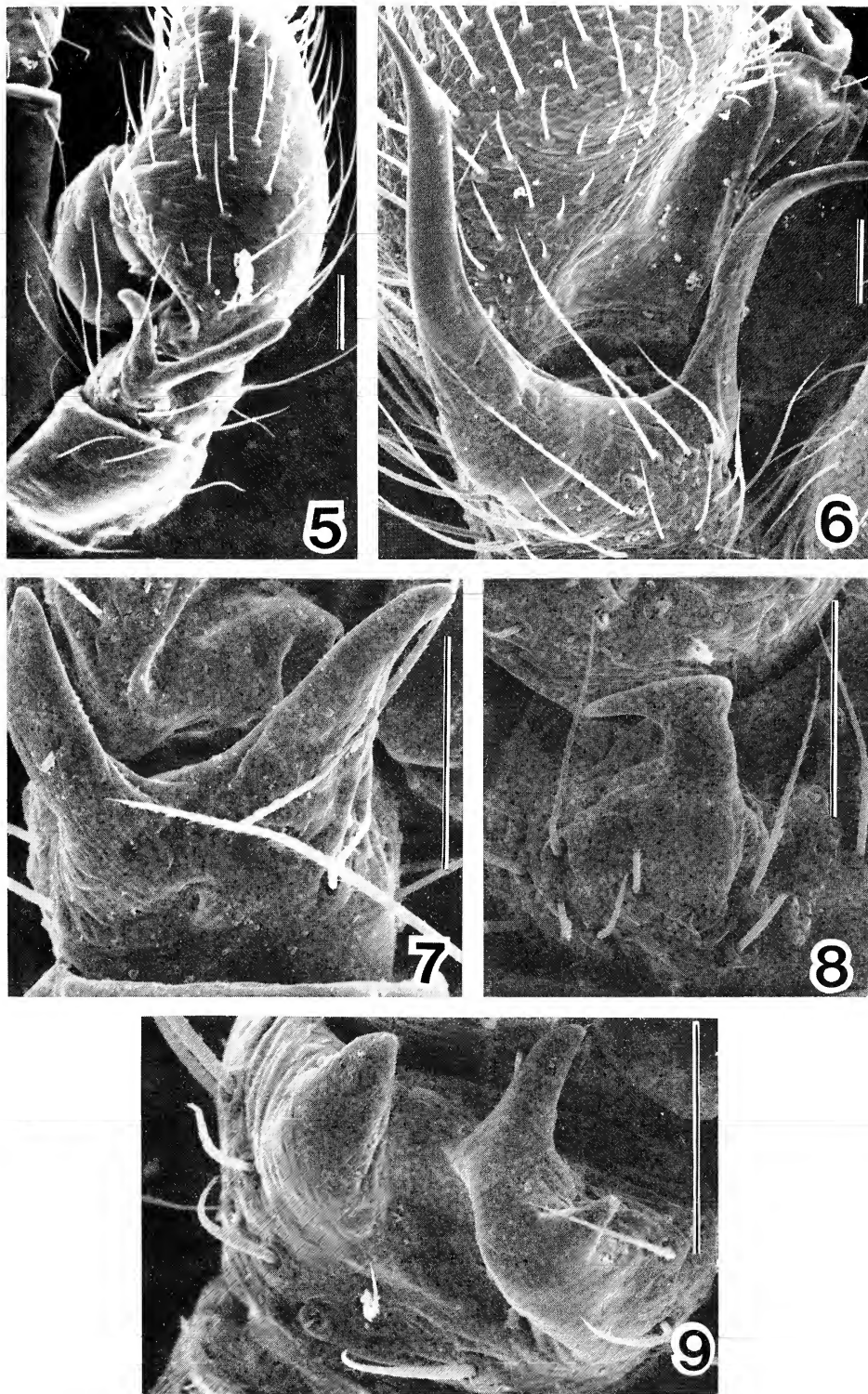
Figs. 5-9.—Male palpal tibial apophyses: 5, *S. (G.) bishopi*; 6, *S. (G.) mexicanus*; 7, *S. (G.) noxiosus*; 8, *S. (S.) venator*; 9, *S. (S.) occidentalis*. Scale = 50 μm.

mexicanus have three pairs of tibial spines on leg I, all other members of the genus have two pairs. In the southwestern United States where *S. (G.) mexicanus* occurs, the few *S. (G.) noxiosus* known are small for the species. It is possible that character displacement in regard to size is taking place, but to establish this requires more specimen material.

NATURAL HISTORY

Synageles are most often collected sweeping grasses and herbaceous vegetation, although they are known from other habitats as well; see the species descriptions for details. The European species occur in the same environment (Bristowe 1958; Engelhardt 1970), although some reports indicate a ground living habitus (Brignoli 1984; Thaler 1983). Life histories have been investigated only sketchily in a few American species; Cutler (1970) provides general details. The primary difficulty in doing life history studies on small salticids is in finding suitable small food items for the young instars. Wayne Maddison (*in litt.*) did have some success in rearing *Synageles* by using Collembola, but it is a very time-consuming process. The most thorough life and natural history was done by Engelhardt (1970) using the European *S. (S.) venator*. Field studies on *Synageles* are even fewer. Abraham (1983) collected numbers of *Synageles* sp. immatures in Utah from the herb, shrub and ground layers in a sagebrush steppe community. Three quarters of the specimens were from the shrub layer, one quarter were from the herb layer, and none were found on the ground.

GENERAL DISTRIBUTION

Synageles contains species which have the most northerly distribution of any antlike salticid. In the Palearctic, *Synageles* reaches the British Isles, southern Scandinavia, and extends through Siberia. The southern range is from the Mediterranean Coast of Africa, through the Middle East and the Central Asian Provinces of the USSR to the Vladivostok area (Proszynski 1976). The northernmost record is from 68°N at Plachino, Yenisey area, Siberia for *S. (S.) venator* (Holm 1973).

In the Americas *Synageles* ranges between southern Canada and southern Mexico. The northernmost record is for *S. (S.) canadensis* at 54°N in British Columbia. The southernmost records are from 17°N in Oaxaca where both *S. (G.) mexicanus* and *S. (G.) noxiosus* occur. Thus the genus has essentially a Holarctic distribution. What is most striking is the distribution of the two subgenera. *Synageles (Synageles)* is found in southern Canada and in the northern Midwest, Rocky Mountain, Great Basin and Pacific Northwest states. *Synageles (Gertschia)* is found in Ontario, the United States exclusive of the areas listed for the nominate subgenus, the Bahamas (Andros), and Mexico. Very little overlap occurs, although both subgenera occur in Ontario, Michigan, and the central and southern part of California. Other possible contact areas are in the central part of the United States westward from Indiana to Nevada, although no joint records are currently available.

There are four species of *Synageles* known from Canada. Only three other species of antlike salticids are known from Canada, *Paradamoetas fontana* (Levi),

Map 1.—General distribution of New World subgenera of *Synageles*. *Synageles (Gertschia)*—solid line; *Synageles (Synageles)*—broken line.

Peckhamia picata (Hentz) and *Synemosyna formica* Hentz. *Paradamoetas* and *Synemosyna* occur only in southern Ontario. *Synageles* not only occurs further north than other genera of antlike salticids, but has a greater diversity in the north than other genera of antlike salticids.

All the other genera of antlike salticids are subtropical or tropical, with or without outliers in the north, eg.: *Myrmarachne*—none in the Nearctic, 10 in Central and South America (Cutler 1981a; Galiano 1969a, 1974), one in Europe, 56 in Africa (Wanless 1978a); *Sarinda*—three in the Nearctic, 14 in Central and South America (Galiano 1965, 1969b); *Synemosyna*—three in the Nearctic, 18 in Central and South America (Cutler 1985; Galiano 1966, 1967).

Genus *Synageles* Simon

Attus Lucas 1836:1.
Salticus C. L. Koch 1837:31 (in part).
Synemosyna Hentz 1850:288 (in part).

Synageles Simon 1876:14; Peckham and Peckham 1889:95 (in part), 1892:59 (in part); Richman and
    Cutler 1979:100; Kaston 1978:248, 1981:952.
Peckhamia Simon 1900:404; Peckham and Peckham 1909:370 (in part); Emerton 1909:233 (in part);
    Gertsch 1934:11.
Gertschia Kaston 1945:16, 1948:450.

Type species.—*Attus venator* Lucas 1836 by subsequent designation (Simon
1876); of *Gertschia, Synemosyna noxiosa* Hentz by subsequent designation
(Kaston 1945).

Description.—Antlike salticids of small size, 2.2-4.8 mm total length. Carapace
flat and low, height from 30-40% length. Ocular quadrangle occupies 65-80%
length of carapace. Eye rows I and III subequal in width. Length of eye field
usually longer than width of widest eye row. Carapace in dorsal view without
constriction, in lateral view with at most a slight declivity behind row III eyes.
Opisthosoma with constriction on anterior part. Male palpus: embolus a spike or
tube, embolic ducts obscure at best in uncleared specimens, with a single
retrolateral tibial apophysis which may be bifid, sometimes with two distinct
apophyses. Epigynum: with two openings leading to convoluted irregular internal
ducts and spermathecae, see illustrations for characteristic shapes and discussions
of subgenera. White scales present in region of row III eyes, and on the
opisthosoma at the sides of the constriction. Scales as viewed by scanning
electron microscopy are: convex and relatively smooth dorsally, sometimes with a
few scattered teeth; a median dorsal groove may be present (shrinkage artifact?).
Color is uniformly dark to light brown, and is not noted in specific descriptions
unless it differs. Legs are pale with pro- and retrolateral dark stripes and
infuscations.

Diagnosis.—There is no single non-genitalic feature that distinguishes *Synageles*
from other salticids. The Peckhams (1892) noted that of all the antlike salticids
only *Synageles* has the ocular quadrangle longer than wide. Their concept of
Synageles at this time included *Peckhamia*. This ratio holds true of most, but not
all, specimens of *Synageles* I have seen. It is also true of most *Peckhamia*. The
only other antlike genus with this ratio is *Sobasina* from the southwest Pacific
(Wanless 1978b). It may also occur in other genera of the Diolenieae (Simon
1901). Ultimately the discrimination of *Synageles* from other antlike salticid
genera depends on the form of the genitalia. In addition, in North America, the
non-genitalic characters of small size, low flat carapace, usually the length of
ocular quadrangle greater than width, and two pairs of ventral spines on leg I
tibia (*S. (G.) mexicanus* has three pair) provide important clues. *Peckhamia* may
be easily confused with *Synageles*, but in *Peckhamia*, the carapace is not as flat,
being more convex in the cephalic area, and has a sharp declivity behind the row
III eyes. Most *Peckhamia* have three pairs of ventral spines on leg I tibia, and the
genitalia are different.

KEY TO NEW WORLD SUBGENERA AND SPECIES
OF *SYNAGELES*

1. Males..2
   Females..8

2. Single bifid palpal tibial apophysis (subgenus *Gertschia*)...................3
   Single non-bifid palpal tibial apophysis, or two separate apophyses
      (subgenus *Synageles*)...5

3. Three pairs of ventral spines on tibia I, two or more retromarginal
      cheliceral teeth...*mexicanus*
   Two pairs of ventral spines on tibia I, a single retromarginal
      cheliceral tooth..4

4. Dorsal cusp of tibial apophysis 1.5-2 times length of
      ventral horn...*bishopi*
   Cusps subequal in length................................*noxiosus*

5. Two tibial apophyses, one is bifid...........................*occidentalis*
   Single palpal tibial apophysis...................................6

6. Embolus points distally, base of embolus not swollen............*canadensis*
   Embolus points to side at about a 30° angle to the wide axis of the
      cymbium..7

7. Base of embolus bulges convexly above long axis of
      embolus (Fig. 33)...*idahoanus*
   Base of embolus while enlarged, does not protrude above long axis of
      embolus (Fig. 37)...*leechi*

8. Epigynal openings medial, leading to laterally directed ducts, at the
      end of ducts are compact coiled spermathecae (subgenus *Gertschia*).......9
   Epigynal openings not medial (subgenus *Synageles*)...................11

9. Three pairs of ventral spines on tibia I, two or more retromarginal
      cheliceral teeth...*mexicanus*
   Two pairs of ventral spines on tibia I, a single retromarginal
      cheliceral tooth..10

10. Posterior margin of epigynum with a broad single notch; internal
      details as in Fig. 13.......................................*bishopi*
   Posterior margin of epigynum smooth, or with two small notches;
      internal details as in Fig. 24.............................*noxiosus*

11. Posterior margin of epigynum with a single medial notch; internal
      details as in Figs. 42, 44.................................*occidentalis*
   Epigynum without a medial notch..................................12

12. Epigynum with posterior margin a flap overhanging epigastric furrow,
      flap with two ovoid lunules; internal details as in Fig. 32........*canadensis*
   Posterior margin of epigynum with two shallow lobes, internal details
      as in Fig. 36...*idahoanus*

Where series were available the minimum distance between the row III eyes was taken for comparison. The reason for choosing this distance is that it is easy to determine and to measure using an ocular micrometer. The more familiar prosomal length measurement in *Synageles* requires special manipulation, because the opisthosoma usually overhangs the prosoma. The spination notation used refers to the ventral spines of the metatarsus and tibia. The numbers separated by dashes refer to prolateral and retrolateral pairs, with the most proximal listed

first, eg.: 1,0-0,1 means a proximal prolateral spine and a distal retrolateral spine; 1,1-1,1 means proximal prolateral and retrolateral spines with distal prolateral and retrolateral spines. All measurements are in millimeters.

Synageles (Gertschia), new subgeneric status

Gertschia was proposed as a new genus by Kaston (1945). Richman and Cutler (1978) considered *Gertschia* as a synonym of *Synageles.* It is proposed here that *Gertschia* be retained as a subgenus of *Synageles* to define a small group of three closely related Nearctic species derived from *Synageles (Synageles).* Speculatively, it may be derived from some *Synageles (Synageles)* species which was isolated in the southwestern United States—northwestern Mexico during some Pleistocene glacial episode.

Diagnosis.—*Gertschia* includes those species of *Synageles* which in the males have a distal bifurcate palpal tibial apophysis, with the cusps extending distally and the greatest width in a dorso-ventral plane. The embolus is thin and distinctly curved, with a length-width ratio 10:1 or more (Figs. 10, 14, 18). Females have a distinctive epigynum with the two openings situated medially, and opening to short tubes extending laterally to compact coiled spermathecae, the spermathecae being well removed from the posterior margin of the epigynum (Figs. 13, 17, 24).

Type species.—*Synageles (Gertschia) noxiosus* (Hentz).

Included species.—*S. (G.) bishopi* n. sp., and *S. (G.) mexicanus* n. sp..

Geographic range.—Mexico: Oaxaca to the southern U.S., north along the west coast of the U.S. to the San Francisco Bay area, and in the Mississippi River region from Kansas northeast to Ontario and Massachusetts, and in the Bahamas.

Synageles (Gertschia) bishopi, new species
Figs. 5, 10-13; Map 2

Synageles scorpiona [lapsus for *scorpionia*]: Peckham and Peckham 1889, 95-96, pl. 6, fig. 72, female; Peckham and Peckham 1892:63, pl. 5, fig. 1d, female [not *Synemosyna scorpionia* Hentz 1845].
Peckhamia scorpiona: Peckham and Peckham 1909, 370-371, pl. 50, fig. 3, female only.
?*Peckhamia scorpionia* Emerton 1909, pl. 12, figs. 6-6a [genitalia not illustrated].

Etymology.—Named after Sherman C. Bishop, arachnologist (and herpetologist) from the eastern United States in the first half of the twentieth century.

Diagnosis.—Sympatric with *S. (G.) noxiosus* in the eastern half of the United States. Males may be distinguished from *S. (G.) noxiosus* by the long, dorsal retrolateral cusp of the palpal tibial apophysis, which is from 1.5-2 times the length of the ventral retrolateral cusp. In *S. (G.) noxiosus* the cusps are subequal in length. Females have a broad single notch on the posterior margin of the epigynum, and the orientation of the internal epigynal tubes is different from that in *S. (G.) noxiosus.*

Description.—*Male holotype:* Total length 2.6. Prosoma 1.19 long, 0.75 wide. Eye field 0.84 long, eye row I 0.58 wide, eye row III 0.57 wide, distance between row III eyes 0.47. Distance eye row II from eye row I 0.18, eye row II from eye row III 0.40. Diameter AME 0.20, ALE 0.10, row II eye 0.03, row III eye 0.10. Femur length leg I 0.72, II 0.53, III 0.50, IV 0.73. Leg order 4123. Leg spination,
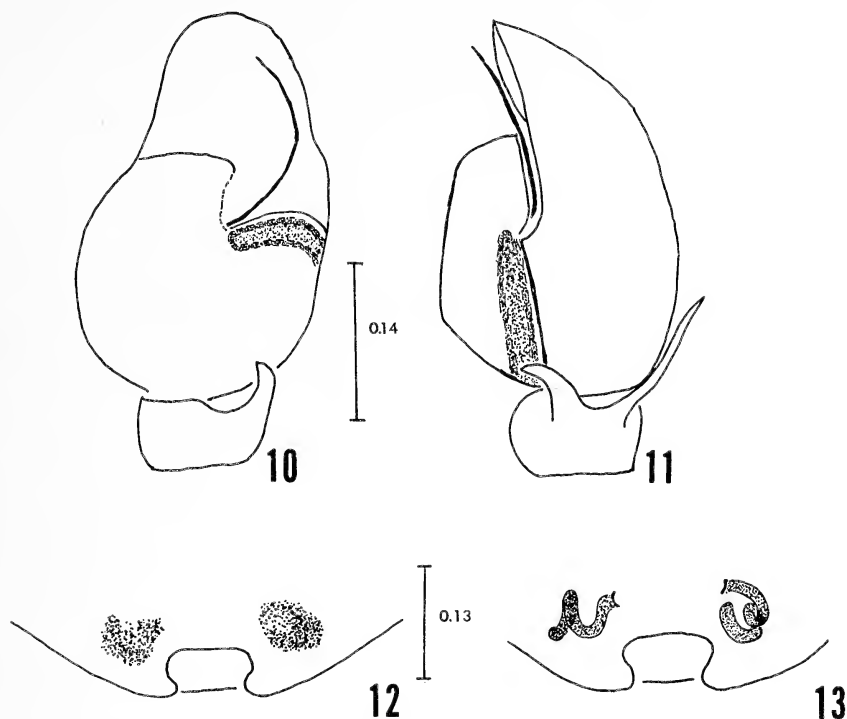
Figs. 10-13.—*S. (G.) bishopi*: 10-11, male palpus; 10, ventral; 11, retrolateral; 12-13, female epigynum; 12, external; 13, internal. Scale in mm.

I metatarsus 1,1-1,1 tibia 1,0-1,1: II metatarsus 1,1-1,1 tibia 0,0-0,1. Fissident bicuspid retromarginal cheliceral teeth. Opisthosoma 1.4 long, 0.8 wide. Color typical for genus.

Distance between row III eyes in 17 males, mean 0.43, SD 0.06, range 0.39-0.55.

Female from Tennessee: Roane Co., Kingston, 3 June 1966 (B. Moulder), on carport (BM). Total length 3.21. Prosoma 1.36 long, 0.80 wide. Eye field 0.88 long, eye row I 0.69 wide, eye row III 0.69 wide, distance between row III eyes 0.60. Distance eye row II from eye row I 0.24, eye row II from eye row III 0.52. Diameter AME 0.22, ALE 0.11, row II eye 0.02, row III eye 0.11. Femur length leg I 0.53, II 0.50, III 0.50, IV 0.71. Leg order 4312. Leg spination, I metatarsus 1,1-1,1 tibia 1,1-1,0; II metatarsus 1,1-1,1 tibia 1,0-0,0. Fissident bicuspid retromarginal cheliceral teeth. Opisthosoma 1.8 long, 1.0 wide. Color typical for genus.

Distance between row III eyes in 16 females, mean 0.50, SD 0.04, range 0.39-0.57.

Discussion.—This species is both sympatric and synchronic with *S. (G.) noxiosus* from the Plains States east to the Atlantic Seaboard. Both species are essentially the same size, and occupy what appears to be similar habitats based on label data. Habitats are: on bark of ponderosa pine, on elm tree, on fence and bushes by stream in forest, in grass and litter of old yard, under logs on gravel, in house, and on side of house. Adults have been collected from March to July, October and December. Most were collected from May to July.
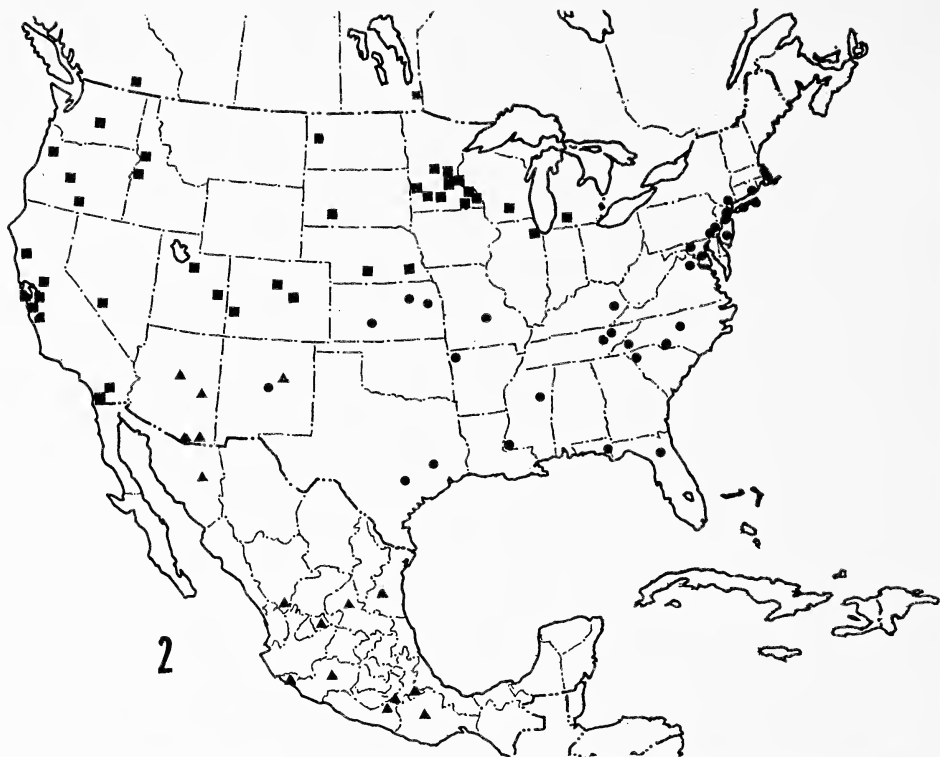
Map 2.—Distribution of *S. (G.) bishopi*—circle; *S. (G.) mexicanus*—triangle; *S. (S.) occidentalis*—square.

Distribution.—*Holotype locality:* U.S.A.: PENNSYLVANIA; *Bucks Co.,* Horseshoe Bend, Neshaminy Creek, NE of Jamison June 1956 (W. Ivie), male (AMNH).

Paratype localities: U.S.A.: FLORIDA; *Alachua Co.,* Gainesville, December 1952 (VIC), female (AMNH): KENTUCKY; *Breathitt Co.,* Quicksand, 27 June 1925 (S. C. Bishop), female (AMNH): MARYLAND; *Washington Co.,* Hagerstown, 9 June 1914 (J. A. Hyslop), female (MCZ): MASSACHUSETTS; *Barnstable Co.,* Woods Hole, 13 July 1901 (H. W. Britcher), male (AMNH): MISSISSIPPI; *Wilkinson Co.,* Centreville, January-July 1944 (A. F. Archer), male (AMNH): NEW JERSEY; *Bergen Co.,* Englewood, 15 June 1939, female (AMNH), Ramsey, 17 June 1934, (W. J. Gertsch), female (AMNH); *Essex Co.,* W. Caldwell, 25 May 1935 (W. A. Strever), male (AMNH); *Ocean Co.,* Lakehurst and Absecon, male (AMNH): NEW YORK; *Nassau Co.,* Seacliff (N. Banks) (155), males, females (MCZ); *Suffolk Co.,* Cold Spring Harbor, 25 June 1903, male, female (AMNH), 8 July 1907 (E. B. Bryant), female (MCZ), Riverhead, 12 July 1949 (R. Latham), male (AMNH); *Westchester Co.,* Yonkers, 20 March 1935 (Woodbury), male (AMNH): NORTH CAROLINA; *Guilford Co.,* Greenshore, 2 June 1949 (E. E. Brown) (130), male (AMNH); *Mecklinburg Co.,* Davidson, 3 May 1949 (E. E. Brown) (253), male (AMNH): PENNSYLVANIA; same data as holotype, male (AMNH): SOUTH CAROLINA; *Oconee Co.,* Clemson, W 82.50 N 34.41, June 1961 (J. A. Payne), male (AMNH): VIRGINIA; *Falls Church Co.,* Falls Church, (N. Banks) (154), female (MCZ).

Other localities: U.S.A.: ARKANSAS; *Benton Co.:* CONNECTICUT; *New London Co.:* FLORIDA; *Liberty Co.:* KANSAS; *Douglas Co.; Pawnee Co.; Riley Co.:* MARYLAND; *Prince Georges Co.:* MASSACHUSETTS; *Plymouth Co.; Suffolk Co.:* MISSISSIPPI; *Okitebbeha Co.:* MISSOURI; *Phelps Co.:* NEW MEXICO; *Bernalillo Co.:* NORTH CAROLINA; *Buncombe Co.:* PENNSYLVANIA; *Philadelphia Co.:* TEXAS; *Bastrop Co.; Walker Co.:* TENNESSEE; *Claiborne Co.*

Synageles (Gertschia) mexicanus, new species
Figs. 2-4, 6, 14-17; Map 2

Etymology.—Named after Mexico, the country of origin of the holotype.

Diagnosis.—The largest species of the genus in the New World, has three pairs of ventral spines on tibia I, and pleurident retromarginal cheliceral teeth. Males have long palpal tibial apophyses, the length of the ventral, retrolateral cusp of the apophysis is at least 50% (usually 60%) of the cymbium length. In the other two species of *Synageles (Gertschia)*, this ratio is rarely 40%, usually around 33% or less. Females have large epigynal openings, densely sclerotized internal epigynal tubes, and a broad shallow flap overhanging the epigastric furrow.

Description.—*Male holotype*: Total length 3.5. Prosoma 1.68 long, 1.23 wide. Eye field 1.04 long, eye row I 0.84 wide, eye row III 0.95 wide, distance between row III eyes 0.80. Distance eye row II from eye row I 0.34, eye row II from eye row III 0.56. Diameter AME 0.28, ALE 0.18, row II eye 0.05, row III eye 0.15. Femur length leg I 1.02, II 0.74, III 0.73, IV 0.98. Leg order 4123. Leg spination I metatarsus 1,1-1,1 tibia 1,1,1-1,1,1; II metatarsus 1,0-1,1 tibia 1,1,0-1,1,1. Two retromarginal cheliceral teeth. Opisthosoma 1.9 long, 1.0 wide. The overall appearance is that of an orange spider, not the usual brown typical of the genus.

Distance between row III eyes in 23 males, mean 0.78, SD 0.10, range 0.57-1.07.

Female paratype from MEXICO: MORELOS; Palo Bolero (AMNH). Total length 4.7. Prosoma 1.9 long, 1.25 wide. Eye field 1.18 long, eye row I 1.02 wide, eye row III 1.18 wide, distance between row III eyes 0.98. Distance eye row II from eye row I 0.36, eye row II from eye row III 0.64. Diameter AME 0.34, ALE 0.20, row II eye 0.05, row III eye 0.20. Femur length leg I 0.99, II 1.01, III 0.87, IV 1.35. Leg order 4213. Leg spination I metatarsus 1,1-1,1 tibia 1,1,1-1,1,1; II metatarsus 1,0-1,0 tibia none. Three retromarginal cheliceral teeth. Opisthosoma 2.9 long, 1.4 wide. Color as in male.

Distance between row III eyes in 15 females, mean 0.77, SD 0.10, range 0.53-0.98.

Discussion.—As the largest New World species, certain allometric trends become evident in *S. (G.) mexicanus*. This species has plurident retromarginal cheliceral teeth, as opposed to the usual bicuspid fissident teeth in the subgenus, and some specimens have three teeth. This is the only species with three pairs of ventral tibial spines on leg I, the usual number is two pairs. In the male the tibial apophysis is proportionately longer than in other species, and the sclerotized portion of the embolus is also proportionately longer. The tips of the male palpal tibial apophyses are often broken, but no broken tips were observed in the female epigynal openings, or along the posterior margin of the epigynum.

Distribution.—*Male holotype locality:* **MEXICO:** DURANGO; 40 miles NE of El Salto, 11 August 1957 (W. J. Gertsch), male, (AMNH).

Paratype localities: **MEXICO:** AGUASCALIENTES; 7.5 miles N of Tepezala, W 102 N 22, 30 August 1965 (Gertsch and Hastings), 3 males, 3 females (AMNH): COLIMA; 5 miles N of Colima, 3 August 1956 (V. Roth and W. J. Gertsch), male (AMNH), 7 miles S of Colima, 2 August 1956 (V. Roth and W. J. Gertsch), female (AMNH): MICHOACAN; 3 miles NE of Patzcuaro, W 101.35 N 19.33, 5 September 1966 (J. and W. Ivie), 13 males (AMNH): MORELOS; Alpoyeca, 28 July 1956 (W. J. Gertsch and V. Roth), female (AMNH), Cuernevaca, 27 July 1956 (V. Roth and W. J. Gertsch), male, 3 females (AMNH): PUEBLA; Tehuacan, 24 July 1956 (W. J. Gertsch and V. Roth), 3 females
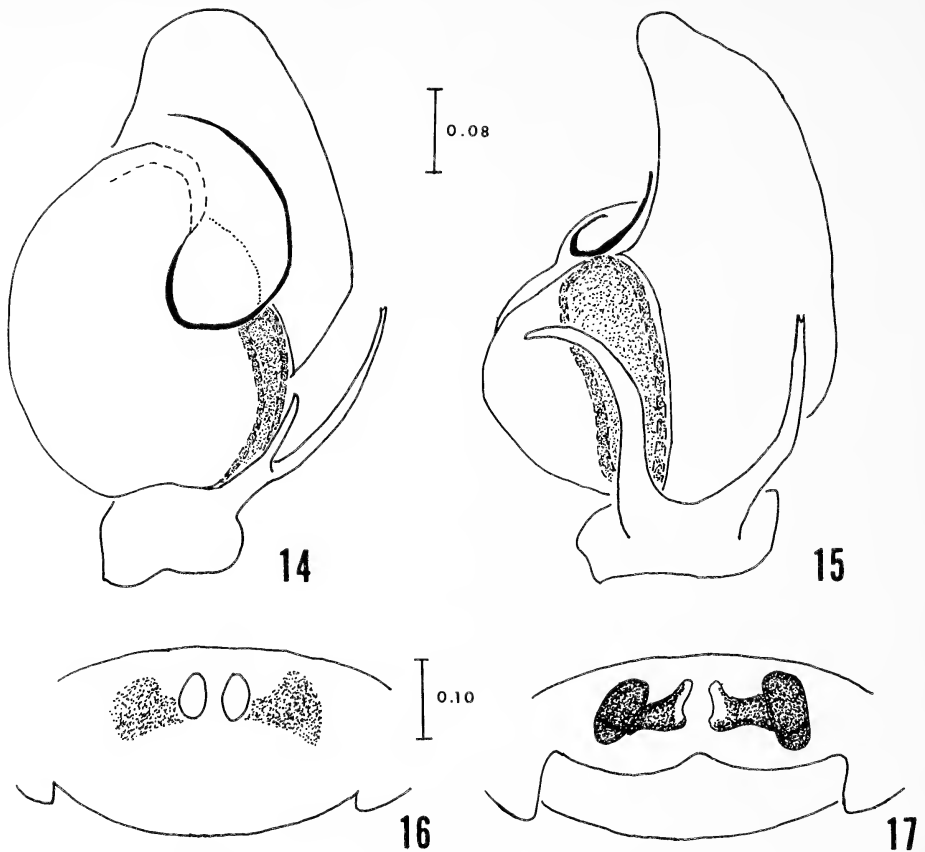
Figs. 14-17.—*S. (G.) mexicanus*: 14-15, male palpus; 14, ventral; 15, retrolateral; 16-17, female epigynum; 16, external; 17, internal. Scale in mm.

(AMNH). **U.S.A.:** ARIZONA; *Cochise Co.*, Garden Canyon, Huachuca Mts., 22 July 1950 (W. S. Creighton), male (AMNH).

Other localities: **MEXICO:** GUERRERO; Taxco, 15 August 1943 (Boliva, Pelaez, Osorio), female (AMNH): MORELOS; Acatlipa, 10 August 1946 (Goodnight, Bolivar, Bonet), female (AMNH): OAXACA; El Catrin, W 96.57 N 17.21, 3 September 1964 (J. and W. Ivie), male (AMNH): SAN LUIS POTOSI; Charcas, July 1934 (Chickering ?), male (MCZ), 7 July 1934 (Chickering ?) male (MCZ): SONORA; Baviacora, 15-20 km E, 110°05′W 20°43′N, 6 August 1983 (V. and B. Roth), male (AMNH): TAMAULIPAS; Victoria, 17 May 1957 (M. Cazier, W. J. Gertsch, R. Schrammel), 3 females (AMNH). **U.S.A.:** ARIZONA; *Coconino Co.*, Lakeview Campground, Lake Mary (7200 feet), 15 June 1974 (C. E. Griswold and R. Jackson), female (CB); *Gila Co.*, 6 miles SW of Whiteriver [Whiteriver is in *Navajo Co.*] (5300 feet), 2 August 1936 (H. H. Poor and F. G. Watson), male (AMNH); *Santa Cruz Co.*, San Rafael Valley, 2 miles E of Patagonia, 22 August 1971 (D. Richman), male (BC): NEW MEXICO; *San Miguel Co.*, Moctezuma Hot Springs, 13 August 1974 (V. Roth), female (AMNH).

Synageles (Gertschia) noxiosus (Hentz)
Figs. 1, 7, 18-24; Map 3

Synemosyna noxiosa Hentz, 1850:288.
Synageles scorpiona [lapsus for *scorpionia*]: Peckham and Peckham 1889:95-96, pl. 6, fig. 72a, male only [not *Synemosyna scorpionia* Hentz, 1845].
Peckhamia scorpiona: Peckham and Peckham 1909:370-371, pl. 51, fig. 72, male only.
?*Peckhamia scorpionia*: Emerton 1909, pl. 12, figs. 6-6a [genitalia not illustrated].
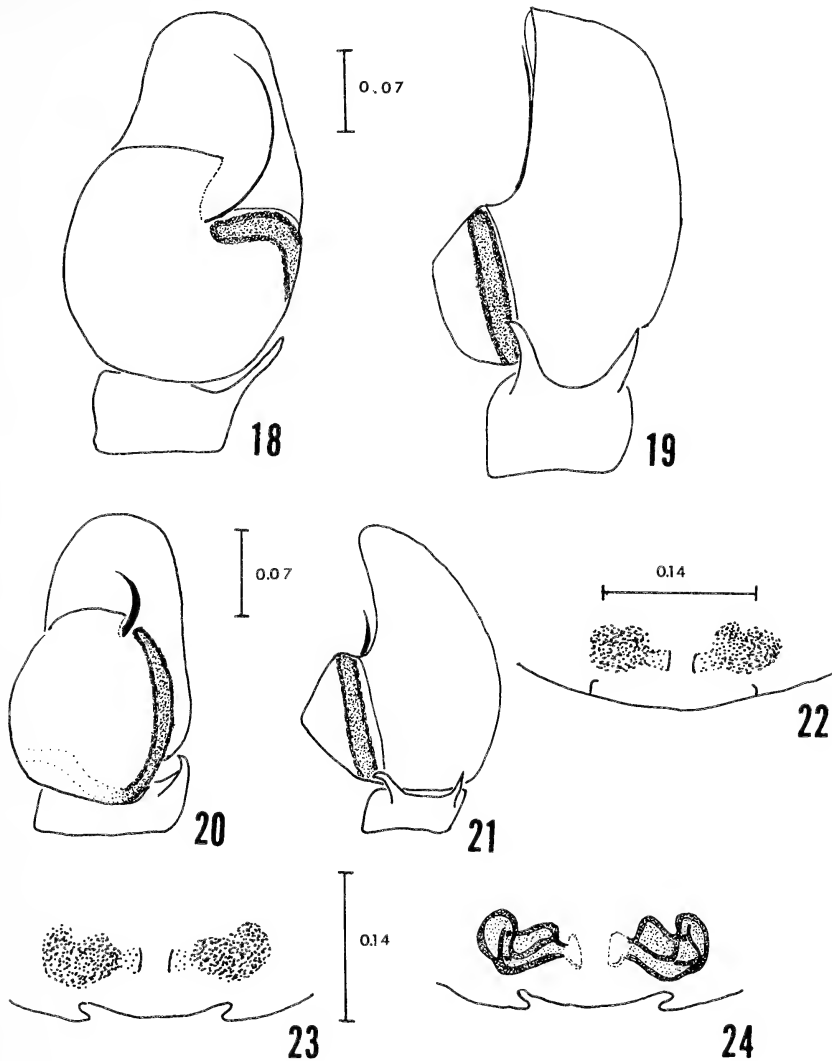
Figs. 18-24.—*S. (G.) noxiosus*: 18-19, male palpus, Tennessee; 18, ventral; 19, retrolateral; 20-21, male palpus, Chihuahua; 20, ventral; 21, retrolateral; 22-24, female epigynum; 22, external, posterior notches absent, New York; 23, external, posterior notches present, Arizona; 24, internal. Scale in mm.

Gertschia noxiosa: Kaston 1945:16-18, figs. 74-76; Kaston 1948:450-451, pl. 88, figs. 1632-1633, pl. 89, figs. 1648-1649, pl. 144, fig. 2137.
Synageles noxiosa [lapsus for *noxiosus*]: Kaston 1978:248, 632-633, female; Richman and Cutler 1978:100.

Diagnosis.—Males have a bicuspid tibial apophysis, both cusps are subequal in length, and the length of the tibial apophysis is 40% or less (usually 33% or less) of the cymbium length. Females have a smooth posterior epigynal margin, or the margin has two small notches. Details of the epigynal tubes are further distinguishing characteristics.

Description.—*Male from CANADA:* ONTARIO; *York Co.*, Toronto, 6 June 1937, (ROM). Total length 2.8. Prosoma 1.18 long, 0.70 wide. Eye field 0.76 long, eye row I 0.57 wide, eye row III 0.56 wide, distance between row III eyes 0.44. Distance eye row II from eye row I 0.18, eye row II from eye row III 0.48.
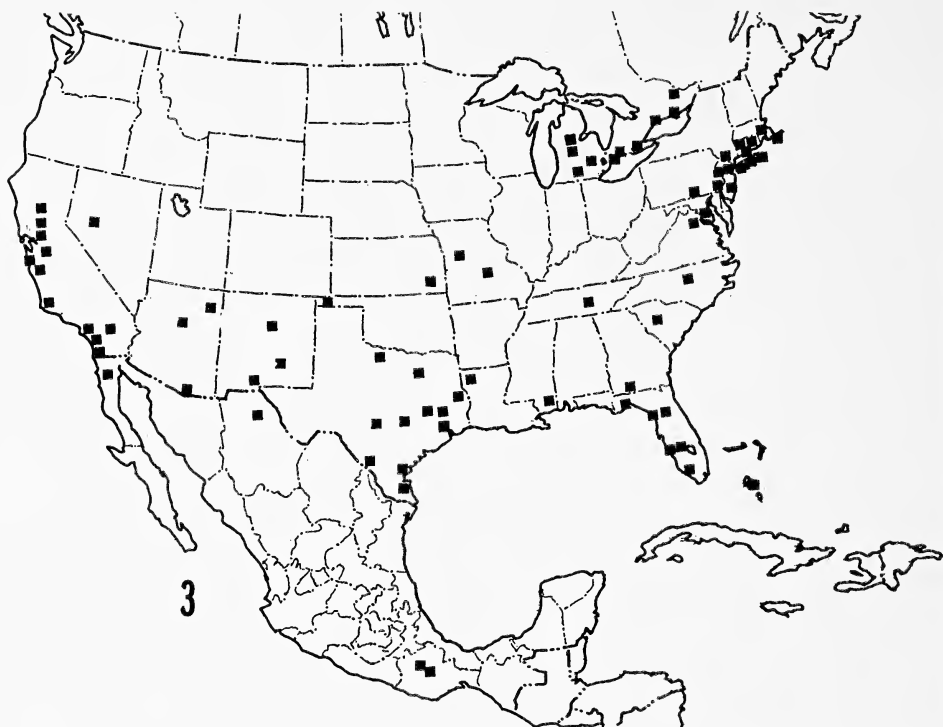
Map 3.—Distribution of *S. (G.) noxiosus*.

Diameter AME 0.16, ALE 0.08, row II eye 0.03, row III eye 0.08. Femur length leg I 0.63, II 0.53, III 0.42, IV 0.63. Leg order 4123. Leg spination I metatarsus 1,1-1,1 tibia 1,1-1,0; II metatarsus 1,1-1,0 tibia 0,0-1,0. Single retromarginal cheliceral tooth. Opisthosoma 1.4 long, 0.6 wide. Color orange overall, markings typical for genus.

Distance between row III eyes in 35 males from U.S.A.: PENNSYLVANIA; Bucks Co., Horseshoe Bend, Neshaminy Creek, NE of Jamison (W. Ivie), (AMNH), mean 0.39, SD 0.02, range 0.37-0.43; in 55 males from other localities, mean 0.43, SD 0.05, range 0.32-0.58.

Female from U.S.A.: NEW YORK; *Bronx Co.*, Pelham Bay Park, 5 June 1963 (B. Cutler), (FSCA). Total length 2.4. Prosoma 1.17 long, 0.70 wide. Eye field 0.77 long, eye row I 0.63 wide, eye row III 0.63 wide, distance between row III eyes 0.53. Distance eye row II from eye row I 0.22, eye row II from eye row III 0.49. Diameter AME 0.24, ALE 0.10, row II eye 0.02, row III eye 0.10. Femur length leg I 0.49, II 0.53, III 0.42, IV 0.70. Leg order 4123. Leg spination I metatarsus 1,1-1,1 tibia 1,1-1,1; II metatarsus 1,1-0,0 tibia 1,1-0,0. Fissident bicuspid retromarginal cheliceral tooth. Opisthosoma 1.2 long, 0.6 wide. Color typical for genus.

Distance between row III eyes in 58 females from U.S.A.: PENNSYLVANIA; *Bucks Co.*, Horseshoe Bend, Neshaminy Creek, NE of Jamison (W. Ivie), (AMNH), mean 0.45, SD 0.03, range 0.40-0.55; in 37 females from other localities, mean 0.51, SD 0.06, range 0.40-0.62.

Discussion.—With the greatest range of any nearctic species, it is of little surprise that it is sympatric with other species in the genus. Its distribution overlaps that of the other two species in *Synageles (Gertschia)*, and also contacts

the range of *Synageles (Synageles) canadensis* and *S. (S.) occidentalis*. The extensive sympatry with *S. (G.) bishopi* is the most puzzling aspect of its distribution. It would be most instructive to determine the parameters of niche overlap in these two species. Unfortunately, the small size of these spiders with attendant difficulties in rearing and distinguishing immatures, means that our understanding of sympatry in this genus will remain unfulfilled. Certainly data from collecting labels do not indicate any habitat differences, and adults appear to mature at the same time in similar localities. Habitats based on label data are: coastal scrub; fence; on ravine bank; sphagnum bog; on wood on shore by marshy pond; elm bark; dead grass (D-Vac); oak woodland; on sandy soil in grassy area; galls on *Solidago*; mesophytic understory of chaparral; woodland climax chaparral; on *Oenothera* on sand dune; on *Baccharis* bushes; low bushes and shrubs; bushes and grasses on hillside; riparian vegetation; snakeweed; crucifers on mesquite dunes; mixed meadow, mostly forbs, little grass. Adults have been taken all months of the year, mostly in May and June.

Hentz's type came from Alabama. The small antlike Nearctic salticids bearing Hentz's specific epithets *noxiosa* and *scorpionia* (and its variant *scorpiona*) have been thoroughly confused since the 1880's. It has been generally accepted since the 1940's (Chickering 1944; Kaston 1945) that *noxiosa* refers to this species, and *scorpionia* refers to a species of *Peckhamia*. Since the types of both are unavailable, and are almost certainly destroyed, it is unlikely that this opinion will be challanged.

Distribution.—*Peripheral localities:* **BAHAMAS:** ANDROS ISLAND; Mangrove Cay, 26 April 1953 (E. Hayden), female (AMNH). **CANADA:** ONTARIO; Ottawa—Carleton Mun., E of Ottawa, Mer Bleue, 14 May to 9 June 1975 (C. D. Dondale and J. Redner), sphagnum bog, female (CNC). **MEXICO:** BAJA CALIFORNIA NORTE; Sierra San Pedro Martir, Melings Ranch (1800 feet), 24 May 1952 (W. S. Creighton), female (AMNH): OAXACA: Monte Albans Ruins, 96°47′ W 17°02′ N, 5 August 1983 (W. Maddison), beating small herbs and bushes near ground on hillside (83-141), female (MCZ). **U.S.A.:** CALIFORNIA; Lake Co., Clear Lake Highlands, 20 May 1959 (R. X. Schick), foothill woodland climax chaparral, female (AMNH).

Other localities: **CANADA:** ONTARIO; *Essex Co.;* Haldimond-Norfolk Mun.; *Kent Co.; Leeds Co., Northumberland Co..* **MEXICO:** CHIHUAHUA; 17.2 miles S of El Sueco, San Jose Barbicora: OAXACA; 39 km NW of Oaxaca. U.S.A: ARIZONA; *Apache Co.; Coconino Co.; Santa Cruz Co.:* CALIFORNIA; *Contra Costa Co.; Lake Co.; Los Angeles Co.; Monterey Co.; Napa Co.; Orange Co.; San Bernardino Co.; San Diego Co.; Santa Barbara Co.; Santa Clara Co.; Santa Cruz Co.:* CONNECTICUT; *Hartford Co.; Litchfield Co.; New Haven Co.; Tolland Co.:* DISTRICT OF COLOMBIA; FLORIDA; *Alachua Co.; Collier Co.; Dixie Co.; Hillsborough Co.; Polk Co.; Wakulla Co.:* GEORGIA; *Thomas Co.:* KANSAS; *Woodson Co.:* LOUISIANA; *Caddo Parish:* MASSACHU-SETTS; *Barnstable Co.; Middlesex Co.; Suffolk Co.:* MICHIGAN; *Calhoun Co.; Gladwin Co.; Livingston Co.; Midland Co.:* MISSISSIPPI; *George Co.:* MISSOURI; *Johnson Co.; Phelps Co.:* NEVADA; *Churchill Co.:* NEW JERSEY; *Bergen Co.; Hunterdon Co.; Ocean Co.:* NEW MEXICO; *Dona Ana Co.; Lincoln Co.; Santa Fe Co.:* NEW YORK; *Nassau Co.; New York Co.; Queens Co.; Rockland Co.; Suffolk Co.:* NORTH CAROLINA; *Durham Co.:* OKLAHOMA; *Cimarron Co.:* PENNSYLVANIA; *Adams Co.:* SOUTH CAROLINA; *Lexington Co.:* TENNESSEE; *Warren Co.:* TEXAS; *Bastrop Co.; Brazos Co.; Dallas Co.; Harris Co.; Kerr Co.; Kleberg Co.; San Patricio Co.; Shelby Co.; Walker Co.; Wichita Co.; Zavala Co.:* VIRGINIA; *Falls Church Co.*

Synageles (Synageles), new subgenus

This subgenus consists of classic *Synageles* in the sense of European authors (Simon 1876; Thaler 1983).
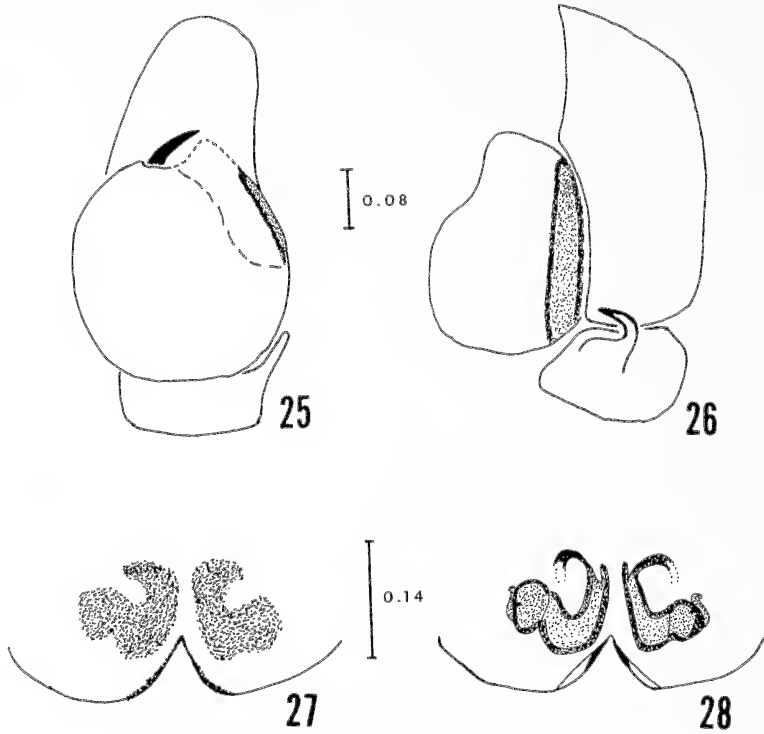
Figs. 25-28.—*S. (S.) venator*: 25-26, male palpus; 25, ventral; 26, retrolateral; 27-28, female epigynum; 27, external; 28, internal. Scale in mm.

Diagnosis.—*Synageles (Synageles)* includes those species which in males have a combination of a non-bifurcate palpal tibial apophysis (Figs. 8, 26, 30, 38), or if bifurcate with an additional distal palpal tibial apophysis (Figs. 9, 40), and an embolus whose length to greatest width ratio is 6:1 or less. Females have a variety of epigynal structures, often with the openings directed laterally or posteriorly. If directed medially, the opening does not lead to short tubes extending laterally to the spermathecae (Figs. 28, 32, 36).

Type species.—*Synageles (Synageles) venator* (Lucas).

Included New World species.—*S. (S.) canadensis* n. sp., *S. (S.) idahoanus* (Gertsch), *S. (S.) leechi* n. sp., *S. (S.) occidentalis* n. sp..

Geographic range.—Includes all of the Old World species known to the author, in the New World from British Columbia to Nova Scotia in Canada, south in the United States to Michigan, the northern prairie and plains states, the Rocky Mountain region, the Great Basin and to Riverside Co. in California.

I have refrained from assigning Old World species other than the type to the subgenus, as that should be left to the revisor of those species.

Synageles (Synageles) canadensis, new species
Figs. 29-32; Map 4

Etymology.—Named after Canada, the country of origin.

Diagnosis.—Males of this species may be distinguished from other members of the genus by the distally pointing embolus, and the configuration of the tibial
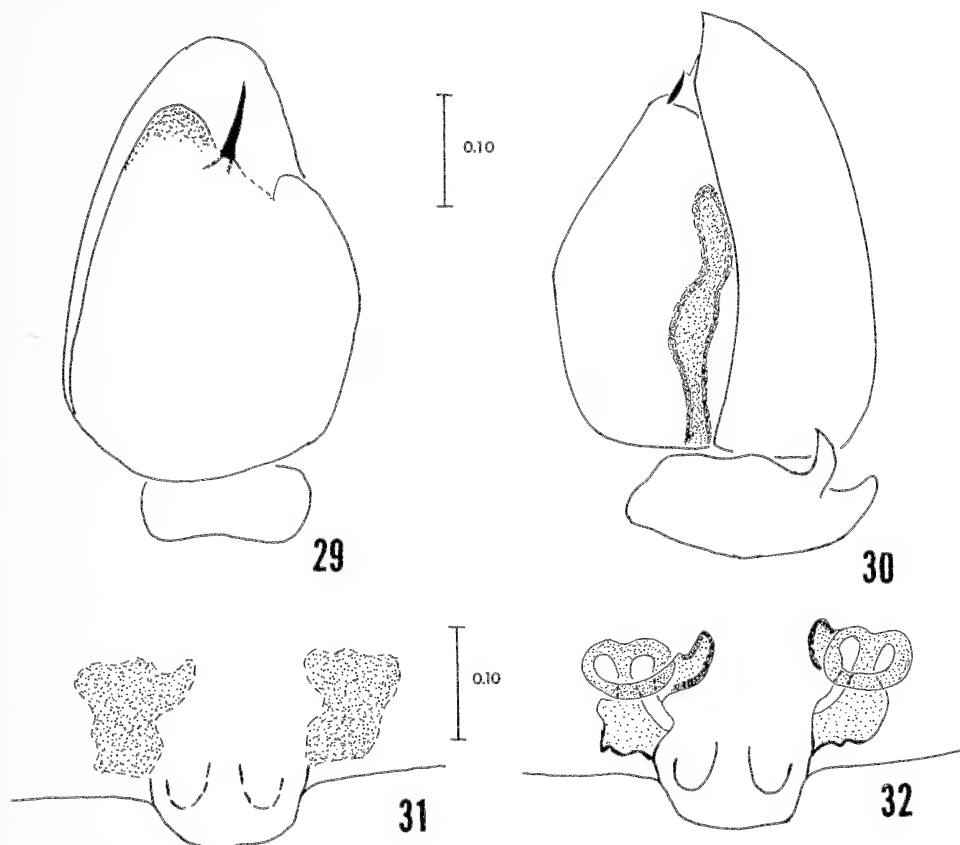
Figs. 29-32.—*S. (S.) canadensis*: 29-30, male palpus; 29, ventral; 30, retrolateral; 31-32, female epigynum; 31, external; 32, internal. Scale in mm.

apophysis. Females have a distinct posteriorly projecting flap of the epigynum with two ovoid lunules, and have a unique configuration of the epigynal tubes. The male palpus of *S. (S.) canadensis* is most similar to that of the palearctic *S. dalmaticus* (Keyserling), but has a different tibial apophysis. The epigynum of female *S. (S.) canadensis* resembles that of the palearctic *S. hilarulus* (C. L. Koch), but there are differences in the details of the epigynal tubes, distance of the tubes to the epigastric furrow, and in the former species the posterior margin of the epigynum is a flap not a notch.

Description.—*Male holotype*: Total length 3.0. Prosoma 1.34 long, 0.78 wide. Eye field 0.84 long, eye row I 0.73 wide, eye row III 0.75 wide, distance between row III eyes 0.67. Distance eye row II from eye row I 0.22, eye row II from eye row III 0.32. Diameter AME 0.20, ALE 0.13, row II eye 0.03, row III eye 0.08. Femur length leg I 0.58, II 0.55, III 0.65, IV 0.97. Leg order 4312. Leg spination I metatarsus 1,1-1,1 tibia 0,1-0,1; II metatarsus 1,0-1,0 tibia 1,0-0,0. Single retromarginal cheliceral tooth. Opisthosoma 1.6 long, 0.7 wide. Color typical for genus.

Female paratype from CANADA: NEW BRUNSWICK; York Co., Fredricton, 20 August 1967 (T. Renault), fall webworm nest, (ROM). Total length 3.3. Prosoma 1.51 long, 1.06 wide. Eye field 0.85 long, eye row I 0.83, eye row III 0.90, distance between row III eyes 0.80. Distance eye row II from eye row I 0.26,

Map 4.—Distribution of *S. (S.) canadensis*—circle; *S. (S.) idahoanus*—square; *S. (S.) leechi*—star.

eye row II from eye row III 0.50. Diameter AME 0.28, ALE 0.13, row II eyes 0.03, row III eye 0.11. Femur length leg I 0.74, II 0.70, III 0.63, IV 0.98. Leg order 4231. Leg spination I metatarsus 1,1-1,1 tibia 1,1-1,1; II metatarsus 0,1-0,0 tibia 0,1-0,0. Single retromarginal cheliceral tooth. Opisthosoma 1.7 long, 1.1 wide. Color typical for genus.

Distance between row III eyes in 5 females, mean 0.75, range 0.60-0.80.

Discussion.—This species occurs across Canada in the boreal and boreo-nemoral forest. The few habitat records suggest that it is an arboreal species. Most records are from the Maritime provinces.

Distribution.—*Holotype locality:* **CANADA:** NEW BRUNSWICK; *Kent Co.,* Kouchibouguac National Park, 14 June 1977 (S. J. Miller), male (CNC).

Paratype localities (all female): **CANADA:** BRITISH COLUMBIA; Prince George, 16 July 1954 (H. R. McCarthy, R. Leech) (RL): NEW BRUNSWICK; *Madawaska Co.,* Green River Field Station, 31 July 1962 (T. Renault), white spruce (TR); *Kings Co.,* Penobsquis, 4 July 1927 (C. A. Frost) (CNC): NOVA SCOTIA; *Cape Breton Co.,* North Sydney, July 1906 (E. B. Bryant): ONTARIO; *Algoma District,* Laird, 3 July 1931 (ROM).

Other localities: **CANADA:** NEW BRUNSWICK; *Kent Co.,* Point Escuminac (47 N, 64.50 W), 17 June 1979 (Wayne and David Maddison), sweeping bog vegetation between road and beach, 2 females (WM): **U.S.A.:** MICHIGAN; Marquette Co., Marquette, 11 June 1973 (W. Maddison), under paper on grass on top of slope to Lake Superior on E side of town, male (WM).

Synageles (Synageles) idahoanus (Gertsch)
Figs. 33-36; Map 4

Peckhamia idahoana Gertsch 1934:11-12, figs. 11-12.
Gertschia idahoana Kaston 1945:17.
Synageles idahoana [lapsus for *idahoanus*] Richman and Cutler 1978:100.

Diagnosis.—The swollen rounded base of the embolus of the male palpus distinguishes this species. *S. (S.) leechi* is similar, but the enlarged base of the embolus has a straight edge. The posterior edge of the epigynum has two shallow lobes, without any lunules. The male palpus of *S. (S.) idahoanus* does not closely resemble that of any of the European species. The female epigynum is similar to
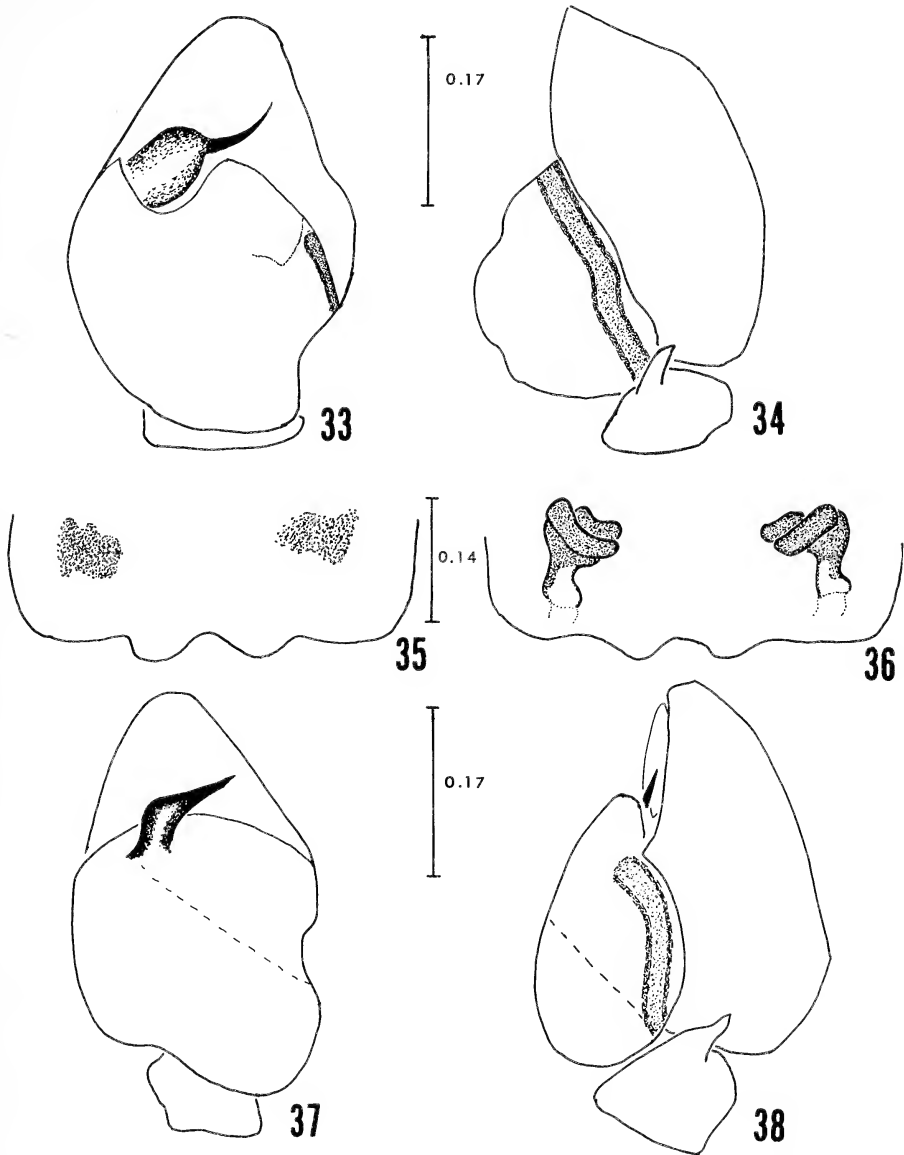
Figs. 33-36.—*S. (S.) idahoanus*: 33-34, male palpus; 33, ventral; 34, retrolateral; 35-36, female epigynum; 35, external; 36, internal. 37-38.—*S. (S.) leechi*: male palpus; 37, ventral; 38, retrolateral. Scale in mm.

that of the palearctic *S. albotrimaculatus gallicus* (Simon) and *S. hilarulus*, but the posterior margin of the epigynum in *S. (S.) idahoanus* has a different shape (as described above). There are also numerous differences in the details of the internal epigynal tubes.

Description.—*Male holotype*: Total length 3.0. Prosoma 1.43 long, 0.88 wide. Eye field 0.77 long, eye row I 0.70 wide, eye row III 0.77 wide, distance between row III eyes 0.65. Distance eye row II from eye row I 0.25, eye row II from eye row III 0.49. Diameter AME 0.21, ALE 0.11, row II eye 0.03, row III eye 0.11. Femur length leg I 0.59, II 0.63, III? IV 0.77. Leg order (leg III missing) 41=2.

Leg spination I metatarsus 1,1-1,1 tibia 1,1-0,0; II metatarsus 1,1-0,0 tibia none. Single retromarginal cheliceral tooth. Opisthosoma 1.5 long, 0.8 wide. Color typical for genus.

Distance between row III eyes in two males, 0.52 and 0.65.

Female from U.S.A.: UTAH; *Kane Co.*, Mt. Carmel, 26 June 1947 (Borys Malkin) (AMNH). Total length 3.1. Prosoma 1.39 long, 0.84 wide. Eye field length 0.80, eye row I 0.73 wide, eye row III 0.80 wide, distance between row III eyes 0.70. Distance eye row II from eye row I 0.24, eye row II from eye row III 0.45. Diameter AME 0.22, ALE 0.13, row II eye 0.03, row III eye 0.10. Femur length leg I 0.60, II 0.57, III 0.52, IV 0.76. Leg order 4123. Leg spination I metatarsus 1,1-1,1 tibia 1,1-1,1; II metatarsus 1,1-1,0 tibia 0,1-0,0. Single retromarginal tooth. Opisthosoma 1.6 long, 1.0 wide. Color typical for genus.

Distance between row III eyes in 10 females, mean 0.70, range 0.47-0.77.

Discussion.—The allotype is an immature specimen, probably a female.

Distribution.—*Holotype, allotype and male paratype locality:* **U.S.A.:** IDAHO; *Twin Falls Co.*, Hollister, 20 May 1931 (D. E. Fox) (AMNH).

Other localities: **U.S.A.:** CALIFORNIA; *Mono Co.*, 10 mi W of Bridgeport, Robinson Creek Campground (7000 feet), 10 July 1975 (C. Griswold), beating *Artemesia/Purshia*, female, 6 small spiderlings (CB); *Placer Co.*, 5 mi W of Emigrant Creek, 9 July 1952 (W. J. Gertsch), female (AMNH); *Tehama Co.*, Deer Creek, 6 July 1952 (W. J. Gertsch), female (AMNH), Mineral, 6 July 1952, female (AMNH): COLORADO—UTAH BORDER; N 41 W 108, 33 fh, female (AMNH): OREGON; *Deschutes Co.*, Redmond, 1 June 1939 (K. Gray and J. Schuh), female (AMNH); *Lake Co.*, Lakeview, 27 June 1951 (Borys Malkin), female (AMNH): UTAH; *Garfield Co.*, Bryce Canyon vicinity, 11 July 1952, female (AMNH); *Morgan Co.*, East Canyon, Wasatch Mountains, W 111.48 N 40.50, 14 June 1942 (W. Ivie), 2 females (AMNH); *Tooele Co.*, Government Creek, 12 June 1946 (Lowell Miller), female (AMNH): WYOMING; *Park Co.*, near Cody, Buffalo Bill State Park, May 1977 (W. Maddison), female (WM): WYOMING?; N 41.73, 33gg, 332, female (AMNH).

Synageles (Synageles) leechi, new species
Figs. 37, 38; Map 4

Etymology.—Named after the arachnologist and collector of the type specimen, Robin E. Leech.

Diagnosis.—In all respects very similar to *S. (S.) idahoanus*, but the base of the embolus is not rounded and has a straight edge. There is no indication that this portion of the embolus is broken, and both right and left palpi have the same form. The shape of the tibial apophysis of *S. (S.) leechi* is closest to that of *S. lepidus*, but the embolus resembles that of *S. (S.) idahoanus*.

Description.—*Male holotype*: Total length 2.6. Prosoma 1.18 long, 0.70 wide. Eye field 0.70 long, eye row I 0.59 wide, eye row III 0.63 wide, distance between row III eyes 0.52. Distance eye row II from eye row I 0.20, eye row II from eye row III 0.39. Diameter AME 0.18, ALE 0.10, row II eye 0.04, row III eye 0.10. Femur length leg I 0.59, II 0.52, III 0.45, IV 0.67. Leg order 4123. Leg spination I metatarsus 1,1-1,1 tibia 1,1-0,0; II meatatrsus 0,1-0,0 tibia none. Single retromarginal cheliceral tooth. Opisthosoma 1.4 long, 0.7 wide. Color typical for the genus.

Discussion.—*S. (S.) leechi* is very similar to *S. (S.) idahoanus*, and may be only a variant form of that species. However, since the few males of *S. (S.) idahoanus* known have essentially identical genitalia, and this specimen is readily distinghished from them, it is best to erect a new species based on it. Unlike in many other genera of salticids, there seems to be a general reluctance to name

new species in the New World *Synageles*, resulting in "overlumping", rather than "oversplitting".

Holotype locality.—CANADA: BRITISH COLUMBIA; Oliver, 5 June 1959 (R. E. Leech) (CNC).

Synageles (Synageles) occidentalis, new species
Figs. 9, 39-46; Map 2

Etymology.—An adjective from the Latin meaning western, referring to the distribution of this species in western North America.

Diagnosis.—Males are the only New World species of *Synageles* with two distinctly separated tibial apophyses. The posterior margin of the epigynum has two shallow lobes overhanging the epigastric furrow as in *S. (S.) idahoanus*, but in addition there is a single medial notch which may be long and narrow, triangular, or shorter and squared off anteriorly. The male palpus overall resembles that of *S. dalmaticus*, but the shape of the tibial apophyses is different. The epigynum of female *S. (S.) occidentalis* is similar to the epigynum of *S. dalmaticus*, but has shorter eipigynal tubes which are closer to the median, and to the posterior of the epigynum.

Description.—*Male holotype:* Total length 2.7. Prosoma 1.16 long, 0.70 wide. Eye field 0.60 long, eye row I 0.59 wide, eye row III 0.60 wide, distance between row III eyes 0.52. Distance eye row II from eye row I 0.20, eye row II from eye row III 0.36. Diameter AME 0.18, ALE 0.08, row II eye 0.03, row III eye 0.08. Femur length leg I 0.56, II 0.50, III 0.45, IV 0.69. Leg order 4123. Leg spination I metatarsus 1,1-1,1 tibia 0,0-0,1; II metatarsus 0,0-0,1 tibia none. Fissident bicuspid retromarginal cheliceral tooth. Opisthosoma 1.4 long, 0.7 wide. Color of prosoma dark orange, rest typical for genus.

Distance between row III eyes in 21 males, mean 0.55, SD 0.04, range 0.47-0.58.

Female paratype from U.S.A.: MINNESOTA; *Ramsey Co.*, Lauderdale, Luther Seminary Grounds, 12 June 1966 (B. Cutler), sweeping *Solidago* (AMNH). Total length 3.1. Prosoma 1.37 long, 0.84 wide. Eye field 0.76 long, eye row I 0.67 wide, eye row III 0.71 wide, distance between row III eyes 0.63. Distance eye row II from eye row I 0.20, eye row II from eye row III 0.42. Diameter AME 0.24, ALE 0.10, row II eye 0.03, row III eye 0.08. Femur length leg I 0.70, II 0.63, III 0.56, IV 0.98. Leg order 4132. Leg spination I metatarsus 1,1-1,1 tibia 1,1-1,1; II metatarsus 1,1-0,0 tibia none. Single retromarginal cheliceral tooth. Opisthosoma 1.7 long, 1.1 wide. Color typical for genus.

Distance between row III eyes in 37 females, mean 0.58, SD 0.06, range 0.47-0.75.

Discussion.—This species has often been confused with *S. (G.) noxiosus* despite its very different genitalia. The ranges of both species meet in Michigan, and there may be additional areas of contact in the north central states. This species and *S. (S.) idahoanus* overlap in the intermontane western United States.

In Washington Co., Minnesota, *S. (S.) occidentalis* is associated with the following species of ants of similar size, on forbs: *Crematogaster lineolata* (Say), *Lasius alienus* Emery, *Prenolepis imparis* (Say) and *Tapinoma sessile* Say. In Minnesota the most consistent ant associate is some species of *Lasius*. Most records are from grassland habitats, often associated with grassland forbs.
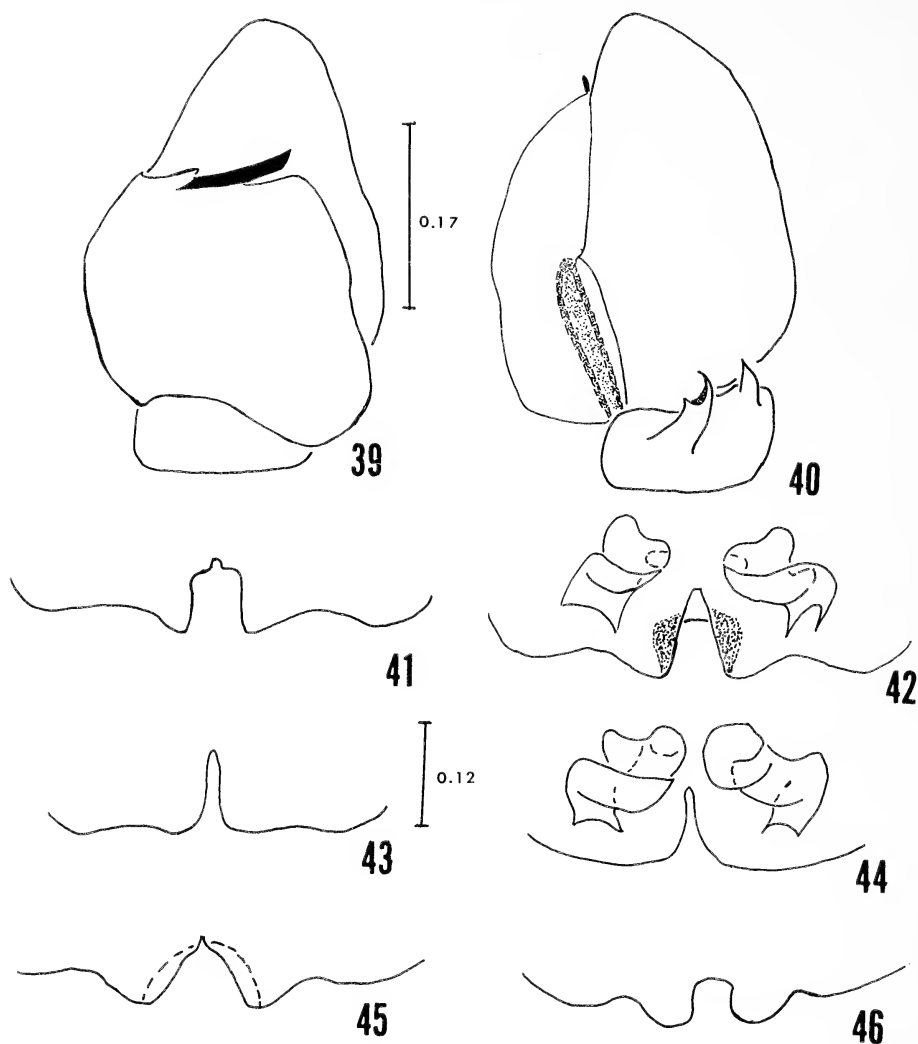
Figs. 39-46.—*S. (S.) occidentalis*: 39-40, male palpus; 39, ventral; 40, retrolateral; 41-46, female epigynum; 41-42, Minnesota; 41, external; 42, internal; 43-44, Utah; 43, external; 44, internal; 45, Idaho, external; 46, California, external. Scale in mm.

Specific habitats recorded are: herbs, sage and shrubs at base of cliff, sand prairie, oak savanna, mixed meadow, *Solidago* stand, *Juncus* swale, swale in dunes area, coastal oak woodland, oak meadow, dry mesic prairie, *Bromus inermis*, and in year old seed pods of *Penstemon grandiflorus*. In Fillmore Co., Minnesota I have taken this species in year-old galls of *Eurosta solidaginis* (Fitch) that were opened by woodpeckers during the previous winter. The spiders constructed retreats in these galls. Both Judd (1964) and Miller (1966) reported *S. (G.) noxiosus* using stem galls originally made by moths on *Solidago* in the same manner. I have not seen the specimens involved, but based on the localities involved (Ontario and Ohio respectively), the determinations were probably correct. Adults have been collected in all months of the year except January and December; most records are from May through July.

Distribution.—*Holotype locality:* U.S.A.: NORTH DAKOTA; *McKenzie Co.*, North Unit Theodore Roosevelt Memorial Park, 26 June 1965 (R. J. Sauer), beating willow along Little Missouri River (AMNH).

Paratype localities: U.S.A.: CALIFORNIA; *Alameda Co.*, Berkeley, hills back of campus, 7 May 1973 (W. M. Middlekauf), female (CB); *San Francisco Co.*, San Francisco, Forest Hill, 27 May 1934, female (CAS); *San Mateo Co.*, near Crystal Springs Reservoir, 21 March 1976 (C. E. Griswold), tall grass near road, male (CB): COLORADO; *Boulder Co.*, Boulder, Flagstaff Canyon (5800 feet), (J. R. Stainer), female (CNC): IDAHO; *Payette Co.*, Payette (north side of town), 20 June 1953 (W. Ivie), female (AMNH); *Washington Co.*, 6 mi W of Weiser, W 117° 04' N 44° 15', 3 May 1962 (W. Ivie), males, females (AMNH): ILLINOIS; *Cook Co.*, Chicago, Palos Park, 11 May 1911 (A. B. Walcott), female (FMN): MINNESOTA; *Ramsey Co.*, Lauderdale, Luther Seminary Grounds, May and June 1966 and 1967, sweeping various meadow habitats, males, females (AMNH, BC, MCZ, UMN): SOUTH DAKOTA; *Jackson Co.*, Badlands National Monument, U.S. Highway 12, 28 June 1966 (L. Pinter), female (MCZ): UTAH; *Lake Co.*, Lake City, Jordan River at 11th South Street, W 111° 54' N40°44', 4 May 1946 (W. Ivie), female (AMNH); *San Juan Co.*, Bluff, 5 September 1937 (G. F. Knowlton), female (AMNH): WISCONSIN; *Walworth Co.*, Sugar Creek Township, 18 July 1938 (D. C. Lowrie), sweeping from auto, 2 females (FMN).

Other localities: CANADA: BRITISH COLUMBIA; Christiana (118.14W 49.01N), 25 July 1980 (W. Maddison), sweeping herbs along railroad, female (WM): MANITOBA; Telford, W95°23' N49°51', 10 June 1964, female (CNC): U.S.A.: ARIZONA; No locality: CALIFORNIA; *Contra Costa Co.; Mendocino Co.; Monterey Co.; Riverside Co.; San Diego Co.; Santa Cruz Co.:* COLORADO; *Lincoln Co.:* MICHIGAN; *Kalamazoo Co.:* MINNESOTA; *Anoka Co.; Fillmore Co.; Hennepin Co.; Lac Qui Parle Co.; Le Sueur Co.; Renville Co.; Sherburne Co.; Wabasha Co.; Washington Co.; Winona Co.:* NEBRASKA; *Dawson Co.; Lancaster Co.:* NEVADA; Esmeralda Co.: OREGON; *Deschutes Co.; Lake Co.; Yamhill Co.:* UTAH; *Grand Co.:* WASHINGTON; *Kittitas Co.:* WISCONSIN; *Dane Co.*

UNPUBLISHED SPECIES NAMES

In my unpublished thesis of 1970, a number of names were created which have no taxonomic status. However, for the sake of completeness, the following list gives the current taxonomic placement of specimens under the thesis names:

This Paper		Thesis Names
S. (G.) bishopi	=	bishopi
S. (G.) mexicanus	=	mexicana
S. (G.) noxiosus	=	canadense males, chaparralicola, creightoni, noxiosa, orarius males, perminima
S. (S.) canadensis	=	canadense females
S. (S.) idahoanus	=	idahoana, ivei, oregonensis
S. (S.) occidentalis	=	araecharactae, colubra, dakota, orarius females

ACKNOWLEDGMENTS

Acronyms for collections cited in text are:

CB   = University of California, Berkeley
BC   = Bruce Cutler
CNC   = Canadian National Collections
AMNH = The American Museum of Natural History
RL   = Robin Leech
BM   = Bennet Moulder
ROM   = Royal Ontario Museum
UMN   = University of Minnesota, Department of Entomology
WM   = Wayne Maddison
TR   = Thaddee Renault

CAS = California Academy of Sciences
MCZ = Museum of Comparative Zoology, Harvard University

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OVIPOSITION SITE SELECTION BY
FRONTINELLA PYRAMITELA (ARANEAE, LINYPHIIDAE)

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ABSTRACT

In the field, the bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae), deposits its eggs in a loosely-woven silk cocoon on or close to the soil. Experimental laboratory studies indicate that gravid females select that type of oviposition site in response to gravitation, soil moisture or atmospheric humidity, and the gross structure of the microhabitat. Under experimental conditions, rates of water loss from *F. pyramitela* egg cocoons are approximately double the rates from cocoons constructed by three species (*Achaearanea tepidariorum, Argyrodes trigonum,* and *Uloborus glomosus*) that oviposit in aerial webs well above the ground. We conclude that desiccation of developing eggs has been an important natural selective force shaping the selection of oviposition sites by bowl and doily spiders.

INTRODUCTION

Habitat selection usually refers to the suite of choices made by an organism that results in its occupation of a particular habitat (Partridge 1978). Often it is useful to partition the choices into functionally specific subsets, to refer, for example, to foraging patch selection, display arena selection, and oviposition site selection. In this more specific context it is possible to discover experimentally the stimuli to which the organism responds as it makes each choice.

Morse (1985) has correctly asserted that the selection of an oviposition site is "one of the most important decisions made by animals that deposit eggs," and that this is particularly so if most of the organism's eggs are deposited at one or only a few sites. Because most spider species do not move their eggs once they are deposited (Comstock 1948; Foelix 1982; but note the egg cocoon-transporting behaviors of the Lycosidae and Pisauridae) and usually distribute their eggs among one or a few clutches (Comstock 1948), their decisions leading to oviposition site selection are certainly crucial. And the importance of the selection process is increased by the fact that hatchlings may remain in the cocoon for long periods (Foelix 1982).

For many web-building spiders (e.g., *Cyclosa, Achaearanea, Uloborus*), the selection of oviposition site is identical to the selection of foraging site, because the egg cocoon is incorporated into the prey-capture web at the time of oviposition. For others, though, the processes of oviposition and web site selection are separate and the selected sites are qualitatively very different. We report here on the oviposition sites chosen in the field by the bowl and doily

spider, *Frontinella pyramitela* (Linyphiidae), and on the environmental cues that the spider responds to during the process of selection.

MATERIALS AND METHODS

Field study.—We removed 17 gravid female *F. pyramitela* from their webs in an old field in LaGrange, NY, during July, 1985, and placed them inside a 1 m³ cube-shaped enclosure which was located in an old field. The enclosure was screened on four sides and on the top but was open on the bottom. The wooden bottom edges of this enclosure rested on a smoothed soil bed which surrounded a one meter square of pasture vegetation (grasses and a mixture of forbes and dried stems of forbes) which had been clipped at the top and sides to fit within the enclosure. The outside of the bottom edge of the enclosure was sealed with fine sand to prevent the escape of the spiders. This entire assembly was surrounded by pasture vegetation similar to what was inside the enclosure.

Eight days after spiders were released into the enclosure, we performed a top-down search of its contents in an attempt to recover as many *F. pyramitela* egg cocoons as possible. As each cocoon was found, we recorded both its location and a description of its microhabitat. We also counted all *F. pyramitela* that we found, and noted their condition.

Laboratory studies.—Gravid female bowl and doily spiders, either mated in captivity or freshly removed from their webs in the field, were placed in 10.2 cm (diameter) by 15.3 cm plastic cylinders which gave the spiders sufficient volume both to construct prey-capture webs and to deposit eggs. In tests of the importance of gravity as a stimulus in oviposition site selection, the ends of each cylinder were covered by polyethylene plastic wrap (e.g., Saran Wrap®) and the chamber was stored horizontally in a larger container in which the atmosphere was saturated with water. Because of overhead lighting, the brightest areas of these cylinders during the day were located on the bottom near either end. In tests of the importance of substrate moisture as a stimulus, one end of each (vertical) cylinder was covered with cheesecloth and the other end rested on a divided bed of white sand, half of which was dry and half of which was moist (darker than the dry sand but with no liquid water visible). Again because of overhead lighting during the day, the sand floors of these containers were uniformly illuminated. Each morning, we recorded the locations of the egg cocoons constructed during the previous night.

Overhead fluorescent bulbs provided light during the day and no light was visible to the spiders during the night. Relative humidity in the laboratory varied between 45% and 60%.

We measured rates of water loss from 16 newly constructed egg cocoons of *F. pyramitela* by individually weighing them before and during seven days of desiccation over a 50% H_2SO_4 bath (33% RH). For contrast, we subjected 48 egg cocoons of *Argyrodes trigonum* (Theridiidae), *Achaearanea tepidariorum* (Theridiidae), and *Uloborus glomosus* (Uloboridae) to the same desiccation regime. After desiccation, the cocoons were dried to constant weight in a low-temperature oven to establish (by subtraction) the total water initially present in each cocoon. They were also opened to determine which cocoons contained only eggs (no spiderlings or parasitoids). Nineteen of the theridiid and uloborid

cocoons contained only eggs, and data from only these were used in later comparisons.

RESULTS

Field study.—During the search of the field enclosure, we found eight egg cocoons belonging to *F. pyramitela*, and two dead and four live *F. pyramitela*. Of the latter, all were still gravid. None of the cocoons was found further than 2 cm from the soil: six were directly on the soil, one was 1 cm and another was 2 cm from the soil surface. All of the cocoons that were in contact with the soil had been constructed in small hollows or between the underside of the wooden frame of the enclosure and the soil (connected to both). The two cocoons found above the soil had been constructed within clumps of dead grass leaves.

Laboratory studies.—Figure 1 shows the locations of 24 egg cocoons relative to the direction of gravity. The distribution of locations is significantly different from random and the mean direction is downward (357° ± 31°; Rayleigh test, $z =$ 17.6, $P < 0.01$). Figure 1 also indicates that $> 91\%$ of the cocoons in the gravitation experiment were constructed in contact with the polyethylene ends of the cylinders (binomial test, $P < 0.001$), and this was the case despite the inability of the silk to adhere to that plastic (Suter et al. in press).

Figure 2 shows the locations of cocoons constructed in vertical cylinders in which the bottoms were divided into moist and dry sections. The 12 spiders unanimously selected the moist side (binomial test, $P < 0.001$) and showed no obvious preference for locations far from the dry sand substrate. As in Fig. 1, Fig. 2 shows evidence that the selection of oviposition site is influenced by the gross structure of the available environment: 92% of the spiders built their cocoons in contact with both the sand and the wall of the cylinder (binomial test, $P = 0.003$).

Desiccation of the 16 egg cocoons of *F. pyramitela* resulted in water loss at a rate nearly twice that of the 19 cocoons of the theridiids and the uloborids (among which there were no statistical differences in rates of water loss). Egg cocoons of *F. pyramitela* lost water at a rate of 0.42% ± 0.1% per hour (70.6% in 7 days) while egg cocoons of the other taxa lost at a rate of 0.27% ± 0.2% per hour (45.4% in 7 days) (T = 3.48, $P < 0.001$).

DISCUSSION

Kaston, in his 1948 work on the spiders of Connecticut, stated that he had never seen the egg sacs of bowl and doily spiders (p. 121). His observation is not surprising given the selection of oviposition sites reported above. The placement of egg cocoons under natural conditions indicates that this aerial web-building spider uses wholly different sets of criteria in selecting sites for prey-capture webs and oviposition. The sites selected for oviposition contained high relative humidity, low light, and were near or on the ground, and all but two were partially enclosed in soil depressions or in small gaps between soil and wood.

Data from the laboratory indicate that gravity, moisture content of the air or substrate, and physical structure of the microhabitat are important variables in oviposition site selection by *F. pyramitela*.

Mean Orientation = 357 deg.
Angular Deviation = 31 deg.
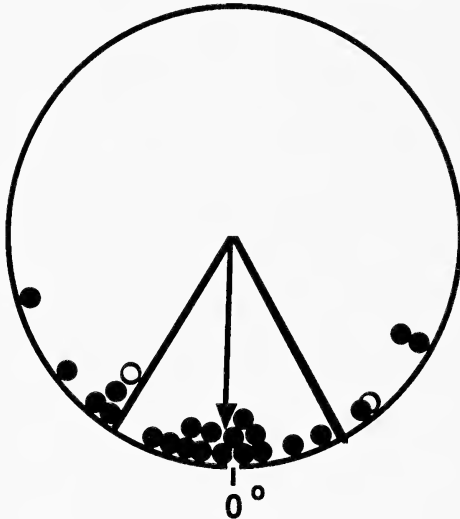**N = 24   P < 0.01**

Fig. 1.—Oviposition sites chosen by 24 gravid spiders in horizontal, cylindrical chambers. In reference to the direction of gravity (0°), the mean orientation of the sites was strongly and significantly downward (357° ± 31°; Rayleigh test, $P <$ 0.01). Only two of the spiders constructed egg cocoons away from the intersection of a cylinder and its plastic end (open circles; binomial test, $P <$ 0.001).

In a horizontal cylindrical environment in which the RH was invariate at 100%, the spiders showed a strong preference for locations that were down (in the direction of gravity) and that had two distinct sides; they nearly always constructed their egg cocoons low against the ends of the cylinders (Fig. 1). The same location is also the brightest location in an experimental cylinder during daylight hours. We discount the importance of light as a cue, however, because nearly all egg cocoons were begun during the night and because the cocoons found in the field were in locations which had very low or negligible light levels.

In a vertical cylindrical environment open to low-RH air at the top and with a choice of moist or dry sand at the bottom, the spiders showed an unequivocal preference for the more moist of the two microhabitats; all egg cocoons were constructed in contact with the moist sand. (Note that no distinction can be made here between the moisture of the sand and the RH of the immediately surrounding air. The spiders may be capable of measuring either or both). In this experiment, too, the spiders displayed a significant tendency to oviposit where the cylinder and one of its ends joined (Fig. 2).

Thus the data from laboratory experiments coincide well with what was found in the field—in selecting a site for oviposition, a female *F. pyramitela* is positively gravitactic and, in that context, chooses a moist site that also is partially enclosed.

The choice of an off-web oviposition site places the gravid female at a risk not shared by spiders that remain on the web while laying eggs. When *F. pyramitela* leaves its web to search for an oviposition site, it leaves its primary source of information and must travel where its detection of predators is greatly hampered. Moreover, the enclosed oviposition sites chosen by *F. pyramitela*, though probably safe from visually-hunting predators, are likely to expose the cocoons to predation by rodents and ants (Hieber 1984). Thus the risk of the search for an
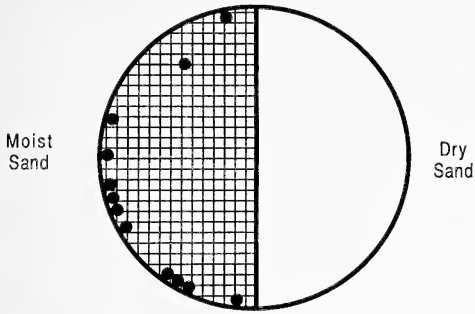
Fig. 2.—Oviposition sites chosen by 12 gravid spiders in vertical, cylindrical chambers resting on sand. All of the spiders constructed their cocoons on moist sand (cross-hatched) in preference to dry sand (binomial test, $P < 0.001$). Eleven of the spiders constructed cocoons in contact with both the sand and the vertical side of the cylinder (binomial test, $P = 0.003$).

oviposition site and the predator pressure on eggs deposited there must be outweighed by the benefits of discovery of a site that is suitable in other ways.

The presence of still, moist air, may be the most important attribute of these oviposition sites. Several authors have postulated that a primary function of egg cocoons in spiders is to retard water loss and the resulting detrimental effects of desiccation on development (Bristowe 1941; Foelix 1982; Opell 1984; Hieber in press). Our investigations of the rates of water loss from egg cocoons of *F. pyramitela* show that, in 33% RH air, about 70% of the water may be lost in seven days, a time that is about half the development time required by the species (median = 15.5 days at 22°C; Suter unpubl. data). That rate of water loss is nearly double the rate from cocoons of two species of spiders that construct their cocoons in open air. One of these, *Argyrodes trigonum*, provides a particularly apt comparison because it often suspends its egg cocoon in the web of *F. pyramitela*. Thus the cocoons of *A. trigonum* are subjected to a relatively dry microclimate (usually > 30 cm above the ground), the one where *F. pyramitela* spends most of its life, and it is not surprising that the eggs of the former become desiccated more slowly under test conditions.

The egg cocoon of *F. pyramitela* is composed of two very loosely-woven layers of silk surrounding the eggs. This covering is open enough to allow the orange color of the eggs to be seen from the outside. In contrast, the egg cocoons of *A. trigonum* and *A. tepidariorum* have as their outer coverings a densely woven and paper-like layer of tanned silk. Opell (1984) and Hieber (in press) have shown that this sort of covering retards water loss from cocoons of some spiders. The absence of such a covering on cocoons of *F. pyramitela* and their high rate of water loss suggests that this spider has evolved orientation behaviors rather than silk spinning behaviors in answer to selective pressures resulting from egg desiccation.

ACKNOWLEDGMENTS

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"SPIDER EAT SPIDER": THE PREDATORY BEHAVIOR OF *RHOMPHAEA* SP. FROM NEW ZEALAND

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ABSTRACT

Rhomphaea sp. from New Zealand captures other spiders which wander onto its web, and ventures onto other spiders' webs to capture the resident. *Rhomphaea* captures spiders by using aggressive mimicry to lure the victim and by throwing a sticky triangular net over the prey. The importance of this unusual method of capturing spiders is discussed in relation to the evolution of this spider.

INTRODUCTION

This work examines the predatory behavior of *Rhomphaea* Simon, a genus of elusive, solitary spiders whose predatory behavior is unknown other than that they eat other spiders (Eberhard 1979; Smith Trail 1980; Horton 1982). The behavior of *Rhomphaea* is of special interest because species from a closely related genus, *Argyrodes*, capture spiders by using stealth (Eberhard 1979), aggressive mimicry (Whitehouse 1986), and engage in an unusual form of foraging—kleptoparasitism (Vollrath 1976; Whitehouse 1986).

Currently there is conjecture surrounding the degree to which the genera *Argyrodes* and *Rhomphaea* are related. Exline and Levi (1962) merged *Rhomphaea* with the genus *Argyrodes*, but some workers disagree with the grouping (e.g., Simon 1895; Forster pers. comm.: opinion based on New Zealand species). More information on the foraging behaviors of the two groups of spiders is needed to ascertain if the behavioral characteristics of the two groups support the merger.

Because the taxonomy of *Rhomphaea* is incomplete, the species studied cannot be named. Two populations of *Rhomphaea* were studied; one at Christchurch, New Zealand (43.32°S; 172.37°E) and one at Te Aroha, New Zealand (37.32°S; 175.43°E). As there were no important behavioral differences between the two populations, data were pooled. Voucher specimens have been desposited at the Otago Museum, Dunedin, New Zealand.

METHODS

Field observations.—Surveys of feeding behavior were conducted in the field during both winter (May 1985) and spring (October 1985) in Christchurch and Te Aroha by inspecting bushes and fences. I recorded the type of web upon which
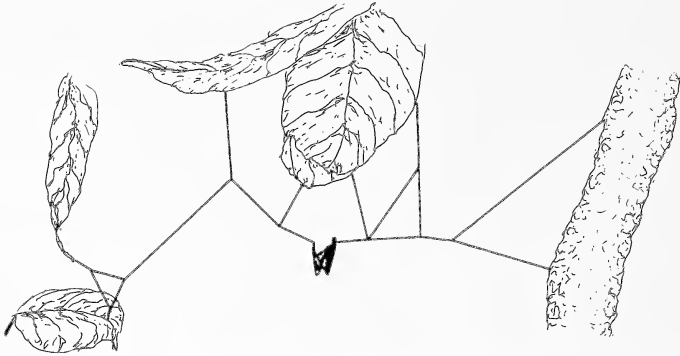
Fig. 1.—Web of *Rhomphaea* located in a bush. *Rhomphaea* is hanging in the middle of the main horizontal thread. Spider is roughly 3 mm long.

Rhomphaea was located, the surrounding habitat, and the activity in which the spider was engaged.

Laboratory studies.—Two types of encounters were staged. The first type was staged in small cylindrical containers (diameter = 5 cm; height = 6 cm) to facilitate spider interaction. The prey spiders were immature *Achaearanea* sp. (Theridiidae), approximately the same size or slightly smaller than the *Rhomphaea*. *Rhomphaea* was either added to the *Achaearanea* sp. cage or vice versa. Spiders were observed for 1-2 h during daylight.

The second type involved *Rhomphaea* responding to prey either on its own web, or on another spider's web. *Rhomphaea*, and potential prey spiders smaller than *Rhomphaea* (which included *Aranea pustulosa* (Walckenaer), *Badumna longinquus* (L. Koch), *Achaearanea* sp., and *Leucauge dromedaria* (Thorell)) established webs in separate spider cages 20 cm long, 8 cm deep, 10 cm wide (see Jackson 1974 for a detailed description of cages). Observations began when either a prey spider was introduced to a cage containing *Rhomphaea* or *Rhomphaea* was introduced to a cage containing a prey spider. The ensuing interaction was observed for 1-2 h. After this period the spiders were often left together for 1-2 days to see if capture occurred.

Maintenance.—Spiders were housed in a room with controlled temperature (22°C-25°C) and light (12:12, L:D). The daylight hours were reversed for the second series of tests and the spiders were observed during their night time.

RESULTS

Habitat.—*Rhomphaea* was found at night in its sparse web (ca 15 cm long) in bushes and other sheltered areas. The web consisted of one main thread, roughly horizontal to the substrate, which had other vertical (secondary) threads ascending from it (Fig. 1). It was usually strung below a branch or ledge in areas where webs of other spiders (such as *Badumna longinquus*, *Achaearanea* sp., and *Cambridgei antipodiana* (White)) were common. *Rhomphaea* usually hung close to the middle of the horizontal thread, 3-8 cm below the branch or ledge. *Rhomphaea* only came out on its web at night. During the day it rested (usually among detritus) by hanging ca 5 mm below a branch or ledge on a single horizontal thread ca 4 cm long.
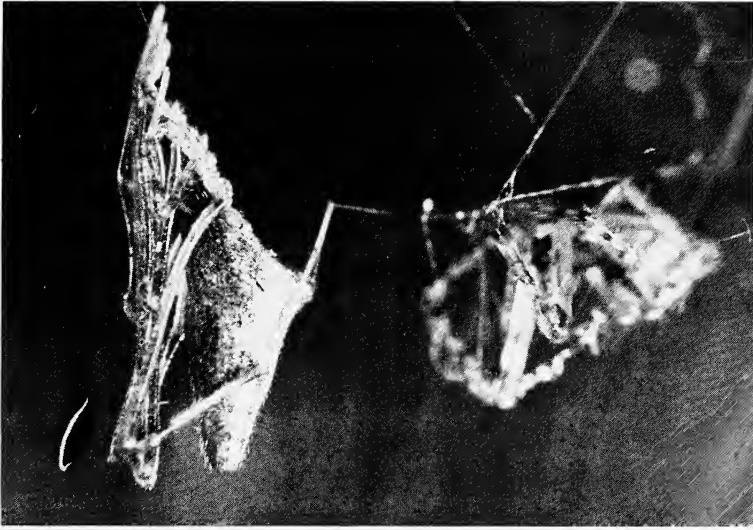
Fig. 2.—*Rhomphaea* (right, foreground) in hunched position next to its recently captured wrapped prey, an *Achaearanea* sp. (left, background). *Rhomphaea* is hanging dorsal side downwards with its legs pulled in close and flexed over its cephalothorax.

Cryptic appearance.—*Rhomphaea* is a small spider (body length: ca 3 mm), with a triangular abdomen, whose body and legs are various shades of light brown. This coloring enabled the spider to blend into its background of dried leaves and twigs. Camouflage was enhanced by the spider adopting the *hunched posture* (Fig. 2) in which all legs (except legs IV) were flexed sharply at the femur-patella joint so that the tibia lay against the femur, and the femora of all its legs lay against the triangular-shaped abdomen. Thus the whole animal resembled a triangular piece of leaf, making detection almost impossible (for a human).

Occasionally, *Rhomphaea* adopted the *extended posture* (Fig. 3), in which legs I and II were held directly anterior to the body.

Field observations.—Of 38 *Rhomphaea* found in the field, 31 were on their own web either in the hunched, extended, or alert posture (see below); two were
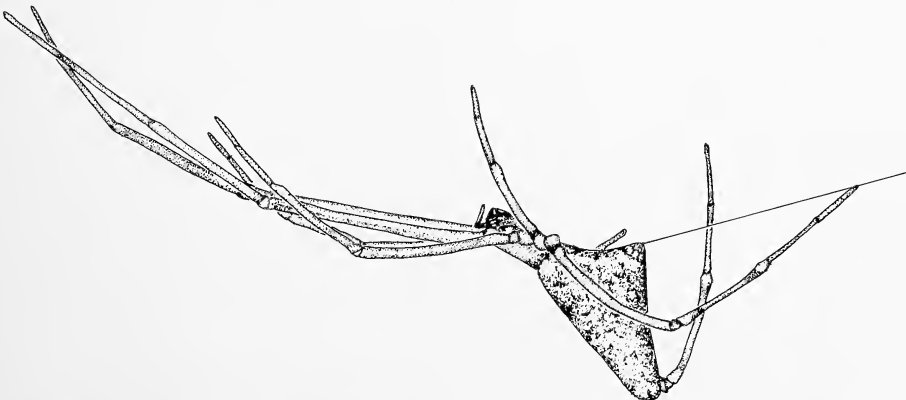

Fig. 3.—*Rhomphaea* in the extended posture. By extending legs I and II anteriorally in this manner, *Rhomphaea* resembles a twig.
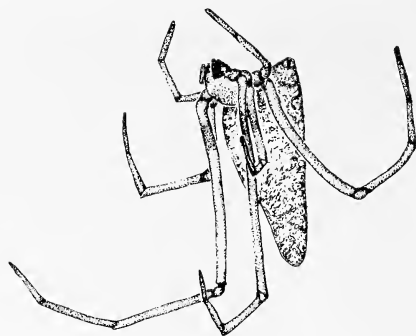
Fig. 4.—The alert posture was assumed by *Rhomphaea* when another spider moved on the same web.

on their own web interacting with other spiders (one *Rhomphaea* had wrapped up an *Achaearanea* sp.; the other was responding to an araneid that was moving onto its web); five were in the webs of other spiders (*Badumna longinquus* (*Rhomphaea* had caught this spider), *Argyrodes antipodiana*, *Leucauge dromedaria*, and two theridiid webs (web owners were not present)).

Elements of predatory behavior.—*Alert posture*: In the alert posture (Fig. 4), *Rhomphaea* extended legs I so that the femora were parallel and dorsal, the tibiae were angled ca 120° to the femora and pointed anteriorly and slightly laterally, while the metatarsi and tarsi were flexed slightly. The femora of legs II (which were lateral to legs I) were also extended dorsally while the tibiae were extended anteriorly. The metatarsi and tarsi of legs II were angled anteriorly so that the tarsal tip was ventral to the animal's mouthparts. Legs III were held ventrally to the spider.

Rotary probing: During rotary probing the spider moved its leg I (mainly at the coxa-trochanter joint) causing the tarsal tip of the leg to describe a circle (diameter: ca 2-6 mm; duration: ca 0.3-1.0 s).

Vibrating techniques: Four vibratory behaviors were observed: standard bouncing, palpating, shuddering, and small pulling. *Standard bounces* occurred intermittently during normal locomotion, just prior to locomotion, or in response to vibrations on the web. Movement by legs III and IV caused the body to oscillate smoothly dorso-ventrally (amplitude: ca 1 mm; duration: 0.5 s per bounce) in bouts of ca nine bounces. To *palpate*, the spider held its long palps in front of the body with the femur directed dorsally and the tibia, metatarsus and tarsus pointing ventrally (towards the silk). *Rhomphaea* moved its palps rapidly dorso-ventrally with the tarsi contacting the silk alternatively at the end of each ventral stroke (rate: ca six per s; amplitude: ca 0.3 mm; duration of bout was variable but was ca 2 s). During *shuddering*, the body of the spider oscillated so rapidly dorso-ventrally that it became a blur (amplitude: ca 0.5 mm; duration: ca 0.25 s). Bouts of shudders occurred at the rate of one per 1-2 s. To *small pull*, all legs in contact with silk were flexed slightly (ca 0.5 mm; duration: 0.1 s; rate: two per s) at the trochanter-femur joint, pulling the silk towards the body and then releasing it slowly in a smooth movement.

Pre-attack behavior: Before attacking its prey, *Rhomphaea* hung from the web by legs I, grasping its dragline with a leg II (Fig. 5a). It then drew more silk out of its spinnerets with first one leg IV and then the other. Thus the tarsi of both legs IV and one leg II held a triangle of silk (Fig. 5a). Large droplets of glue were

present on the silk as it was drawn out of the spinnerets. These covered the thread between the legs IV and continued over half way up the sides of the triangle towards leg II. Almost as soon as the net was complete, *Rhomphaea* scooped.

Scoop: When the approaching prey was 2-3 mm away, *Rhomphaea* scooped (Fig. 5b) by moving the triangular net towards the prey with both legs IV in unison. As legs IV moved the net towards the prey, the leg II that was holding the upper corner of the net also moved towards the prey. If the net adhered to the prey, up to ca three more nets were cast over the victim at a rate of ca two per s. If *Rhomphaea* missed the prey with the scoop, it immediately ate the triangular net.

Post-attack behavior: Once the prey was entangled, *Rhomphaea* approached and began wrapping it quickly with alternating sweeps of legs IV (ca six attachments per s) for ca 2 s. It bit the prey's leg then either continued to wrap or paused a few seconds while the victim's struggles subsided. A wrapped prey was covered with only enough strands of silk to bundle its legs against its body (Fig. 2). Finally the prey was carried higher in the web via a thread from the prey to the spider's spinnerets that was held by leg IV.

Sequences of behavior observed in the laboratory.—*Rhomphaea* first responded to prey spider's movements by assuming the alert posture. If the prey continued to move, *Rhomphaea* often began luring it by palpating, shuddering and/or giving small pulls while in the alert posture. The prey spider usually responded to the displays by rushing towards the predator who assumed the pre-attack posture (the resulting vibrations continued to lure the prey), and attacked by scooping.

Rhomphaea frequently made mistakes when it scooped. Sometimes the pre-attack position was assumed too soon, and *Rhomphaea* either scooped in front of the victim missing it, or the prey stopped short. One *Rhomphaea* in a densely woven juvenile *Achaearanea* sp. web scooped in the opposite direction to the prey.

Rhomphaea on its own web caught *Leucauge dromedaria* and *Achaearanea* sp. at least once, and attempted to catch *Aranea pustulosa*. On the prey's web *Rhomphaea* caught *Achaearanea* sp. and *Aranea pustulosa*. The prey responded at least once to palpating and small pulls by moving towards *Rhomphaea*. Surprisingly, simply walking on the web routinely lured prey (8 out of 15 recorded observations). However, *Rhomphaea* often rotary probed or palpated while walking, and these movements may have been what actually attracted the prey.

DISCUSSION

Aggressive mimicry.—*Rhomphaea* produces vibrations on the web of the prey spider which cause the prey to respond to *Rhomphaea* as if it were food caught on the web, and run towards *Rhomphaea* who is therefore an aggressive mimic. By thus manipulating the behavior of the potentially dangerous prey, *Rhomphaea* presumably enjoys greater ease and less danger when catching prey than if the prey's behavior was uncontrolled. The advantages resulting from manipulating the prey's behavior have probably resulted in the majority of specialized web-invading araneophagic spiders adopting aggressive mimicry (see Whitehouse 1986).
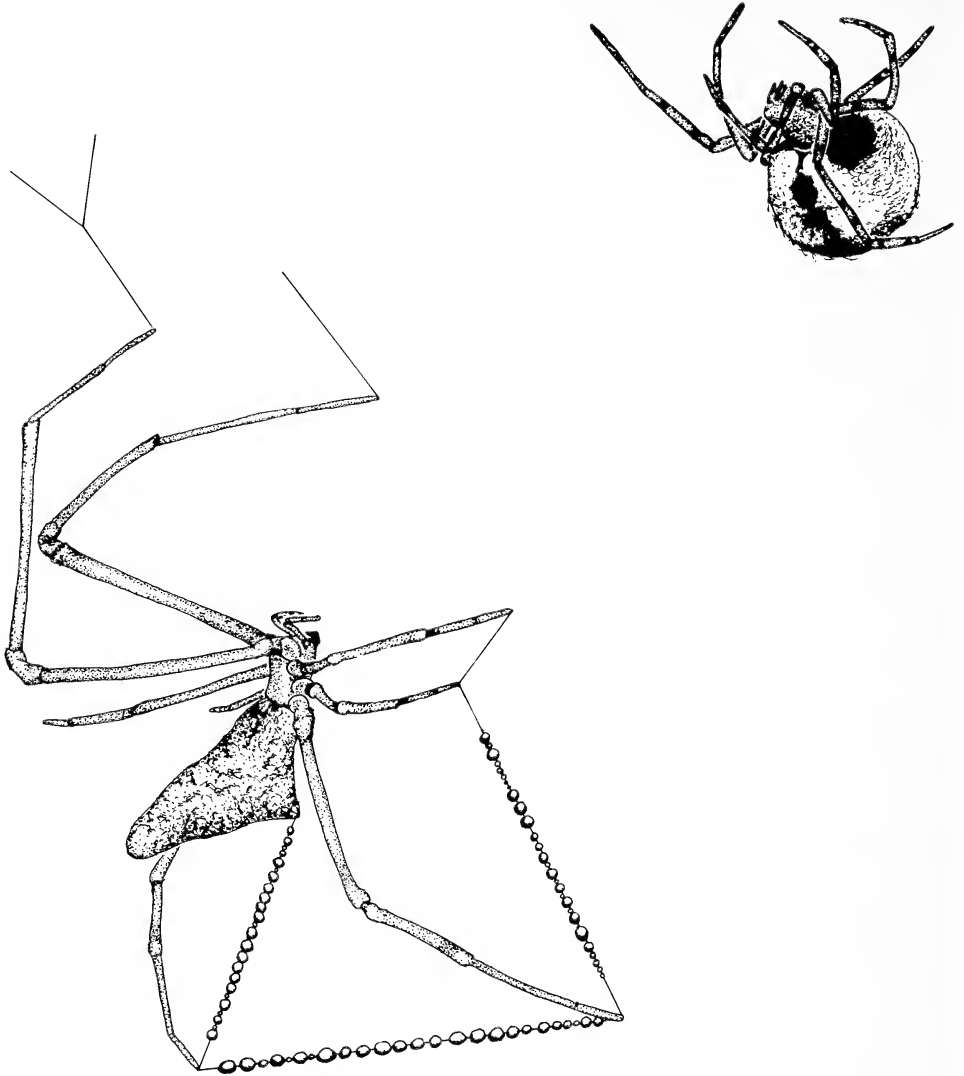
Fig. 5a.—*Rhomphaea* (bottom, left) holding its triangle net just prior to catching the *Achaearanea* sp.

These advantages may explain why *Rhomphaea* employs specialized vibratory techniques even though walking alone was effective at luring prey. *Rhomphaea* responded to prey lured while walking by momentarily stopping, perhaps to "read" the vibrations of the prey accurately. *Rhomphaea* may thus need to stop in order to accurately gauge where to cast the net.

The standard bounce rarely lured prey, and may be primarily defensive, rather than predatory. Stick-mimicking phasmids and mantids rock backward and forward or side to side in a manner suggested to resemble a leaf or stem being gently blown by a breeze in the forest (Robinson 1969). The standard bounce also fits this imagery, and may be used by *Rhomphaea* to conceal itself from its own visually hunting predators.

Comparisons with the genera *Ariamnes* and *Argyrodes*.—*Ariamnes*: Exline & Levi (1962) merged the genus *Ariamnes* with *Rhomphaea* and *Argyrodes*.
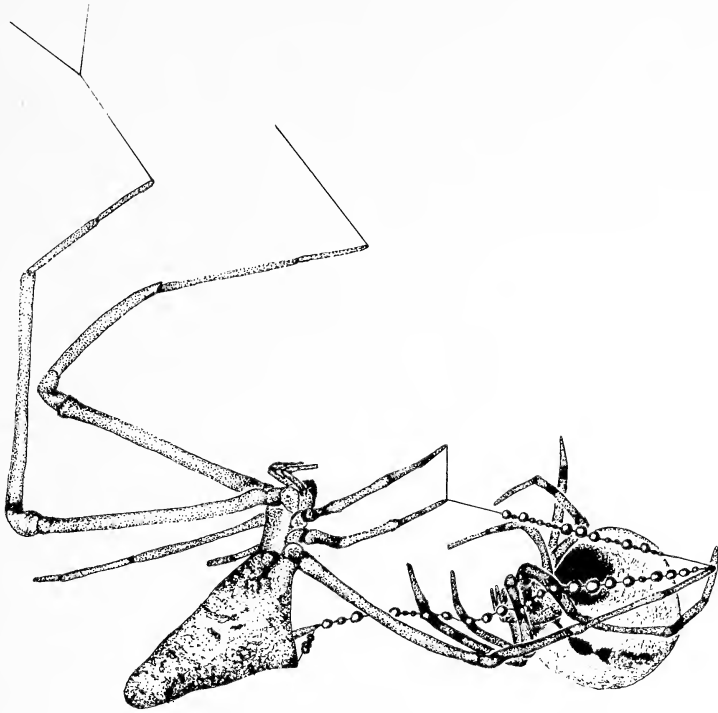
Fig. 5b.—*Achaearanea* sp. is lured towards a *Rhomphaea* which scoops with a triangle net, catching the spider. To scoop, legs IV are rotated ventrally at the trochanter-femur joint.

Ariamnes colubrinus (Keyserling) (Clyne 1979) and *Ariamnes attenuatus* (O. P. Cambridge) (Eberhard 1979) use a similar scooping behavior to that of the New Zealand *Rhomphaea* to catch their prey. However, *Ariamnes* has relatively longer legs than *Rhomphaea* and unlike *Rhomphaea*, neither species of *Ariamnes* appears to use a leg II to form a complete triangle. By using leg II the triangular net is no longer apexed at the spider who may thus enjoy greater safety from the prey should the net be misthrown. Another difference is that *Ariamnes attenuatus* has modified hairs with which to hold the sticky silk (Eberhard 1979) whereas New Zealand *Rhomphaea* has no such hairs (Whitehouse unpubl. data). A third difference is that *Ariamnes* is only known to catch spiders and flies on its own web, while *Rhomphaea* ventures onto foreign webs to capture prey.

Argyrodes: This genus is well known for its kleptoparasitic species some of which are also araneophagic. *Argyrodes antipodiana* uses a different method to lure and capture spiders than species from the genera *Rhomphaea* and *Ariamnes*. Instead of ensnaring them in a net, *A. antipodiana* lunges, encircling the prey with legs I and II, and pulls the spider in towards its mouth (Whitehouse 1986). This method is similar to that used by species of *Mimetus* (Jackson & Whitehouse 1986).

Evolution.—The degree to which the genera *Argyrodes*, *Ariamnes*, and *Rhomphaea* are related and whether they should be treated as one or three genera is unclear. Presumably their common ancestor was a web-builder which caught prey by wrapping it with silk in a manner similar to that of many other theridiids such as *Achaearanea* sp. The behavioral repertoires of *Argyrodes*,

Ariamnes and *Rhomphaea* have diverged in different directions from such an ancestor. The genus *Argyrodes* (as represented by *A. antipodiana*) now lunges at prey with legs I. In contrast the New Zealand *Rhomphaea*, and species of *Ariamnes* all catch prey by scooping. This behavior may be a synapomorphy linking *Rhomphaea* more closely to *Ariamnes* than *Argyrodes*.

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WATER SURFACE WAVES GENERATED BY THE MALE PISAURID SPIDER *DOLOMEDES TRITON* (WALCKENAER) DURING COURTSHIP BEHAVIOR

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ABSTRACT

The semi-aquatic spider *Dolomedes triton* inhabits the littoral zone of ponds and lakes. During the mating season male *D. triton* perform displays consisting of leg-waving, single or successive jerks, and palpal drumming. The jerks cause bursts of concentric water surface waves which may provide information for the female. Jerk-generated waves are considerably regular in the time course, have a duration of 900 ± 145 ms, and do not contain frequencies above 55 Hz. In contrast, terrestrial insects trapped at the water surface generate wave stimuli which are long lasting (in most cases > 2 s), irregular in the time course, and usually include frequencies above 55 Hz (Lang 1980; Bleckmann 1985a). Thus wave signals produced by male *Dolomedes* during courtship behavior lack "prey" (insect) wave characteristics, which may ensure that female *Dolomedes* and other surface dwelling predators do not regard the courting males as insect prey.

INTRODUCTION

The fishing spider *Dolomedes triton* (Walckenaer) inhabits the littoral zone of lakes and ponds (Carico 1973; Bleckmann and Rovner 1984). Fishing spiders prey opportunistically on aquatic- and semiaquatic insects, as well as terrestrial insects that have fallen into the water (Carico 1973; Williams 1979; Bleckmann and Barth 1984). In addition these spiders catch vertebrates such as small fish, frogs, and tadpoles (Gudger 1922; Bleckmann and Lotz 1987). *D. triton* detects, recognizes, and localizes its prey with the aid of water surface waves (Bleckmann and Barth 1984; Bleckmann and Lotz 1987). Terrestrial insects trapped at the water surface generate wave stimuli which are long lasting (in most cases > 2 s), irregular in the time course, and usually include frequencies above 55 Hz (Lang 1980; Bleckmann 1985a). Consequently, artificial wave stimuli with these characteristics effectively elicit prey capture behavior in *Dolomedes* (Bleckmann and Barth 1984; Bleckmann 1985a).

Fishing spiders live in a complex vibratory environment. Not only prey objects, but abiotic sources such as leaf, seed, or twig fall also generate water surface waves. These types of wave stimuli are short-lasting (< 1 s, Bleckmann 1985a), have a regular time course (if compared with insect waves), and rarely contain

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frequencies above 50 Hz (Lang 1980). The same holds for the waves generated by small fish, toads, and tadpoles when they contact the water surface (Bleckmann and Lotz 1987). *D. triton* responds to this type of wave stimulus in less than 2% of the cases with prey capture attempts (Bleckmann 1985a; Bleckmann and Lotz 1987). Wind-generated water surface oscillations constitute a third type of vibration with which fishing spiders have to deal. Wind-generated wave stimuli do not have frequencies above 10 Hz (Bleckmann and Rovner 1984). Like web spiders (Klärner and Barth 1982; Masters 1984) and spiders hunting on a solid substrate (Hergenröder and Barth 1984), *D. triton* rarely can be induced to attack a vibrator below a frequency of 10 Hz (Bleckmann and Barth 1984).

During the mating season male *Dolomedes* perform displays of leg-waving, palpal drumming, and jerks. The jerks, especially, cause easily visible bursts of concentric surface waves, which may provide information for the female (Roland and Rovner 1983). This raises the question whether and how the wave stimuli generated by the courting male differ from prey waves and water disturbances caused by abiotic sources. To solve this question we have recorded surface waves caused by male *D. triton*. Our experimental results show that jerk-generated wave stimuli resemble abiotically or vertebrate-generated wave stimuli in many aspects, i.e., they have a regular time course, a mean duration of less than 1 sec, and an upper frequency limit which rarely exceeds 55 Hz. This suggests that courtship signals are unlikely to be misinterpreted as insect prey stimuli by female *Dolomedes* or by other surface-dwelling predators (Bleckmann 1985b).

GENERAL METHODS

We used mature male and female *Dolomedes triton* for the experiments. All the spiders were collected in Athens, Ohio, USA, and housed individually in small jars (diameter 13-15 cm). The jars, which were filled a few cm deep with fresh water, contained a floating piece of styrofoam, serving as a resting site. The spiders were fed once a week with at least one fly (*Calliphora vicina*). We blinded all spiders by covering their eyes with correction fluid (Tipp-Ex = Liquid Paper®), because intact *Dolomedes* tend to respond to the slightest movement of the experimenter with fright reactions (Bleckmann and Barth 1984), thus being less suitable for experimentation. Spiders were given at least one day to acclimate to the blindess. For the experiments, we introduced a female spider to the experimental tank (50 x 60 cm, water depth 5.5 cm) and encouraged it to move around over the water surface. To minimize wave reflections, the experimental tank had a flat bank (slope 15-20°) covered with foam rubber. The entire experimental setup rested on air bags, which attenuated wave stimuli caused by vibrations of the building by at least 33 dB in the range 5-100 Hz (Bleckmann and Lotz 1987). After a waiting period of about 30 minutes, a male spider was introduced into the experimental tank on the side opposite the resting female. In most cases the male soon began with the first phase of courtship behavior.

The behavior of *D. triton* had been filmed previously with a a Cine-8 high-speed camera (Visual Instrumentation Corp., Model SP-1) at 100 frames per sec. We used a Lafayette Super 8 Analyzer (Model 926) with a frame counter to perform a frame-by-frame analysis.

A submerged emitter electrode, carefully placed close (5-10 cm) to the female spider, measured the wave stimuli. The method of wave measurement is based on
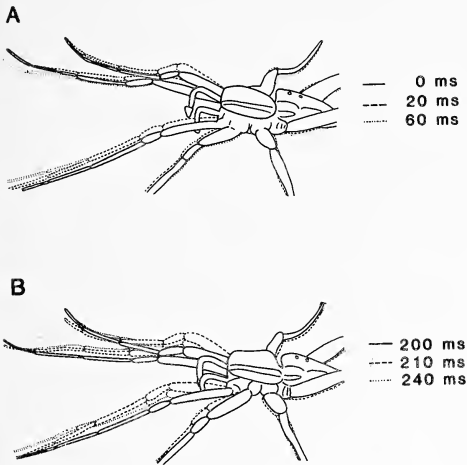
A

—— 0 ms
--- 20 ms
········ 60 ms

Fig. 1.—Leg movements of male *D. triton* during two successive jerks. The drawings are based on high-speed cinematography.

B

—— 200 ms
---- 210 ms
········ 240 ms

the principle that the electrical resistance between the emitter electrode inserted into the circuit of a Wheatstone bridge (Phillips PR 9307) and a receiver electrode depends on the depth of immersion of the latter. When the water surface is motionless, the Wheatstone bridge can be balanced. Any change in the water level at the receiver electrode disequilibrates the bridge and delivers in the range of 0-0.5 mm a voltage output which is linear to the wave amplitude. We stored the demodulated output of the Wheatstone bridge on an FM-tape (Howell CR 3000). For analysis the wave recordings were digitalized (Digital Equipment Corp., Minc 11; 512 data points, dwell time 3.1 or 3.9 ms), and stored on floppy disc for further processing. The frequency content of the wave stimuli was evaluated on the basis of the -60 dB bandwidth of the power spectra.

RESULTS

After introduction to the experimental tank which housed the female or after contacting the dragline of the female on land or water, male *D. triton* usually begin the first phase of signaling. This involves leg-waving and jerks (Roland and Rovner 1983). The former includes lifting legs I, usually in irregular alternation, with these legs typically being held extended straight or just slightly arched. Most often, the tarsus describes a vertically elliptical path. The leg-waving is presumably a long-distance visual signal (ibid.). At irregular intervals, while holding all the legs in contact with the substrate, the male performs one to three jerks. Each results from one or, more typically, two partial flexions and extensions at the femoro-patellar joint of legs I and, to a much lesser degree, legs II (Fig. 1). In the one case studied by single frame analysis, visible surface waves arose 20 ms after the initial jerk movement started. Then, 200 ms after the first jerk, which lasted for about 40 ms, the male displayed a second jerk which, within 30 ms, also generated a visible wave signal. In general, a noticeable effect of a jerk on water is a burst of concentric surface waves spreading outward from the male. In response to the male approach, the female may also generate water surface waves by rapidly vibrating her pedipalps. However, we did not attempt to record any female-generated wave stimuli.
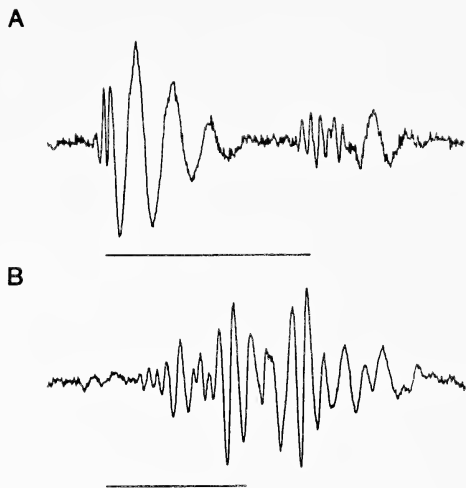
A

B

Fig. 2.—Two representative examples of jerk-generated wave stimuli produced by a single jerk (A) or by three successive jerks (B). The distance between the spider (reference point middle of the prosoma) and the wave measuring electrode is about 10 cm in A and 15 cm in B. Both stimuli were bandpass filtered from 10 to 1000 Hz. Time bar in A and B 500 ms.

Male-generated wave stimuli are sinusoidal and—if caused by a single jerk—click-like (Fig. 2A), i.e., these stimuli are short-lasting and have a regular downward frequency modulation which is probably caused by the dispersion relationship of capillary water surface waves (Sommerfeld 1970; Bleckmann and Schwartz 1982). If measured at a distance of 5-20 cm, wave signals generated by up to three successive jerks (Fig. 2B) have a mean duration of 900 $\pm$ 145 ms and an upper frequency limit of 55 Hz. The spectral amplitude maximum of these signals is found at around 7.3 $\pm$ 2.6 Hz ($N=5$, $n=25$) (Fig. 3).

DISCUSSION

The courtship signaling of spiders often exploits the predominant sensory modality in the prey detection system of the family or other taxon (Robinson 1982). Therefore it is not surprising that male *D. triton* use vibratory signals to court a female. In our experiments both the male and female spiders were allowed to move freely. The wave-measuring electrode was usually placed close to the female. However, the distance between the male and the wave-measuring electrode often exceeded 10 cm. Due to the strong damping of high-frequency water surface waves and the dispersion characteristics of the water-air interface (Sommerfeld 1970) our recordings may be biased—with respect to the waves a female experiences if close to the male—in that they have a too low upper frequency limit and a too long duration. However, the distance between male and female varies during courtship displays, i.e. depending upon the distance, the female will experience different wave stimuli. This makes it unlikely that the wave parameters of frequency content, duration, and amplitude have to be within a narrow range in order to transmit species-specific information. Female *Dolomedes* know the distance a wave signal has travelled (Bleckmann and Barth 1984), and there are strong indications that they weigh a wave stimulus according to that distance (Bleckmann 1987).

According to our results a wave stimulus produced by a single jerk is not very specific. Whenever the water surface is set into oscillation by a short-lasting (click-like) event, (i.e., by a falling leaf, seed, or twig) wave stimuli of short
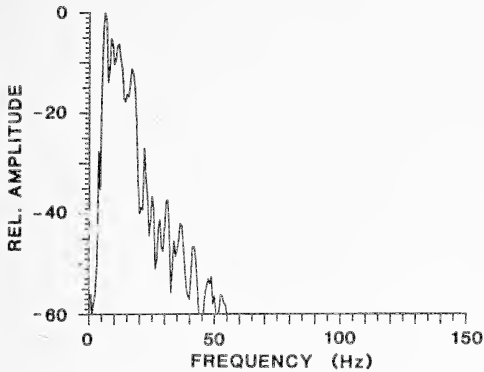
Fig. 3.—Representative example of the power spectrum of a jerk-generated wave stimulus produced by male *D. triton* during courtship display. Wave stimuli produced by one or two successive jerks were not distinguished.

duration, a regular time course, and a regular frequency downward modulation result (Bleckmann 1985a). The upper frequency limit of these stimuli rarely exceeds 50 Hz (Lang 1980; Bleckmann 1985a). As has been shown, click-like waves trigger prey capture behavior in *Dolomedes* in less than 2% of the cases even if the amplitude of these signals is far above threshold and the upper frequency limit reaches 78 Hz, i.e. includes frequencies unique to insect generated waves (Bleckmann 1985a). Thus even at close distance a courting male is unlikely to be misinterpreted as insect prey as long as it generates vibrations by a single jerk. The question remains, however, whether and how male-generated courtship stimuli can be recognized as such.

Male *Dolomedes* often perform two or even three jerks in quick succession. The upper frequency limit of 55 Hz and the mean duration of less than 1 sec still guarantees that these stimuli are insufficient to release prey capture behavior (Bleckmann 1985a). However, because a falling leaf or seed generates only one click at a time and place, it may well be that the quick repetition of two or even three jerks is one cue which enables the female to identify the male stimulus as such.

The best studied example of vibratory courtship behavior in spiders is that of the nocturnal Central American wandering spider *Cupiennius salei* (Keys.), which lives on banana plants, agaves, and bromeliads (Barth and Seyfarth 1979). Courting male *Cupiennius* produce a series of syllables, each of which consists of several impulses (Rovner and Barth 1981; Schüch and Barth 1985). The responsiveness of female *C. salei* to artificial courtship signals can be altered by changing the syllable duration, the intersyllable pause duration, or the syllable frequency content (W. Schüch, unpublished; Barth 1985). A single wave pulse generated by a courting male *Dolomedes* may be defined as a syllable. When approaching a female, a male *D. triton*, from time to time, generates a syllable. However, a regular timing of syllables was not discovered, at least not by simple visual observation.

Broadcast courtship displays are often replaced by low-range types of signals as soon as a mate has been attracted at close distance (Markl 1985). In addition to jerk-signals, male and female *Dolomedes* generate small, but visible, waves by palpal drumming. Although our recording device was not sensitive enough to detect these signals, it may well be that they contain additional species and sex-specific cues used by the female *Dolomedes* to identify a mate. Only careful further studies can show whether fishing spiders have a communication system

based on the exchange of vibratory signals equally sophisticated as that reported for some water striders (Wilcox 1972, 1979).

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ECOMORPHOLOGICAL FACTORS INFLUENCING
PREY USE BY TWO SYMPATRIC SPECIES
OF ORB-WEB SPIDERS, *ARGIOPE AURANTIA*
AND *ARGIOPE TRIFASCIATA* (ARANEIDAE)

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ABSTRACT

Two species of orb-web spiders, *Argiope aurantia* Lucas and *Argiope trifasciata* (Forskal) were used
to analyze how accurately spider and web characteristics could predict the type, size, and number of
prey captured. The ecomorphological hypothesis proposes that spider and web characteristics
determine what subset of the prey population actually will be captured. Prey size and taxa are
functions of web height, web diameter and spider size. Mesh density is a poor predictor of these
parameters. The number of prey captured by spiders is not correlated with any spider or web
characteristic except mesh density of *A. aurantia*. Species-specific differences in spider and web
characteristics occurred until both species reached maturity (October). The major differences were that
A. trifasciata were smaller and matured later than *A. aurantia*. These differences were accompanied by
species-specific differences in the size and taxa of prey, but these parameters also converged during
October. Differences in the two species may have evolved because of (1) exploitation competition, (2)
non-competitive resource partitioning, or (3) interference competition. The diet overlap of the two
species was generally high but increased even higher in October. Therefore, it is doubtful that dietary
differences were sufficient to prevent exploitation competition.

INTRODUCTION

The morphology of trophic structures in predators may influence the size and
type of prey captured (= ecomorphological hypothesis, see Wiens and Rotenberry
1980). Therefore, species-specific differences in morphology may partition prey
between species (Hutchinson 1959; but see Wiens and Rotenberry 1980, 1981).
However, the effect of predator morphology on foraging and resource
partitioning rarely has been tested on individuals in the field (Wiens and
Rotenberry 1980). For spiders, body or leg size may determine the maximum size
of prey (Brown 1981; Murakami 1983). In general, overall foraging success
apparently is affected by seasonal and yearly changes in both prey characteristics
(abundance, size, and taxa) (Riechert and Luczak 1982) and spider characteristics
(size, activity, and web) (Riechert and Luczak 1982; Howell and Ellender 1984).

Different species of spiders appear to divide food resources by differences in
size, foraging behavior, or spatial and temporal activity patterns (Uetz 1977;
Turner and Polis 1979). Differences in foraging behavior, morphology, web

height, and web location may lead to differential capture of prey (Enders 1974; Uetz et al. 1978; Olive 1980, 1981a; Brown 1981). Such species specific differences ultimately may result from competition (Enders 1974; Olive 1980; Brown 1981).

The relationships of spider size and web characteristics to foraging characteristics of two orb-web spiders, *Argiope aurantia* Lucas and *Argiope trifasciata* (Forskal) were analyzed because these spiders commonly occur in the same habitats and with similar daily activity patterns. Therefore, partitioning of prey resources is predicted (see Brown 1981). The ecomorphological hypothesis was tested to determine which, if any, spider or web characteristics were good predictors of prey characteristics. Temporal and species-specific differences in spider size, web characteristics, and prey captured were described and compared.

MATERIALS AND METHODS

The study was conducted in old fields and disturbed areas in the Radnor Lake State Nature Area, Nashville, Tennessee, from July through October from 1981-1984. Major components of the vegetation included several species of grass, goldenrod (*Solidago* sp.), ironweed (*Vernonia* sp.), and smartweed (*Polygonum* sp.). Other vegetation included pasture rose (*Rosa* sp.), ragweed (*Ambrosia artenisiifolia*, and thistle (*Cirsium vulgare*).

Argiope aurantia and *Argiope trifasciata* (Araneidae) are located easily because of their relatively large size, their habit of sitting in the hub of their large orb-webs (see Reed et al. 1969), the zig-zag stabilimentum at the hub (see Lubin 1974; Tolbert 1975; Horton 1980), and their diurnal habits. The webs of *Argiope* are built in vegetation of old fields and disturbed sites (Enders 1973; Tolbert 1979; Sholes and Rawlins 1979; Olive 1981b). Large prey are wrapped in silk before being carried to the hub while small prey are bitten and carried directly to the hub (see Robinson 1969; Robinson et al. 1969; Hardwood 1974). Maturity is reached in September and October (see Olive 1980; Howell and Ellender 1984). Adult female (> 20 mm) *Argiope* are much larger than adult males (< 10 mm). In September, mature males stop building their own web and are usually located near female webs (Olive 1982). There is only one generation per year: egg production occurs in September and October (Olive 1980; Horton and Wise 1983), the young overwinter in the egg sac, and emergence is in April and May (Tolbert 1977).

The following data were collected: (a) description of the spider (species, total length, abdomen width), (b) web parameters (diameter at the widest point, height from the ground to the hub, and mesh density = number of web spirals per centimeter of web in the middle of the lower spiral zone), and (c) prey captured (prey number per spider per observation period = number of prey captured by a spider during a day of observation; prey size = total length; and prey taxa = order of prey). A prey item was considered captured after it had been wrapped by the spider or carried to the hub. During 1981 and 1982, prey were collected from the webs daily, identified and measured in the laboratory. During 1983 and 1984, prey were identified and measured in the web daily. A bias in the observed number of prey captured per day may occur because prey with a short handling time may be consumed before it was observed or prey with a long handling time may be included in more than one observation period (Fairweather and Underwood 1983). The first bias was possible, but it was unlikely that prey were

Table 1.—Length, taxa, and number of prey captured as a function of spider size class. An one-way ANOVA and a G-test of independence are used to test differences between size classes (X = mean prey length (mm), SD = standard deviation, N = total number of prey, M = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method, $P < 0.05$).

	Spider Size (mm)											
	A. aurantia						A. trifasciata					
	6-10	11-15	16-20	21-25	26-30		6-10	11-15	16-18	19-21	22-25	
Length:						F						F
X	8.7	12.1	12.7	13.0	12.5	1.58	6.6	9.8	11.7	11.4	11.2	6.60
SD	3.04	6.28	4.28	4.85	5.58	ns	2.06	3.40	3.51	3.81	3.83	<0.001
N	7	11	216	235	32		11	39	105	79	5	
							a	ab	c	bc	abc	
Taxa:						G						G
OR	0.0	72.7	31.4	25.5	11.1	30.17	18.2	2.6	18.1	15.2	0.0	32.06
HY	57.1	18.2	35.4	34.0	44.4	<0.01	18.2	51.3	53.3	64.6	20.0	<0.01
CO	14.3	9.1	14.1	23.8	25.0		9.1	20.5	17.1	11.4	40.0	
Other	28.6	0.0	19.1	16.6	19.4		54.5	25.6	11.4	8.9	40.0	
N	7	11	220	235	36		11	39	105	79	5	
Number:						G						G
1	100.0	90.0	65.5	64.1	41.2	18.93	88.9	64.3	54.5	61.7	75.0	17.27
2	0.0	10.0	25.7	21.6	35.3	ns	0.0	28.6	34.8	17.0	25.0	ns
3	0.0	0.0	6.8	10.5	11.8		11.1	7.1	7.6	14.9	0.0	
4	0.0	0.0	1.4	3.3	5.9		0.0	0.0	3.0	4.3	0.0	
≥5	0.0	0.0	0.7	0.7	5.9		0.0	0.0	0.0	2.1	0.0	
M	7	10	148	153	17		9	28	66	47	4	

included in more than one observation period because we monitored individual prey that spiders captured in previous observations.

All statistical methods, including a t-test for unequal variances (t'), were from Sokal and Rohlf (1981). After careful consideration, spider and web characteristics were placed in classes instead presented as continuous data because this more clearly demonstrated important trends. Furthermore, most hypotheses address classes of observations, e.g., low versus high webs, large versus small webs, etc. Some data form natural classes (e.g., orders of prey taxa) and are analyzed more clearly by combining spider and web characteristics into classes for use in contingency tables. Data were pooled from 1981-1984.

RESULTS

Ecomorphology.—*Spider size:* Spider size and web characteristics generally influence the size and type of prey captured. However in some cases, there were no clear patterns. Prey size changed significantly with an increase in spider size classes for *A. trifasciata* but not *A. aurantia* (Table 1). The *A. trifasciata* in the smallest class (6-10 mm) captured significantly smaller prey than spiders in larger classes (16-18 and 19-21) (see Table 1). Significantly different prey taxa were captured by different spider size classes of both species (Table 1). The number of prey captured by different spider size classes was not significantly different for either species (Table 1).

Web diameter: For both species, spiders from different web diameter classes captured significantly different sizes of prey (Table 2). *Argiope aurantia* in large

Table 2.—Length, taxa, and number of prey captured as a function of web diameter. An one-way ANOVA and a G-test of independence are used to test differences between web diameter classes ($\bar{X}$ = mean prey length (mm), SD = standard deviation, N = total number of prey, M = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method, $P <$ 0.05).

		A. aurantia						A. trifasciata			
	0-20	20-30	30-40	40-50	50-70		0-20	20-30	30-40	40-50	
Length:						F					F
$\bar{X}$	9.5	12.0	13.3	13.1	12.3	4.55	10.0	12.2	10.5	10.3	4.71
SD	3.10	4.11	4.74	4.83	5.24	$P<0.01$	3.70	3.75	3.35	3.88	$P<0.01$
N	24	90	191	135	60		20	75	103	35	
	a	ab	b	b	ab		cd	c	d	d	
Taxa:						G					G
OR	12.5	20.0	29.8	34.8	26.2	45.71	15.0	16.0	10.7	17.1	11.40
HY	41.7	54.4	38.2	25.2	13.1	$P<0.001$	50.0	58.7	52.4	54.3	ns
CO	25.0	12.2	16.8	21.5	27.9		15.0	18.7	13.6	17.1	
Other	20.8	13.3	15.2	18.5	32.8		20.0	7.7	23.3	11.4	
N	24	90	191	135	61		20	75	103	35	
Number:						G					G
1	80.0	63.8	63.0	62.1	67.5	12.51	73.3	70.6	56.1	50.0	12.72
2	20.0	22.4	26.0	23.0	20.0	ns	20.0	15.7	33.3	35.0	ns
3	0.0	10.3	7.1	12.6	7.5		6.7	9.8	7.6	10.0	
4	0.0	1.7	2.4	2.3	5.0		0.0	3.9	3.0	0.0	
≥ 5	0.0	1.7	1.6	0.0	0.0		0.0	0.0	0.0	5.0	
M	20	58	127	87	40		15	51	66	20	

web diameter classes (30-40 and 40-50 cm) captured larger prey than spiders in the small web diameter class (0-20 cm), and *A. trifasciata* in a middle web diameter class (20-30 cm) captured larger prey than spiders with larger web diameters (30-40 and 40-50 cm) (see Table 2). Prey taxa also were significantly different for *A. aurantia* using different web diameter classes: the frequency of Hymenoptera decreased, and the frequency of Orthoptera increased with an increase in web diameter (Table 2). There was no significant difference in prey taxa captured by *A. trifasciata* using different web diameter classes (Table 2). The number of prey captured in different web diameter classes was not significantly different for either species (Table 2).

Web height: Both prey size and taxa were significantly different for each species using different classes of web height (Table 3). Larger prey were captured by *A. aurantia* in lower web height classes (< 100 cm), but the prey captured by *A. trifasciata* in a middle web height class (40-60 cm) were larger than prey captured by spiders in other web height classes (20-40 and 60-80 cm) (see Table 3). In general, more Orthoptera and fewer Hymenoptera and Coleoptera were captured in lower webs by both species. There was no significant difference in the number of prey captured by spiders using webs of different height (Table 3).

Mesh size: The size of prey captured in different mesh size classes was significantly different for *A. trifasciata* but not *A. aurantia* (Table 4). Mean prey size decreased with increased mesh density for both species, but the high variance in *A. aurantia* obscured statistical significance. Prey taxa were not significantly different for either species using different mesh size classes (Table 4). The number of prey captured in webs of different mesh size classes was significantly different

Table 3.—Length, taxa, and number of prey captured as a function of web height. An one-way ANOVA and a G-test of independence are used to test differences between web height classes ($\bar{X}$ = mean prey length (mm), SD = standard deviation, N = total number of prey, M = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method, $P <$ 0.05).

	Web Height (cm)									
	A. aurantia						A. trifasciata			
	20-40	40-60	60-80	80-100	>100		20-40	40-60	60-80	80-120
Length:						F					F
$\bar{X}$	13.4	13.1	12.5	13.3	10.1	4.14	7.9	11.8	10.3	10.8	3.15
SD	4.80	4.75	4.54	4.68	4.48	$P<0.01$	3.50	3.79	2.97	3.63	$P<0.05$
N	66	183	157	54	41		13	119	65	35	
	a	a	a	a	b		c	d	c	cd	
Taxa:						G					G
OR	44.9	36.1	20.4	19.2	2.5	55.88	9.1	22.0	3.0	5.9	30.87
HY	20.3	30.4	45.9	34.6	42.5	$P<0.001$	36.4	55.1	59.1	52.9	$P<0.001$
CO	14.5	16.5	14.6	30.8	15.0		18.2	7.6	24.2	29.4	
Other	20.3	17.0	19.1	15.3	40.0		36.4	15.3	13.6	11.8	
N	69	194	157	52	40		11	118	66	34	
Number:						G					G
1	74.5	63.8	68.2	58.3	52.2	17.87	62.5	68.3	58.1	40.0	16.43
2	12.8	25.2	21.8	33.3	26.1	ns	12.5	23.2	32.6	35.0	ns
3	6.4	9.4	7.3	8.3	8.7		25.0	3.7	7.0	25.0	
4	4.3	0.8	1.8	0.0	13.0		0.0	3.7	2.3	0.0	
≥5	2.1	0.8	0.9	0.0	0.0		0.0	1.2	0.0	0.0	
M	47	127	110	36	23		8	82	43	20	

for *A. aurantia* but not *A. trifasciata* (Table 4). More prey per spider were captured by *A. aurantia* using smaller mesh size classes (Table 4).

There was not a close correlation (correlation coefficient = 0.15-0.46) between different spider and web characteristics. Therefore, the effect of a particular characteristic on prey capture was largely independent of other spider or web characteristics.

Temporal differences.—*Spider size:* Spider size, web characteristics, and prey size and taxa changed weekly. Females of both species grew over most of the summer (Fig. 1a). However, spider length showed no significant increase after September 1 for *A. aurantia* and after September 16 for *A. trifasciata* (Fig. 1a) suggesting that these spiders were either adult or penultimate females.

Web characteristics: Web diameters of *A. aurantia* (F(4,361) = 13.52 $P <$ 0.001) and *A. trifasciata* (F(4,153) = 8.25 $P <$ 0.001) changed significantly over time (Fig. 2a). Mean web diameter of *A. aurantia* was largest during early September but that of *A. trifasciata* continually increased to the end of the season. Mean web height significantly increased over time for *A. trifasciata* (F(4,157) = 6.372 $P <$ 0.001) but not *A. aurantia* (F(4,370) = 1.13 ns) (Fig. 2b).

Prey: The mean length of prey captured by all spiders showed a significant increase over time for *A. trifasciata* (F(4,234) = 11.27 $P <$ 0.001) but not *A. aurantia* (F(4,537) = 1.43 ns) (Fig. 1b). The identity of prey changed significantly over time for both species (Table 5). The frequency of Coleoptera was high during early September for *A. aurantia*, and the frequency of Hymenoptera increased over time for both species (Table 5). Coleoptera, Hymenoptera, and Orthoptera were the major prey types (Table 5). The major Coleoptera was the

Table 4.—Length, taxa, and number of prey captured as a function of web mesh size. An one-way ANOVA and a G-test of independence are used to test differences between mesh size classes ($\bar{X}$ = mean prey length (mm), SD = standard deviation, N = total number of prey, M = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method, $P <$ 0.05).

| | Mesh (/cm) | | | | | | | | |
| | A. aurantia | | | | A. trifasciata | | | | |
	1-2	3-4	5-6		1-2	3-4	5-6	>6	
Length:				F					F
$\bar{X}$	12.6	11.3	7.6	2.58	12.6	9.3	8.3	7.0	3.12
SD	6.45	5.16	2.07	ns	4.07	4.40	3.17	2.65	P<0.05
N	66	38	7		8	45	14	9	
					a	ab	ab	b	
Taxa:				G					G
OR	15.7	12.8	28.6	9.62	0.0	15.9	7.1	0.0	15.42
HY	45.7	28.2	57.1	ns	37.5	50.0	35.7	22.2	ns
CO	14.3	12.8	0.0		37.5	18.2	14.3	11.1	
Other	24.3	46.2	14.3		25.0	15.9	42.9	66.7	
N	70	39	7		8	44	14	9	
Number:				G					G
1	50.0	66.7	100.0	21.05	85.7	69.7	72.7	66.7	4.04
2	18.8	29.6	0.0	P<0.001	14.3	24.2	18.2	16.7	ns
3	15.6	0.0	0.0		0.0	3.0	9.1	16.7	
4	15.6	0.0	0.0		0.0	0.0	0.0	0.0	
≥5	3.1	3.7	0.0		0.0	3.0	0.0	0.0	
M	32	27	7		7	33	11	6	

soldier beetle, *Chauliotgnathus pennsylvanicus* (Cantharidae) (82% of Coleoptera). The major Hymenoptera was the honeybee, *Apis mellifera* (49%). Other families of Hymenoptera (e.g., Vespidae) that commonly visit flowers were also important prey items. Two families of Orthoptera were captured: Acrididae and Tettigoniidae. Lepidoptera were occasionally important in *A. aurantia's* diet.

Comparisons of the two species.—*Body size:* Although there were species-specific differences in size, web characteristics, temporal patterns, and prey size and taxa there were also many similarities. *Argiope aurantia* was significantly larger than *A. trifasciata* as adult and pentultimate females (Table 6), and always significantly larger during the same biweekly period (July F(1,8) = 11.86 $P <$ 0.01, August F(= 1,25) = 18.23 $P <$ 0.001, Sept. 1-15 F(1,144) = 103.42 P = 0.001, Sept. 16-30 F(1,137) = 28.09 $P <$ 0.001, Oct. 1-15 F(1,111) = 51.60 $P <$ 0.001, and Oct. 16-30 F(1,34) = 5.88 $P <$ 0.05; Fig. 1a). The largest difference in length was during early September where *A. aurantia* had reached adult size, but *A. trifasciata* were still immature.

Web characteristics: Web height of *A. aurantia* and *A. trifasciata* was not significantly different (Table 6). Web diameter was significantly different with *A. aurantia* building a larger web (Table 6). Webs of *A. aurantia* were significantly higher and larger than webs of *A. trifasciata* during early periods but converged towards the end of the season (Web diameter: July–August t'= 2.73 $P <$ 0.05, Sept. 1-15 F(1,114) = 25.69 $P <$ 0.001, Sept. 16-30 F(1,156) = 5.82 $P <$ 0.05, Oct. 16-30 F(1,166) = 0.98 ns, Oct. 16-30 F(1,58) = 0.12 ns; and Web height: July–August t'= 3.44 $P <$ 0.01, Sept. 1-15 F(1,116) = 8.16 $P <$ 0.01, Sept. 16-30 F(1,156) = 0.02 ns, Oct. 1-15 F(1,168) = 0.18 ns, and Oct. 16-30 F(1,58) = 0.09 ns; Fig. 2).
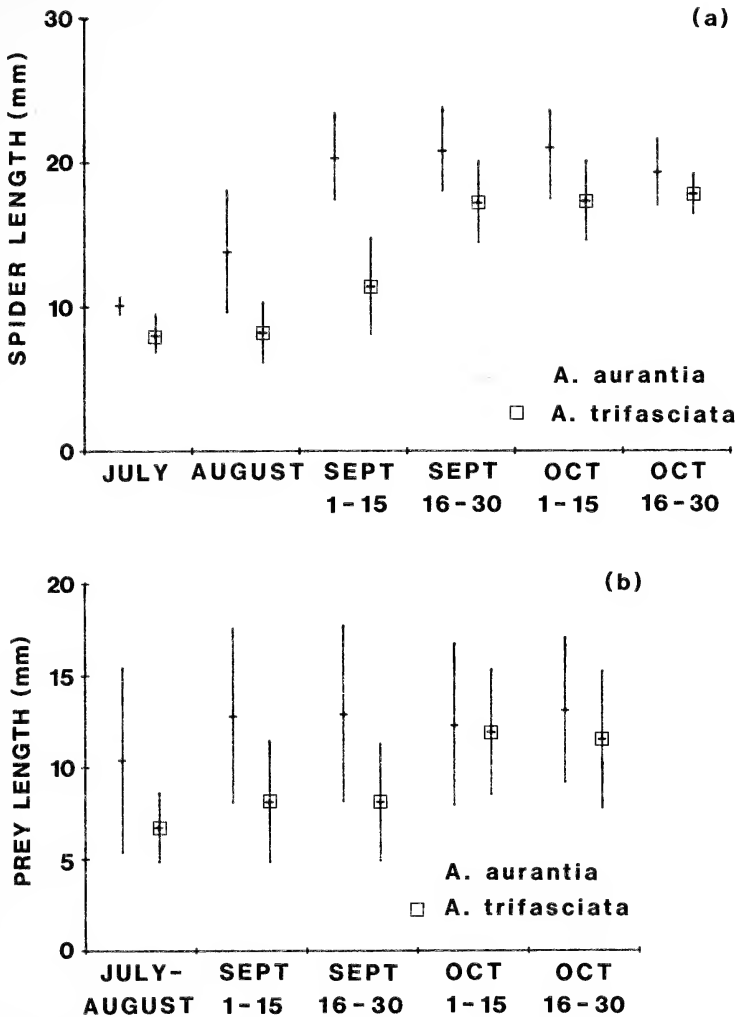
Fig. 1.—Mean (± 1 standard deviation) (a) spider and (b) prey length of *Argiope* during biweekly periods. See text for comparisons over time and among species.

Prey: The length of prey captured by *A. aurantia* was significantly larger than that captured by *A. trifasciata* (Table 6). *Argiope aurantia* took significantly larger prey than *A. trifasciata* during early periods but prey sizes converged during October when almost all spiders were adults (July-August $t' = 3.00$ $P <$ 0.05, Sept. 1-15 $F(1,116) = 15.55$ $P < 0.001$, Sept. 16-30 $F(1,211) = 19.00$ $P <$ 0.001, Oct. 1-15 $F(1,244) = 0.59$ ns, and Oct. 16-30 $F(1,95) = 3.70$ ns; Fig. 1b). Significantly different prey taxa were captured by *A. aurantia* and *A. trifasciata* overall and through most of the biweekly periods until late October (Table 5). There was a tendency for *A. aurantia* to capture more Orthoptera and *A. trifasciata*, more Hymenoptera.

DISCUSSION

Web-building spiders are a good example of sit-and-wait predators (Schoener 1969; Riechert and Luczak 1982). These spiders remain in one site until prey
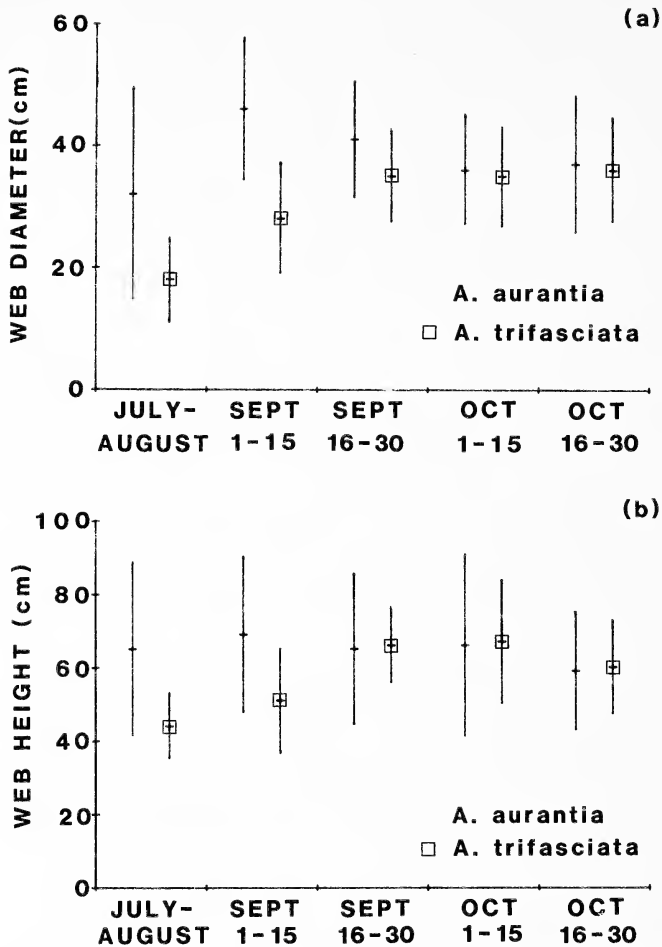
Fig. 2.—Mean (± 1 standard deviation) (a) web diameter and (b) height of *Argiope* during biweekly periods. See text for comparisons over time and among species.

move within attack range and thus cannot influence the number and type of prey encountering the web except by placement of the web in a good micro-habitat (Turnbull 1973). Therefore, spiders should select web-sites or heights that allow the greatest encounter and capture rates (e.g., near flowering plants) (Riechert 1974, 1976; Riechert and Tracy 1975; Uetz et al. 1978; but see Enders 1973, 1977; Colebourn 1974; Schoener and Toft 1983). The best method to evaluate web-site quality is a bioassay of prey capture at different sites (see Castillo and Eberhard 1983).

In summary, prey size and taxa are functions of web height, web diameter and spider size. Mesh density is a poor predictor of these parameters. The number of prey captured by spiders is not correlated with any spider or web characteristic except mesh density of *A. aurantia*.

Proponents of the ecomorphological hypotheses have proposed that spider and web characteristics determine which subset of the prey population actually will be captured (Olive 1980, 1981a; Brown 1981; Murakami 1983). During this research more Orthoptera were captured at low web sites and more Hymenoptera and Coleoptera, at higher web sites by both species (also see Uetz et al. 1978; Olive

Table 5.—Taxa of prey captured by *A. aurantia* (A.a.) and *A. trifasciata* (A.t.) over time with all years combined. The relative frequency of prey is identified to order for each time period. All periods are biweekly except July-August. A G-test of independence is used to test differences between time periods and species (N = total number of prey, ns = not significant, HY = Hymenoptera, OR = Orthoptera, CO = Coleoptera, LE = Lepidoptera, DI = Diptera, HE = Hemiptera, HO = Homoptera, ME = Mecoptera, Other = Other insects, and AR = Araneae).

	Sept. 1-15		Sept. 16-30		Oct. 1-15		Oct. 16-30		Total	
	A.a	A.t.	A.a.	A.t.	A.a.	A.t.	A.a.	A.t.	A.a.	A.t.
Taxa:										
CO	38.0	15.4	15.1	21.7	9.9	17.2	7.4	11.6	21.7	15.9
HY	14.1	30.7	36.6	47.8	50.4	59.4	51.9	53.6	33.2	54.3
OR	27.1	0.0	30.2	0.0	23.1	13.3	25.9	23.2	26.4	14.2
LE	6.8	0.0	2.9	0.0	0.8	1.6	0.0	0.0	4.2	0.4
DI	4.2	23.1	4.4	4.3	0.8	3.1	3.7	1.4	3.4	3.8
HE	2.1	7.7	2.0	0.0	5.0	2.3	3.7	2.9	2.7	2.9
HO	1.6	0.0	0.0	17.4	0.0	0.8	0.0	1.4	0.7	3.3
ME	2.1	15.4	2.4	4.3	0.8	0.8	7.4	4.3	2.2	2.9
Other	3.6	7.7	5.9	0.0	5.0	1.6	0.0	1.4	4.5	1.7
AR	0.5	0.0	0.5	4.3	4.1	0.0	0.0	0.0	1.3	0.4
N	192	13	205	23	121	128	27	69	554	239
Differences between species:										
G	23.02		39.65		20.85		2.53		56.07	
P	<0.01		<0.001		<0.05		ns		<0.001	

Temporal Differences: *A. aurantia* G = 116.19 $P < 0.001$
A. trifasciata G = 56.65 $P < 0.01$

1980; Pasquet 1984a). This suggests that orb-web spiders may influence the type of prey encountered by use of different web sites (see Tolbert 1979; Olive 1980; Biere and Uetz 1981; Greenstone 1984). Larger webs encounter more and larger prey by either covering more area (Olive 1980) or being positioned in the path of large and active prey (Uetz et al. 1978; Howell and Ellender 1984). In this study, larger prey were captured by *A. aurantia* with larger webs. However, smaller prey were captured by *A. trifasciata* with larger webs. Furthermore, overall capture rates of prey by both species were not influenced by web diameter. The encounter rate with smaller prey may increase with denser mesh (Uetz et al. 1978; Murakami 1983). The decrease in mean prey size captured by *A. trifasciata* with an increase in mesh density tends to support this hypothesis; however, it does not explain why (for *A. aurantia*) there was no change in prey size, and there was a decrease in the overall capture rate with an increase in mesh density.

Larger and more dense webs may retain large or clumsy prey (e.g., Orthoptera) longer thus decreasing the probability of escape (Olive 1980, 1981a). Another predator, an antlion, attempted to capture larger ants when its pit was larger (Heinrich and Heinrich 1984). Mean prey size of *A. aurantia* and *A. trifasciata* increased with an initial increase in web diameter, after which there was an apparent asymptote in *A. aurantia* or even a decline in *A. trifasciata* such that larger webs did not capture larger prey. Large Hymenoptera were captured less frequently by *A. aurantia* in large webs possibly because Hymenoptera may avoid or escape larger webs better than other prey (see Olive 1980). Furthermore, no increase in prey size with mesh density suggests that mesh size does not improve chances of retaining prey.

Table 6.—Mean adult spider length, prey length, web height, and web diameter. ($\bar{X}$ = mean, SD = standard deviation, and n = sample size). A one-way ANOVA is used to test the differences between species (ns = not significant).

Species		Spider Length (mm)	Prey Length (mm)	Web Height (cm)	Web Diameter (cm)
A. aurantia	$\bar{X}$	20.6	12.7	66	41
	SD	2.63	4.62	21.2	10.0
	n	312	542	353	350
A. trifasciata	$\bar{X}$	17.5	11.0	64	35
	SD	2.39	3.43	14.6	8.0
	n	110	239	137	137
Differences between species:					
	F	119.2	23.3	0.90	42.6
	P	<0.001	<0.001	ns	<0.001

Growth may increase efficiency at handling prey (Olive 1980; Riechert and Luczak 1982) and thus spiders may capture larger prey as they increase in size (Murakami 1983; Brown 1981). This is a general trend observed in other predators (Turner 1979; Mittelbach 1981; Werner and Mittelbach 1981; Polis 1984 and included references). In the present study, prey size generally increased with size of *A. trifasciata*, but smaller individuals of *A. aurantia* occasionally captured large prey making it unclear exactly how spider size affects size of prey captured.

Temporal differences.—Temporal (weekly or yearly) changes in foraging success may be affected by several factors. For example, large prey are most available in late summer or early fall (Olive 1980, 1981b; Pasquet 1984b). Insects feeding on nectar and pollen (e.g., cantharid beetles, bees, and wasps) increase locally when plants are in flower (Olive 1980). Flowering phenology and subsequent insect activity may explain the increase in Coleoptera captured by *A. aurantia* during early September and the increases in Hymenoptera captured by *A. aurantia* and *A. trifasciata* in October. Other habitat changes may result in seasonal changes in *Argiope* diet (Olive 1980; Brown 1981; Horton and Wise 1983; Howell and Ellender 1984).

Temporal changes in spider size and web characteristics affect foraging. The growth of *A. trifasciata* partially explains the increase in prey size and changes in prey taxa captured over time. Increases in Hymenoptera in the diet over time are related to seasonal increases in web height of *A. trifasciata*, and the decrease in web diameter of *A. aurantia*. Therefore, changes in web characteristics increase the frequency of encounter and capture of a particular prey. Alternately, environmental variability is known to influence prey availability and temporal differences in diet (see Wiens 1977). Both diet and web characteristics reflect changes in the preferred habitat over time (Brown 1981; Howell and Ellender 1984). *Argiope* spp. are flexible in habitat use and occasionally shift habitats in response to increased prey availability (Olive 1980; Brown 1981). For example, as *A. trifasciata* grows it moves from a low grassy site to high sites with many herbs in flower (see Olive 1980). Such movement not only increases web height but also allows the capture of more Hymenoptera and Cantharidae. Thus dietary or web changes may be a function of habitat rather than diet being a direct function of web characteristics.

Resource partitioning.—Several different selective forces have been hypothesized as important in the evolution of species-specific differences. (1) Exploitation competition causes differences in the use of prey (Abrams 1975; Thomson 1980) or habitat (Schoener 1974). (2) Differences in diets may result from non-competitive partitioning of resources due to autecological adaptation to different habitats or foraging methods (Wiens 1977; Bloom 1981). (3) Interference competition can produce in temporal, spatial, or behavioral avoidance of the dominant species by the subordinate species (Case and Gilpin 1974; Carothers and Jaksic 1984; Polis and McCormick 1987).

Comparisons between *Argiope* spp. showed differences in size, web characteristics, and prey. *Argiope aurantia* captured larger prey and more Orthoptera than did *A. trifasciata*; *A. trifasciata* captured more Hymenoptera than *A. aurantia*. Web and habitat differences are known to contribute to dietary differences in spider species (see Enders 1974; Brown 1981; Riechert and Cady 1983; Wise and Barata 1983).

Dietary differences also were influenced by temporal differences in spider and web characteristics. *Argiope trifasciata* captured smaller prey than those captured by *A. aurantia* until October when both species were mature resulting in both spider and prey size convergence (see Turner and Polis 1979; Polis 1984). Dietary convergence in October was influenced further by the observed convergence in web characteristics. Finally, use of the same habitat(s) (with prey availability similar for both species) may also contribute to the October convergence in diet and web characteristics.

Both species ate the same major taxa of prey. Therefore, it is doubtful that dietary differences are large enough to prevent exploitation competition. For this and other reasons, it is not clear if exploitation competition even occurs between *A. aurantia* and *A. trifasciata* (see Horton and Wise 1983; McReynolds and Polis in prep.). The observed dietary differences appear to be due to varying non-competitive abilities of *A. aurantia* and *A. trifasciata* to handle and capture different prey (Olive 1980, 1981a) or to autecological differences in habitat use and foraging methods (see Wiens 1977; Bloom 1981). Alternately, interference by the larger *A. aurantia* can exclude *A. trifasciata* from preferred habitats and prey (Case and Gilpin 1974; Carothers and Jakosic 1984; McReynolds in prep.). Under these conditions, a temporal shift may occur because the larger *A. aurantia* can effectively exclude *A. trifasciata*. Further research is needed to separate these hypotheses.

ACKNOWLEDGMENTS

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LIFE CYCLE AND COURTSHIP BEHAVIOR OF THE BURROWING WOLF SPIDER *GEOLYCOSA TURRICOLA* (TREAT) (ARANEAE, LYCOSIDAE)

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ABSTRACT

The life cycle and male and female courtship behavior of the burrowing wolf spider *G. turricola* are
described. *Geolycosa turricola* is found to have a two-year life cycle rather than the one-year cycle
previously reported. Copulation occurs in late summer following a period of cohabitation of the
mature male and a penultimate female. Spiders were collected during cohabitation and the courtship
video recorded. Male *G. turricola* engage in a series of leg waves and body movements followed by a
copulatory position face down in the burrow of the female. The courtship pattern is generally similar
to that of other lycosids except for the lack of palpal waving and abdominal movements. It is thought
that cohabitation provides a pre-courtship opportunity for sexual communication thereby mitigating
the loss of some elaborate display elements.

INTRODUCTION

Courtship behavior among wolf spiders (Lycosidae) involves patterns of leg and
palpal movements and abdominal vibrations (Bristowe and Locket 1926; Kaston
1936; Rovner 1968) and often includes the exchange of chemical cues and the
production of substrate vibrations and acoustic signals (e.g., Uetz and Stratton
1982; Tietjen and Rovner 1982). However, considerable variation in courtship
pattern exists among lycosid species (Platnick 1971), and little is known of the
specifics of the courtship of groups that have adopted unusual life strategies such
as burrowing and web building (e.g., *Geolycosa* and *Sosippus*). Here we describe
the phenology and basic courtship behavior of the obligate burrowing wolf spider
Geolycosa turricola (Treat). We compare the behavioral characteristics of this
species to those described for other wolf spiders and discuss the importance of

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variation in courtship patterns among burrowing and non-burrowing forms in relationship to the burrowing life strategy.

The genus *Geolycosa* is distributed widely throughout North America, with the greatest species diversity occurring in the southeastern United States (Wallace 1942). *Geolycosa turricola* (Treat) is one of the most widely distributed species and is found in New England, along the eastern seaboard, in Northern Florida and in the Florida panhandle (Wallace 1942). We have discovered several populations in central Mississippi.

Geolycosa generally prefer well drained or sandy habitats (Wallace 1942; McCrone 1963). The spiders construct burrows shortly after dispersing from their mother's burrow and are thought to remain in the same burrow for life, enlarging it as they grow (Wallace 1942; McQueen 1983).

MATERIALS AND METHODS

The life cycle of *Geolycosa turricola* was deduced from periodic observations of populations in Oktibbeha County, Mississippi and Santa Rosa County, Florida over a period of four years.

Courtship was observed in 10 pairs of *G. turricola* that were collected in August 1984 in Oktibbeha County, Mississippi about 12.8 km north of the Mississippi State University campus. A detailed description of the habitat and dynamics of that population is being prepared (Miller and Miller, in prep.). We have reported that *G. turricola* engage in a period of pre-courtship cohabitation in which mature males and penultimate females share the female's burrow (Miller and Miller 1986). The spiders used in this study were collected during that time, returned to the laboratory, and held until the females matured.

Penultimate females were provided with artificial burrows constructed of paper half-cylinders that were situated in sand with the open side of the cylinder against the glass of 75 L aquaria. The females adopted the burrows without hesitation and, in each case, lined the paper burrow with silk. Movements of the females inside their burrows were difficult to observe in this setup because the females deposited silk on the glass thus obstructing our view. However, females could be easily observed when they positioned themselves at the burrow entrance, the typical position during courtship (see below). Females constructed turrets at the burrow entrance with bits of grass that were provided. Males were held in wire cages adjacent to the burrow of their mate. Each of the females molted successfully to maturity.

Courtship was allowed to proceed (male was released from his cage) within 24 h after the final molt of the female. The courtship bouts were video recorded. Video tapes were analyzed with the aid of a multiple event timer computer program (DeAngelis and Miller 1985). Field observations indicated that courtship takes place in the early evening hours and, thus, most courtship bouts were recorded between 1800 and 2000 h. Recordings were made in low room lighting, and the laboratory temperature was around 22°C. No attempt was made to record sounds made during courtship. Copulation was allowed to continue until termination at which time the males were removed for further experimentation.

Twenty-four h after completion of copulation, one-half of the males were reintroduced to the female with which they had previously copulated, and one-half to a strange and previously mated female. The courtship behavior of these

pairs was observed to determine if mated females would accept a second male and if males would court females with which they had not cohabitated (second group of five). Each of the ten males was also introduced in turn to mature females without burrows, to empty burrows previously occupied by mature females, and to turret material from burrows of mature females. The difficulty in finding and collecting mature males made reuse of the males for these latter experiments a necessity.

RESULTS

Life cycle.—Emerton (1912) believed that *Geolycosa turricola* completed its life cycle in one year. Wallace (1942) concurred and reported finding mature males in spring and early summer (May to July) in Florida. These observations are not consistent with those we have made in Mississippi. We believe that *G. turricola* has a two year life cycle with copulation occurring in late summer (August and September). Females overwinter and produce young in spring (late April through June). Those young overwinter and mature in their second summer. This is consistent with the pattern of other *Geolycosa*; e.g., *G. fatifera* (Hentz), *G. missouriensis* Chamberlin, and *G. pikei* (Marx) (Wallace 1942).

Pattern of courtship behavior.—Male courtship was typically of short duration ($\bar{x} = 1.2$ min, SD $= 0.78$, $n = 10$). Two distinct phases in male courtship are distinguishable: (1) approach, and (2) contact. Prior to their release, males engaged in a brief exploration of their cages and then oriented toward the female's burrow. Unless disturbed, males remained in that position until released.

The approach phase includes those behaviors of the male that occur at a distance beyond the reach of the female's forelegs and as part of his movement toward her. Several separate approaches may be made by the male depending on the intensity of the aggressive behavior of the female (Fig. 1).

An approach may include combinations of four distinct behaviors: (1) foreleg-waving, (2) foreleg-tapping, (3) retreat, and (4) palpal-drumming. During a foreleg-wave, the leg is drawn back, raised, stretched high above the cephalothorax (Fig. 2), and then lowered. The legs are often waved alternately in a "bicycling" motion. No palpal drumming or abdominal vibrations are observed during foreleg-waves. The male walks toward the female's burrow during leg waves.

Foreleg-tapping behavior is interspersed with foreleg-waving. Foreleg-tapping, which the male performs while in a stationary position, involves quick, jerky downward "taps" of one or both forelegs (on occasion one of the second legs will tap simultaneously with the first leg on the same side). The forelegs do not touch the ground during the taps. The legs are held high for this part of the display (Fig. 2 shows a typical starting position for a leg tap). Leg waving movements of the female (described below) that are given during male leg-waving may cause the male to stop and engage in leg-tapping.

If the female displays aggression (described below) toward the approaching male, the male quickly retreats and immediately engages in palpal-drumming movements. The male's palps were never observed to make contact with the sand substrate of the aquarium. In the retreat behavior, the male quickly steps or jumps back and lowers his body to the ground (similar to the posture shown in Fig. 2). The male remains in this position only for a short time before resuming

ORIENTATION

FORELEG
WAVES & TAPS

(.25)

APPROACH

RETREAT

PALPAL
DRUMMING

TAPPING ———(.10)———→

SPARRING———(.26)———→

CONTACT

PUSH & HOLD—(.2)———→
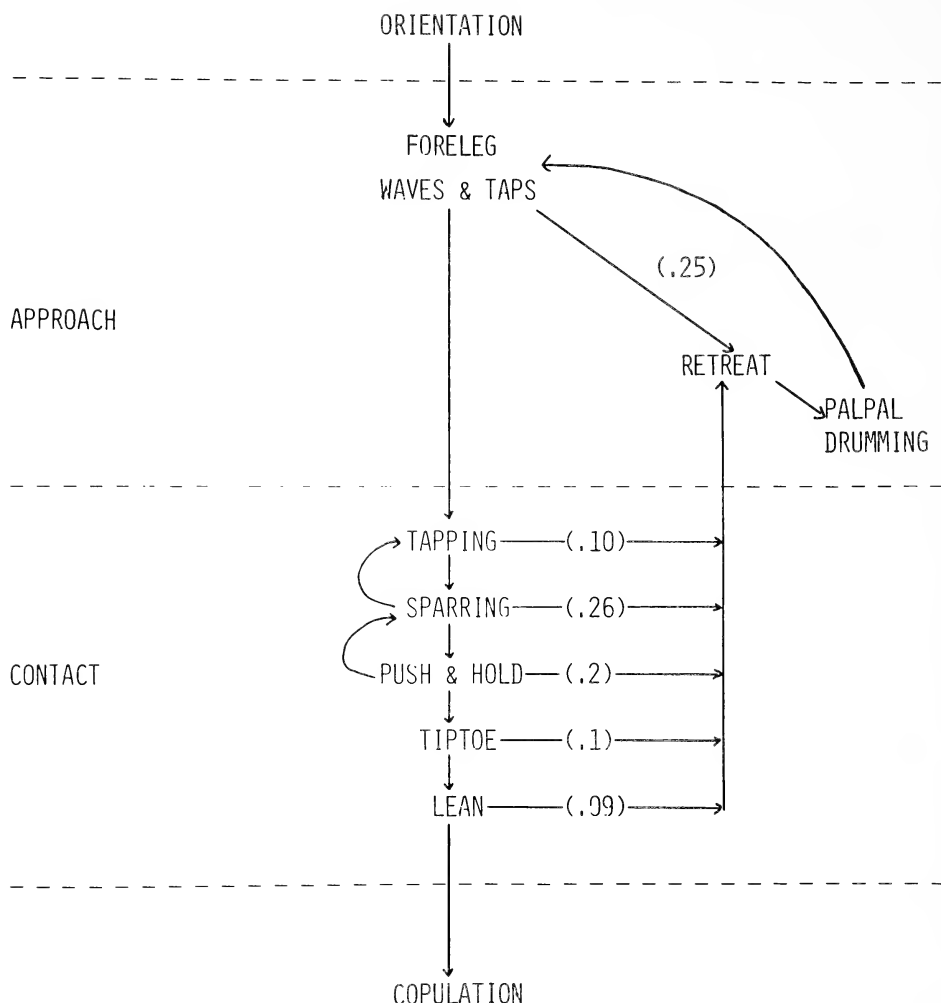
TIPTOE———(.1)———→

LEAN———(.99)———→

COPULATION

Fig. 1.—Sequence of elements of courtship behavior of male *Geolycosa turricola*. Numbers in parentheses indicate the proportion of the total number of retreat moves that were initiated at various places in the sequence. Behaviors are explained in the text.

his approach ($\bar{x} = 7.25$ s, SD $= 3.1$, $n = 31$, n refers to the total number of retreats observed in the 10 males studied). Males may retreat at any point in the courtship sequence in response to aggression by the female. However, two-thirds of male retreats occurred during approach or early contact (tapping and sparring, Fig. 1).

The contact phase of the male courtship is that period when the male and female are close enough to each other to touch. Contact courtship may be interrupted by aggressive moves of the female that prompt the male to initiate another approach or to return to an earlier behavior in the contact courtship sequence (Fig. 1). The contact phase involves five distinct behaviors: (1) leg-tapping, (2) sparring, (3) push-and-hold, (4) tiptoe, and (5) lean.

Leg-tapping movements of the male during the contact phase are functionally similar to those described above except that individual "taps" often make contact with the female's forelegs or cephalothorax. Leg-tapping by the male stimulates
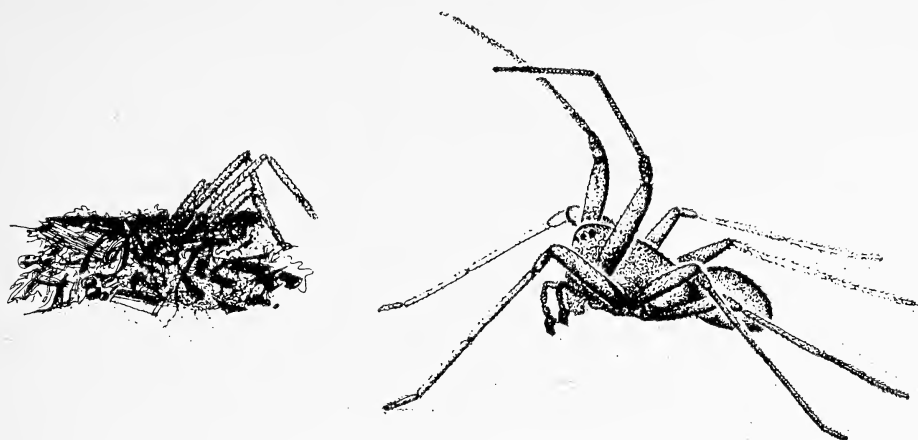
Fig. 2.—Approach of courting male *G. turricola.*

the female to engage in foreleg sparring with him. During sparring, the male attempts to push the female's forelegs down and hold them against the turret in what we term the push-and-hold behavior. If he succeeds in holding her forelegs down, he begins the tiptoe movement in which he raises his body high above hers (Fig. 3). This is the first time during courtship (with the exception of instances where female attacks take her out of her burrow; see description below) that the female would be able to see the proximal portions of the male's forelegs, his venter, and his palps (Fig. 3). The male engages in no palpal or abdominal movements during this time.

If the female shows no aggressive behavior, the male begins to lean forward into the burrow from the tiptoe position. This behavior involves "walking" his forelegs across the female's back and, thus, requires that he release his hold on her forelegs (Fig. 3). The successful male will eventually adopt a copulatory position face down in the burrow.

Behaviors during the contact phase always occur in a specific sequence (Fig. 1). The sequence may be interrupted at any step by aggressive displays of the female. If the male is interrupted during the tapping behavior (25% of total retreats were initiated during this time), he will retreat and begin a new approach. If the contact courtship sequence is interrupted during tapping, the male retreats (10% of total retreats) and begins another approach. Interruption of the male during sparring or the push-and-hold phase prompts the male to either retreat (26% and 20% of total retreats respectively) and begin another approach or to return to the previous behavior in the contact sequence (e.g., he will return to sparring if he is interrupted during the push-and-hold). Our observations indicate that the more intensive the female aggressive behavior that initiated the break in the sequence, the more likely it is that the male will retreat and begin a new approach. If the contact sequence is interrupted during the tiptoe or the lean, regardless of the intensity of the female aggressive behavior, the male retreats and begins a new approach.

In a typical courtship bout, the female adopts a position at the burrow entrance just below the rim of the turret. In this position, her forelegs, which are draped over the turret, could be visible to the approaching male, but she cannot
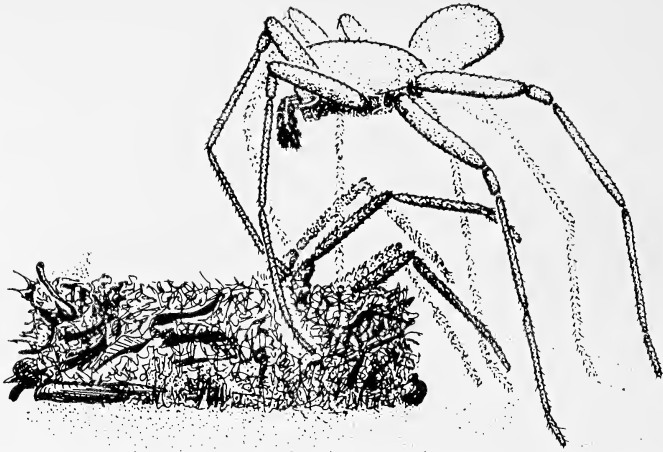
Fig. 3.—Tiptoe behavior (beginning of the lean behavior) of male *G. turricola*.

see the male (Fig. 2). As the male moves into contact range, the distal portions of his legs (which are held high) come into her field of view.

Females engage in several distinct behaviors during courtship: (1) leg-waving, (2) sparring, (3) attack, (4) quiescence. Female leg-waving is not as distinctive a behavior as that of the male. Female leg-waves consist of gentle, slow up and down movements of one or both first legs. These waves, like the male leg-waves, are given during the male's approach phase.

Female aggressive behavior may take the form of an overt attack or may consist of quick leg movements. Aggressive behavior is observed during both the approach and contact phases of courtship. During an attack, the female lunges from her position just below the turret rim to a position with her midsection over the turret, her first legs raised high and her chelicerae spread. From this position, she is able to see the male. The female is quiescent during most of the courtship. We observed no significant palpal movements by the female.

Variations in typical courtship pattern.—In two instances females remained below the burrow entrance (out of the male's visual field) during male approach. In these two cases, the male engaged in a normal approach (presenting leg-waves and leg-taps but no retreat or palpal-drumming behaviors). When the male reached the burrow entrance, he slowly probed the tunnel with his forelegs and proceeded into the tunnel until he made contact with the female. The female reacted by gently pushing the male out of the burrow. When the male had backed out of the burrow and the female had reached the entrance, she engaged in an attack. The male retreated and then began another approach.

In one of these two cases, the female dropped back below the turret rim but remained at the entrance (Fig. 2), and the male proceeded with courtship display. In the other case, the female retreated to the bottom of her burrow after the first attack, and the male was forced to coax her out a second time before courtship could proceed. Copulation occurred in both cases.

Copulation.—Except for the burrow entrance, which is somewhat flared, the diameter of *Geolycosa* burrows are just large enough to allow passage of one spider. Because of this, copulation must occur at the burrow entrance where the female can position herself over the turret thereby making room for the male to adopt a position face down in the burrow. Except for the vertical position,

copulation is typical of that described for other lycosids (e.g., Rovner 1974). Copulation typically lasts over an hour ($\bar{x} = 1.6$ h, SD = 0.25, $n = 10$).

Male mating success and mate finding.—All males that were offered a second female proceeded through normal courtship. In every case, once-mated female *Geolycosa* rejected a second male regardless of previous experience with that male. Rejection behavior involved repeated attacks by the female during the male approach. Fewer than five such attacks ($\bar{x} = 4.2$, SD = 1.1, $n = 45$, n refers to the total number of female attacks observed) were sufficient to cause the male to cease further attempts.

When previously mated males were offered females without burrows, empty burrows of mature females, or turret material, they engaged in orientation behavior and proceeded with an approach. Males courting females without burrows proceeded through a normal approach and into the contact phase. These males were eventually rejected by the females.

Males exposed to the empty burrows of mature females engaged in normal approaches followed by foreleg searches of the empty burrow (see description above). Such males made several probes. Males courting turret material made normal approaches and engaged in leg tapping of the material.

DISCUSSION

The mechanism by which the mature male *G. turricola* finds the penultimate female is unknown (Miller and Miller 1986). However, given the stationary position of the female and the relatively wide spacing of burrows in some *Geolycosa* populations (pers. obs.), one possibility is that long range attraction of the male is mediated by aerial pheromones given off by the immature female. The existence of aerial attractants has been predicted for burrow dwelling spiders (Robinson 1982).

The use of draglines for attracting males from a distance (Tietjen 1977) seems unlikely. *Geolycosa* rarely wander more than a few cm from their burrows, even during foraging (pers. obs.). We also presently have little evidence that immature female *Geolycosa* produce percussive or stridulatory sounds to attract mature males, although further investigation in this area is needed.

Certain components of the courtship of *G. turricola* are similar to those described for other lycosids. The foreleg-high approach posture of the males is similar to the courtship posture of mature male *Lycosa carolinensis* Walckenaer (Farley and Shear 1973; pers. obs.) and *L. malitiosa* Tullgren (Costa 1975). Leg-waving and leg-tapping has been observed in male *Pardosa* (e.g., Den Hollander and Dijkstra 1974; Koomans et al. 1974), *Schizocosa* (e.g., Uetz and Denterlein 1979) and *Lycosa* (Rovner 1968). Palpal-drumming by the male is similar in form to that described for other lycosids (e.g., *L. rabida* Walckenaer, Rovner 1968).

However, *G. turricola* courtship differs from the typical lycosid pattern (Robinson 1982) in the absence of pronounced abdominal vibrations and ritualized palpal movements. Palpal movements may provide visual stimulation of the female (e.g., palpal rotation of *L. rabida*, Rovner 1968), percussive sound (e.g., palpal-drumming of *Schizocosa mccooki* Montgomery, Stratton and Lowrie 1984) or acoustic signals (e.g., sound produced by palpal stridulation, Rovner 1975). Abdominal vibrations may provide vibratory, acoustic or visual signals. Subtle abdominal movements produce substrate vibrations in some spiders

(Rovner and Barth 1981), but the abdomen of male lycosids does not generally touch the substrate during vibrations (Rovner 1968, pers. obs.). Acoustic sounds are not likely in *G. turricola* since abdomen-prosoma type stridulatory organs (Legendre's type a, 1963) are not known for lycosids (Uetz and Stratton 1982). Although the abdomen of the male *G. turricola* is probably visable to the female during the male's tiptoe display, we observed no significant movements of the abdomen during that time.

A reduction of the visual component of courtship (non-sound producing palpal movements and abdominal vibrations) may reflect the relatively greater importance of chemotactic communication during cohabitation over visual courtship signaling by the male. There is evidence that visual signals are not as important in lycosid courtship as chemotactic, vibratory and acoustic signals. Wolf spiders are thought to have poor visual acuity (Homann 1931), and the experimental removal of the palps of courting male *L. rabida*, and, thus, the removal of the palpal rotation display, did not prevent the mating success of the male under laboratory conditions (Rovner 1968). Cohabitating male *Geolycosa* position themselves face down in the burrow and, in order for courtship to proceed, must exit the tunnel (Miller and Miller 1986). Our observations indicate that the male is, in fact, gently pushed from the burrow by the mature female. This close contact between the mature male and female provides a pre-courtship opportunity for the male to stimulate the female and, thus, may lead to a less elaborate courtship, such as we observe here. However, pre-courtship contact alone may not negate the necessity of visual display. Some lycosids (e.g., *L. helluo* Walckenaer, Nappi 1965; *S. mccooki*, Stratton and Lowrie 1984) require contact between male and female to initiate courtship but still engage in fairly elaborate visual display, and we show here that *G. turricola* males signal vigorously with their palps in some situations during courtship. Further, the presence of distinctive epigamic coloration on the distal foreleg segments of most *Geolycosa* (Wallace 1942) suggests some importance of visual display in these spiders. The possible significance of the less well-developed visual display in *G. turricola* requires experimental studies.

Our results indicate that female *G. turricola* are obstructed in their view of the approaching male until he is very close to the burrow. Although this may contribute to the relative unimportance of visual display on the part of the male, it might also suggest a greater emphasis on vibration or sound production and chemical signaling. With regard to sound production in burrowing spiders for example, ctenizid males that are approaching the burrows of mature females drum the ground with their first pair of legs (Buchli 1969). However, our observations suggest that vibratory and airborne sounds are not important in *Geolycosa* courtship. We believe that the lack of such sounds is to a large extent mitigated by chemical signaling during cohabitation and courtship. However, as we mentioned earlier, the possibility of vibration or sound production in these spiders needs further investigation.

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DOS NUEVAS ARAÑAS CANGREJO (ARANEAE, THOMISIDAE) DE MEXICO

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ABSTRACT

Synema lopezi n. sp. and *Tmarus tamazolinus* n. sp. from the State of México are described and illustrated.

RESUMEN

Se hace la descripción de las nuevas especies *Synema lopezi* y *Tmarus tamazolinus*, del Estado de México.

INTRODUCCION

El género *Synema* (Simon 1864), de amplia distribución mundial, está representado por 119 especies (Bonnet 1959; Brignoli 1983) de las cuales cinco se encuentran en Norte América: *Synema viridans* (Banks 1896), *S. neomexicanum* Gertsch 1939; *S. parvulum* (Hentz 1847), de Estados Unidos y México; *S. aequinoctiale* (Taczanowski 1872) y *S. madidum* Pickard-Cambridge 1895 de México y Guyana. Son arañas pequeñas que se localizan entre el follaje de arbustos y en flores. Se caracterizan por tener un caparazón convexo con espinas; la primera hilera de ojos es muy recurvada y los tarsos de las patas I tienen uñas con seis a doce dientes.

El género *Tmarus* Simon 1875, al igual que *Synema*, está ampliamente representado en todos los continentes con 125 especies (Bonnet 1959; Brignoli 1983), de las cuales siete pertenecen a Norte América: *Tmarus unicus* Gertsch 1936, *T. minutus* Banks 1904, *T. floridensis* Keyserling 1884, *T. rubromaculatus* Keyserling 1880, *T. angulatus* (Walckenaer 1837), de Estados Unidos y Canadá y *T. corruptus* Pickard-Cambridge 1892, *T. separatus* Banks 1898, de México. Son arañas de talla pequeña, viven sobre las plantas, descansando en una ramita, a la cual rodean con sus dos últimos pares de patas presionando el cuerpo sobre ella. La coloración es generalmente grisácea, pudiendo ser confundidas con un brote o cicatriz de la rama.

En este trabajo se describe una especie nueva del género *Synema* y otra del género *Tmarus* de México.

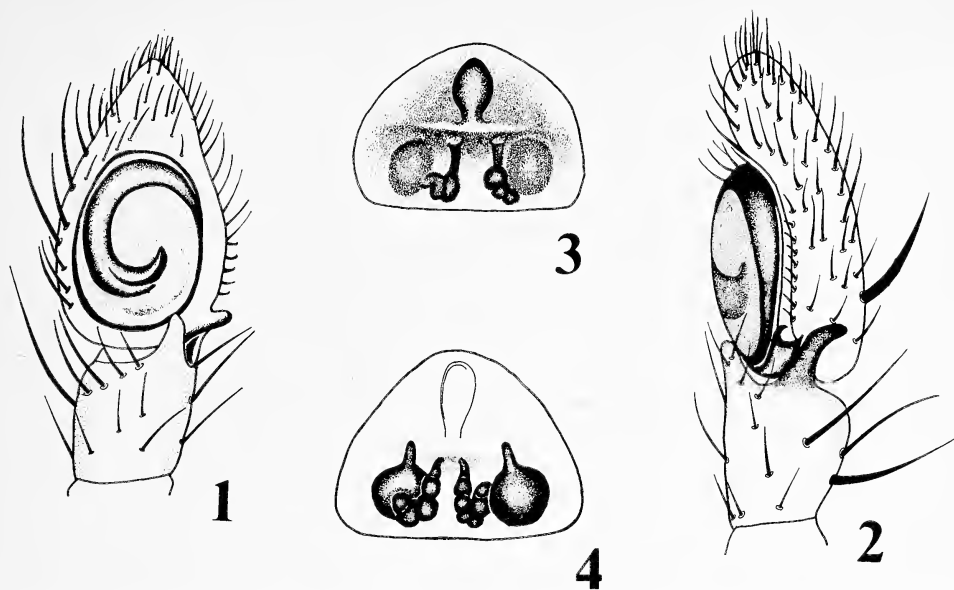*Synema lopezi*, nueva especie
Figs. 1-4

Datos del tipo.—Holotipo macho recolectado en San Francisco Oxtotilpan, Estado de México, 2400, bosque de pino-encino, 14 de mayo 1985 (M. Jiménez) y los siguientes paratipos: 4 agosto 1983, 25 mayo 1984, 12 julio 1984, 8 mayo 1985, 12 junio 1984 (M. Jiménez) todos de la misma localidad del tipo. El tipo será depositado en la colección del Laboratorio de Acarología (Fac. de Ciencias, Universidad Nacional Autónoma de México), con excepción de un paratipo que será depositado en la Colección del Centro de Inestigaciones Biológicas de Baja California Sur.

Macho.—Longitud total 2.62-3.57 mm; longitud del caparazón 1.25-1.60 mm, y anchura 1.25-1.60 mm (13 ejemplares). Caparazón muy convexo, de color amarillo claro a amarillo oro márgenes con una línea negra y escasas espinas largas en el dorso; primera hilera de ojos más estrecha y menos recurvada que la segunda; ojos laterales bien separados, en tubérculos blancos a grisáceos; ojos medios anteriores separados dos díametros, ojos medios posteriores, tres diámetros, ambos pares encerrados en un círculo blanco, clípeo con cinco espinas largas cerca de su borde; quelíceros sin ninguna mancha. Patas III y IV más cortas y color amarillo clara, patas I y II más largas y oscuras que las posteriores y con anulaciones; femur I 1.5-2.0 mm, con cinco espinas dorsales y seis o siete lateroexternas, cero ventrales; tibia I 1.12-1.60 mm, con cinco espinas dorsales, tres espinas lateroexternas, tres laterointernas, tres pares ventrales; metatarso I 1.12-1.47 mm, con dos espinas laterointernas, dos lateroexternas, cuatro dorsodistales y dos ventrales; fémur II 1.75-2.60 mm, con cinco dorsales; tibia III 1.0-1.37 mm, con dos espinas dorsales, dos laterointernas, dos lateroexternas, seis pares ventrales. Opistosoma amarillo con granulaciones blancas y una franja transversa castaño oscuro en su borde caudal, la cual se continúa hacia los costados y rodea a las hileras; vientre amarillo clara con una mancha oscura cerca de las hileras que son amarillo oro. Femur del pedipalpo del mismo tamaño que la patela y tibia juntos; tibia con una apófisis ventral pequeña y una apófisis retrolateral que se dirige hacia atrás del cimbio; el émbolo delgado, se origina en la parte media del bulbo y se enrolla alrededor del mismo, de tal forma que la punta queda cerca de una pequeña saliente del cimbio en su margen lateroinferior (Figs. 1 y 2).

Hembra.—Longitud total 2.8-3.5 mm, longitud del caparazón 1.37 mm y anchura 1.37 mm (dos ejemplares). Estructura general y coloración similar a la del macho. Epiginio tan largo como ancho, con una depresión oval anterior; las aperturas de los tubos copuladores se localizan en medio del atrio; espermatecas globosas lisas y con órganos espermáticos anteriores cortos, tubos copuladores espiralados.

DISCUSION

Los especímenes de *Synema lopezi*, sp. nov. presentan características afines a *S. parvulum*, pero difieren en lo siguiente: el émbolo de *S. parvulum* que se origina en el extremo distal del bulbo enrollándose en el mismo 1.25 veces; la depresión anterior del epiginio es triangular amplia y rodeada de sedas cortas; las

Figs. 1-4.—*Synema lopezi* sp. nov.: 1, 2, macho, pedipalpo; 1, vista ventral; 2, vista lateral; 3, 4, hembra, epiginio; 3, vista ventral; 4, vista dorsal.

aperturas de los tubos copuladores están bien separados y se localizan a los lados del atrio.

**Distribución.**—Conocida sólo para la localidad de los tipos.

Etimología.—Se dedica la presente especie al Biol. David J. López Cortés, quien recolectó parte del material estudiado.

Tmarus tamazolinus, nueva especie
Figs. 5, 6

Datos del tipo.—Holotipo macho recolectado en San Francisco Oxtotilpan, Edo. de México, 2400, bosque de pino-encino, 13 junio 1984 (M. Jiménez y D. López) y los siguientes paratipos: 13 junio 1984, 12 junior 1985 (M. Jiménez y D. López) todos de la misma localidad del tipo. El tipo y cinco paratipos serán depositados en la colección del Laboratorio de Acarología (Fac. de Ciencias, Universidad Nacional Autónoma de México). Un paratipo será depositado en la Colección del Centro de Investigaciones Biológicas de Baja California Sur.

Macho.—Longitud total 3.9-4.8 mm; longitud del caparazón 1.4-1.9 mm y anchura 1.3-1.8 mm (seis ejemplares). Caparazón de color claro con manchas oscuras; área ocular clara con una línea blanca media entre los ojos anteromedios y posteromedios; en la región media dorsal se localiza una mancha blanca formando un tridente que se irradia hacia adelante y hacia los lados del caparazón; la hilera de ojos anterior menos curvada que la posterior; ojos medios anteriores más chicos que los medios posteriores, sobre pequeños tubérculos; ojos anterolaterales ligeramente más grandes que los posterolaterales, ambos pares sobre tubérculos separados; clípeo casi horizontal, con cinco sedas largas y delgadas cerca del borde ventral y con manchas oscuras a cada lado; quelíceros amarillo claro y con manchas oscuras y sedas largas y delgadas; el artejo distal de color blanco y el proximal sin dientes en ambos márgenes; esternón redondo y
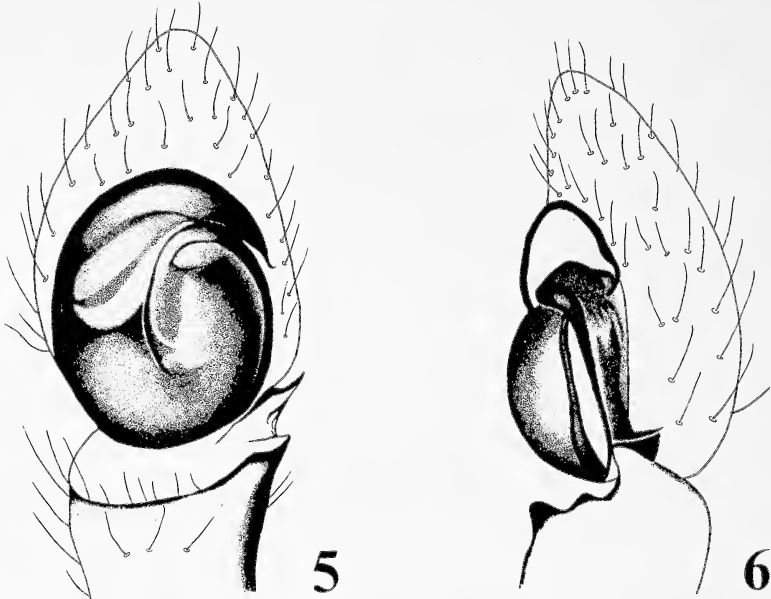
Figs. 5, 6.—*Tmarus tamazolinus* sp. nov., macho, pedipalpo: 5, vista ventral; 6, vista lateral.

con bordes oscuros y abundantes sedas pequeñas delgadas y negras en su superficie. Patas amarillo claro salpicadas con manchas grises y sin escópula; femur I 1.50-2.70 mm, con dos espinas dorsales, cuatro laterointernas y numerosas sedas cortas y delgadas; tibia I 1.40-2.60 mm, con dos espinas dorsales, tres pares laterales, dos espinas ventrales y un anillo oscuro distal; basitarso I 1.60-2.10 mm, con cuatro pares de espinas ventrales y múltiples sedas delgadas y cortas; tibia III 0.7-1.0 mm, con dos pares de espinas dorsolaterales, una espina ventral. Opistosoma grisáceo con un tubérculo en la región posterior y una banda lanceolada clara en la parte anterior, los costados son gris oscuro, cambiando gradualmente hacia el vientre el cual se ve bordeado de una franja blanca gruesa con manchas oscuras que encierran una franja oscura media; hileras amarillo claro con el ápice gris oscuro y numerosas sedas. Pedipalpos con patela corta; tibia con una apófisis retrolateral y apófisis ventral bicúspida pequeña; émbolo corto y ancho que termina en una punta curva (Figs. 5 y 6).

DISCUSION

Tmarus tamazolinus sp. nov. se parece a *T. angulatus* (Walckenaer 1837) pero difiere en que la segunda especie presenta una y apófisis retrolateral y una apófisis ventral en forma de gancho; la punta del émbolo en más corta.

Distribución.—Conocida sólo para la localidad de los tipos.

Etiomología.—El nombre específico se refiere a "tamazolín" que en náhuatl significa "sapo" por la forma del prosoma de la araña.

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Doy mis más sinceros agradecimientos al Dr. C. D. Dondale por la confirmación de las especies descritas así como por la revisión del manuscrito y a

los doctores: W. B. Peck y R. Johansen N. por sus atinados comentarios y sugerencias al mismo. Este trabajo fué realizado con el apoyo económico del Centro de Investigaciones Biológicas de Baja California Sur, A. C., el Consejo Nacional de Ciencia y Tecnología (CONACyT) y la Secretaría de Programación y Presupuesto (SPP).

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TIME BUDGET AND PREY OF *NEPHILA CLAVIPES* (LINNAEUS) (ARANEAE, ARANEIDAE) IN SOUTHERN TEXAS

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ABSTRACT

From diurnal and nocturnal observations of the araneid spider, *Nephila clavipes* (Linnaeus), in two locations in Texas, old pasture and scrub forest habitat, rates of prey capture, types of prey utilized and time budgets can be estimated. This species had no preferred prey types. It was never observed in a retreat but was always at the hub except when replacing silk or molting. Spiders at both locations had similar time budgets and schedules but differed significantly in the types of prey captured and the estimated contribution of each prey type to the spider diet. Despite these differences, the number of prey and the estimated dry weight of prey captured by each spider was not different between the two locations. Compared to other araneids, *N. clavipes* in Texas captured a relatively low number of prey per hour, the prey were small relative to spider size, and web investment appeared high. *N. clavipes* may be required to hunt as much as it does because it is large relative to the insects upon which it preys.

INTRODUCTION

Many spiders that build orb webs must renew the orb regularly. To understand how these spiders budget their time and energy resources between foraging and growth, more information is needed concerning foraging success and the expense of the materials and movement in web building. Important factors in both the time and energy budgets include the frequency of orb renewal, the frequency and efficiency of silk recycling, and the types and capture rates of prey utilized. Environmental factors such as prey size relative to spider size, predation and climate may influence the time spent at the hub actively hunting. Opposition of predation pressure and the need to hunt may have played a role in the evolution of structures placed on or around the orb, (such as stabilamenta and barrier webs, Lubin 1973, 1975; Eberhard 1973; Tolbert 1975), of hunting at night (A. Mahler pers. comm.) and of hunting from a retreat. During the summers of 1983 and 1984 I surveyed the diurnal and nocturnal activities of individual *Nephila clavipes* (Linnaeus) in two Texas locations. Observations on time budgets and activity schedules, web-renewal behavior and prey are presented here. *N. clavipes* is a large araneid (1-3 g when gravid) with a web of two parts: a viscid orb and mazes of silk forming barriers dorsal and ventral to the spider at the hub of the orb (Robinson and Robinson 1973a). Females were observed to feed primarily on insects much smaller than themselves, renew some or all of the orb daily, and hunt nearly twenty-four hours a day.

STUDY SITES

Brazoria County.—In July, 1983, spiders were observed for twenty-one days near Sweeny, Texas (Brazoria County). *N. clavipes* occurred primarily in two habitats: scrub forest and tall grass areas in an abandoned pasture, and cut grass. Most individuals studied were in the former habitat. A major recent disturbance in Brazoria was the infestation by the imported red fire ant, *Solenopsis invicta*, that has greatly reduced the diversity of the insect fauna (J. E. Rawlins pers. comm.).

Galveston County.—In August, 1984, spiders were studied for 30 days at the University of Houston Coastal Center, Galveston County, Texas. The site is used for a study of the cultivation of Chinese tallow trees (*Sebum sebiferum*). This forms a scrub forest similar in appearance to that found in Brazoria County. There were several hived and feral honeybee colonies (*Apis melifera*). *S. invicta* was present, but not in the densities observed at the Brazoria site. I studied *N. clavipes* where it was most dense: in the less tended stands of tallow trees and along unused roads. No other large araneids were common at either site during the study.

METHODS

The survey method followed that of Turnbull (1960) and Castillo and Eberhard (1983). Spiders along a 200 m path were checked at regular intervals throughout the observation period. Each individual was observed for approximately 15 seconds, unless unusual behavior was in progress. Each survey included all spiders along the path, between 12 and 28 spiders (Table 1). In five surveys the spiders were checked at hourly intervals. In six surveys, the spiders were checked at half-hourly intervals starting from the time the first orb was finished until the last spider had begun to remove its orb, usually 0800 to 2400. Observations between 0100 and 0800 were made at hourly intervals to determine the time of web removal and rebuilding.

During the first check of each survey, spiders were scored as hunting or not hunting. Pre-molt spiders do not appear to hunt; they are not considered in the analysis of hunting behavior and success. At each subsequent check two types of spider behaviors were scored. Of behaviors that were observed directly, the spiders were scored as sitting at the hub, sitting in thermoregulatory positions (described by Robinson and Robinson 1974), feeding, spinning or removing silk, or moving on the orb, barriers or support lines of the web. Behavior that could be deduced from physical evidence included addition or removal of orb silk (increases or decreases in the amount of silk of the orb relative to the previous observation) and prey capture. *N. clavipes* stores all prey at the hub of the orb. Except for very small insects, consumed in less than one-half hour, the prey captured over the previous half hour could be observed.

Only diurnal (0600-1900), hourly direct observations of hunting spiders were used to construct the time budgets. This restriction was necessary to eliminate the bias towards nocturnal observations in Brazoria and diurnal observations in Galveston. Both direct and indirect observations of spider behaviors were used to construct the time schedules of the various activities. At the beginning of each

Table 1.—Dates, times, time intervals and number of individuals observed in each of the prey-capture censuses. * = Diurnal censuses hourly until first spider finished spinning, nocturnal censuses hourly after last spider began removing silk.

Site	Date	Time	Intervals	N
Brazoria 1983	17 July	1830-0130	hourly	15
	19 July	0530-1830	hourly	17
	20 July	1830-0230	half-hourly	20
Galveston 1984	1 August	0630-1930	hourly	28
	4 August	1900-0300	half-hourly*	25
	8 August	0500-1830	half-hourly*	16
	10 August	1800-0300	half-hourly*	13
	15 August	0500-1830	half-hourly*	13
	17 August	1800-0100	half-hourly*	14
	21 August	0400-0500	hourly	15
	23 August	0600-1100	hourly	12

check in Galveston, the temperture, cloud cover and (in nocturnal surveys) presence of dew were recorded.

Insects observed in the orb were placed in a size class (in 2 mm increments) and when possible, the order or family was determined. Insects in the 2 mm size class were not identified and are presented as miscellaneous small insects. Dry weights for identified prey items were estimated using the equations of Schoener (1980, Table 1) for temperate insects. Schoener's equation for "total insects" was used for unidentified prey items.

Prey capture rates were calculated using only observations of hunting spiders. Individual prey capture rates were calculated as the number of prey divided by the number of hours that individual was observed. The prey capture rate for all animals in a survey is the total number of prey for that survey divided by the sum of hours of all hunting spiders observed. Within each week, the numbers of prey captured during the diurnal and nocturnal censuses were compared using paired t-tests on spiders that were present for both censuses. From the observations of five randomly selected spiders that were present at both the diurnal and nocturnal survey in each week, individual prey-capture records were compared using repeated-measure analysis. These analyses compared the four weeks at Galveston and compared the two sites. Prey capture was too infrequent to allow comparisons between individual webs or between microhabitats within a study area.

A simultaneous study of approximately 200 marked females provided background information on the sizes of the individuals, patterns of orb renewal, and the proportion of pre-molt females. These individuals were observed each morning for six days each week. Observations of prey captured have been added to the data from the surveys in the discussion of the variety of insects captured and eaten by *N. clavipes* in southern Texas. The sizes of the spiders in each location were determined by measuring either the length of the entire first leg (Brazoria County) or the length of the tibia plus patella of the first leg (Galveston County). I switched to the latter measurement as it is obtained more accurately from spiders on webs. The two measurements are correlated and the former were converted to tibia plus patella length using an allometric equation derived from preserved females (after Vollrath 1983).

RESULTS

Background population information.—Only females were observed in this study. At both sites, the spiders were approximately fifth to eighth instar (between 0.5 and 1.4 cm tibia + patella length). In Galveston, there was a shift in the distribution of sizes in the population over the month, with the smallest instars dropping out completely by the end of August, and an increasing number of mature females. The only observed causes of mortality were failed molts and, in Galveston, cannibalism between females.

One to three days before a spider molted, it stopped renewing its orb, or replaced the viscid orb with a nonviscid platform (Christenson et al. 1985; the skeleton web of Robinson and Robinson 1973b). The condition of the orb was used to judge whether or not a spider was immediately pre- or post-molt (the new orb was not usually built until the day following the molt). Pre- and post-molt spiders did not appear to be actively hunting; only one individual was ever seen to capture prey from an old orb, and prey capture is unlikely on a non-viscid platform.

At any one time in the Galveston County population, 0 to 22% of the spiders used in the surveys were premolt. Premolt females were not included in the surveys done in Brazoria County.

Time budgets and orb renewal.—The time budgets were calculated using only diurnal (0600-1900) hourly direct observations of hunting spiders' behaviors (Fig. 1). The time budgets are not significantly different between the two locations (likelihood ratio G-test, Sokal and Rohlf 1981). By 0600 all hunting spiders had some viscid spiral in place. Diurnal prey capture is definitely impossible only when a spider is moving on the barrier webs (M). The spiders moved onto the barrier webs during the day to escape a disturbance, or, rarely, to chase a kleptoparasite or a male. In both locations, the spiders could potentially capture prey 98% of the day.

Spiders replaced between one-third and all of the orb between 2200 and 1100, most completed the new portion of the orb by 0930 (Fig. 2). The amount of new silk in the orb on any day was a function of the weather of the previous day (Higgins in prep). The spiders spun the viscid spiral in concentric sections with pauses at the hub between sections. The spiders also returned to the hub if disturbed while spinning. While at the hub, a spider could capture prey and no spinning would be done until it finished feeding.

Nocturnal orb removal took place between 2200 and 0400, with peak activity at 0100 (Fig. 2). Dewfall appears important in triggering orb renewal. I compared the distribution of the initiation of orb removal over the night between nights with and without dewfall. Spiders began removing the orb significantly earlier on the evenings when there was dew fall, compared to when there was no dewfall (Chi-square = 23.39, df = 5, $p < 0.001$). Web removal by spiders that were abandoning a location may occur earlier in the night. The spider removed one-fourth to one-third of the orb in a wedge-shaped piece, then progressively enlarged the hole in a manner similar, but not identical, to the slow-removal pattern described by Carico (1986) (Higgins in prep.). Many of the radii of the orb were constructed during the orb-removal process. Orb removal could take several hours, with the spider pausing at the hub to consume the silk or to capture prey. The amount of silk removed by a spider that was abandoning a web
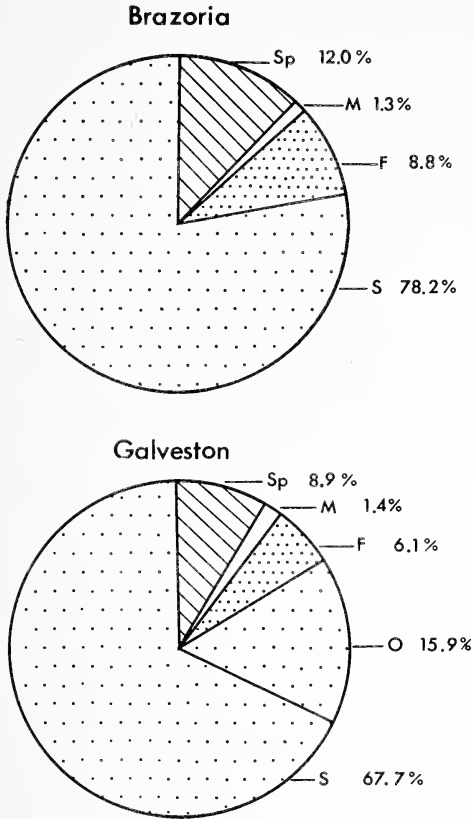
Brazoria

Galveston

Fig. 1.—Diurnal time budget of *N. clavipes* in Galveston and Brazoria counties. S = waiting at the hub, O = thermoregulatory posture (orientation of abdomen to sun), F = feeding, S = spinning, M = moving on the barriers, frame or support strands. Prey capture was possible during all behaviors except movement off of the orb. Thermoregulatory positions were not recorded in Brazoria. The distributions are not significantly different.

site was variable, but many such spiders consumed most of the orb and barriers. Abandonment of intact webs was only seen in cases of cannibalism, heavily damaged webs, or when the spider was leaving to lay eggs. Orb rebuilding by spiders staying at the same location commenced immediately after the silk of the old orb had been consumed. Non-viscid platforms of premolt spiders were also built at this time by removal of some or all of the old orb and replacement with radii and scaffolding, but no viscid spiral. The stabilimenta were not always added at night.

During the orb removal process, most females spent some time moving on the barriers, frame and support strands. In some cases the spiders were obviously reinforcing the strands. The density of silk in the barriers was variable and was probably changed at this time.

Orb removal may occur during the day if the orb was wet by rainfall. On the one census day with rain, four of the ten actively hunting spiders removed sections of the orb when it rained, and one rebuilt a portion of the removed area after the rain had stopped. The cause of the variation in response to rainfall is unclear but appears related to the amount of water actually reaching the orb.

Prey types caught by *Nephila clavipes*.—Insects were scored as captured if they were observed to be attacked or stored at the hub, rejected if the female was observed to remove the insect from the orb, and ignored if the insect was in the orb but the spider was not observed to approach it. In Brazoria County, 90 prey-captures were recorded with 31 observations of rejected or ignored prey. In Galveston County, 164 prey-captures were recorded with no observations of
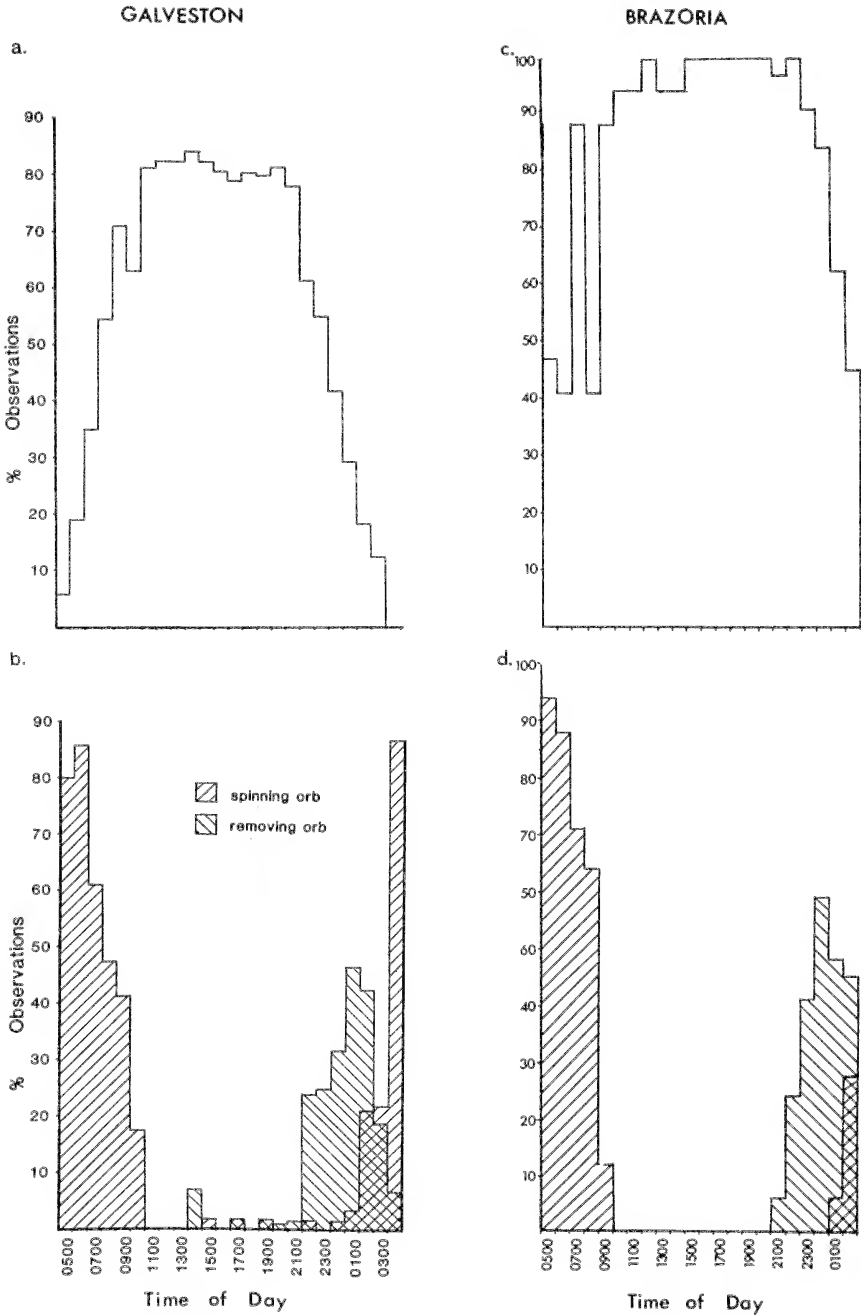
Fig. 2.—Activity schedule of female *N. clavipes* in Galveston and Brazoria Counties. The percentage of total observations is plotted against the time of day. Sunrise occurred at about 0700, sunset at about 2030: a, The percentage of individuals hunting in Galveston. At no time are all spiders hunting because of the presence of pre- and post-molt individuals in the population; b, The schedule of web renewal in Galveston; c, The percentage of individuals hunting in Brazoria. Non-hunting pre- and post-molt individuals were not used in this portion of the study; d, the schedule of web renewal in Brazoria.
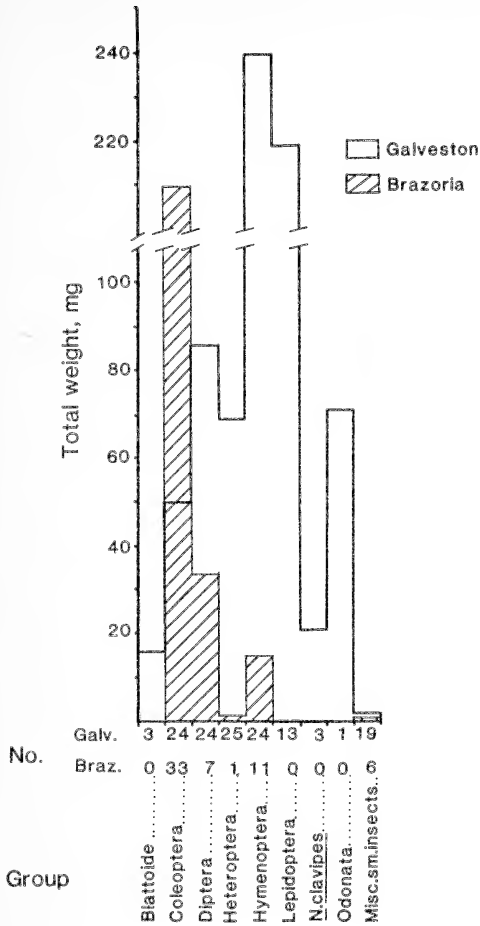
Fig. 3.—Numbers and estimated dry weights of prey identified to order. Dry weights of insects estimated from equations provided in Schoener (1980), *N. clavipes* weight estimated from weights of live spiders of equivalent size.

rejected prey. Of prey observed, 66% were identified in Brazoria County and 83% in Galveston County. The common beetles were identified to family level in Brazoria County. The numbers and estimated weights of identified prey in each order are presented in Fig. 3. Both the numbers and the weight of prey of each order are significantly different between the two locations (Chi-square for numbers of prey = 38.35, df = 5, $p < 0.001$; Chi-square for weights of prey = 605.2, df = 7, $p < 0.001$; categories with expected values of less than 1.66 were included as "Others" in the calculation of Chi-square). Lepidoptera and Hymenoptera, mostly bees, were the major sources of prey weight in the Galveston County population, whereas Coleoptera contributed the most in Brazoria County.

The histogram of body length of all observed prey (Fig. 4a) includes observations of prey capture from both the survey study and the population study. The distributions are significantly different (G = 16.60, df = 7, $p = 0.02$, lumping all prey greater than 15 mm). In both locations a large proportion of the items captured were less than 4 mm body length: 52% in Galveston and 45% in Brazoria (90% if the alate ants are included, see below). These small insects were mostly dipterans, hymenopterans and coleopterans. They contribute little to the total weight of prey captured (6% in Brazoria and 4% in Galveston, Fig. 3). The

a.

b.   c.
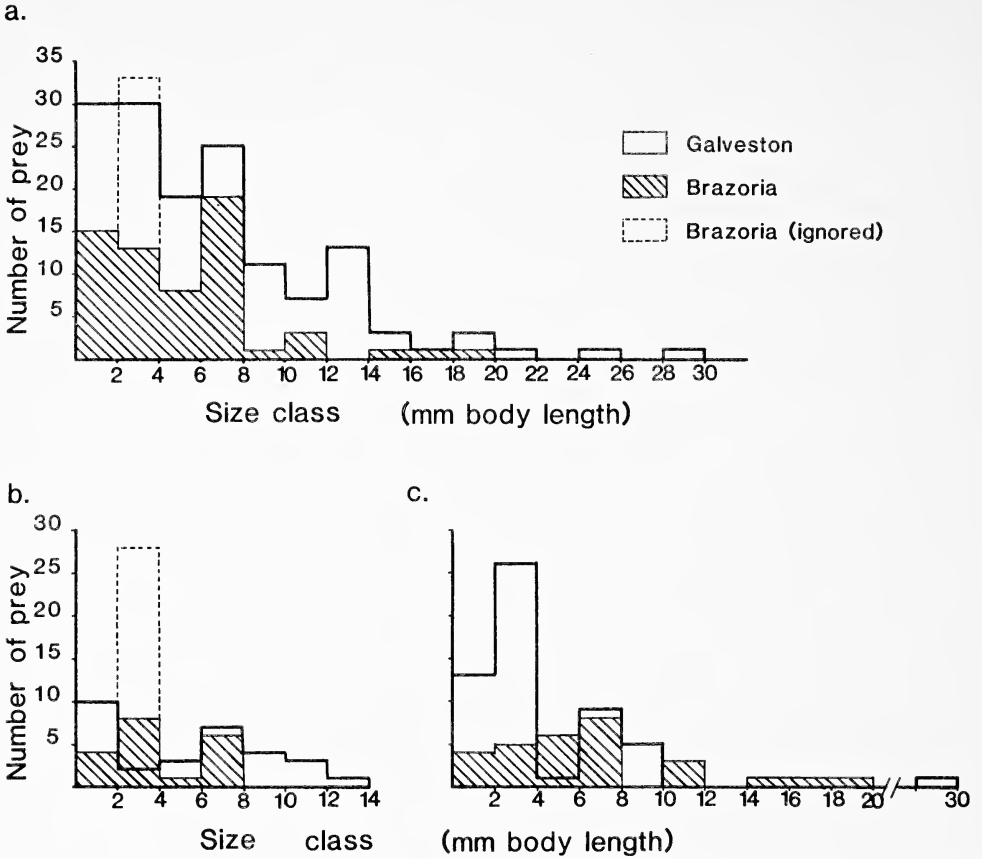
Fig. 4.—Distribution of body lengths of prey caught by *N. clavipes* at both locations. Stippled outline indicates the alate ants observed in the orbs (but ignored by the spiders) in Brazoria County: a, all prey captured; b, diurnal surveys only; c, nocturnal surveys only.

distributions of prey body lengths observed in the diurnal and nocturnal surveys are presented in Figs. 4b, c. A G-test of independence (Sokal and Rohlf 1981) was done to compare the effects of time (diurnal or nocturnal) and locality on the distribution of prey sizes. The three-way interaction of time, site and prey size was significant (G = 25.68, df = 4, $p < 0.001$). The sizes of prey are significantly different between diurnal and nocturnal surveys at each location (G = 30.09, df = 8, $p < 0.001$) and the locations are significantly different at each time (G = 32.68, df = 8, $p < 0.001$). These interactions can be partly explained by the differences in the types of prey observed at the different sites. The diurnal prey in Galveston County (bees, large Diptera, Lepidoptera) were larger than the nocturnal prey (small Coleoptera and Diptera). In Brazoria County, the diurnal prey (alate ants and Diptera) were smaller than the nocturnal (scarabs and other beetles).

N. clavipes showed individual variation in response to small (less than 4 mm) and potentially dangerous insects. During the diurnal survey in Brazoria there was an emergence of 3-4 mm alate ants, and while three spiders ignored them, another ate them immediately. Only five of 33 alates observed in orbs were eaten by spiders during the survey. The ignored alate ants were observed both escaping and being eaten by kleptoparasites; it is doubtful many of these small insects would still be in the orb when the spider removed and consumed it at the end of

the day. The spiders in Galveston County were often observed removing insects of less than 2 mm body length from their orbs. In addition, two spiders in Brazoria rejected (removed from the orb) 5-6 mm wasps that were captured by other spiders, and one female "ignored" a 30 mm beetle that did a lot of damage as it removed itself from the orb.

Prey-capture rates.—*N. clavipes* required at least one half-hour to consume most insects. Significantly more prey captures were observed when observations were done at half-hour rather than hour intervals in Galveston (paired t-test t = 2.03, df = 10, $p < 0.05$), with no change in the size range of prey observed. The smallest size class of prey is understimated with either schedule, but I assumed that prey of less than 2 mm body length were not energetically important to the diet even though they may be numerically important (Kajak 1965; Nyffler and Benz 1978).

The pattern of prey capture over twenty-four hours was similar at both sites (Fig. 5). Potentially, the spider can capture insects any time there are viscid strands in place. However, in Galveston County, all observed prey captures occurred between 0500 and 2300, with most occurring between 0800 and 2200. In Brazoria County, all but one of the prey captures observed occurred between 0600 and 2400 (Fig. 5). The rate of prey capture was almost constant through the day and peaked at dusk (1900 to 2200). In Galveston, this peak corresponded to the evening drop in temperature (Fig. 5). This may reflect an increase in the number of flying insects, as Buskirk (1975) observed in Costa Rica. The distribution of prey capture was similar in Brazoria County, with an additional small increase in prey capture between 1100 and 1300, due in part to the alate ants.

Considering only the surveys done at half-hour intervals, the diurnal and nocturnal prey-capture rates were not significantly different within weeks in Galveston (paired t-test). Prey capture was highly variable from web site to web site; between 47 and 73% of the spiders captured prey during any one survey (considering only surveys done at half-hour intervals). The variation between individuals was greater than the variation between Brazoria and Galveston, or between weeks at Galveston County. There was no indication at either site of a relationship between prey capture and web-site tenacity.

In Galveston County, an average of 24% of the spiders captured at least one prey item greater than 4 mm body length during a single survey (32% during diurnal observation periods and 19% during nocturnal observation periods). The prey-capture rate of prey items greater than 4 mm body length was approximately half that of the total prey-capture rate (0.03 prey items per spider per hour, diurnal or nocturnal).

In Brazoria County, the nocturnal prey capture rate was higher than the diurnal prey capture rate. This is the opposite of Galveston County (Table 2). A higher proportion of spiders captured prey in Brazoria than in Galveston (Chi-square = 5.02, df = 1, $p < 0.02$). In Brazoria, 45% of the spiders captured prey equal to or larger than 4 mm during any one survey (29% during diurnal observations, 53% during nocturnal observations). The diurnal prey-capture rate for insects greater than 4 mm was the same as in Galveston (0.03 prey items per spider per hour), but the nocturnal rate was almost double (0.07 prey items per spider per hour).
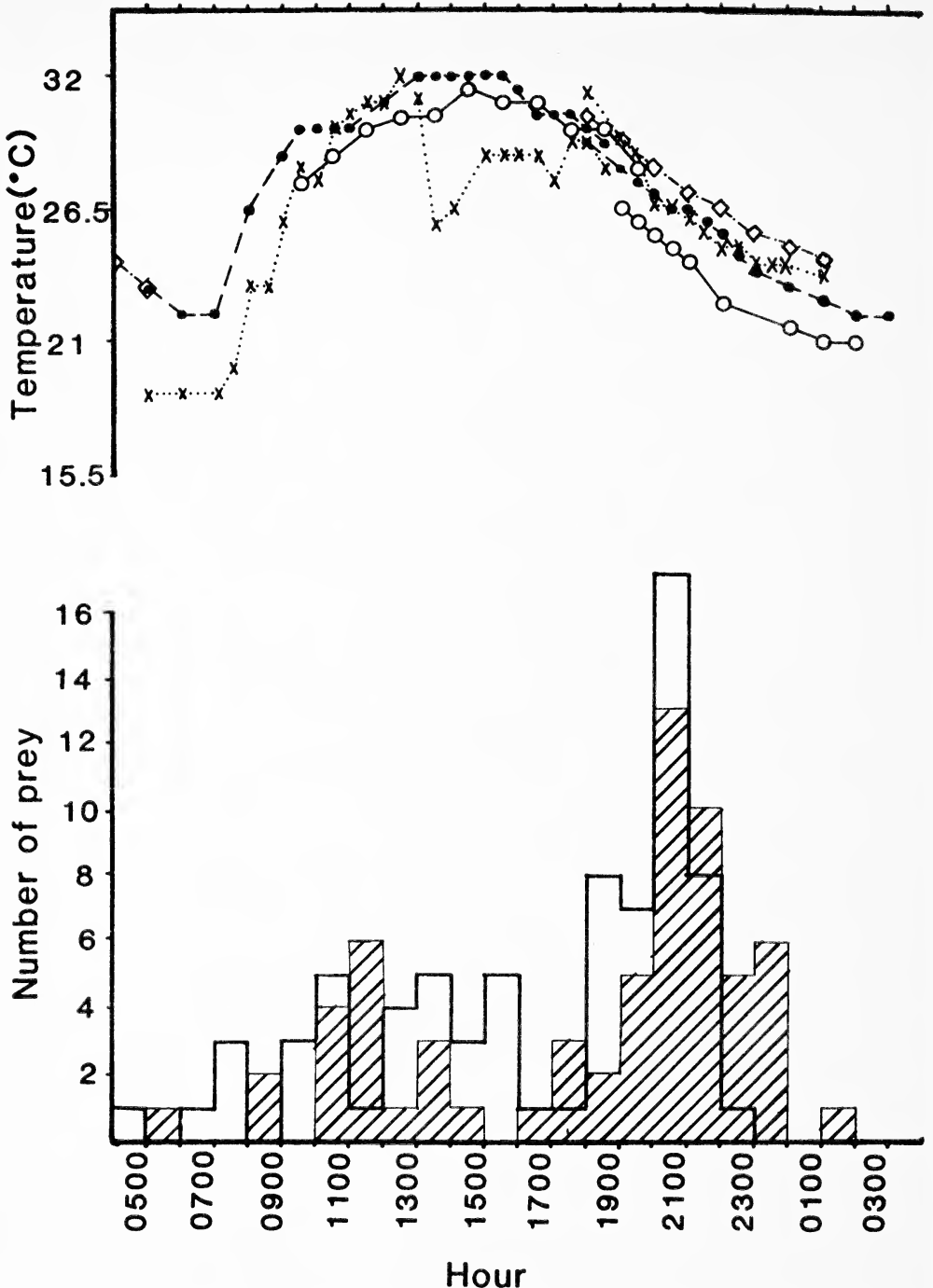
Fig. 5.—Prey capture in both locations and temperatures in Galveston County. Brazoria is hatched, Galveston is clear. Ignored prey are not included (see text). Temperature lines as follows: open circles = Aug 1, 4; black circles = Aug 8, 10; X⋯X = Aug 15, 17; diamonds = Aug 21, 23.

The total weight of prey captured by each spider during each survey was calculated (Fig. 6). I used only the data from the Galveston surveys done at half-hourly intervals but all of the Brazoria surveys. A total of 228.2 mg of prey were

Table 2.—Prey capture rates (number of prey captured per spider) observed in Brazoria County, July, 1983, and Galveston County, August, 1984. Overall prey-capture rates are based on 12 hour days and 10 hour nights. The rates for Galveston County are calculated using only the data from surveys done on half-hour intervals.

Place	Time	Spider-hours	Number of Prey	Prey Capture Rates	
				Per Hour	Per Survey
Brazoria	Diurnal	255	19	0.075	0.894
	Nocturnal	270	29	0.107	1.07
	OVERALL	525	48	0.091	—
Galveston	Diurnal	294	20	0.068	0.816
	Nocturnal	334	45	0.135	1.35
	OVERALL	628	65	0.104	—

observed caught in Brazoria County (50 spiders, 53 prey items), and 164.0 mg in Galveston County (67 spiders, 56 prey items). There were no significant interactions between the three factors of time of day, site, and mg prey captured (G-tests). Therefore, the between-site difference in prey sizes does not affect the estimated dry-weight of prey captured by a spider during a survey.

DISCUSSION

The activity schedules and time budgets of *N. clavipes* in the two locations in southern Texas are the same. The patterns of orb renewal are the same and are similar to those observed in the tropics for *N. clavipes* (pers. obs.) and *N. maculata* (Fabricius) (Robinson and Robinson 1973a). *N. clavipes* in southern Texas appears to have a wide range of acceptable prey. The prey caught are dependent upon the geographic location and probably also upon the microhabitat of the individual spider (Brown et al. 1985). The large number of small prey in the diet of the Texas populations is similar to the diet in studies of *N. clavipes* in Louisiana (Brown et al. 1985) and Peru (Rypstra 1985).

Web renewal and recycling.—The spiders were unable to capture prey only a short period of time each night. The length of time was dependent on whether the spider replaced all of the orb or only a section; in the former case there was a period of one or two hours when there was no viscid silk, in the latter, there was always some viscid silk. Hunting spiders are believed to respond to moving insects in the orb anytime they are not satiated. Even when not hunting, *N. clavipes* remains at the hub of the orb, and that is where molting occurs.

Web renewal patterns have not been studied in most araneids, and the extent and efficiency of silk recycling are not known. Although silk recycling has been carefully studied in *Araneus diadematus* Clerck (Breed et al. 1964; Peakall 1971; Peakall and Witt 1976) and is here reported for *N. clavipes*, it is known that there are araneids which either abandon the orbs or remove them and discard the silk (M. Robinson, pers. comm.; pers. obs.). This may be more common among the araneids with reduced orbs (Robinson and Robinson 1975) and the uloborids, with non-viscid orbs (Eberhard 1971). Web renewal and silk recycling patterns are important for understanding the evolution of foraging behavior within araneid species (Lubin 1973) and between araneids and other web-dependent spiders (Janetos 1982).
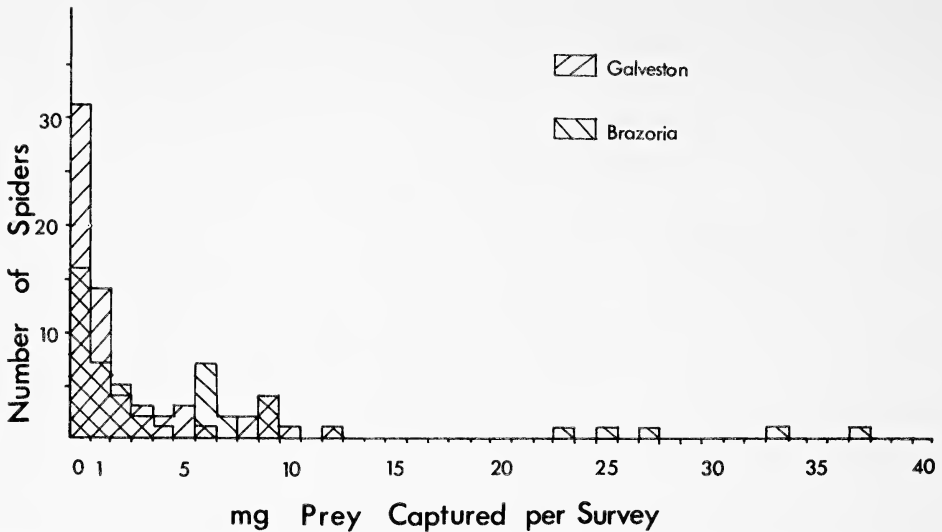
Fig. 6.—The frequency distribution of mg prey captured per spider per survey. There is no interaction between the time of the survey (diurnal or nocturnal), the location and the amount of prey captured (G-test for the 3-way interaction = 3.85, 4 df, ns; G-test for each of the 2-way interactions also not significant).

Prey captured.—The main difference between the two sites is the types of prey taken. The numbers and weights of each prey type are significantly different between sites (Fig. 3). These differences indicate that, like other web dependent spiders studied in several locations or over long periods of time, *N. clavipes* will take most common insects (Kajak 1965; Turnbull 1960; Robinson and Robinson 1970, 1973a; Nyffler and Benz 1978; Olive 1980). *N. clavipes* does not specialize on any one prey type (see also Turnbull 1960; Wise and Barata 1983) or size range (Olive 1980, Nentwig and Wissel 1986). However, the variable response to small Hymenoptera reflects selectivity by individuals (Castillo and Eberhard 1983). In Brazoria, most of the spiders ignored the alate ants and small wasps that were common during the diurnal census, but in Galveston *N. clavipes* consumed most insects caught in the orb regardless of size. This may be an indication of energetic stress in Galveston. Antagonistic interactions have been reported by Rypstra (1985) in response to artifically reduced food levels. Interactions such as female-female cannibalism and female-female and male-female displacement were common on Galveston but not at Brazoria, and may be additional indications of energetic stress.

Part of the between-size difference in prey types caught probably reflects differences in prey availability between the two locations. No samples were made of prey availability because of the difficulty in sampling insect types used by spiders (Kajak 1965; Robinson and Robinson 1973a; Uetz et al. 1978; Castillo and Eberhard 1983). The prey captured by *N. clavipes* in Galveston County were taxonomically diverse (Fig. 3). Of the orders reported as prey of other araneids, only Orthoptera were never observed. The main prey types (Diptera and Hymenoptera) were also caught by *N. clavipes* in Panama (Robinson and Mirick 1971). In contrast to the observations from Brazil (Vasconcellos-Neto and Lewinsohn 1986) and Panama (Robinson and Mirick 1971), Lepidoptera were not common prey in Texas but the contribution to the diet (estimated dry weight) was

Table 3.—Results of Chi-square and rank-order tests on prey types captured for between-site differences within species. Chi-square tests were computed over all prey types for contingency tables with smallest cells lumped into "Others". Species: *A. a.* = *Araneus quadratus*, *A. c.* = *Araneus cornutus*, *A. b.* = *Argiope bruennichi*, *N. c.* = *N. clavipes*. Sources: 1. Kajak 1965, table 3. 2. Nyffler and Benz 1978, tables 1, 2, and 3. 3. Present Study. * = Data presented only as percentages and totals. Data presented here are estimates; total absolute difference over the four stations between these totals and original totals = 4. ** = Rank order test not computed because ranks are identical. *** = Rank order test not computed because of large number of ties.

	Species				
	A. a.		*A.c.*		*N. c.*
				A. b	
Location (Source)	Poland (1)	Switzerland (2)	Poland (1)	Switzerland (2)	U.S.A. (3)
Number of Sites	3	1	3	5*	2
Total Prey Obs. at each site	44, 34, 47	173	131, 199, 299	873, 377, 244, 215, 90	90, 164
Chi-square	19.56 (Poland)	32.9 (both)	60.3	179.5	38.35
df	8	9	8	16	5
P	<0.025	<0.001	<0.0015	<0.001	<0.001
Rank-order Test	**	$t = 4.6$, ns	**	$W = 0.431$, $\chi^2 = 17.24$ $df = 8$, $p < 0.05$	***

high. The large number of Heteroptera and honeybees in Galveston reflects the abundance of heteropteran pests found on the Chinese tallow trees (W. Shield, pers. comm.) and the honeybee hives at the research station. The diversity of prey captured in Brazoria County is lower than in Galveston County and probably reflects reduced insect diversity due to fire ant predation (J. E. Rawlins, pers. comm.). The most common prey by number and weight in Brazoria are coleopterans (40% of total prey, 80% of weight); many of these are large, nocturnal beetles (Scarabeidae, Elateridae and Lampyridae). Large beetles were never observed in the webs of *N. clavipes* at the Galveston site and are not reported as common prey in New Orleans (Brown et al. 1985) or in Panama (Robinson and Mirick 1971).

As comparison with other interpopulation studies of araneid foraging, Table 3 presents statistical analysis of published prey lists. All between-site differences in numbers of prey captured by one species are significant (Chi-square tests). In these studies as in the current study, the spiders are taking different proportions of the various prey types at different sites, however all but *N. clavipes* rank the prey types in the same order (Kendall's tau and Kendall's Coefficient of Concordance, Siegel 1956).

Most observations of other Araneidae have indicated that large proportions of the diets consist of small insects (Kajak 1965; Nyffler and Benz 1978; Olive 1980). Kajak, and Nyffler and Benz treated small prey as unimportant since the contribution of these items to the total estimated weight of prey captured is small. In all populations of *N. clavipes* where prey records have been kept, a large proportion of the prey were of small body size. A high capture rate of small prey is possible in *N. clavipes* because the viscid spiral is closely spaced for a spider of this size (Uetz et al. 1978) (4-6 viscid strands/cm in penultimate and adult females in Texas). Nentwig and Wissel (1986) found experimentally that most spiders prefer prey of 50-80% of the spiders' body length. Few prey items recorded in these studies fall within this range (7-12 mm for a spider of tibia + patella length

Table 4.—Comparisons of prey-capture rates of different araneids. * = Prey-capture rates are underestimates due to observation methods. Kajak presents the data as prey-capture per 24 hours total time of observations not given. ** = Data given as prey-capture per spider-hour. Sources: 1 = present study. 2 = Robinson and Robinson 1973a. 3 = Robinson and Robinson 1970. 4 = Olive 1980. 5 = Kajak 1965. 6 = Buskirk 1975.

Species	Location	Source	Total Time	Prey Capture Observed	Estimated PC/Hour
Nephila clavipes	Texas	1	1131 spider-hours	85	0.08
*N. maculata**	New Guinea	2	3237 web-days (24 h)	6039	0.08
Argiope argentata	Panama	3	2809 web-days (12 h)	4672	0.21
A. trifasciata	U.S.A.	4	61.5 web-hours	40	0.65
Araneus trifolium	U.S.A.	4	37.2 web-hours	24	0.65
*A. cornutus**	Poland	5	24 web-hours	6.7	0.3
*A. quadratus**	Poland	5	24 web-hours	2	0.08
*Metabus gravidus***	Costa Rica	6	—	—	1.70

= 1 cm). Rypstra (1985) reported that in Peru 85% of the prey were no greater than 5 mm body length. Brown et al. (1985) found many small prey in the diet of *N. clavipes* in Louisiana (11 to 93%), with the exact proportion dependent upon the microhabitat. In the current study, 52% of the prey in Galveston and 45% in Brazoria were 4 mm or smaller in body length, and the proportion of spiders capturing larger prey was low. Insects that are small relative to the spider's size may be very important in the diet in these populations. It may also be that occasional capture of very large insects is important. Interestingly, these studies of *N. clavipes* prey are all of populations at the edges of the distribution of this species (Levi 1980).

The prey-capture rates observed in the two Texas populations are very similar to that calculated from the data of Robinson and Robinson (1873a) for *N. maculata* (Table 4). However, the average weight of prey captured each day by *N. maculata* is estimated as 15 mg, or 1.5 times the observed capture in Brazoria, 2.5 times that in Galveston. Therefore, *N. maculata* is capturing a larger proportion of large insects. The prey-capture rates calculated from the data of Robinson and Robinson (1973a) and calculated for *N. clavipes* (this study) are much lower than prey-capture rates estimated from data available for other araneids (Table 4). However, the former may be an underestimate as the methods of Robinson and Robinson did not allow the observation of small insects that may form a part of the diet.

N. clavipes does not easily fit into any of the foraging models proposed for web-dependent spiders (Enders 1975; Olive 1980; Janetos 1982, 1984; Rypstra 1982). *Nephila* females are large araneids (gravid females often weigh over 2 g) with large, complex webs. In theory, a large predator that is dependent upon relatively small prey should spend large amounts of time or energy searching for prey (Sutherland and Moss 1985). For orb-weaving spiders, this means increased time at the hub or increased energy invested in the orb, both observed in *N. clavipes*.

Comparison of this study with studies of smaller araneids provides insight into the possible relationship between prey capture and hunting time. *Metabus gravidus* (Cambridge) has the highest per-hour capture rate reported for orb-building spiders (1.70 items per spider per hour, Buskirk 1975). Buskirk found

that *M. gravidus* individuals spent between three and eight hours hunting. The time spent hunting by each individual was inversely correlated with its hunting success on the previous day. Eberhard (1973), studying *Uloborus diversus* (Marx), found that web construction was inversely related to the frequency of prey capture. Other researchers have observed orb-web spiders without webs, found in retreats in the vegetation (Kajak 1965; Eberhard 1971, 1973; Nyffler and Benz 1978; Olive 1980; A. Mahler pers. comm.; pers. obs.). By comparison, *N. clavipes* was always found at the hub of the orb, even when molting. Other large araneids such as *N. maculata* (Robinson and Robinson 1973a), *Cyrtophora moluccensis* (Doleschall) (Lubin 1973), *Araneus cornutus* Clerck and *A. quadratus* Clerck (Kajak 1965; Nyffler and Benz 1978) were observed to hunt most of the time; how many other orb-weaving spiders are on the orb nearly 24 hours per day is unclear. The spiders' position at the hub increases its exposure to potential predators. (Predators on *N. clavipes* are not common in the temperate locations (Moore 1977; pers. obs.) but are very common in the tropical locations (pers. obs.)). These species are reported to either hunt from retreats (many *Araneus* species) or build barrier webs (*N. clavipes, N. maculata* and *C. moluccensis*). Hunting from retreats or building auxillary web structures such as stabilimenta and barrier webs may have evolved in large araneids to maximize hunting time in the presence of predators.

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BLACK-STRIPE PHENOTYPES IN THE SPIDER
ENOPLOGNATHA OVATA (ARANEAE, THERIDIIDAE)

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ABSTRACT

In this paper we describe black-stripe phenotypes of the polymorphic theridiid *Enoplognatha ovata*
(Clerck) found among reared broods and natural populations from coastal Maine. Among reared
spiders, black stripes were deposited over the typical color phenotypes *lineata*, *redimita* and *ovata*,
and appeared to assort independently of the typical color morphs. Black stripes occurred more
frequently among males than females, although the difference in incidence between the sexes was not
statistically significant. Among 17 natural populations, black-stripe morphs were far more frequent
among males than females, suggesting the possibility that black striping is associated with sex
determination in *E. ovata*.

INTRODUCTION AND METHODS

The theridiid spider *Enoplognatha ovata* (Clerck) displays a conspicuous color
polymorphism characterized by three distinct phenotypes: (1) *lineata*, with a
creamy yellow opisthosoma (Fig. 1a); (2) *redimita*, exhibiting two dorsolateral red
stripes (Fig. 1b); and (3) *ovata*, characterized by a solid red shield covering most
of the dorsal opisthosoma (Fig. 1c). The genetic basis of color expression is
detailed in a model by Oxford (1983) in which three color alleles (C^1, C^r, C^0) at a
single autosomal locus determine the phenotypes *lineata, redimita* and *ovata*. The
alleles exhibit a dominance hierarchy whereby *ovata* (C^0) is dominant to *redimita*
(C^r) which is in turn dominant to *lineata* (C^1). A linked regulatory gene
determines the timing of red pigment deposition in *redimita* and *ovata* during
development (either early, during third or fourth instar, or late, upon final ecdysis
to maturity). Biochemical aspects of pigment deposition in *E. ovata* are addressed
elsewhere (Seligy 1969, 1972), and the reader is directed to many discussions of
the ecological and evolutionary aspects of this color polymorphism (Oxford 1976,
1983, 1985; Oxford and Shaw 1986; Hippa and Oksala 1979, 1981; Wise and
Reillo 1985).

Oxford (1976) reported that some *E. ovata* exhibit black stripes in addition to
one of the typical color phenotypes just described. We recently discovered black-
striped phenotypes among the offspring of field-collected broods of *E. ovata* from
eastern North American populations. Below we describe the patterns observed
and present preliminary estimates of the incidence of the black-stripe trait in
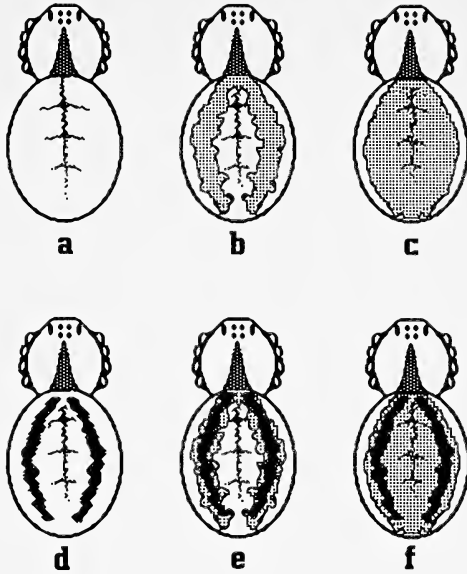natural populations.

Fig. 1.—Typical color morphs (a) *lineata* (b) *redimita*, and (c) *ovata*, with corresponding black-stripe morphs below (d-f).

Fifty-seven *E. ovata* females with egg sacs were collected from several locations in Acadia National Park, Maine, USA during August 1985. None of these females exhibited the black-stripe character. Over the following year broods from these phenotypically known females were reared in cages based on a design by Oxford and Pitts (1981) or in individual glass vials as described in Seligy (1971) and Oxford (1983). Spiderlings from caged broods were isolated into individual glass vials upon reaching 4th instar, where they remained until maturity (6th instar) or death.

RESULTS AND DISCUSSION

The black-striped phenotype appeared in broods of five field-collected females. Black-striped individuals appeared with *lineata*, *redimita* and *ovata* background phenotypes. The black-stripe character results from a dark pigment deposited over the typical color morph patterns. Figure 1(d-f) depicts the combination black stripe/color morph phenotypes for the background patterns *lineata, redimita* and *ovata*. In individuals with a background *lineata* pattern, the striped morph appears as two dark lines that vary from dull grey to shiny black. The stripe width is also variable. Some individuals exhibit thin stripes, whereas others show broad bands with occasional horizontal bars bridging the two main stripes. In black-striped *redimita* individuals, the black stripes often coincide so completely with the dorsolateral red stripes that this phenotype can easily be mistaken for the black-striped *lineata* morph. Closer examination may reveal a triangle of red pigment left unmasked by the stripes at the anterior end of the opisthosoma or occasional patches of red along the margins of the black stripes. The pattern in black-striped *ovata* individuals is readily identified by the black stripes circumscribing the *ovata* red shield; occasionally red pigment can also be detected beyond the margins of the black stripes.

Black-stripe pigmentation was deposited by the end of the fourth instar and was detected in second and third instars in some individuals. Not all striped

PROGENY PHENOTYPES

Mother's phenotype			lin.	red.	ova.	b/l	b/r	b/o	n	N	#b/n	tot.#b/N
OVA	♂		4	-	3	2	-	1	10	17	3/10	4/17
	♀		6	-	-	-	-	1	7		1/7	
LIN	♂		6	-	-	4	-	-	10	22	4/10	4/22
	♀		12	-	-	-	-	-	12		0/12	
RED1	♂		7	4	-	3	-	-	14	21	3/14	7/21
	♀		2	1	-	2	2	-	7		4/7	
RED2	♂		1	3	-	2	1	-	7	12	3/7	5/12
	♀		1	2	-	1	1	-	5		2/5	
RED3	♂		1	-	-	2	2	-	5	8	4/5	5/8
	♀		2	-	-	1	-	-	3		1/3	

OVA = *ovata*   RED = *redimita*   LIN = *lineata*

Fig. 2.—Summary table for broods exhibiting black-stripe phenotpyes: b/l = black-stripe morph over *lineata* pattern, b/r = black-stripe morph over *redimita* pattern, b/o = black-stripe morph over *ovata* pattern, "b" in last two columns refers to black stripes over any pattern.

young instars retained the black stripes. Some black-striped spiders changed phenotype during the fourth instar or upon ecdysis to fifth instar: three black-striped *lineata* spiders became indistinguishable from typical *lineata*, and one black-striped *redimita* spider became a typical *redimita*. Spiderlings that developed both black-stripe and red pigments indicate that black pigments can be deposited earlier in development than *redimita* or *ovata* pigments. Careful scrutiny of some third- and fourth-instar black-striped *redimita* and black-striped *ovata* spiders revealed that red pigments were deposited beneath black stripes already in place.

The distribution of phenotypes among the five broods exhibiting the black-stripe trait is given in Fig. 2. The character appears to assort independently of the *lineata, redimita* and *ovata* traits, suggesting that it is controlled by a locus (or loci) independent of the autosomal locus controlling the typical color phenotypes. The black-stripe trait is more frequent among male than female offspring from broods exhibiting the character (37% vs. 24%, respectively, Fig. 2), although this difference is not statistically significant (Chi-square = 1.64, df=1, P = 0.200).

Preliminary field census data from 17 populations reveal a sex-based bias in appearance of the trait. In all populations sampled, black-stripe morph frequencies were dramatically higher among males (Fig. 3). However, these frequencies should be interpreted with caution. Black-stripe frequencies in males may be over-estimated due to observers confusing the black-stripe morphs with dark patterns associated with the digestive diverticulae showing through the body wall (Seligy 1969; Oxford 1983). Laboratory examination of specimens is required to confirm phenotype assignments. Despite possible identification problems, the census data indicate that the black-stripe phenotype is more frequent among males than females and hence may be associated with sex-determination in *E.*

SITE	SEX	BLACK STRIPE	N	FREQ. BLACK STRIPE
DC	M	17	245	.069
	F	–	383	–
OCR1	M	6	15	.400
	F	–	35	–
OCR2	M	3	14	.214
	F	1	37	.027
OCR3	M	3	14	.214
	F	1	37	.027
OCR4	M	4	19	.211
	F	1	31	.032
OCR5	M	8	22	.364
	F	1	28	.036
OCR6	M	8	12	.667
	F	–	38	–
C	M	8	51	.157
	F	–	102	–
FT2	M	3	17	.176
	F	–	36	–
FT3	M	7	15	.467
	F	1	35	.029
OTT.PT.	M	12	51	.235
	F	–	73	–
TI	M	20	36	.556
	F	1	66	.015
G	M	18	37	.486
	F	–	73	–
J	M	17	38	.447
	F	1	66	.015
MP	M	13	39	.333
	F	1	61	.016
NL1	M	7	34	.206
	F	–	66	–
GCP	M	4	23	.174
	F	–	41	–
TOTAL	M	158	668	.237
	F	8	1208	.006

Fig. 3.—Frequencies of black-striped morphs from seventeen Maine populations, censused mid-July 1986.

ovata. G. S. Oxford also found the black-stripe trait more frequently among males in both reared broods and field populations (G. S. Oxford, unpublished data).

The genetic mechanism underlying the inheritance of this trait is unclear. The genetics of black-stripe expression in *E. ovata* may resemble the recessive, sex-linked inheritance of dark pigments of *Eupteryx* leafhoppers (Stewart 1986). Alternatively, gene(s) for the trait may be autosomal and its expression may be partially sex-limited (G. S. Oxford, pers. comm.). The most direct method of determining the inheritance of black striping would be to cross black-striped spiders of known ancestry; unfortunately, matings with lab-reared *E. ovata* have proven mostly unsuccessful (personal observation; Oxford 1983). In view of the difficulties of obtaining black-stripe crosses and censusing the morphs in natural populations, we feel it is worthwhile to present patterns based on preliminary data. We hope these data and ideas serve as incentives for future research.

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>
> *A-us y-us* Bates 1932:18, fig. 4. NEW SYNONYMY.
>
> *A-us z-us*: Miranda 1948:98 (misidentification); Harris 1951:3 (in part?). (*nec A-us z-us* Zimmer).

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Figs. 27-34.—Right chelicerae of species of *A-us* from Timbuktu: Figs. 27, 29, 31, 33.—Dorsal views; Figs. 28, 30, 32, 34.—Prolateral views of movable finger; Figs. 27-28: *A-us x-us*, holotype male; Figs. 29-30: *A-us w-us*, male; Figs. 31-32: *A-us z-us*, holotype male; Figs. 33-34; *A-us t-us*, male. Scale = 1.0 mm.

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