The Journal of
ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY

THE JOURNAL OF ARACHNOLOGY

A REVISION OF THE *METAPHIDIPPUS ARIZONENSIS* GROUP (ARANEAE, SALTICIDAE)

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ABSTRACT

The *Metaphidippus arizonensis* group contains two species, *Metaphidippus arizonensis* (Peckham and Peckham) and *M. helenae* (Banks). The two species share similar genitalic morphology. *M. arizonensis* occurs in both tall and shortgrass habitats in the central grasslands from southern Alberta to eastern Minnesota south to Arizona and New Mexico. *M. helenae* occurs in the interior basins of North Dakota, Utah, and Wyoming, and in saline marshlands of central California. Both species are redescribed and *M. glacialis* (Scheffer) is synonymized with *M. arizonensis.*

INTRODUCTION

During the 1970's we were independently engaged in biological studies of *Metaphidippus arizonensis* (Peckham and Peckham) at the southern and northern ends of its range (these studies to be published separately). It became apparent that there was some confusion in the taxonomy of the species, particularly concerning the status of *M. glacialis* (Scheffer). As a result, we decided to determine if indeed two species were represented. In a search for similar species we found that only one other North American species is closely related, *M. helenae* (Banks). It has been suggested that *M. tillandsiae* Kaston may belong in this species group, but the genitalia are of a different type. This small species group bears epigynal resemblances to two Siberian and Mongolian species described by Prozynski (1979). He noted an external epigynal similarity to *M. glacialis* in his *Dendryphantes biankii,* but internally they are different. However, the internal epigynal structure of his *D. czekanowskii* bears a close resemblance to the internal epigynal structures seen in the *M. arizonensis* group. Both of these Palearctic species are represented by only three female specimens; if males become available, they would be of considerable interest.

METHODS

Certain measurements for statistical purposes were standardized. These were all done on field collected females, males being relatively rarer in collections. Three populations of *M. arizonensis* were tabulated separately. Fewer specimens of *M. helenae* were available, so these measurements were pooled. All measurements throughout this paper are in millimeters.

SYSTEMATICS

Metaphidippus F. O. P. - Cambridge 1901.
Metaphidippus arizonensis group.

This small group may be readily distinguished from other *Metaphidippus* by genitalic characters. Males have a retrolateral palpal tibial apophysis which bifurcates near the tip forming a small hook. This is an oddity in North American members of the genus, the others have the tibial apophysis simple. The unexpanded bulb of the palpus is large compared to the cymbium. Females have a large external epigynum, which has a peculiar general appearance, resembling that of an insect face (Figs. 8 and 16). The internal genitalia are simple consisting of spermathecae with a loop (Figs. 9-11 and 17). Scale ultrastructure as viewed by scanning electron microscopy (Figs. 1 and 2) exhibits the predominantly three shafted morphology typical of "dendryphantine" salticids (Cutler 1981, Hill 1979).

KEY TO SPECIES

1. Males 2
   Females 3

2. Embolus in ventral view broadly spatulate, tip not twisted and acuminate . . . .
   . . . . *helenae*
   Embolus in ventral view not broadly spatulate, tip twisted and acuminate . . . .
   . . . . *arizonensis*
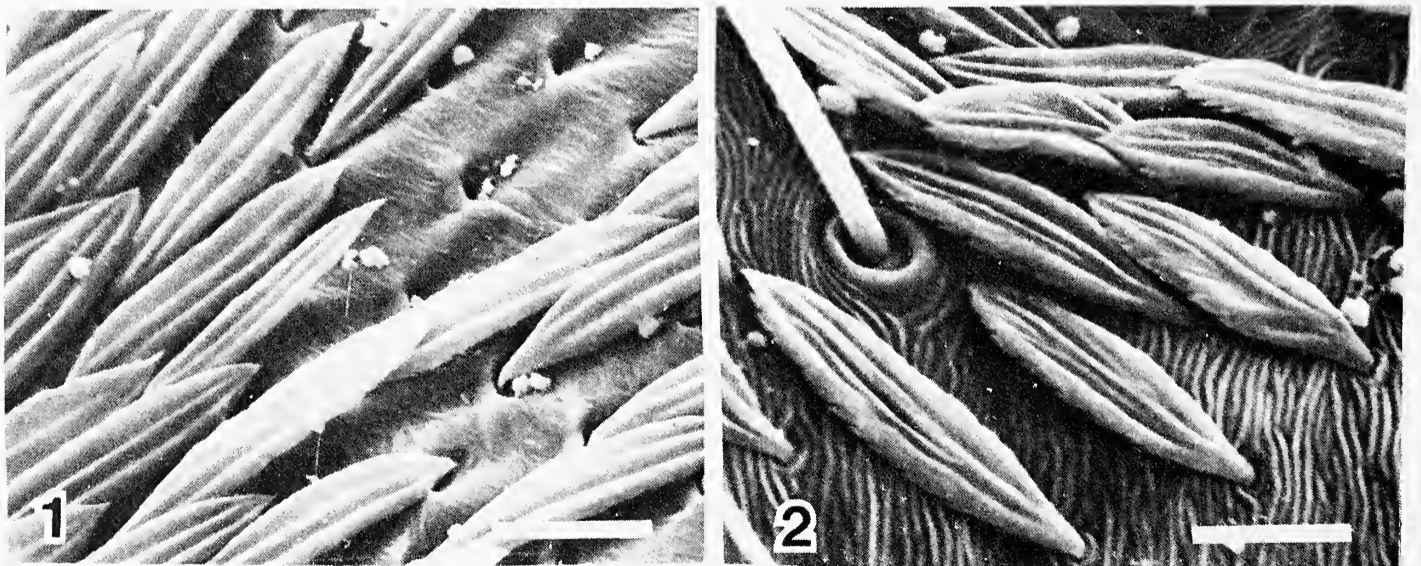
Figs. 1-2.—*Metaphidippus arizonensis,* Cedar Creek male: 1, scales between row III eyes; 2, opisthosoma, lateral. Both markers = 25 μm.

3. External epigynum with sclerotized rims of openings perpendicular to the long axis of the opisthosoma (Fig. 16); interior epigynum with loop of spermathecae posterior to epigynal openings (Fig. 17) . . . . *helenae*
External epigynum with sclerotized rims of openings parallel to the long axis of the opisthosoma (Fig. 8); interior epigynum with loop of spermathecae at level of epigynal openings (Figs. 9-11) . . . . *arizonensis*

Metaphidippus arizonensis (Peckham and Peckham)
Figs. 1-11, Map 1

Dendryphantes arizonensis Peckham and Peckham 1901:326, pl. 28, f. 2, 1909:463, pl. 36, f. 7.
Metaphidippus arizonensis: Petrunkevitch 1911:622.
Dendryphantes glacialis Scheffer 1905:7, 1906:124, f. 3, 4, 8; Peckham and Peckham 1909:463, pl. 37, f. 7. **NEW SYNONYMY.**
Metaphidippus glacialis: Bonnet 1957:2814.

Notes.—The Peckham's type was compared by Dr. H. W. Levi, and agrees with the other specimens discussed here; it is a male from an unknown locality in Arizona. Scheffer's specimens are unavailable or lost; letters to Kansas brought no response, and the specimens are not at the AMNH, CAS, MCZ, or the U.S. National Museum. [Apparently Scheffer described a number of species in 1905 in the Industrialist. These descriptions were repeated (as new) the next year in the Transactions of the Kansas Academy of Sciences. The latter publication is much more readily available in libraries, and contains illustrations not in the original description.]

Male (Arizona, Chevelon Ranger District).—Total length 4.6, carapace 2.22 long, 1.67 wide. Eyerow I width 1.18, eyerow III width 1.19, eyefield length 0.89. Eye diameters:
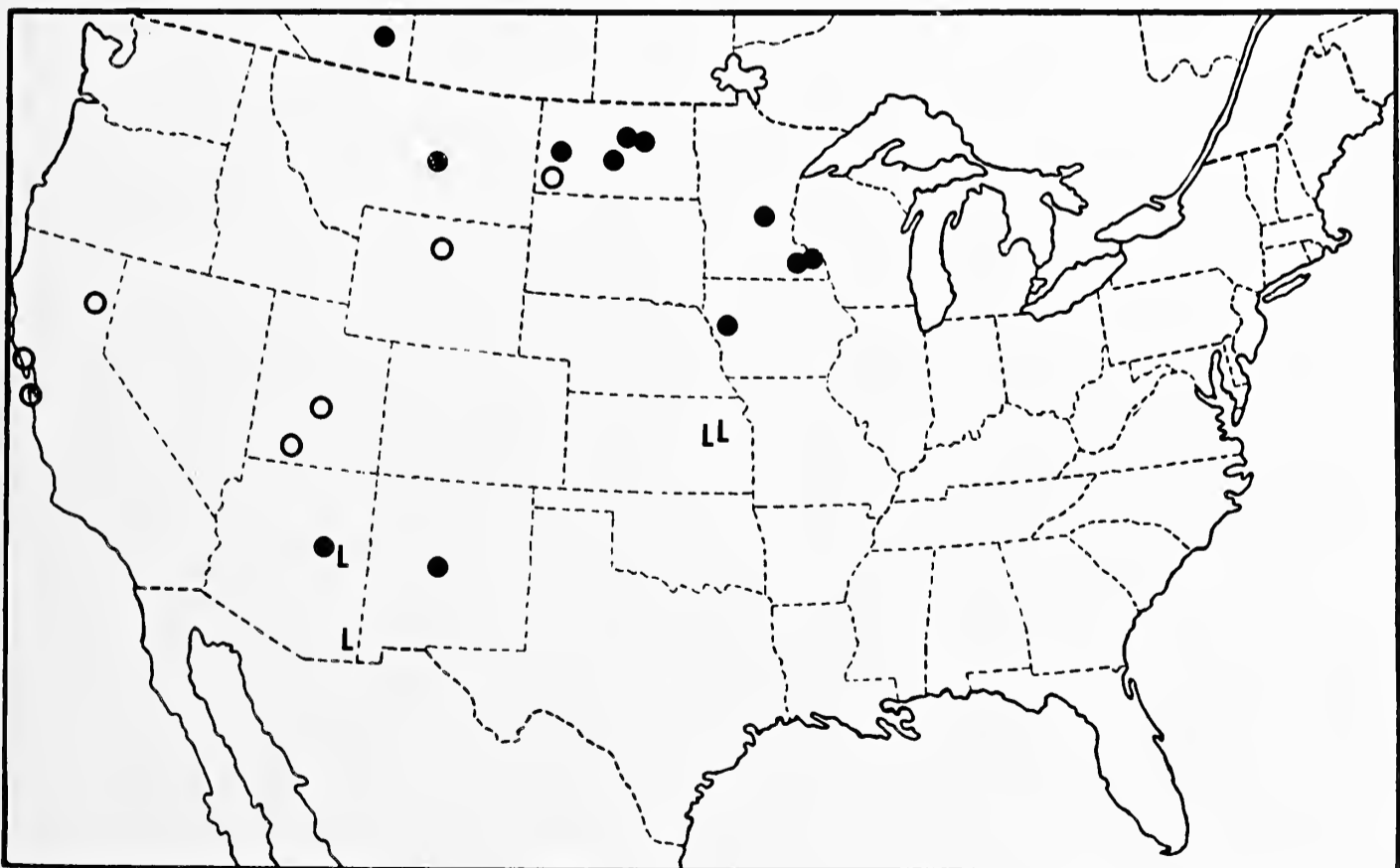
Map 1.—Ranges of *Metaphidippus arizonensis* (closed circles = examined specimens, L = literature records) and *M. helenae* (open circles).

Table 1.—Analysis of variation in populations of *M. arizonensis*. Femur = length of femur I, epigynum = minimum distance between sclerotized rims of epigynum, carapace = width of eyerow III. Column means followed by the same letter are not significantly different, one-way ANOVA, P ≤ 0.05.

| Population | n | FEMUR | | EPIGYNUM | | CARAPACE | |
		X̄±S.D.	Range	X̄±S.D.	Range	X̄ ±S.D.	Range
Cedar Creek	35	1.23±0.08[a]	1.04-1.42	0.19±0.02[a]	0.13-0.23	1.23±0.07[a]	1.13-1.40
Kellogg	12	1.39±0.08[b]	1.18-1.48	0.20±0.02[a]	0.15-0.23	1.34±0.10[b]	1.12-1.42
Chevelon	31	1.26±0.08[a]	1.09-1.50	0.18±0.02[a]	0.12-0.23	1.25±0.07[a]	1.07-1.50

AME 0.28, ALE 0.17, PME 0.06, PLE 0.14. Distance ALE-PME 0.24, PLE-PME 0.30. Femora lengths I 1.37, II 1.14, III 1.08, IV 1.31. Leg formula I, IV, II, III. Spines Leg I, dorsal femoral 5, tibia 3-3, metatarsus 2-2. Color pattern see figure 3.

Female (Arizona, Chevelon Ranger District).—Total length 5.7, carapace 2.41 long, 1.81 wide. Eyerow I width 1.27, eyerow III width 1.29, eyefield length 0.95. Eye diameters: AME 0.27, ALE 0.16, PME 0.07, PLE 0.15. Distance ALE-PME 0.25, PLE-PME 0.32. Femora lengths I 1.34, II 1.12, III 1.09, IV 1.40. Leg formula IV, I, II, III. Spines as in male. Color pattern see figure 7.

Three populations of females were chosen for numerical comparison. Two were from Minnesota, Allison Savanna — Cedar Creek, Anoka Co. (these sites are adjacent, separated only by a county road) and Kellogg, Wabasha Co.; and, one from Arizona, Chevelon Ranger District, Coconino Co. Three measurements were obtained from specimens: from the carapace, the width of eyerow III; from an appendage, the length of right femur I; from the opisthosoma, the narrowest point between the sclerotized rims of the epigynum. Table I summarizes the data. Note that one of the Minnesota populations resembles the Arizona population, whereas the other Minnesota population had members that were significantly larger. Chi-square tests for independence of characters within populations were nonsignificant. In addition to the identity in genitalic morphology, it appears that morphometrically there are no great differences in northern and southern populations of this species, other than local population differences.

Distribution.—From Alberta through Montana and North Dakota to southeast Minnesota, south through Kansas to New Mexico and Arizona. Does not occur west of the Rocky Mountains.

Material examined.—CANADA: **Alberta**, Medicine Hat (Carr), female (AMNH). UNITED STATES: **Arizona**; *Coconino Co.*, Sitgreaves National Forest, T13N, R13E, sections 17-20, 30, 35, west of Bart's Crossing (7000 feet) summer months 1969 to 1973, on forbs and seedling pine trees (D. T. Jennings), one male, numerous females (AMNH); **Iowa**; *Woodbury Co.*, four miles ENE of Hornick, 14 June 1970, sweeping upland prairie on bluff (B. Cutler), female (FSCA); **Minnesota**; *Anoka Co.*, Helen Allison Savanna, Nature Conservancy Area, E. of E. Bethel, April to October 1978 to 1980, on forbs in and sweeping sand prairie (B. Cutler), numerous males and females (AMNH and BC); *Anoka and Isanti Cos.*, Cedar Creek Natural History Area, E. of E. Bethel, April to October late 1970's to 1981, on forbs in and sweeping sand prairie (B. Cutler), numerous males and females (BC); *Wabasha Co.*, 3 miles SE of Kellogg, spring and summer months from 1974 to 1978, sweeping sand prairie (B. Cutler and R. Huber), 3 males, numerous females (BC); *Winona Co.*, Whitewater Game Refuge 1 mile E. of Beaver, 31 July 1982, in retreats on heads of *Lespedeza* (B. Cutler), numerous females (BC); **Montana**; *Petroleum Co.*, 1.5 miles S., 5 miles W. of Winnett, May 1971, sweeping disturbed short grass plains (N. E. Rees), male, female (BC); **New Mexico**; *Socorro Co.*, 21 miles E. of San Antonio, 28 June 1975, on roadside table in desert grassland (R. Carter), male (BC); **North Dakota**; *McHenry Co.*, Denbigh Sand Dune Reserve, 27 June 1970, on brush (P. D. Tobin), female (FSCA); 14 miles SW of Towner,
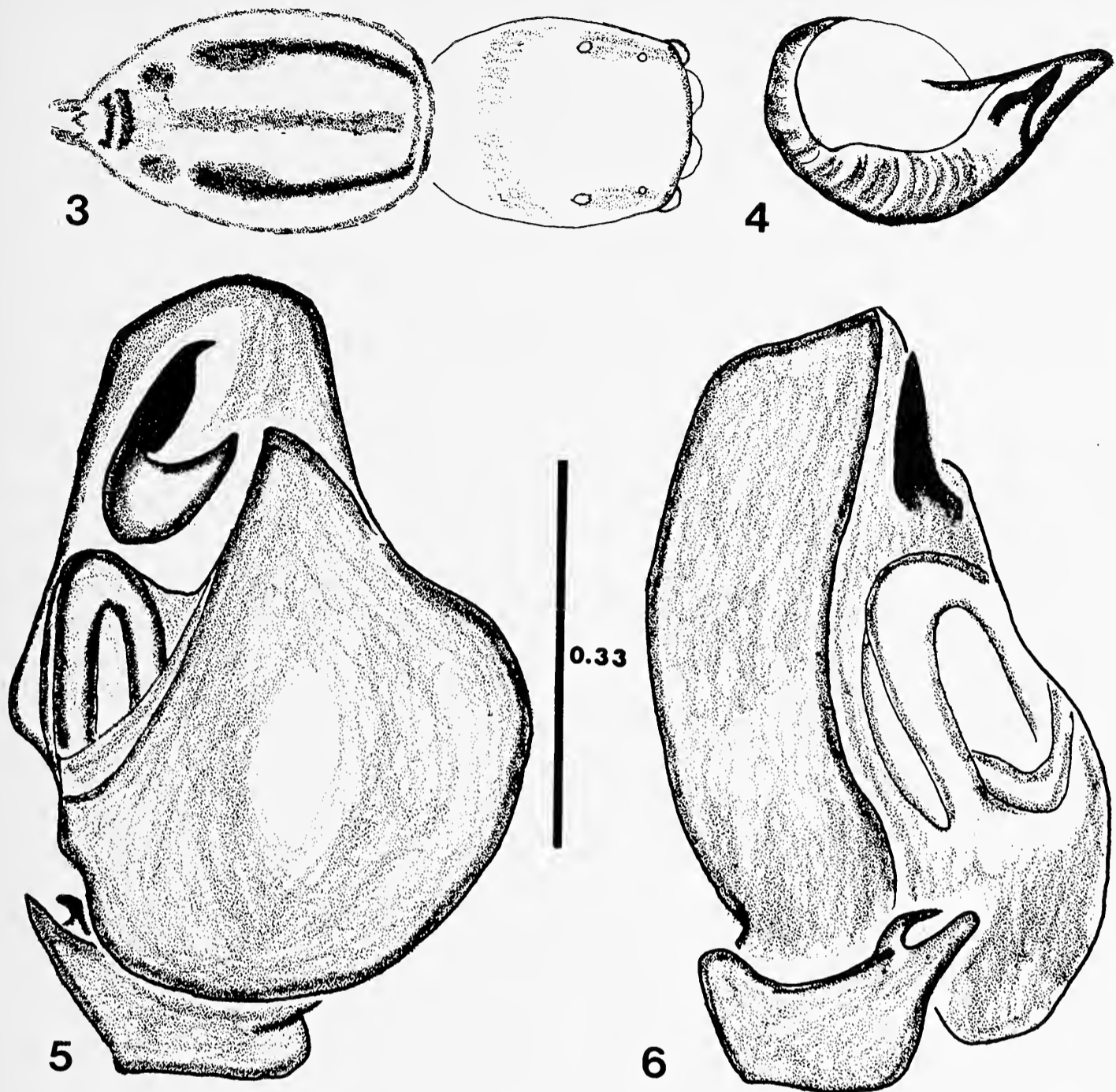
Figs. 3-6.—*Metaphidippus arizonensis* males: 3, Chevelon specimen, dorsal view; 4, Cedar Creek specimen, apical view of palpal tibia after removal of tarsus; 5, Chevelon specimen, ventral view of palpus; 6, Cedar Creek specimen, retrolateral view. Scale line in mm does not pertain to dorsal body view.

15 June 1971, brushing grass (P. D. Tobin), female (FSCA); *McLean Co.,* Garrison, near Douglas Creek Bay, 4 July 1970, on weeds (P. D. Tobin), male (FSCA); *Williams Co.,* Williston, 13 June 1973, male on plant in field, females in nests in dry plants in field (D. Maddison), male, three females (WM).

In addition, the following literature records are believed to be reliable: Scheffer's specimens were from **Kansas:** Pottawatomie Co., St. George, and Riley Co., Manhattan; Jung and Roth (1974) Ari-zona: *Cochise Co.,* Chiracahua Mountains; Jennings (1973) *Coconino Co.,* Sitgreaves National Forest, Chevelon Ranger District, Dudley Burn, sec. 20, T13N, R14E (7100 feet), 24 July 1970, female and egg retreat in dead stem of *Tragopogon pratensis* L. (AMNH). Although Worley and Pickwell (1927) have been listed as recording this species (as *D. glacialis*) from Nebraska, they only noted that it was possibly present.

Metaphidippus helenae (Banks)
Figs. 12-17, Map 1

Dendryphantes helenae (Banks) 1921:101-102, f. 5.
Metaphidippus helenae: Gertsch 1934:18.
Dendryphantes sausalitanus Chamberlin 1925:137, f. 57-58, Gertsch 1934:18 (synonymy with *M. helenae*).

Notes.—In the vial with the two female paratypes in the MCZ is a left palpus of a male, this is probably the left palpus of the holotype which is missing from that specimen.

Male holotype.—Total length 4.3, carapace 1.85 long, 1.42 wide. Eyerow I width 1.00, eyerow III width 1.00, eyefield length 0.73. Eye diameters: AME 0.28, ALE 0.18, PME 0.07, PLE 0.15. Distance ALE-PME 0.18, PLE-PME 0.23. Femora lengths: I 1.19, II 0.97, III 0.92, IV 1.15. Leg formula I, IV, II, III. Spines, leg I dorsal femoral 4, tibia 3-3, metatarsus 2-2. Range of total length in five males 3.4-4.4. Color pattern faded in this specimen, see Figure 12 for unfaded appearance.

Female (paratype in CAS).—Total length 5.2, carapace 2.01 long, 1.54 wide. Eyerow I width 1.16, eyerow III width 1.15, eyefield length 0.95. Eye diameters: AME 0.30, ALE

0.33
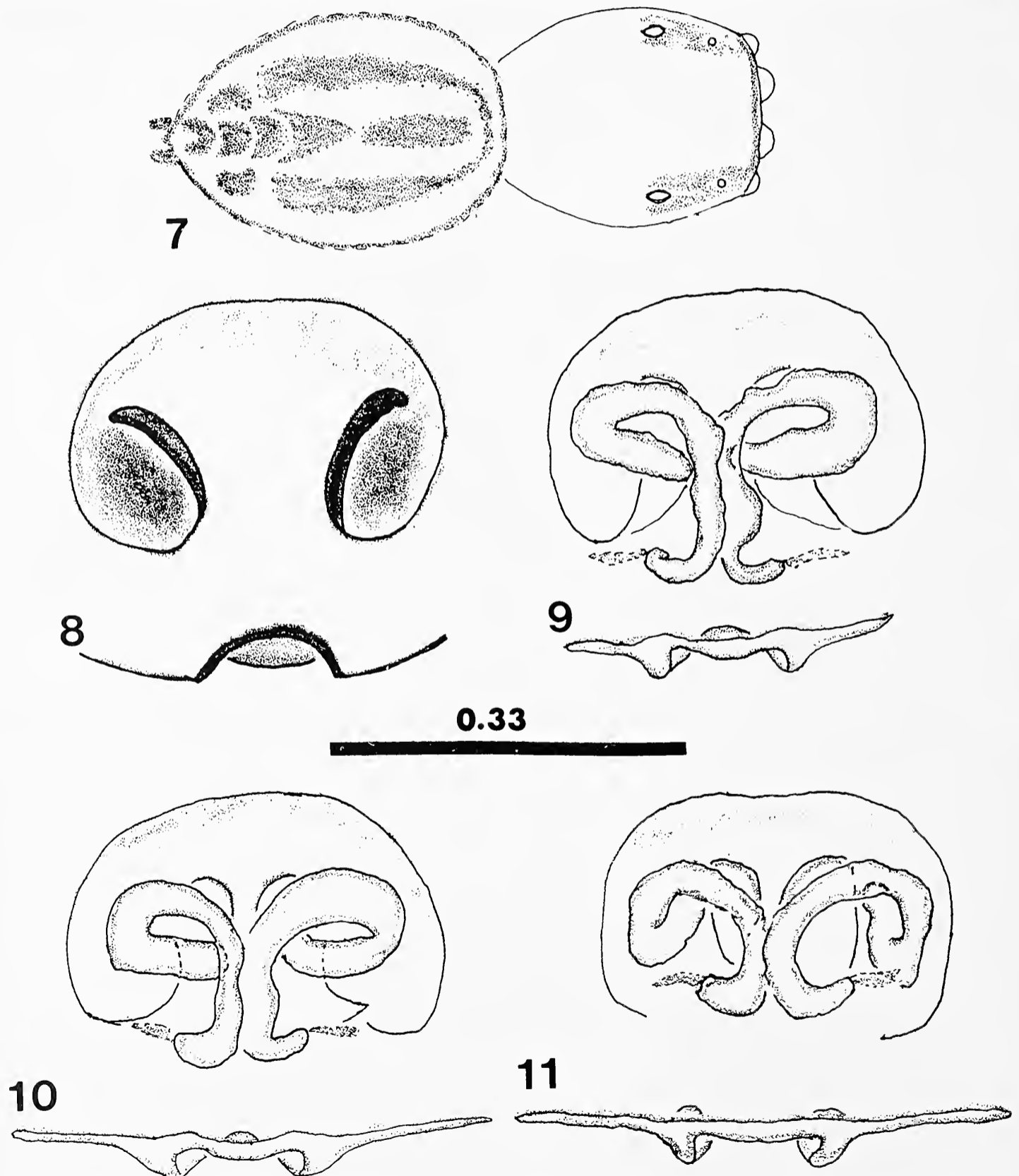
Figs. 7-11.—*Metaphidippus arizonensis* females: 7, Chevelon, dorsal view; 8, Chevelon, epigynum. 9-11. Variation in internal copulatory tubes. 9, Cedar Creek specimen; 10-11, Chevelon specimens. Scale in mm does not pertain to dorsal body view.

0.17, PME 0.07, PLE 0.15. Distance ALE-PME 0.18, PLE-PME 0.25. Femora lengths: I 1.20, II 1.00, III 0.99, IV 1.22. Leg order I, IV, II, III. Spination and color pattern as in male, see figure 13 for unfaded specimen. In eight female specimens measured: the width of eyerow III, mean 1.19, range 1.10-1.37; the length of right femur I, mean 1.15, range 1.00-1.25; the minimum width between the epigynal rims, mean 0.09, range 0.07-0.13.

Distribution.—Northern California, western North Dakota, southern Utah, north central Wyoming.

**Material examined.**—UNITED STATES: **California,** *Lassen Co.,* 13 mi S. of Ravendale, 5 June 1970, ex *Sesymbrium* (P. Rude), male (CB); *Marin Co.,* 4 mi N. of Novato, 10 April 1972, *Salicornia* marsh, Devac (E. Schlinger), male (CB); *San Francisco Co.,* San Francisco, 7 April 1918 (Helen van Duzee), male holotype, female paratype (CAS), San Francisco, 2 female paratypes (MCZ); **North Dakota;** *McKenzie Co.,* Theodore Roosevelt National Park, North Unit, 11 July 1970, sweeping herbs and shrubs in wooded gulley (K. V. Stone), female (FSCA); **Utah;** *Kane Co.,* Coral Pink Sand Dunes, near Kanab, 19 June 1974, on sagebrush with eggs in retreat (D. T. Jennings), female (BC); *Sevier Co.,* Richfield, 25 May 1930 (W. J. Gertsch), 2 females (AMNH); **Wyoming;** *Bighorn Co.,* 6 mi E. of Shell on Highway 14, sweeping grasses and shrubby bushes in area of low shrubby vegetation and many rocks (W. Maddison), male, 2 females (WM); Shell, 23 June 1965, saltbush (W. D. Fronk), male (BC).

The distribution of these two species overlaps in western North Dakota. *M. helenae* is found in interior basins and along the Pacific coast, whereas *M. arizonensis* is a grassland species found from the eastern edge of the tall grass prairie, through the short grass plains, and into mountain meadows. Undoubtedly both species will be found in more sites,
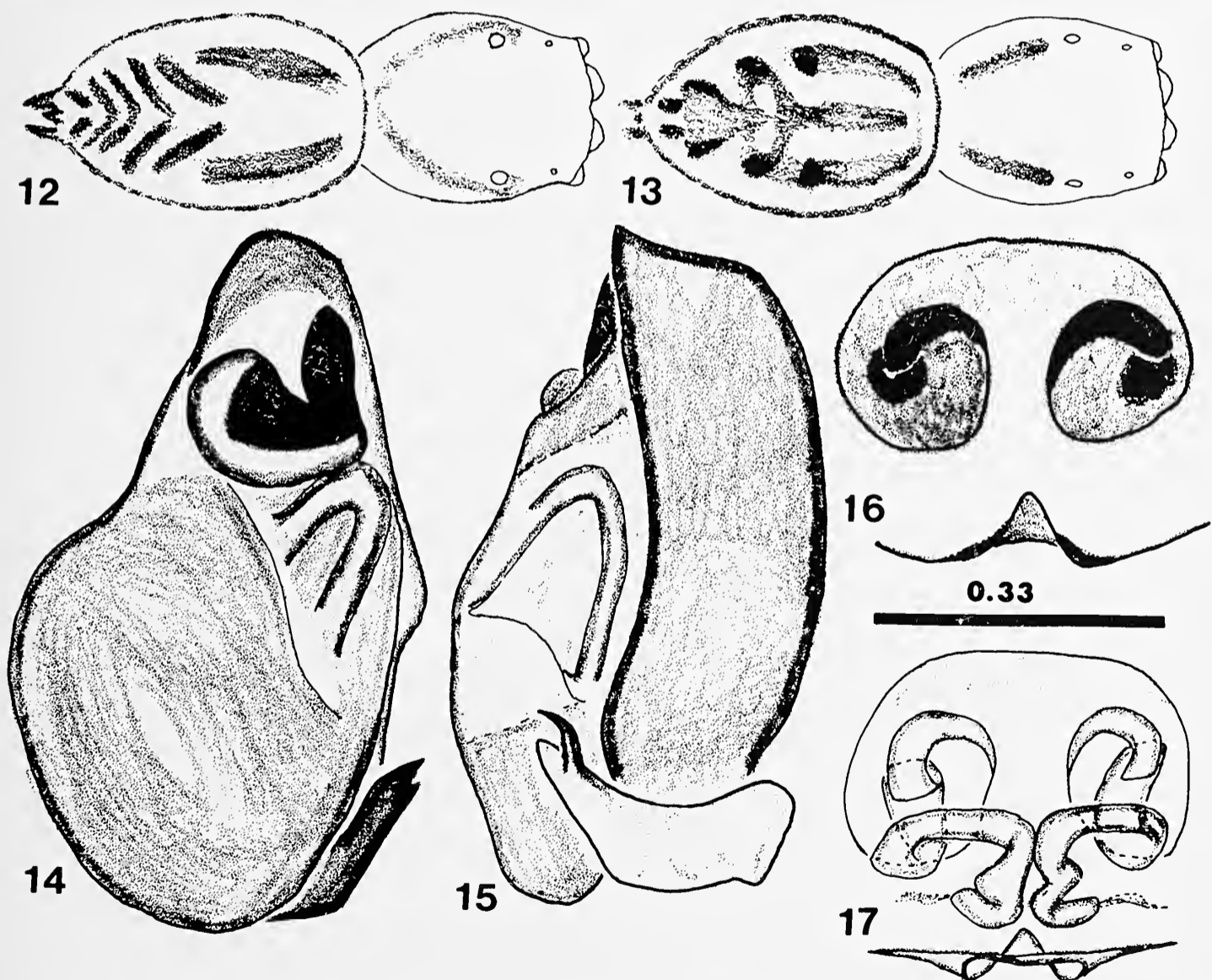
Figs. 12-17.—*Metaphidippus helenae:* 12, Male, Wyoming, dorsal view (California coastal specimens have the chevrons reduced, and the stripes extend to the posterior of the opisthosoma); 13, Female, Kane County, Utah, dorsal view (Dark spots may be less prominent in other specimens); 14, Male palpus, Wyoming, ventral view, 15, retrolateral view; 16, Female, Kane County, Utah, epigynum, 17, internal copulatory tubes. Scale in mm does not pertain to dorsal body views.

because the interior of the continent where they live is poorly collected relative to the eastern grassland fringes and the coastal and desert areas. They may have different habitat preferences, but this is not clearly established by the label data.

ACKNOWLEDGMENTS

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REVISION DEL GENERO *HURIUS* SIMON, 1901
(ARANEAE, SALTICIDAE)

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ABSTRACT

The genus *Hurius* is redefined to include the male diagnostic characters. Males of *Hurius* can be distinguished by the unidentate chelicerae with four or five teeth on promargin and by the presence of two big retrolateral apophyses on the palpal tibia. *Spinurius* Mello-Leitão, 1941 is newly synonymized and *H. aeneus* (Mello-Leitão, 1941); a new combination is established. Males of *H. vulpinus* and females of *H. aeneus* are described for the first time. Two new species are described: *Hurius petrohue* from Chile and *H. pisac* from Peru.

INTRODUCCION

El género *Hurius* Simon, 1901 fue descripto originalmente con una sola especie, *H. vulpinus* Simon, 1901, basada sobre ejemplares femeninos. Al estudiar colecciones de material indeterminado pertenecientes al Museum of Comparative Zoology, se halló un lote con hembras y machos de *H. vulpinus,* lo que permite ampliar la diagnosis del género con los caracteres del palpo del macho, hasta ahora desconocidos, que son muy particulares.

En 1944, Mello-Leitão incorporó dos especies al género, *H. costulatus* y *H. tristis.* La primera de estas especies fue transferida (Galiano, 1970) al género *Tullgrenella* como un sinónimo de *T. quadripunctata.* En cuanto a *H. tristis* debe ser excluída del género y transferida a otro taxon que se publicará próximamente.

En el presente estudio se incorporan al género dos especies, *H. petrohue* n. sp. y *H. pisac* n. sp. y se considera que *Spinurius* Mello-Leitão, 1941 es un sinónimo de *Hurius,* por lo que se establece *Hurius aeneus* (Mello-Leitão, 1941) nueva combinación. Se describen por primera vez las hembras de esta especie.

Nada se conoce sobre la biología de las especies de *Hurius,* pero todos los ejemplares provienen de áreas montañosas ubicadas en la Cordillera de los Andes o en la Precordillera. Es probable que vivan bajo piedras.

Material y métodos.—Las medidas se expresan en milímetros y fueron tomadas según se explica en una publicación anterior (Galiano, 1963). La quetotaxia se menciona según el sistema de Platnick y Shadab (1975) con ligeras modificaciones. Las abreviaturas son las siguientes: OMA, OLA, OMP y OLP, ojos medios anteriores, laterales anteriores,

medios posteriores y laterales posteriores, respectivamente; p, prolateral, r, retrolateral, v, ventral, d, dorsal, ap, apical; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia":MCZ, Museum of Comparative Zoology; MNHN, Muséum National d'Histoire Naturelle, París; MLP, Museo de La Plata.

Hurius Simon, 1901

Hurius Simon 1901a: 583, 585 (n. gen.) Petrunkevitch 1928:202. Neave 1939:702. Roewer 1954: 1184. Bonnet 1957:2237. Brignoli 1983:627.
Spinurius Mello-Leitão 1941:187 (n. gen.). Roewer 1954:1185. Brignoli 1983:628, 749 *(Spinutius, lapsus)*. **NUEVA SINONIMIA.**

Diagnosis (revisada).—Quelíceros con tres o más dientes en el promargen como en *Sitticus* Simon, 1901, del cual se diferencia por tener un diente en el retromargen, muy cercano a la base de la uña, y por presentar dos apófisis tibiales en el palpo. Se distingue de *Scoturius* y *Atelurius* cuyos quelíceros son semejantes, por la forma del palpo.

Descripción.—Prosoma robusto (ancho 44-47% del largo), mitad anterior de la región torácica en el mismo nivel que la cefálica. Estría torácica pequeña, algo alejada de los ojos posteriores. Area ocular más ancha que larga, más ancha atrás que adelante y con los OMP más próximos a los OLA que a OLP. El largo del área ocular representa aproximadamente el 40% del largo del prosoma. Clípeo bajo, menor que el radio de OMA. Esternón relativamente angosto, ancho del extremo anterior igual a la base del labio. Láminas maxilares redondeadas. Quelíceros paralelos, verticales, surco ungueal muy breve; promargen con tres dientes, a menudo los dos mayores sobre una base común y uno a tres pequeños dientes suplementarios; retromargen con un diente, situado muy próximo a la base de la uña. Patas espinosas. Pata III siempre más corta que la IV. Palpo del macho con dos apófisis tibiales retrolaterales muy desarrolladas, de las cuales la inferior está recubierta por gruesas cerdas. El émbolo es breve y nace en el borde prolateral superior del bulbo. Epigino con mecanismo de anclaje formado por uno o dos bolsillos de ubicación variable. Las aberturas de entrada se continuan por un ancho conducto más o menos cilíndrico, que desemboca en una cámara esferoidal de la cual parte por un lado un delgado conducto ciego (con glándulas en el extremo) y por otro las espermatecas, que son esféricas y ubicadas a cada lado de la línea media.

Especie tipo.—*Hurius vulpinus* Simon, 1901b.

Hurius vulpinus Simon, 1901
Figs. 1-7

Hurius vulpinus Simon 1901b:154 (1 hembra Lectotypus y 1 hembra Paralectotypus, de Ecuador: Quito, en MNHN, examinado); 1901a:583, 585 fig. 708. Petrunkevitch 1911:658; 1928:202. Roewer 1954:1184. Bonnet 1957:2237. Galiano 1963:363, lám. 19, fig. 16.

Descripción de la hembra Nº 7923 MACN.—Largo total 3.93. Prosoma: largo 1.70, ancho 1.30, alto 0.70. Clípeo, alto 0.06. Area ocular: largo 0.73; ancho de hilera anterior 1.08; de hilera posterior 1.20; distancia OLA-OMP 0.16; OMP-OLP 0.18; diámetro OMA 0.36. Estría torácica, situada 0.26 más atrás del borde posterior de OLP. Quelíceros con surco ungueal muy breve; retromargen con un diente muy próximo a la base de la uña; promargen con cuatro dientes (dos angulares mayores) sobre una base común. Patas IV-I-III-II. 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 l. Tibias I v 2-2-1p; II v lr-lr-lp, p 1; III v lp-lp, p 1-1, r 1-1-1; IV v lp-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v ap 2, p 1-2, r 1-2; IV v lp-2, p 1-2, r 1-1-2. Epigino: El borde posterior grueso y esclerosado, con dos profundos bolsillos infundibuliformes de anclaje, en cuyos bordes y parte interna se implantan largas cerdas plumosas de función desconocida. Los orificios de entrada a los conductos de las espermatecas se abren en el campo medio del epigino, seguidos por anchos conductos que desembocan en una cámara esferoidal, que a su vez se conecta por medio de un conducto espiral con la espermateca, esférica, mediana y relativamente pequeña. (Figs. 5-7). Aspecto y color en alcohol: prosoma pardo anaranjado, con la región cefálica amarilla, con
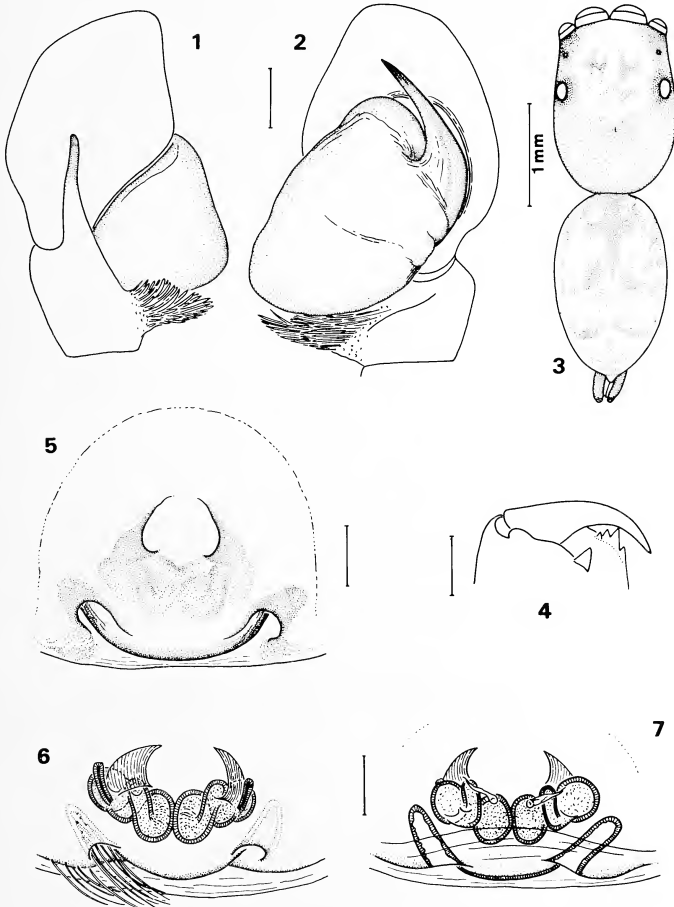
Figs. 1-7.–*Hurius vulpinus* Simon, macho: 1 palpo, retrolateral; 2, palpo, ventral; 3, cuerpo; 4, quelícero, cara posterior. Hembra: 5, epigino; 6, epigino clarificado, vista ventral (se dibujan los pelos de un solo lado); 7, el mismo, vista dorsal. Escala 100μ, salvo indicación.

manchas marmoradas de guanina blanca que se ven por transparencia. Sobre la región torácica, líneas radiantes pardas a partir de la estría. Pelos pardos y blancos, entremezclados; una mancha de pelos blancos sobre la estría y dos manchas en el medio del área ocular; pelos blancos en el margen anterior, alrededor de los ojos anteriores y en el espacio entre OLP y OMP; pelos blancos en los costados y en el declive torácico. El espacio bajo los OLA ocupado por pelos blancos. Desde el borde externo de cada OMA salen largos pelos blancos dirigidos oblicuamente, convergentes en la línea media. Quelíceros amarillentos, con pelos blancos en la cara anterior. Patas pardo amarillento, con abundantes pelos blancos. Palpos amarillos, con tarsos pardo claro con abundantes pelos blancos. Opistosoma amarillo pardusco, con manchas de guanina blanca que se ven por transparencia y bandas pardas con pelos pardo rojizo que forman un diseño de bandas en V invertidas. Vientre amarillo, con manchas de guanina blanca; en el medio, una banda pardusca.

Descripción del macho Nº 7923 MACN.—Largo total 3.60. Prosoma: largo 1.80, ancho 1.33, alto 0.83. Clípeo, alto 0.11. Area ocular: largo 0.80; ancho de hilera anterior 1.13; de hilera posterior 1.21; distancia OLA-OMP 0.18; OMP-OLP 0.23; diámetro OMA 0.36. Estría torácica, situada 0.25 más atrás del borde posterior de OLP. Láminas maxilares con ángulo redondeado. Esternón algo estrechado adelante, levemente más angosto que la base del labio. Quelíceros paralelos, verticales. Surco ungueal muy breve, retromargen con un diente muy cercano a la base de la uña; promargen con cuatro dientes, los dos angulares sobre una base común y dos más pequeños hacia la base de la uña. Patas IV-I-III-II. Quetotaxia: Fémures I d 1-1-1, p ap 2, r ap 1; II d 1-1-1, p ap 2, r 1-2; III d 1-1-1, p 1-2, r ap 2; IV d 1-1-1, p ap 2, r ap 2. Patellas I-IV p 1, r l. Tibias I v 2-2-2, p 1-1, r 1-1; II v lr-2-2, p 1-1, r 1-1; III, IV d 1, v 1-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2, p ap 1; III, IV v ap 2, p 1-2, r 1-1-2. Palpos: (Figs. 1 y 2). Aspecto y color en alcohol: esencialmente como en la hembra. Largos pelos blancos dirigidos hacia adelante forman una banda que baja desde el espacio OMA-OLA hasta el borde del clípeo. También hay pelos blancos bordeando los ojos y en la cara anterior de los quelíceros. Patas pardo claro amarillento, con abundantes pelos blancos. Tarso I pardo con pelos pardos abundantes. Palpo pardo claro con fémur amarillo y pelos al tono. Los pelos de la apófisis tibial inferior son pardo negruzco. Opistosoma como el de la hembra, con un *scutum* pequeño, basal dorsal, anaranjado (Fig. 3).

Observaciones.—Variación en la quetotaxia: hembras, fémur IV p ap 2, r ap. 1 Tibias I v 2-2-lr; II p 1-1, r 1-1-1; III v lp-2. Metatarso III v lp-2. Machos, fémures I p ap 1. Patella I p 1. Tibia II v lr-lr-2. Metatarsos I, II p 0, r 0; III, IV v lp-2.

Material estudiado.—ECUADOR: *Tungurahua,* Baños (1800 m elev.), 10 April 1939 (col. W. C. Macintyre), 1 macho, 3 hembras (MCZ), 1 macho, 1 hembra Nº 7923 (MACN), July 1938, 1 hembra Nº 7924 (MACN).

Hurius petrohue, nueva especie

Figs. 8-14

Etimología.—El nombre específico es un sustantivo en aposición; corresponde a la denominación de la localidad típica.

Diagnosis.—Se diferencia de *H. vulpinus* por presentar los bolsillos de anclaje en la parte anterior del epigino y porque la apófisis tibial inferior del palpo es mucho más larga.

Descripción del Holotypus hembra.—Largo total 4.57. Prosoma: largo 1.83, ancho 1.40, alto 0.80. Clípeo, alto 0.08. Area ocular: largo 0.80; ancho de hilera anterior 1.18;

de hilera posterior 1.30; distancia OLA-OMP 0.18; OMP-OLP 0.25; diámetro OMA 0.40. Estría torácica situada 0.25 más atrás del borde posterior de OLP. Quelíceros pequeños, verticales, paralelos. Surco ungueal muy breve. Retromargen con un diente muy cercano a
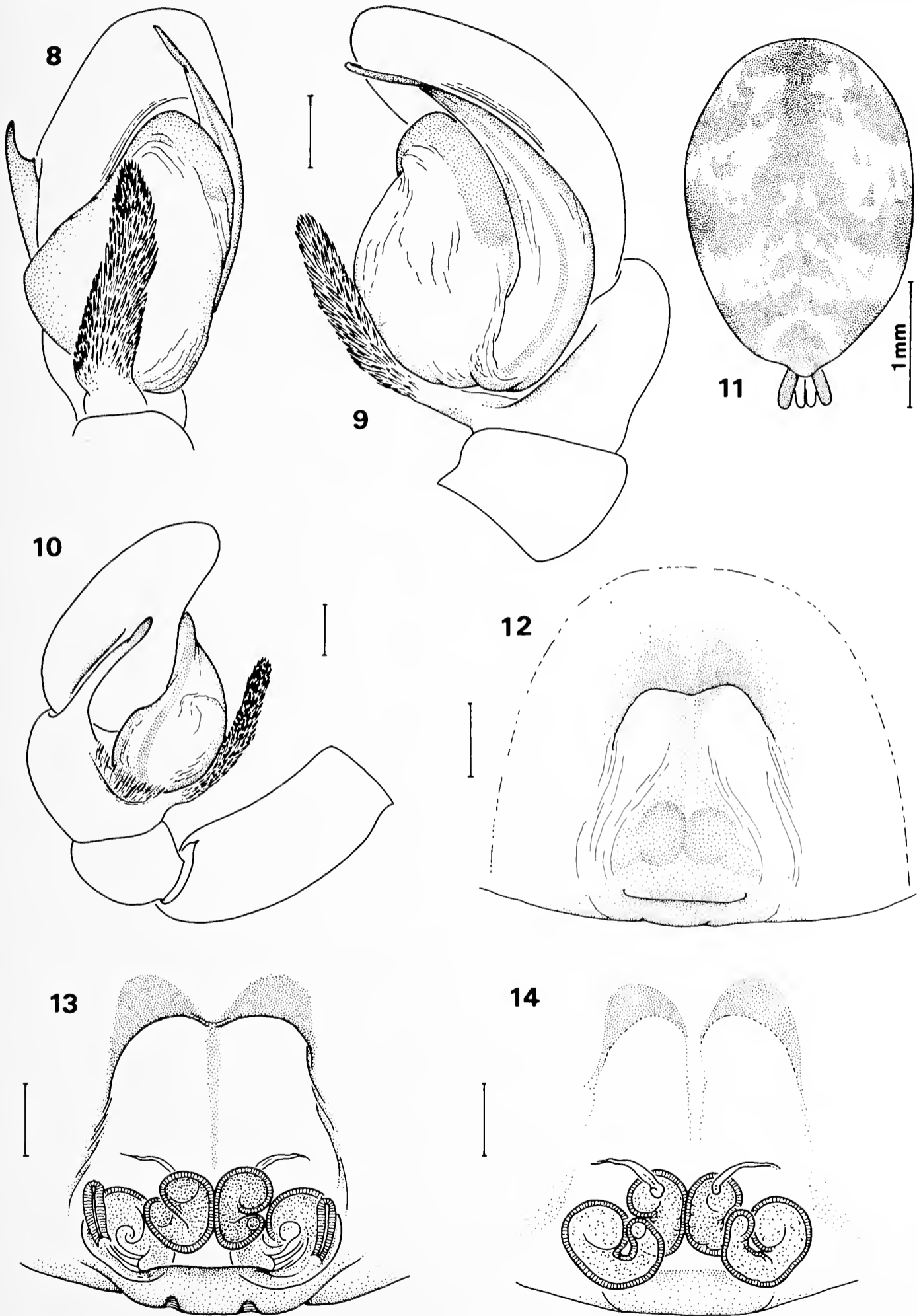
Figs. 8-14.–*Hurius petrohue* sp. n., paratipo macho: 8, palpo, ventral; 9, palpo, prolateral; 10, palpo, retrolateral. Holotipo hembra: 11, opistosoma, dorsal; 12, epigino; 13, epigino clarificado, vista ventral; 14, el mismo, vista dorsal. Escala 100 μ, salvo indicación.

la base de la uña; promargen con cinco dientes, los dos angulares mayores y sobre una base común. Patas IV-I-III-II. Quetotaxia: Fémures I, 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, v 2-2; II v lr-lr; III p 1, r 1; IV v 1p-2, p 1, r 1. Metatarsos I, II v 2-2; III v 1-2, p 1-2, r ap 2; IV v 1-2, p ap 2, r 1-2. Epigino: dos grandes bolsillos de anclaje situados contiguos y en el extremo anterior del epigino. Borde posterior engrosado. Entrada de los conductos próximos al reborde. Espermatecas contiguas, medianas. (Figs. 12-14). Aspecto y color en alcohol: prosoma pardo rojizo oscuro, con el borde anterior de la región cefálica algo más claro. Pelos blancos y pardo rojizos, distribuidos formando manchas de la siguiente manera: pelos blancos en el margen anterior y entre OMA y OLA y detrás de cada OLP. Pelos blancos bajo los OLA; en el clípeo, largos pelos blancos formando una barba orientada hacia adelante y cubriendo en parte la base de los quelíceros. Clípeo amarillo. Pelos blancos en los costados y en el declive torácico. El resto del prosoma con pelos pardo rojizos. Quelíceros amarillentos con pelos blancos. Opistosoma amarillo con grandes manchas pardas (Fig. 11). Patas pardas, las primeras más oscuras; la mitad basal de los fémures y patellas y la parte media de tibias y metatarsos, amarillentos. Palpos amarillos, con anillos pardos en base de patella, tibia y tarso, con abundantes pelos blancos. Esternón pardo negruzco.

Descripción del Paratypus macho N$^{\underline{o}}$ 7922 MACN.—Largo total 3.66. Prosoma: largo 1.63, ancho 1.22, alto 0.70. Clípeo, alto 0.10. Area ocular: largo 0.68; ancho de hilera anterior 1.03; de hilera posterior 1.11; distancia OLA-OMP 0.16; OMP-OLP 0.23; diámetro OMA 0.33. Estría torácica pequeña, situada 0.23 más atrás del borde posterior de OLP. Quelíceros verticales, paralelos. Surco ungueal muy breve; retromargen con un diente cercano a la base de la uña; promargen con tres dientes, dos de ellos sobre una base común. Es posible que exista un cuarto diente pequeño, que se ha desprendido. Patas IV-I-II-III. Quetotaxia: Fémures I, II, III d 1-1-1, p ap 2; IV d 1-1-1, p ap 1, r ap 1; Patella IV r 1. Tibias I v lr-2-1p, p 1-1; II v lr-lr, p 1; III p 1-1, r 1-1; IV v 1-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v ap 2, p ap 2, r 1-1; IV v 1-2, p 1-2, r 1-1-2. Palpo: las dos apófisis tibiales muy largas; la retrolateral con el borde superior interno dentado; la ventral con gruesos, largos y densos pelos negros. El émbolo nace en el extremo inferior prolateral del bulbo; grueso en la mayor parte del trayecto se afina apicalmente. (Figs. 8-10). Aspecto y color en alcohol: prosoma pardo oscuro, con el margen anterior levemente más claro, con algunos pelitos blancos entre los ojos. El resto cubierto por pelos pardo negruzcos. Clípeo con una banda amarilla de guanina que abarca el espacio bajo los cuatro ojos; sin barba. Quelíceros rojizos, esternón pardo. Opistosoma pardo y amarillo, con diseño semejante al de al hembra, excepto que en el dorso basal hay un *scutum* pardo oscuro. Patas pardas, las primeras más oscuras que las otras, con tarsos negruzcos con abundantes pelos negros. Las otras patas anilladas de pardo oscuro negruzco, con anillos poco evidentes.

Observación.—Variación en la quetotaxia, hembras: fémures I, II d 1-1-1. Metatarso III p ap 2, r ap 2.

Material estudiado.—CHILE: *Llanquihue;* Petrohue, 19-20 marzo 1965 (col. H. W. Levi), 1 hembra Holotypus, 1 hembra Paratypus (MCZ), Volcán Oscorno, E. slope above Petrohue (400-1000 m elev.), 21 de marzo 1965 (col. H. W. Levi), 1 hembra, 1 macho Paratypi N$^{\underline{o}}$ 7922 (MACN).

Hurius aeneus (Mello-Leitão, 1941) nueva combinación
Figs. 15-21

Spinurius aeneus Mello-Leitão 1941:187, fig. 80, t. xi fig. 53 [macho Holotypus, de R. Argentina: Tucumán; Bañado, (col. Birabén), N$^{\underline{o}}$ 14.989 (MPL), examinado]. Roewer 1954:1184.

Medidas del Holotypus macho.—Prosoma: largo 1.77, ancho 1.53, alto 0.93. Clípeo, alto 0.10. Area ocular: largo 0.97; ancho de hilera anterior 1.33; de hilera posterior 1.50; distancia OLA-OMP 0.23; OMP-OLP 0.26; diámetro OMA 0.43.

Descripción del macho Nº 5035 MACN.—Largo total 4.47. Prosoma: largo 2.03, ancho 1.72, alto 1.10. Clípeo, alto 0.11. Area ocular: largo 0.98; ancho de hilera anterior 1.43; de hilera posterior 1.57; distancia OLA-OMP 0.26; OMP-OLP 0.29; diámetro OMA
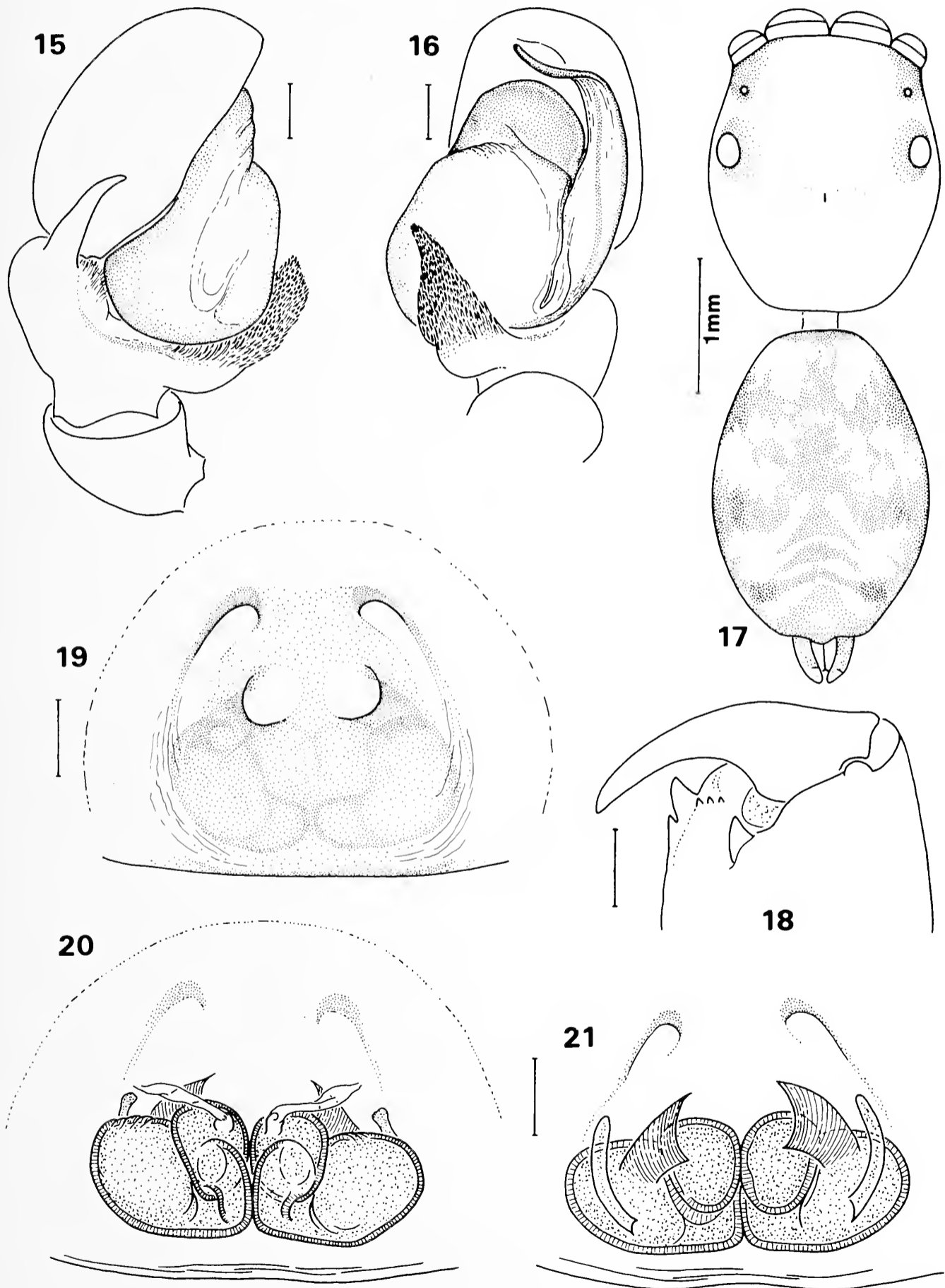
Figs. 15-21.—*Hurius aeneus* (Mello-Leitão), macho: 15, palpo, retrolateral; 16, palpo, ventral; 17, cuerpo; 18, quelícero, cara posterior. Hembra: 19, epigino; 20, epigino clarificado, vista dorsal; 21, el mismo, vista ventral. Escala 100 μ, salvo indicación.

0.43. Estría torácica 0.15 más atrás del borde posterior de OLP. Quelíceros paralelos, verticales; surco ungueal corto; retromargen con un diente fuerte; promargen con dos dientes sobre una base común (el angular mayor) y dos o tres dientes pequeños, en hilera orientada hacia el fondo del surco ungueal. (Fig. 18). Patas I-IV-III-II. Quetotaxia: Fémures I d 1-1-1, p ap 2; II d 1-1-1, p ap 2, r ap 2; III d 1-1-1, p 1-2, r ap 1; IV d 1-1-1, p ap 2, r ap 2. Patellas I-IV p 1, r 1. Tibias I v 2-2-2, p 1-1, r 1-1; II v 1-1-2, p 1-1-1, r 1-1; III-IV d 1-1, v 1-2, p 1-1-1, r 1-1-1. Metatarsos I v 2-2, p 1-1; II v 2-2, p 1-1, r 1; III v 2-2, p 1-2, r 1-2; IV v 2-2, p 1-2, r 1-1-2. Palpos: (Figs. 15 y 16). Aspecto y color en alcohol: prosoma alto y ancho, la región cefálica levemente deprimida entre los OLP que son bastante salientes. Color pardo oscuro, con la región cefálica pardo claro y abundantes pelos pardos y amarillos entremezclados. En la región cefálica los pelos se disponen en un patrón semejante al que se observa en algunas especies de *Sitticus:* en cada mitad del área ocular, los pelos se orientan divergiendo de una imaginaria línea longitudinal de modo que se orientan de cada lado hacia afuera (hacia los ojos laterales) y hacia la línea media del cuerpo, donde se encuentran con los correspondientes del lado opuesto. Entre los OLP y OMP y entre los OMA y OLP hay manchas de pelos blancos; también abundan en la región torácica. Bajo los OLA hay largos pelos blancos, que se dirigen hacia adelante y forman un fleco en el borde del clípeo, donde se confunden con los largos pelos blancos que cubren la cara anterior de los quelíceros. Esternón y piezas bucales pardo claro. Opistosoma amarillento, con manchas pardas formando tres anchas bandas transversas, vinculadas entre sí por manchas con forma de V invertida, más cortas (Fig. 17). Vientre amarillo, con ancha banda media parda. En la mitad basal del dorso, un *scutum* anaranjado, brillante. Patas pardas, las primeras más oscuras, con la mitad de tibias y metatarsos más claras, formando una anillación poco evidente. Tarsos I pardo oscuro, con abundantes pelos largos de ese color, que cubren todo el artejo. Palpos pardo claro, con abundantes pelos blancos; apófisis tibial ventral con pelos pardo oscuro cobrizo.

Descripción de la hembra N⁰ **7848 MACN.**—Largo total 5.66. Prosoma: largo 2.30, ancho 1.98, alto 1.13. Clípeo, alto 0.08. Area ocular: largo 1.11; ancho de hilera anterior 1.66; de hilera posterior 1.90; distancia OLA-OMP 0.26; OMP-OLP 0.33; diámetro OMA 0.51. Estría torácica situada 0.06 más atrás del borde posterior de OLP. Quelíceros como los del macho. Patas IV-I-III-II. Quetotaxia: Fémures I d 1-1-1, p ap 2; II, III, IV d 1-1-1, p ap 2, r ap 1. Patellas III, IV r 1. Tibias I v 2-2-2; II v 1-2-2, p 1-1; III, IV lp-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v lp-2, p 1-2, r 1-2; IV v 2-2, p 1-2, r 1-1-2. Epigino: dos bolsillos de anclaje poco profundos en posición anterior. Conductos y espermatecas parecidos a los de *H. vulpinus.* (Figs. 19-21). Aspecto y color en alcohol: esencialmente como en el macho, pero con el prosoma algo más ancho y alto. Color como en el macho, pero con las manchas claras del opistosoma menos notables. Las patas con anillos pardo oscuro más marcados que en el macho, con parte basal de fémures y patellas amarillos. Palpos pardo claro, con ápice de fémur, base de tibia y de tarso, pardo oscuro.

Observaciones.—El ejemplar típico es un macho que carece de palpos. El aspecto general, el color y la presencia de un área dorsal endurecida en el opistosoma permite afirmar que se trata de un espécimen adulto. La publicación original muestra que en el momento de tomarse la fotografía ya faltaban los palpos; la fig. 80 es un dibujo que me ha permitido identificar a los ejemplares que aquí se describen. Seguramente por un error de imprenta, al comienzo de la descripción original de la especie aparece el símbolo de hembra, aunque se está describiendo el macho cuyo palpo se ilustra. Esta confusión llevó a Roewer a mencionar que Mello-Leitão describió macho y hembra. Hay también inexactitudes en la descripción de los caracteres por parte del autor, p.e., solo menciona dos dientes en promargen; dice que los ojos de la segunda hilera están separados de los OLA

por el doble del espacio que los separa de OLP, menciona un clípeo densamente barbado y describe la patella I como sin espinas. Como se ha podido comprobar estudiando el tipo, se trata de fallas de observación.

En otros ejemplares estudiados se ha observado la siguiente variación en la quetotaxia: machos, tibias II d 1; III, IV v 2-2, p 1-1-1-1, r 1-1-1-1. Metatarsos III, IV r 2-1-2. Hembras, tibias I p 1-1; II v lp-2-lr; III v 2-2, r 1-1-2; IV v 2-2. Metatarso IV v lp-2.

Material estudiado.–R. ARGENTINA: *Córdoba:* Santa Rosa de Calamuchita, marzo-abril 1958 (col. M. J. Viana), 3 machos N° 5035 (MACN); San Alberto, Las Calles, 10 junio 1972 (col. G. Williner), 2 hembras N° 7848 (MACN); La Falda, marzo 1951 (col. M. J. Viana), 1 hembra N° 7847 (MACN).

<p style="text-align:center">

Hurius pisac, nueva especie
Figs. 22-24

</p>

Etimología.–El nombre específico es un sustantivo en aposición; corresponde a la denominación de la localidad típica.

Diagnosis.–Se distingue de las otras especies por tener un solo bolsillo de anclaje impar y medio en el epigino.

Descripción del Holotypus hembra.–Largo total 4.80. Prosoma: largo 2.00, ancho 1.57, alto 0.93. Clípeo, alto 0.07. Area ocular: largo 0.90; ancho de hilera anterior 1.40; de hilera posterior 1.52; distancia OLA-OMP 0.21; OMP-OLP 0.26; diámetro OMA 0.46. Estría torácica situada 0.28 más atrás del borde posterior de OLP. Quelíceros con un diente en retromargen y cuatro en promargen. Quetotaxia: Fémures I d 1-1-1, p ap 2; II, III, IV d 1-1-1, p ap 2, r ap 1. Patellas II p 1; III, IV r 1. Tibias I v 2-2-2; II v lr-lr-2, p 1-1; III v ap 2, p 1-1, r 1-1-1; IV v lp-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 lp-2, p 1-1-2, r 1-1-2 (muchas de las espinas se han caído y la quetotaxia se establece por los puntos de inserción). Epigino: un bolsillo de anclaje impar y medio en la parte anterior del epigino. Espermatecas muy grandes. (Figs. 22-24). Aspecto y color en
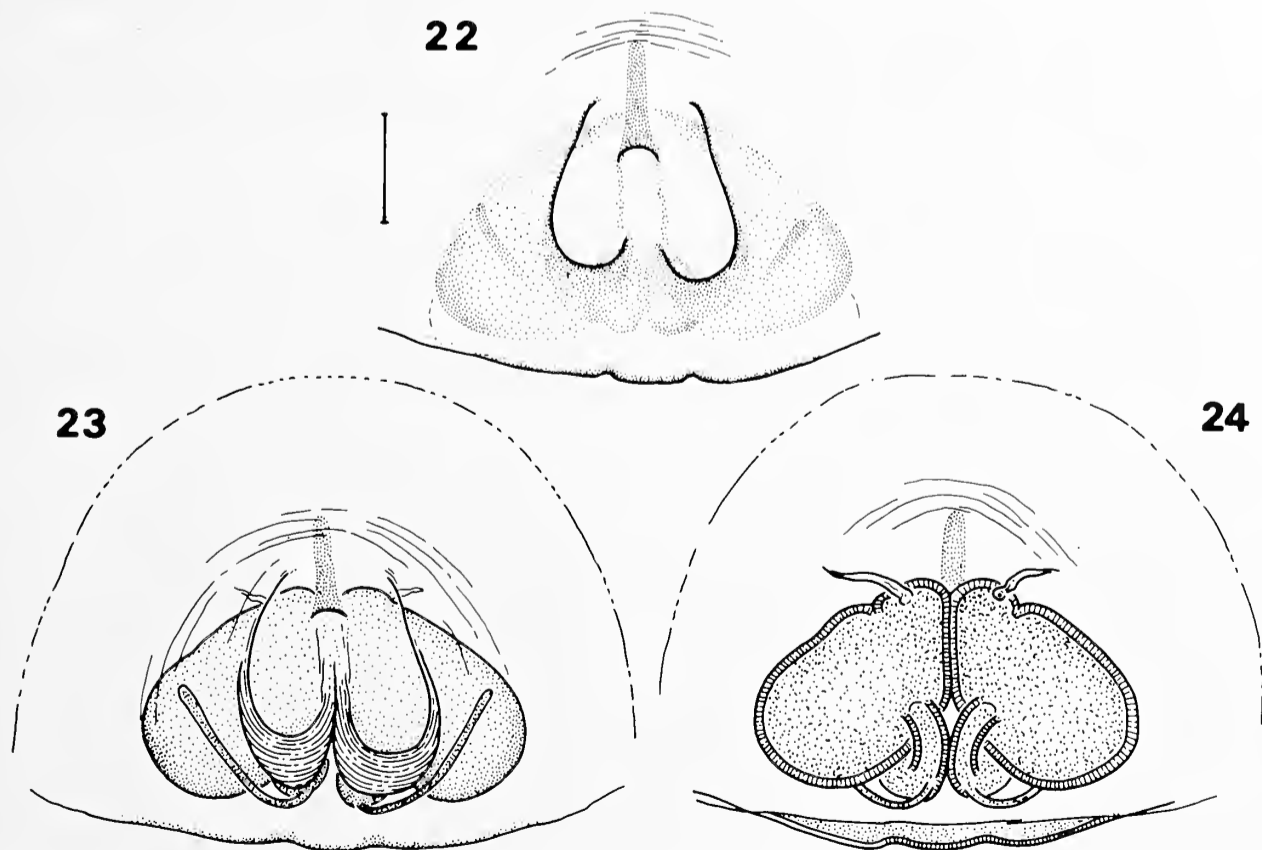
Figs. 22-24.–*Hurius pisac* sp. n., holotipo hembra: 22, epigino; 23, epigino clarificado, vista ventral; 24, el mismo, vista dorsal. Escala 100 μ.

alcohol: prosoma robusto, pardo, con la región cefálica negruzca. Hay una mancha con forma de Y, cuyo extremo posterior apoya en la estría, de color amarillento, que transparenta manchas de guanina blanca. El margen anterior de la región cefálica es amarillento. Opistosoma amarillento con manchas pardo oscuro, que forman en la línea media una sucesión de triángulos pardos, algunos con los brazos oblicuamente prolongados hacia los costados. Lados amarillos con manchitas pardo negruzco. Patas amarillo pardusco, con anillos pardo oscuro en ápice de fémur, base de patella, base y ápice de tibia y base de metatarso y tarso. Palpos amarillentos con una manchita parda en base de patella, tibia y tarso.

Observación.—El Holotypus es el único ejemplar conocido hasta el momento.

Material estudiado.—PERÚ: *Departamento Cusco;* Pisac (3000 m elev.), 13 enero 1983 (col. A. Roig), 1 hembra Holotypus Nº 7927 (MACN).

AGRADECIMIENTOS

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NEW GROUPS AND SPECIES BELONGING TO THE NOMINATE SUBGENUS *PARUROCTONUS* (SCORPIONES, VAEJOVIDAE)

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ABSTRACT

The nominate subgenus of the North American genus *Paruroctonus* Werner, 1934, comprises three infragroups, differentiated primarily by cheliceral and pectinal characters, and named after *P. gracilior* (Hoffmann, 1931), *P. boreus* (Girard, 1854), and *P. stahnkei* (Gertsch and Soleglad, 1966). The gracilior infragroup is monotypic. The boreus infragroup comprises four microgroups (10 species), named after *P. boreus, P. becki* (Gertsch and Allred, 1965), *P. xanthus* (Gertsch and Soleglad, 1966), and *P. baergi* (Williams and Hadley, 1967). The stahnkei infragroup comprises four microgroups (15 species), named after *P. stahnkei, P. shulovi* (Williams, 1970), *P. borregoensis* Williams, 1972, and *P. williamsi* Sissom and Francke, 1981. New synonyms include: *P. boreus* (= *Vejovis auratus* Gertsch and Soleglad, 1966); *P. gracilior* (= *Vejovis pallidus* Williams, 1968). New species and subspecies include: *P. bantai saratoga,* n. ssp. (southern Death Valley); *P. shulovi nevadae,* n. ssp. (southern Nevada); *P. simulatus,* n. sp. (western Great Basin); *P. coahuilanus,* n. sp. (Cuatro Cienegas basin, Coahuila). The gracilior and boreus infragroups are primarily allopatric, but both are sympatric with the stahnkei infragroup. Species within an infragroup are primarily allopatric, exceptions involving essentially allotopic species.

INTRODUCTION

The scorpion genus *Paruroctonus* Werner, 1934, is distributed throughout most of western North America, and contains at least thirty species. Recently, two subgenera were defined, including *Smeringurus* Haradon, 1983, and two species groups were delimited within the nominate subgenus (Haradon, 1984a, 1984b). The complexity of this genus is revealed further by the descriptions herein of two new species and two new subspecies, prompting an effort at this time also to put the various species and groups in the nominate subgenus into a sharper hierarchical perspective. Where necessary, to clearly differentiate or synonymize species, supplementary data are given for certain previously described forms. A key complementing those in Haradon (1984a, 1984b) is also provided.

METHODS

Relatively new characters involving the tarsal and pedipalpal macrosetae are explained in the accompanying illustrations, and in more detail by Haradon (1984a). For examples of the superior setae and mid-retrosuperior (mrs) seta on the basitarsus see Figures 7-8, and for examples of the retrosuperior and retroinferior terminal setae on the telotarsus see Figures 15-16.

Most of the measurements used herein are defined by Stahnke (1970). Pectinal measurements are shown in Figures 17-18. The cheliceral fixed digit length is taken dorsally in a straight line from the digit's tip to the bicusp's proximal base. The length of each distal tine on the cheliceral movable digit is taken dorsally in a straight line from the tip to the point of common divergence; the ratio, inferior tine length/superior tine length, is primarily useful only when the superior tine is short and essentially triangular (when elongate and curved the planes and the proximal limit are indefinite).

Statistical data include the observed range (sample mean ± one standard deviation, n = sample size). Acronyms of specimen depositories are explained below in the acknowledgments.

SUBGENUS *Paruroctonus* Werner, 1934

Uroctonoides Hoffmann, 1931:405; not Chamberlin 1920:36.
Paruroctonus Werner, 1934:283 (Jan.); Gertsch and Allred 1965:9 (subgenus of *Vaejovis* Koch, 1836; in part); Gertsch and Soleglad 1966:3 (subgenus of *Vaejovis;* in part); Williams 1972:2 (in part), 1974:15 (in part), 1980:31 (in part); Hjelle 1972:26 (in part); Soleglad 1973:353, 355 (in part); Francke and Soleglad 1981:241, 243 (in part).
Hoffmanniellius Mello-Leitão, 1934:80 (June).

Type species.—*Uroctonoides gracilior* Hoffmann, 1931.

Diagnosis.—Nominate subgenus, differentiated by: metasomal segments I-IV without short, reddish, intercarinal setae ventrally; metasomal segment III length/width ratio in adult males 1.8 or less, junveniles and adult females 1.7 or less, immatures 1.6 or less; carapace length/pectine length ratio in adult females 1.2 or more; pectinal teeth in females 22 or fewer (rarely 23 or 24); adult carapace length usually less than 6.5 mm in males and 7.0 mm in females.

Comparisons: Subgenus *Smeringurus* has numerous short, reddish, intercarinal setae ventrally on metasomal segments I-IV, and differs significantly in the other four characters above (see Haradon 1983).

Distribution.—Western North America, southern Canada southward into Aguascalientes and Baja California Sur in Mexico.

Subordinate taxa.—The subgenus *Paruroctonus* comprises three infragroups (defined below): gracilior infragroup (one species), boreus infragroup (10 species), stahnkei infragroup (15 species).

Vaejovis minckleyi Williams, 1968a, assigned to *Paruroctonus* by Stahnke (1974:138), exhibits only some of the characteristics that in combination define *Paruroctonus*, and is here excluded from this genus.

Remarks.—One of the more striking dichotomies in the nominate subgenus is that between the generally large species with many pectinal teeth and the generally small species with few pectinal teeth. Although there are exceptions in each group, the divergent tendencies in size and pectinal tooth counts, as well as in several coincident characters, are quite conspicuous. This dichotomy is also supported by the observations that the two groups are widely sympatric, whereas the species within each group are, with few exceptions, allopatric. However, one of the large species, *Paruroctonus gracilior* (Hoffmann, 1931), is geographically removed and morphologically divergent from the other large species, and in various characters tends to link the large and small species. The link is completed by *Paruroctonus becki* (Gertsch and Allred, 1965) among the large species and *Paruroctonus stahnkei* (Gertsch and Soleglad, 1966) among the small species, each of

which is intermediate to *P. gracilior* and most or all of the other species in their respective groups with respect to infragroup characters 1-3 (see infragroup diagnoses below) as well as in the number of retroinferior terminal setae on the telotarsi, the number of primary denticle rows on the pedipalp movable finger, and the development of denticles on the inferior carina of the cheliceral fixed digit. The various characteristics shared by *P. gracilior* and the remaining large species (i.e., infragroup characters 5-10) all appear plesiomorphic, relative to the outgroup subgenus *Smeringurus,* and thus do not necessarily support a closer relationship than one between *P. gracilior* and the small species, a relationship for which, likewise, no synapomorphies are known. Therefore, the classification that, in my opinion, best describes the available observations is one involving three infragroups; namely, gracilior, boreus (including *P. becki*), and stahnkei.

GRACILIOR INFRAGROUP

Diagnosis.—An infragroup of nominate subgenus *Paruroctonus* differentiated by: (1) cheliceral fixed digit with inferior carina confined distally, does not extend proximally to level of bicusp (see Gertsch and Soleglad 1966:fig. 33); (2) cheliceral movable digit with superior distal tine essentially triangular, inferior distal tine length/superior distal tine length ratio 3.1-3.2 (see Gertsch and Soleglad 1966:fig. 35); (3) carapace length/cheliceral fixed digit length ratio 3.3-4.1 (rarely 4.2); (4) basitarsus III with five superior setae, including three distal plus two proximal (3+2; rarely 4+2, and only among arenicolous specimens); (5) pectinal teeth in males 23-32 (more than 95% with 24-32), females 15-21 (more than 95% with 18-21); (6) pedipalp movable finger length/palm length ratio in adult males and females 1.1-1.2; (7) carapace length/pectine length ratio in adult males 0.9-1.0, adult females 1.2-1.3; (8) humerus with three (occasionally four) inframedial macrosetae on proximal 3/5 of internal surface; (9) pedipalp primary denticles, excluding proximal row, total 42-61 on fixed finger, 54-75 on movable finger; (10) adult carapace length in males 4.1-6.6 mm, females 4.8-7.2 mm.

Comparisons: the boreus infragroup (below) differs in characters 1-4; the stahnkei infragroup (below) differs primarily in characters 1-4, but also significantly in 5-10.

Distribution.—Southeastern Arizona, eastward to Big Bend region of Texas, southward to Aguascalientes in Mexico.

Included species.—*P. gracilior* (Hoffmann, 1931).

Paruroctonus gracilior (Hoffmann)

Uroctonoides gracilior Hoffmann, 1931:406, figs. 42-43; Gertsch 1958:15, 17.
Paruroctonus gracilior: Werner 1934:283, fig. 363; Stahnke 1957:253, 1961:206, 1974:136, 137, 138, figs. 10A, 11A, 11B; Williams 1972:3, 1980:31, 32, figs. 35A-B, 36C-D; Soleglad 1972:73, 1973:355, tbl. 2; Sissom and Francke 1981:97-98, 102, 107, figs. 7-12, 33-35; Francke and Soleglad 1981:242, fig. 22.
Vejovis (Paruroctonus) gracilior: Gertsch and Allred 1965:9; Gertsch and Soleglad 1966:6, 26-30, figs. 13, 18, 21, 23, 33-35, tbl. 3; Williams 1968a:7.
Hoffmanniellus gracilior: Gertsch and Soleglad 1966:26 (in synonymy); Williams 1972:3 (in synonymy). Misspelling of *Hoffmanniellius* Mello-Leitão, 1934:80.
Vejovis (Paruroctonus) pallidus Williams 1968a:6-11, figs. 4-6, tbl. 2; Diaz-Nájera 1975:7, 20. **NEW SYNONYMY.**
Paruroctonus pallidus: Williams, 1972:3; Soleglad 1972:73, 1973:355, tbl. 2; Stahnke 1974:138; Sissom and Francke 1981:98, 102.
Uroctonus gracilior: Diaz-Nájera 1975:2 (erratum).
Vaejovis gracilior: Diaz-Nájera 1975:2, 6, 8, 20.

Types.—*Uroctonoides gracilior:* Lectotype male (adult) from Mexico, Aguascalientes, Tepezala (C. C. Hoffmann), tagged #1. Depository: American Museum of Natural History.

Vejovis pallidus: Holotype male (adult) from Mexico, Coahuila, 0.5 kilometer SW Cuatro Cienegas (S. C. Williams, et al.). Depository: California Academy of Sciences, Type No. 10174.

Diagnosis.—See infragroup diagnosis above.

Description.—Supplementing above diagnosis, Gertsch and Soleglad (1966:26), and Sissom and Francke (1981:97). Basic fuscous pattern (see Gertsch and Soleglad 1966: figs. 18, 21) varies from dark and distinct to obsolete. Cheliceral fixed digit without denticles on inferior carina. Humeral macrosetae: internals include one supramedial, three (occasionally four) inframedials on proximal 3/5; four dorsals; usually three external medials, middle seta often small in immatures and juveniles. Brachial macrosetae: four internals. Chela: palm with eight major carinae moderately to well developed and granular in both sexes, intercarinal surfaces weakly to moderately concave; macrosetae include two or three on internal carina, usually four on ventrointernal carina, usually eight or nine flanking ventral carina, none on fixed finger, one long internal proximal and sometimes one short internal at mid-length of movable fingers; fingers essentially unscalloped in both sexes; primary denticles in seven rows on movable finger, six on fixed finger; supernumerary denticles well developed, six on fixed finger, seven on movable finger. Basitarsi I-III: not conspicuously compressed laterally; superior setae on I-III irregularly distributed, usually three distal plus two proximal on III; mrs seta on I at most only slightly offset from superior setae, on II moderately offset, on III set well apart from superior setae. Telotarsal setae I-IV: proinferiors 1,2,2,2; two each promedials, prosuperiors, retrosuperiors and retromedials; usually one retroinferior; one retroinferior terminal. Ungues I-IV about 1/3 as long as telotarsus. Pectines extend to proximal margin of femur IV in males, to 1/4 length of trochanter IV in females. Metasomal carinae: ventral and ventrolaterals I-III in males essentially smooth to crenulate (often strongly so), in females smooth to weakly crenulate, IV entirely crenulate in both sexes. Metasomal setae: counts variable; ventrals I-IV primarily 3-4,5-6,5-6,5-7; ventrolaterals I-V primarily 2-3,4,4-5,4-6, 7-15; dorsals I-IV 0,1,1,2 (fewer than 5% with 1,1,1,2).

Variation.—Some specimens from arenicolous populations had on basitarsus III, in addition to the usual 3+2 superior setae, a sixth seta (variably developed) between and prolateral to the proximal and distal groups, resulting in a 4+2 pattern; distinctly smaller extraneous setae might also be present, particularly in arenicolous specimens.

The ventrolateral metasomal seta counts varied considerably, including on V; e.g., eight to 15 (80% with nine to 12) in Texas and New Mexico, seven to nine (68% with eight) in southeastern Arizona, and seven to nine, normally eight, in Cuatro Cienegas basin of Coahuila.

Adult carapace lengths varied considerably among the samples; e.g., 4.1-5.0 mm (Chiricahua Mts., Arizona), 4.5-6.5 mm (Big Bend region, Texas), and 6.0-7.2 mm (Cuatro Cienegas basin, Coahuila).

Remarks.—*Paruroctonus pallidus,* distinguished from *P. gracilior* originally (Williams 1968a:7) by apparent differences in pigmentation and in the metasomal carinae, and further (Sissom and Francke 1981:98, 102) by apparent differences in metasomal seta counts, is here considered an arenicolous pigmentation variant of *P. gracilior.* The range in variation in the development of the metasomal carinae and the metasomal seta counts in *P. gracilior* subsumes that of *P. pallidus.* When detectable, vestigial traces of fuscosity in *P. pallidus* specimens conform to the general pattern characteristic of *P. gracilior.* The

Table 1.—Diagnostic characteristics of the four microgroups constituting the boreus infragroup of the nominate subgenus *Paruroctonus*.

Character		*xanthus*	*becki*	*boreus*	*baergi*
Carapace length/cheliceral fixed digit length		7.0-9.0	5.5-6.5	7.0-9.0	7.0-9.0
Pedipalp movable finger length/ palm length		1.4-1.6	1.1-1.3	1.1-1.2	1.1-1.2
Pedipalp primary denticles, rows on movable finger		7	6-7	6	6
less proximal row, fixed finger		>80	<80	<80	<80
movable finger		>90	<90	<90	<90
Pedipalp fingers, scalloping: (A) not, (B) proximally	♂	C	A	A,B	B
only, (C) multiscalloped	♀	C	A	A	A
Basitarsus II mid-retrosuperior seta (A) present (B) absent		B	A	A	B
Basitarsus III superior setae:		10-11	6	6	7-11
(A) in distal plus proximal rows, (B) in single file		B	A	A	A,B
Telotarsi II-IV retroinferior terminal setae		2	1	2	2
Telotarsi III retrosuperior setae		6-7	2	2	2-4

amount of fuscosity typical of a population is often correlated with the darkness of the substrate, and in several *Paruroctonus* species considerable variation in pattern intensity exists (Haradon 1983:253, 261).

The above synonymy is based on the examination of *P. pallidus* paratypes (CAS, OFF); the lectotype and two cotypes of *P. gracilior* (AMNH); and approximately 120 other specimens of *P. gracilior* from previously reported material (Gertsch and Soleglad 1966; Sissom and Francke 1981) from Arizona, New Mexico, Texas and Chihuahua.

BOREUS INFRAGROUP

Diagnosis.—An infragroup of nominate subgenus *Paruroctonus* differentiated by combination of: (1) cheliceral fixed digit with inferior carina extending proximally at least to level of bicusp (see Gertsch and Soleglad 1966:fig. 39); (2) cheliceral movable digit with superior distal tine elongate and curved, inferior distal tine length/superior distal tine length ratio less than 3.0; (3) carapace length/cheliceral fixed digit length ratio 5.5-9.0; (4) basitarsus III with six or more superior setae, arranged in distal plus proximal rows (4+2 to 5+2) or in essentially single file; (5) pectinal teeth in males 24-39 (except 20-23 in some populations of *P. bantai* and *P. baergi*, or rarely 23 in several other species), females 18-24 (except some populations 16-17 in *P. bantai* and 13-17 in *P. baergi*, or rarely 17 in several other species); (6) pedipalp movable finger length/palm length ratio in adult males and females 1.1-1.6; (7) carapace length/pectine length ratio in adult males 0.8-1.0, adult females 1.2-1.4 (except 1.6-1.8 in *P. utahensis*); (8) humerus with three inframedial macrosetae on proximal 3/5 of internal surface (except two in *P. baergi*); (9) pedipalp primary denticles, excluding proximal row, total 25-90 fixed finger, 35-103 movable finger (rarely 35 or 36); (10) adult carapace length generally 4.5-6.0 mm in males, 5.0-7.0 mm in females.

Comparisons: The gracilior infragroup (above) differs in characters 1-4; the stahnkei infragroup (below) differs primarily in character 5, but also significantly in 6-10. Exceptional males with fewer than 24/24 and females with fewer than 17/18 pectinal teeth differ from the stahnkei infragroup in having 35 or more primary denticles (less proximal row) on pedipalp movable finger in combination with either dorsal metasomal setae I-IV 0,0,0,1 *(P. bantai)*, or mrs seta absent on basitarsus II and either three internal inframedial macrosetae on humerus or one retromedial seta on telotarsus III (baergi group).

Distribution.—Western North America, southern Canada southward into northern Baja California Norte, Sonora and Chihuahua in Mexico.

Subordinate taxa.—The boreus infragroup comprises four primarily allopatric elements, differentiated as follows and in Table 1.

BOREUS MICROGROUP. Diagnosis: combination of carapace length/cheliceral fixed digit length ratio 7.0-9.0; basitarsus II with mrs seta. Distribution: Rocky Mountains region westward to Pacific coastal mountains (excluding northwest coast), southern Canada southward to northern Arizona and northern Baja California Norte (excluding Mojave and Sonoran Deserts). Included taxa: *P. boreus* (Girard, 1854); *P. silvestrii* (Borelli, 1909); *P. bantai* (Gertsch and Soleglad, 1966); *P. bantai saratoga*, n. ssp.; *P. arnaudi* Williams, 1972.

BECKI MICROGROUP. Diagnosis: carapace length/ cheliceral fixed digit length ratio 5.5-6.5. Distribution: Western and southern Great Basin, southwestward through Mojave Desert to San Jacinto Mountains and edge of Colorado Desert in California. Included species: *P. becki* (Gertsch and Allred, 1965).

XANTHUS MICROGROUP. Diagnosis: pedipalp primary denticles, excluding proximal row, total 82-90 on fixed finger, 98-103 on movable finger; pedipalp movable finger length/palm length ratio 1.4-1.6 in both sexes; pedipalp fingers multi-scalloped in adults of both sexes (see Gertsch Soleglad 1966:fig. 32); telotarsus III with six or seven retrosuperior setae. Distribution: Sand dunes, southeastern California and extreme northwestern corner of Sonora. Included species: *P. xanthus* (Gertsch and Soleglad, 1966).

BAERGI MICROGROUP. Diagnosis: combination of carapace length/ cheliceral fixed digit length ratio 7.0-9.0; pedipalp primary denticles on movable finger in six rows; basitarsus II without mrs seta. Distribution: Loose sandy soils, primarily dunes, associated with Colorado River and Rio Grande drainages, from southern Utah to northern Mexico. Included species: This microgroup, named after *P. baergi* (Williams and Hadley, 1967), and including *P. utahensis* (Williams, 1968b), is discussed in detail by Haradon (1984a).

Remarks.—The boreus and gracilior microgroups, where sympatric with the arenicolous baergi microgroup, occupy more compact soils; the boreus microgroup, where sympatric with the becki microgroup, tends to occupy higher elevations.

Paruroctonus boreus (Girard)

Figs. 1-2

Scorpio (Telegonus) boreus Girard, 1854:267-269, zool. plt. xvii, figs. 5-7 (in part, not record from Eagle Pass, Texas).
Buthus boreus: Wood 1863a:110, 1863b:368.
Vejovis boreus: Marx 1888:91; Gertsch 1958:6 (in part, not synonymy with "*Vejovis silvestrii*").
Vaejovis boreus: Ewing 1928:12; not Bugbee 1942:320 (= *Paruroctonus utahensis;* see Sissom and Francke 1981:94); not Diaz-Nájera 1975:13 (= *Paruroctonus silvestrii*).
Vejovis aquilonalis Stahnke, 1940:101.
Vejovis (Paruroctonus) boreus: Gertsch and Allred 1965:9 (in part, not synonymy with "*Vejovis silvestrii*"); Gertsch and Soleglad 1966:7.

Vejovis (Paruroctonus) aquilonalis: Gertsch and Allred 1965:9; Gertsch and Soleglad 1966:42 (in part, see Sissom and Francke 1981:94).

Vejovis (Paruroctonus) auratus Gertsch and Soleglad, 1966:7 (key), 34, 44-47 (description), figs. 55, 58, tbl. 6 (in part, holotype only). **NEW SYNONYMY.**

Vaejovis (Paruroctonus) boreus: Hjelle 1972:22.

Paruroctonus aquilonalis: Williams 1972:3; Soleglad 1972:74, 1973:355, Stahnke 1974:138; Sissom and Francke 1981:94.

Paruroctonus auratus: Williams 1972:3, 1976:2, 1980:47; Soleglad 1972:75 (in part), 1973:355 (in part); Stahnke 1974:138; Sissom and Francke 1981:96 (in part).

Paruroctonus boreus: Williams 1972:3, 1976:2; Soleglad 1972:74, 1973:355; Stahnke 1974:138; Sissom and Francke 1981:93.

Type.—*Scorpio (Telegonus) boreus:* Female (adult) from the "Valley of the Great Salt Lake of Utah", collected by "Capt. Howard Stansbury". Depository: United States National Museum.

Girard (1854) based his description of *P. boreus* on a single specimen, which was last reported to have been examined by Marx (1888). The 18 pectinal teeth reported by Girard (1854:267, 268, fig. 6) indicate the original specimen to be a female.

Figs. 1-4.—Right pedipalpal segments, internal views: 1, *P. boreus,* chela; 2, *P. boreus,* brachium; 3, *P. bantai,* chela; 4, *P. bantai,* brachium. Key: dsm = distal supramedial seta; circle = trichobothrium. Scale = 1.0 mm.

Figs. 5-6.—Metasomal segment V, ventral views: 5, *P. bantai bantai;* 6, *P. bantai saratoga,* n. ssp. Scale = 1.0 mm.

Vejovis aquilonalis: Holotype male (adult) from U.S.A., Arizona, (Coconino County), 30 mi. S Grand Canyon on Hwy. 64; locality corrected by Sissom and Francke (1981: 94). Depository: California Academy of Sciences.

Vejovis auratus: Holotype female (adult) from U.S.A., California, San Bernardino County (Death Valley Natl. Mon.), Saratoga Springs. Depository: American Museum of Natural History.

Diagnosis.—A species of subgenus *Paruroctonus,* boreus infragroup (cheliceral fixed digit with inferior carina extending proximally to level of bicusp; pectinal teeth 24-35 in males, 18-23 in females, pedipalp primary denticles, excluding proximal row, 37-52 on fixed finger, 44-68 on movable finger), and boreus microgroup (carapace length/cheliceral fixed digit length ratio 7.0-9.0; basitarsus II with mrs seta), differentiated by combination of: (1) pedipalp fingers in adult male deeply scalloped proximally, closed fingers form wide gap, in adult female weakly scalloped, closed fingers form a narrow proximal gap (see Gertsch and Soleglad 1966:figs. 24, 25); (2) fuscous markings generally absent in interocular triangle and do not extend to posterior margin on tergites II-VI (see Gertsch and Soleglad 1966:figs. 6, 8); (3) ventrolateral metasomal setae on IV 3, on V 6; (4) ventral metasomal setae I-IV 3,3,3,4; (5) dorsal metasomal setae I-IV 0,1,1,2; (6) ventrolateral metasomal carinae I-III smooth with few posterior crenulations; (7) ventral metasomal carinae I-III obsolete to smooth; (8) brachium with four long internal macrosetae (Fig. 2); (9) chelal palm macrosetae include two on internal carina (both long) and two on ventrointernal carina (proximal long, distal short) (Fig. 1).

Comparisons: *P. silvestrii* has (1) weakly scalloped pedipalp fingers in adult males and essentially unscalloped fingers in adult females; *P. silvestrii* and *P. arnaudi* have (2) extensive fuscous markings in interocular triangle and extending to posterior margin on tergites II-VI (see Gertsch and Soleglad 1966:figs. 7, 9), (3) ventrolateral metasomal setae on IV 4, on V 7, and (4) ventral metasomal setae I-IV 3,4,4,5; *P. bantai* (see below) differs primarily in characters 5-9.

Distribution.—Western North America, from southern Canada to northern Arizona and to coastal mountains of southern California, essentially excluding northwest coastal region and the Mojave and Sonoran Deserts.

Table 2.—Numbers of ventral and ventrolateral metasomal setae in subspecies of *Paruroctonus bantai.*

Carina	Setae	P. b. bantai Metasomal Segment					P. b. saratoga Metasomal Segment				
		I	II	III	IV	V	I	II	III	IV	V
Ventral	2/2	3									
	2/3	13									
	3/3	26	42	42	36	41	62	60	49		7
	3/4				5	1		2	10		17
	4/4				1				3	62	38
Ventro-lateral	2/2	42	33	17			62				
	2/3		6	11							
	3/3		3	14	42			62	62	60	
	3/4									2	
	4/4					30					
	4/5					11					
	5/5										
	5/6					1					
	6/6										62

Remarks.–*Paruroctonus boreus* is the most widely mentioned *Paruroctonus* species in the technical and popular literature (often combined with *Vaejovis* or *Vejovis*), and the above synonymy includes only the first citation of each name, major taxonomic accounts, new synonyms and misidentifications. The bibliographic data given herein for Girard (1854), a report contained in a rare volume, corrects a recurring error that began with Wood (1863b:369).

The above diagnosis of *P. boreus* is based primarily on specimens from the Great Basin, including the Great Salt Lake Desert. The inter- and intrapopulation variability of many other characters in *P. boreus* is considerable, and still being studied.

Examination of the holotype of the nominal species *Paruroctonus auratus* revealed no significant differences between it and the Great Salt Lake Desert (topotypic) population of *P. boreus*. The subtle differences in metasomal and telson proportions between *P. auratus* and *P. boreus* reported by Gertsch and Soleglad (1966:45) were found to be insignificant using large samples of the latter species. As in certain other congeners (see Remarks to gracilior infragroup above), many arenicolous populations of *P. boreus*, including the topotypic populations of *P. boreus* and *P. auratus*, have essentially lost the basic fuscous pattern characteristic of this species (see Gertsch and Soleglad 1966:figs. 6, 8), and simply represent pigmentation variants.

Paruroctonus bantai (Gertsch and Soleglad)
Figs. 3-6

Vejovis (Paruroctonus) bantai Gertsch and Soleglad, 1966:6 (key), 20-23 (description), figs. 12, 22, 29, tbl. 2; Williams and Hadley 1967:112; Williams 1970:8.
Paruroctonus bantai: Williams 1972:3, 1976:2; Soleglad 1972:75, 1973:355, tbl. 2; Stahnke 1974: 138.

Type.–*Vejovis bantai:* Holotype female (adult) from U.S.A., California, Inyo County, Saline Valley, Warm Springs Road, Station 94, 8 May 1960 (B. Banta). Depository: California Academy of Sciences, Type No. 10193.

Diagnosis.–A species of subgenus *Paruroctonus*, boreus infragroup (cheliceral fixed digit with inferior carina extending proximally to level of bicusp; pectinal teeth 20-28 in males, 16-20 in females; pedipalp primary denticles, excluding proximal row, 28-35 on fixed finger, 37-49 on movable finger), and boreus microgroup (carapace length/cheliceral fixed digit length ratio 7.0-9.0; basitarsus II with mrs seta), differentiated by combination of: (1) pedipalp fingers in adult male deeply scalloped proximally, closed fingers form wide gap, in adult female weakly scalloped, closed fingers form narrow gap; (2) fuscous markings generally absent in interocular triangle and do not extend to posterior margin on tergites II-VI; (3) ventrolateral metasomal setae on IV 3, on V 4 or 6; (4) ventral metasomal setae I-IV 3,3,3,3-4; (5) dorsal metasomal setae I-IV 0,0,0,1; (6) ventrolateral metasomal carinae I-III granular; (7) ventral metasomal carinae I-III smooth to granular; (8) brachium with three long macrosetae on internal surface, dsm seta inconspicuous (Fig. 4); (9) pedipalp chelal macrosetae inconspicuous or absent (Fig. 3), except occasionally one short proximal on internal or ventrointernal carina, especially in females and juveniles.

Comparisons: *P. silvestrii* differs in characters 1-9, *P. arnaudi* differs in characters 2-9, and *P. boreus* differs in characters 5-9 (see *P. boreus* diagnosis above).

Description.–Supplementing above diagnosis and Gertsch and Soleglad (1966:20). Adult carapace lengths in males 4.9-6.2 mm, in females 5.5-7.4 mm. Chelicera: fixed digit with denticles on inferior carina; on movable digit, superior distal tine elongate and

curved, about 1/2 as long as inferior distal tine. Trichobothria typical of genus in number and distribution. Humeral macrosetae: internals include one supramedial, three inframedials on proximal 3/5; four dorsals; usually three external medials, middle seta smallest and occasionally absent. Chela: supernumerary denticles well developed, six on fixed finger, seven on movable finger. Basitarsi I-III: not conspicuously compressed laterally; superior setae on I 2+2 or 3+2, II 3+2 or 4+2, III 4+2; mrs seta on I-III stout, short and distinctly offset from superior setae. Telotarsal setae I-IV: proinferiors 1,2,2,2; two each promedials, prosuperiors, retrosuperiors, retromedials; retroinferiors 1,1,2,2; retroinferior terminals 1-2,2,2,2. Ungues about 3/5 as long as telotarsus. Pectines in adult males extend to about 3/4 length of trochanter IV, in adult females to slightly beyond coxa IV or to about 1/3 length of trochanter IV. Telson setae: two long ventroanteriorly, two long at subaculear tubercle, others short or inconspicuous.

Distribution.—Saline Valley and southern Death Valley, California

Remarks.—Two subspecies of *P. bantai* are delimited as follows.

Paruroctonus bantai bantai (Gertsch and Soleglad)
Figs. 3-5

Synonymy.—Same as for species (see above).

Diagnosis.—A subspecies of *P. bantai* differentiated by combination of: ventrolateral metasomal setae on segment II 2 (90% of specimens), on V 4 (Fig. 5) (fifth seta, if present, smaller and offset from others); ventral metasomal setae on segment IV 3 (90% of specimens), on V 3 (rarely 4); pectinal teeth in males (79%) 23 or fewer, females (75%) 17 or fewer.

Comparisons: *P. bantai saratoga*, n. ssp., differs in all five characters (see diagnosis below).

Table 3.—Numbers of pectinal teeth in subspecies of *Paruroctonus bantai* and *Paruroctonus shulovi*, and in *Paruroctonus simulatus*, n. sp.

	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
P. b. bantai																		
Males										3	13	9	10	6	3			
Females						4	20	7	1									
P. b. saratoga																		
Males												3	3	13	21	11	7	2
Females						1	7	32	23	1								
P. s. shulovi																		
Males								6	12	15	6							
Females	1	4	33	44	11													
P. s. nevadae																		
Males											1	4	7					
Females			2	7	9	4												
P. simulatus																		
Males									1	2	10	9	4	1	1			
Females		1	4	8	4	7	2											
P. coahuilanus																		
Males								2		6	11	6	1					

Variation.—Total adult length of males 37-50 mm, females 50 mm. Adult carapace length of males 4.9-6.2 mm, females 5.5-6.6 mm. Variation in the numbers of metasomal setae is presented in Table 2. Pectinal tooth counts in males 20-25, females 16-19 (Table 3). Pedipalp primary denticles, excluding proximal row, total 28-35 (32.15 ± 1.91, n = 39) on fixed finger, 37-47 (41.77 ± 2.01, n = 39) on movable finger. The dsm seta on the internal brachial surface, and the chelal internal setae, are generally inconspicuous from the late immature state on.

Distribution.—Saline Valley, California.

Specimens examined.—U.S.A.: CALIFORNIA;*Inyo County,* Saline Valley, 21 September 1971 (D. Giuliani), 1 male (CAS), Saline Valley, June 1959 (B. Banta), 7 males, 4 females (CAS), 4 July 1959 (B. Banta), 2 males, 3 females (CAS), 5 July 1959 (B. Banta), 3 males, 2 females (CAS), 22 November 1959 (B. Banta), 2 males (CAS), 27 November 1959 (B. Banta), 6 males (CAS), 28 November 1959 (B. Banta), 1 males, 1 female (CAS), 3 March 1960 (B. Banta), 1 male (CAS), 6 March 1960 (B. Banta), 1 female (CAS), 3 April 1960 (B. Banta), 1 male, 2 females (CAS), 8 May 1960 (B. Banta), 1 male (CAS), 3 April 1962 (B. Banta), 1 male, 3 females (CAS).

Paruroctonus bantai saratoga, new subspecies
Fig. 6

Type.—*Paruroctonus bantai saratoga:* Holotype male (adult) from U.S.A., California San Bernardino County, Death Valley Natl. Mon., Saratoga Springs, salt flats, 11 June 1970 (M. A. Cazier, L. Welch, O. F. Francke). Depository: California Academy of Sciences, Type. No. 15057.

Diagnosis.—A subspecies of *P. bantai* differentiated by combination of: ventrolateral metasomal setae on segment II 3, on V 6 (Fig. 6); ventral metasomal setae on segment IV 4, on V 4 (72% of specimens); pectinal teeth in males (90%) 24 or more, females (87%) 18 or more.

Comparisons: *P. bantai bantai* differs in all five characters (see diagnosis above).

Description of male holotype.—Measurements: Table 4. Pedipalp primary denticles on fixed fingers 4,5,7-6,8,10-8,12-14, movable fingers 5,8-6,9,9-11,14,9-10. Metasomal setae: dorsals 0,0,0,1; dorsolaterals 0,1,1,2; laterals 1,0,0,02; ventrolaterals 2,3,3,3,6; ventrals 3,3,3,4,4.

Allotype.—Measurements in Table 4.

Variation.—Total adult length of males 50-60 mm, females 50-60 mm. Adult carapace length of males 5.2-6.1 mm, females 6.0-7.4 mm. Variation in the numbers of metasomal setae is presented in Table 2. Pectinal teeth in males 22-28, females 16-20 (Table 3). Pedipalp primary denticles, excluding proximal row, total 28-35 (32.26 ± 1.38, n = 62) on fixed finger, 39-49 (43.81 ± 2.16, n = 62) on movable finger. The dsm seta on the internal brachial surface, and the chelal internal setae, are generally inconspicuous or absent in subadult and adult specimens.

Etymology.—The name "saratoga" refers to the type locality.

Distribution.—Salt flats at Saratoga Springs, southern Death Valley, California.

Specimens examined.—Paratypes. U.S.A.: CALIFORNIA; *San Bernardino County,* Death Valley Natl. Mon., Saratoga Springs, 11 June 1970 (M. A. Cazier, L. Welch, O. F. Francke), 29 males, 31 females (OFF), allotype (CAS).

STAHNKEI INFRAGROUP

Diagnosis.—An infragroup of nominate subgenus *Paruroctonus* differentiated by combination of: (1) cheliceral fixed digit with inferior carina extending proximally at

Table 4.—Measurements (in millimeters) of type specimens of new *Paruroctonus* species and subspecies. L = length, W = width, D = depth.

	P. bantai saratoga		*P. shulovi nevadae*	*P. simulatus*		*P. coahuilanus*
	Holotype male	Allotype female	Holotype female	Holotype male	Allotype female	Holotype male
Total L	50.7	56.2	40.6	38.6	41.6	41.6
Carapace L	6.1	7.0	4.5	4.4	5.3	5.0
Mid-length W	5.0	5.5	3.6	3.6	4.0	4.0
Posterior W	5.8	6.5	4.6	4.0	4.8	4.6
Median eyes W	1.2	1.4	1.0	1.0	1.0	1.0
Mesosoma L	13.8	17.4	10.5	10.7	12.7	11.4
Metasoma I L/W	3.2/3.1	3.3/3.6	2.2/2.2	2.6/2.2	2.5/2.4	2.8/2.7
II L/W	3.9/3.0	3.9/3.4	2.6/2.0	3.0/2.1	2.9/2.2	3.2/2.6
III L/W	4.1/2.8	4.1/3.2	2.8/2.0	3.2/2.0	3.1/2.1	3.4/2.4
IV L/W	5.1/2.8	5.1/3.2	3.4/1.8	4.0/1.8	3.9/2.0	4.2/2.2
V L/W	7.6/2.8	7.7/3.2	5.2/1.8	5.8/1.8	6.0/2.0	6.1/1.9
Telson L/W	6.9/2.7	7.7/3.4	4.7/1.9	5.0/1.7	5.2/2.2	5.4/1.6
Ampulla L/D	4.0/2.3	4.3/2.6	2.8/1.6	3.0/1.4	3.4/1.7	3.2/1.4
Chelicera palm L/W	1.6/1.3	2.4/1.6	1.5/1.2	1.0/1.0	1.3/1.2	1.4/0.9
Fixed digit L	0.8	0.9	0.6	0.6	0.7	0.9
Movable digit L	1.5	1.6	1.2	1.0	1.4	1.5
Humerus L/W	5.1/1.7	5.6/2.0	3.6/1.2	4.0/1.2	4.4/1.4	3.8/1.4
Brachium L/W	5.4/2.3	5.9/2.3	4.0/1.2	4.0/1.6	4.6/1.8	4.0/1.7
Pedipalp palm L/W	5.3/4.8	6.0/5.0	3.9/2.6	4.0/2.6	4.4/2.9	4.7/2.9
Fixed finger L	4.6	5.1	3.2	3.0	3.7	2.9
Movable finger L	6.4	6.8	4.2	4.0	4.9	4.2
Pectine L	6.2	5.2	3.2	4.6	3.9	4.4
Dentate L	5.9	4.1	2.4	3.9	2.8	3.8
Basal L/W	1.7/1.4	1.7/1.2	1.0/0.6	1.0/0.9	1.2/0.8	–
Pectinal teeth	25/25	19/18	15/15	21/21	16/16	19/19

least to level of bicusp (see Gertsch and Soleglad 1966:fig. 36); (2) cheliceral movable digit with superior distal tine essentially triangular or elongate and curved, inferior distal tine length/superior distal tine length ratio 3.0 or less; (3) carapace length/cheliceral fixed digit length ratio 4.2-8.0; (4) basitarsus III with six or more superior seta, arranged in distal plus proximal rows (4+2 to 6+2) or in essentially single file; (5) pectinal teeth in males 13-23 (except 26-27 in one new species; rarely 24 in *P. stahnkei* or *P. simulatus*, n. sp.), females 8-17 (except 18 in one new species); (6) pedipalp movable finger length/palm length ratio in adult males 0.8-1.0 (except 1.0-1.1 in shulovi microgroup), adult females 1.0-1.1; (7) carapace length/pectine length ratio in adult males 1.0-1.2, adult females 1.5-2.2 (except 1.4-1.5 in *P. stahnkei*, and 1.4 in shulovi microgroup); (8) humerus with two inframedial macrosetae on proximal 3/5 of internal surface (except two to three in shulovi microgroup); (9) pedipalp primary denticles, excluding proximal row, total 17-47 on fixed finger, 22-57 on movable finger; (10) adult carapace length generally 3.0-5.0 mm in males, 3.5-5.5 mm in females.

Comparisons: the gracilior infragroup (above) differs primarily in characters 1-4, but also significantly in 5-10; the boreus infragroup (above) differs primarily in character 5, but also significantly in 6-10. Specimens with pectinal tooth counts exceeding 23/24 in males or 17/17 in females (see Haradon, 1984b) have 34 or fewer primary denticles on pedipalp movable finger; all species in the boreus infragroup have 35 or more primary denticles on the movable finger.

Distribution.—Western and southern Great Basin, southward into Sonoran Desert and Baja California Sur; also Chihuahuan Desert.

Subordinate taxa.—The stahnkei infragroup comprises four primarily allopatric elements, differentiated as follows and in Table 5.

STAHNKEI MICROGROUP.Diagnosis: combination of carapace length/ cheliceral fixed digit length ratio 4.2-5.0; telotarsi II-IV with one retroinferior terminal seta (similar to Fig. 16). Distribution: Northern Sonoran Desert. Included species: *P. stahnkei* (Gertsch and Soleglad, 1966).

SHULOVI MICROGROUP. Diagnosis: combination of carapace length/ cheliceral fixed digit length ratio 7.0-8.0; basitarsus II with mrs seta. Distribution: Western and southern Great Basin. Included taxa: *P. shulovi* (Williams, 1970); *P. shulovi nevadae*, n. ssp.; *P. simulatus*, n. sp.

BORREGOENSIS MICROGROUP. Diagnosis: basitarsus II without mrs seta. Distribution: Southern Great Basin, southward into northwestern Sonora and northern Baja California Sur. Included species: This microgroup, named after *P. borregoensis* Williams, 1972, is discussed in detail by Haradon (1984b).

WILLIAMSI MICROGROUP. Diagnosis: combination of carapace length/cheliceral fixed digit length ratio 4.8-5.8; telotarsi II-IV with two retroinferior terminal setae. Distribution: Chihuahuan Desert. Included species: *P. williamsi* Sissom and Francke, 1981; *P. pecos* Sissom and Francke, 1981; *P. coahuilanus*, n. sp.

Paruroctonus shulovi (Williams)
Figs. 7-10, 15, 17-20

Vejovis (Paruroctonus) shulovi Williams, 1970:7-11, figs. 5, 6, tbl. 3.
Paruroctonus shulovi: Williams 1972:3, 1976:2, tbl. 1; Soleglad 1972:74, 1973:355, tbl. 2; Stahnke 1974:138.

Type.—*Vejovis shulovi:* Holotype female (adult) from U.S.A., California, Inyo County, Death Valley Natl. Mon., Grapevine Spring, 4 miles E Ubehebe Crater, 12 April 1968 (S. C. Williams, V. F. Lee, J. Bigelow). Depository: California Academy of Sciences.

Diagnosis.—A species of subgenus *Paruroctonus*, stahnkei infragroup (cheliceral fixed digit with inferior carina extending proximally to level of bicusp; pectinal teeth 18-22 in males, 11-17 in females; pedipalp primary denticles, excluding proximal row, 24-31 on fixed finger, 34-42 on movable finger; basitarsus II with mrs seta; dorsal metasomal setae I-IV 0,1,1,2), and shulovi microgroup (carapace length/cheliceral fixed digit length ratio 7.0-8.0; cheliceral fixed digit with denticles on inferior carina), differentiated by: (1) telotarsi II-IV with two retroinferior terminal setae (Fig. 15); (2) basitarsus III with seven (5+2) superior setae (Figs. 9-10); (3) pedipalp fingers in adult male deeply scalloped proximally, closed fingers form wide gap (Fig. 19), in adult female weakly to moderately scalloped proximally, closed fingers form narrow to moderate gap (Fig. 21); (4) pedipalp palm length/width ratio in adult males 1.3-1.4.

Comparisons: *P. simulatus*, n. sp., differs in characters 1-4 (see below).

Description.—Supplementing above diagnosis and Williams (1970:7). Total adult length of male 35-40 mm, females 35-45 mm. Adult carapace length of males 3.8-4.8 mm, females 4.2-5.6 mm. Trichobothria typical of genus in number and general distribution. Humeral macrosetae: internals include three inframedials on proximal 3/5, one supramedial; four dorsals; usually two external medials on distal 3/5, small middle seta occasionally present. Brachial macrosetae: four internals. Chela: supernumerary denticles well

developed, six on fixed finger, seven on movable finger; primary denticles in six rows on both fingers; macrosetae include two on internal carina (both long), two on ventrointernal carina (proximal long, distal short), one short internal on fixed finger, two internal on movable finger (proximal long, mid-length short). Basitarsus I-III: slightly compressed laterally; superior setae on I 3+2 irregularly set, II 4+2, III 5+2; mrs seta on I long and in line with proximal superior setae, on II about 2/3 as long as superior setae and generally set well apart from superior setae. Telotarsi I-IV setae: proinferiors 1,2,2,2; two each promedials, prosuperiors, retrosuperiors and retromedials; retroinferiors and retroinferior terminals 1,2,2,2. Pectines in adult males extend to 2/3 to 3/4 length of trochanter IV, adult females to or slightly beyond distal edge of coxa IV. Metasomal setae: dorsals 0,1,1,2; dorsolaterals 0,1,1,2; laterals 1,0,0,0,2; ventrolaterals 3,4,4,5,6-8; ventrals 3,4,4, 5. Telson of adult male granular.

Variation.—Pedipalp palm length/width ratio in adult males 1.3-1.4 (1.32 ± 0.02, n = 9), adult females 1.4-1.6 (1.46 ± 0.05, n = 39). Variation in other characters is discussed under subspecies.

Distribution.—Death Valley in California, and southern Nevada.

Paruroctonus shulovi shulovi (Williams)
Figs. 7-10, 15, 17, 19-20

Synonymy.—Same as for species (see above).

Diagnosis.—A subspecies of *P. shulovi* differentiated by combination of: pectinal posterior basal length/maximum basal width ratio in adult females 1.8-2.3 (1.96 ± 0.11, n

Table 5.—Distribution and diagnostic characteristics of the four microgroups constituting the stahnkei infragroup of the nominate subgenus *Paruroctonus*.

Character	*stahnkei*	*williamsi*	*shulovi*	*borregoensis*
Desert region	Sonoran	Chihuahuan	Great Basin	Mojave to Vizcaino
Carapace length/cheliceral fixed digit length	4.2-5.0	4.8-5.8	7.0-8.0	6.8-8.6
Cheliceral fixed digit, inferior denticles (A) absent (B) present	A	A	B	B
Pedipalp movable finger length/ palm length, adult male	1.0	0.9-1.0	1.0-1.1	0.8-1.0
Pedipalp primary denticles, rows on movable finger	7	6-7	6	6
less proximal row, fixed finger	37-47	27-34	24-34	17-30
movable finger	43-57	33-43	34-44	22-38
Pedipalp fingers, adult male: (A) unscalloped, (B) scalloped	A	A	B	A,B
Pedipalp palm carinae, adult female: (A) granular, (B) smooth	A	B	A	B
Humeral internal inframedial macrosetae	2	2	2-3	2
Basitarsus II mid-retrosuperior seta (A) present, (B) absent	A	A	A	B
Telotarsi II-IV retroinferior terminal setae	1	2	1-2	2
Carapace length/pectine length ♀	1.4-1.5	1.6	1.4	1.5-2.2

= 49); pectine length/dentate margin length ratio in adult females 1.4-1.6 (1.54 ± 0.05, n = 49) (Fig. 17); pectinal teeth in males (85%) 18-20, females (88%) 11-14; metasomal segment V with 7/7 or fewer ventrolateral setae (78% of specimens).

Comparisons: *P. shulovi nevadae,* n. ssp., differs significantly in all four characters (see below).

Variation.—Pectinal tooth counts varied as in Table 3. Ventrolateral setae on metasomal segment V (sample n = 58) varied as follows: 6/6 (15), 6/7 (20), 7/7 (10), 7/8 (10), 8/8 (3); seventh and eighth setae were generally smaller than and offset from other six. Pedipalp primary denticles, excluding proximal row, 24-31 (28.51 ± 1.63, n = 45) on fixed finger, 34-42 (37.72 ± 2.12, n = 43) on movable finger.

Distribution.—Northern Death Valley, California.

Specimens examined.—U.S.A.,: CALIFORNIA; *Inyo County,* Death Valley Natl. Mon., Scotty's Ranch (3000 feet), 13 April 1968 (M. A. Cazier, et al.), 3 males 25 females (CAS, OFF), Grapevine Spring, 4 mi. E Ubehebe Crater (2100 feet), 12 April 1968 (S. C. Williams, V. F. Lee), 2 males, 8 females (CAS), 1 mi. N Ubehebe Crater (2100 feet), 12 April 1968 (S. C. Williams, V. F. Lee), 5
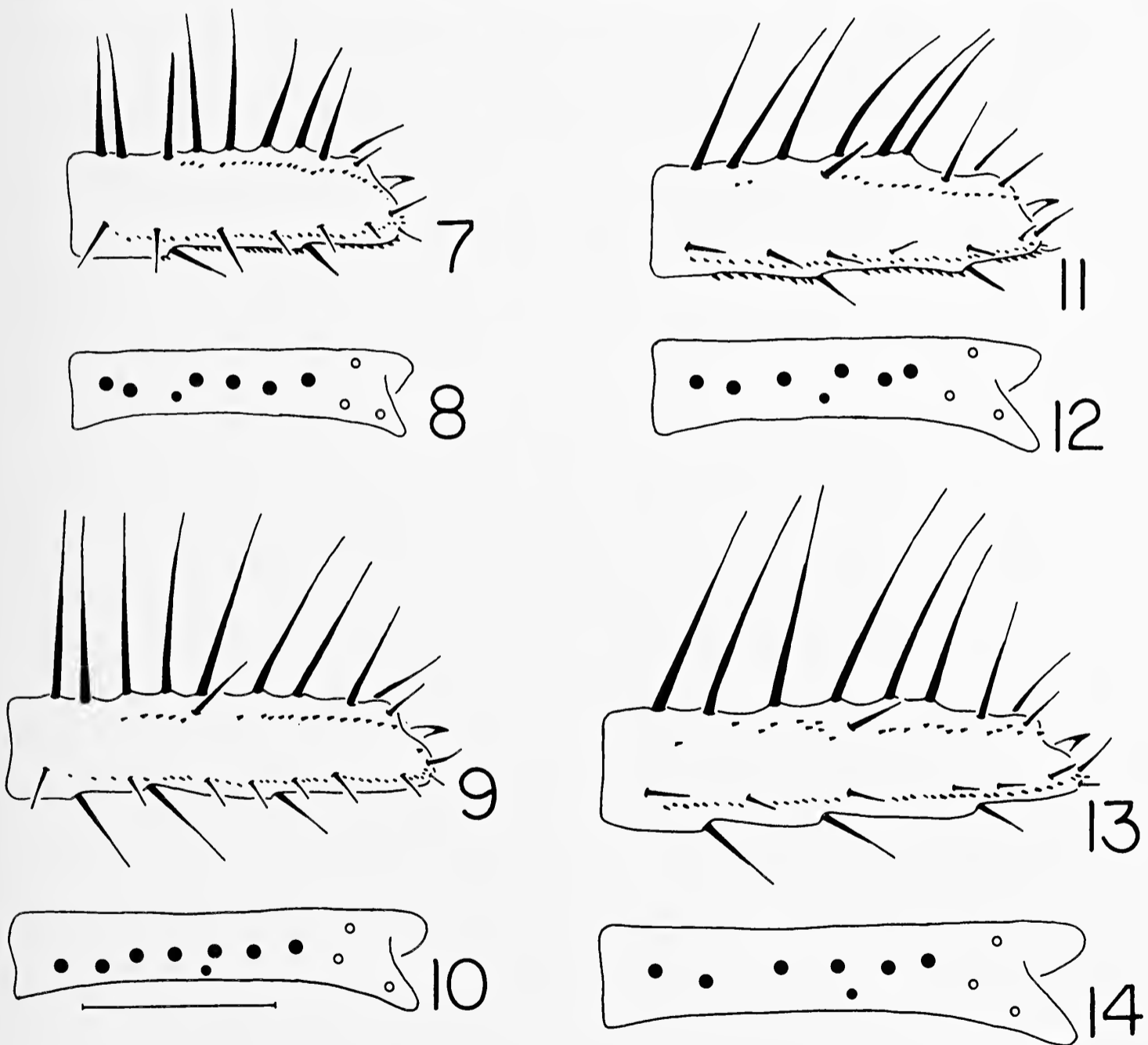
Figs. 7-14.—Right basitarsi. Figs. 7-10, *P. shulovi:* 7, basitarsus II, retrolateral view; 8, basitarsus II, superior view; 9, basitarsus III, retrolateral view; 10, basitarsus III, superior view. Figs. 11-14, *P. simulatus,* n. sp.: 11, basitarsus II, retrolateral view; 12, basitarsus II, superior view; 13, basitarsus III, retrolateral view; 14, basitarsus III, superior view. Key to setae: large solid circles = diagnostic superior setae; small solid circle = mid-retrosuperior (mrs) seta; small open circles = landmark setae. Scale = 1.0 mm.
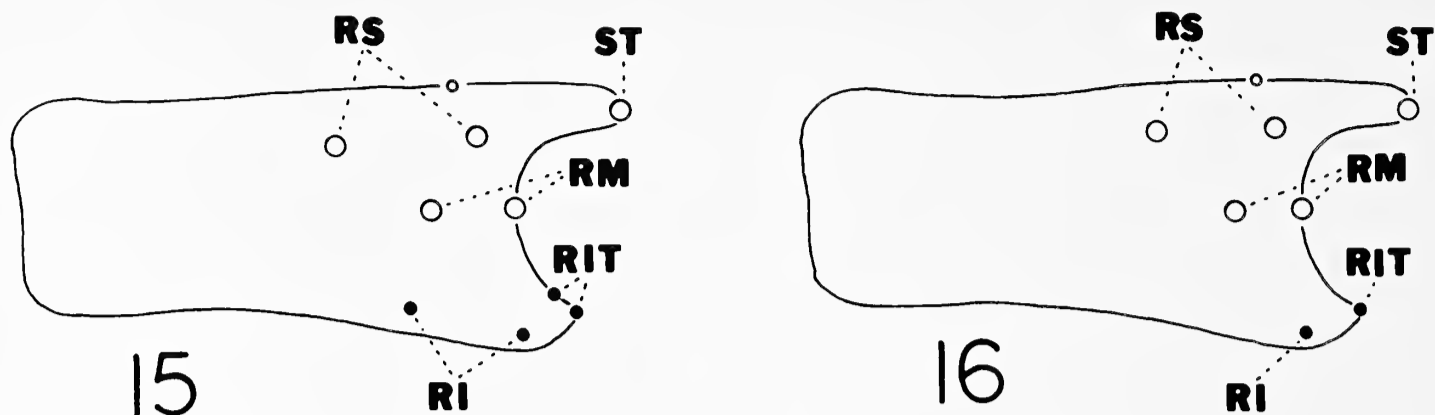
Figs. 15-16.—Right telotarsi, retrolateral views: 15, *P. shulovi;* 16, *P. simulatus*, n. sp. Key to setae: solid circles = diagnostic setae; open circles = landmark setae; RI = retroinferior; RIT = retroinferior terminal; RM = retromedial; RS = retrosuperior; ST = superoterminal.

males, 4 females (CAS), N side Ubehebe Crater Rd., 1.8 mi. W jct. Hwy. 72, 14 October 1977 (J. Hjelle, W. Savary), 6 males, 4 females (CAS), Mesquite Springs Campground, 14 October 1977 (J. Hjelle, W. Savary), 1 female (CAS), Mesquite Springs, 5 June 1970 (M. A. Cazier, et al.), 4 males, 4 females (OFF), Mesquite Springs, 10 June 1970 (M. A. Cazier, et al.), 2 males, 1 female (OFF).

Paruroctonus shulovi nevadae, new subspecies
Fig. 18

Type.—*Paruroctonus shulovi nevadae:* Holotype female (adult) from U.S.A., Nevada, Clark County, Corn Creek Field Station, 4-5 April 1971 (S. D. Slightham). Depository: California Academy of Sciences, Type No. 15062.

Diagnosis.—Adult male unknown. A subspecies of *P. shulovi* differentiated by combination of: pectinal posterior basal length/maximum basal width ratio in adult females 1.5-1.8 (1.65 ± 0.10, n = 12); pectine length/dentate margin length ratio in adult females 1.3-1.4 (1.39 ± 0.04, n = 12) (Fig. 18); pectinal teeth in males (92%) 21-22, females (91%) 15-17; metasomal segment V with 7/8 or 8/8 ventrolateral setae (88% of specimens).

Comparisons: *P. shulovi shulovi* differs significantly in all four characters (see above).
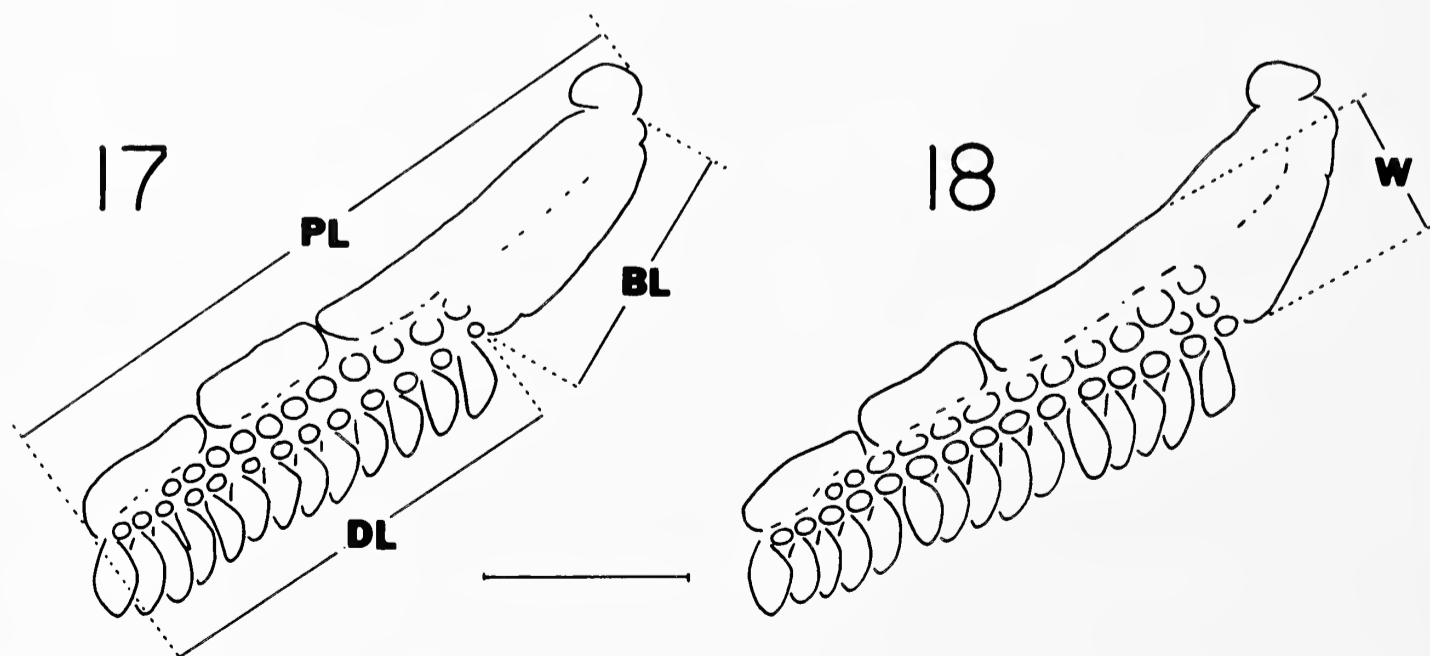
Figs. 17-18.—Right pectines: 17, *P. shulovi shulovi;* 18, *P. shulovi nevadae*, n. ssp. Key: BL = basal length; DL = dentate length; PL = pectine length; W = basal width. Scale = 1.0 mm.

Description of female holotype.—Measurements: Table 4. Pedipalp primary denticles on fixed fingers 3,4,6-5,7,9-8,17, movable fingers 5,6-5,8,8,11,8. Metasomal setae: dorsals 0.1,1,2; dorsolaterals 0,1,1,2; laterals 1,0,0,0,2; ventrolaterals 2,3,3,4,7-8; ventrals 3,4,4,5.

Variation.—Pectinal tooth counts varied as in Table 3. Ventrolateral setae on metasomal segment V (sample n = 17) varied as follows: 6/7 (1), 7/7 (1), 7/8 (9), 8/8 (6). Pedipalpal primary denticles, excluding proximal row, total 26-31 (28.65 ± 1.40, n = 23) on fixed finger, 35-42 (38.12 ±1.68, n = 24) on movable finger.

Etymology.—The name "nevadae" refers to the state to which this subspecies is largely restricted.

Distribution.—Southern Nevada and extreme southeastern Inyo County, California.

Specimens examined.—Paratypes. U.S.A.: NEVADA; *Clark County,* Corn Creek Station, 4-5 april 1971 (S. D. Slightham), 4 males, 10 females (CAS); *Nye County,* 0.8 mi. N California-Nevada border, along State Rt. 29, 12 August 1974 (R. M. Haradon, W. E. Savary), 1 female (CAS); CALIFORNIA; *Inyo County,* 5 mi. N Tecopa (1400 feet), 1 February 1970 (V. Lee), 1 male (CAS).

Paruroctonus simulatus, new species
Figs. 11-14, 16, 21-22

Type.—*Paruroctonus simulatus:* Holotype male (adult) from U.S.A., Nevada, Mineral County, 7 miles N Hawthorne, dunes SE Walker Lake, 15 August 1974 (R. M. Haradon, W. E. Savary). Depository: California Academy of Sciences, Type No. 15063.

Diagnosis.—A species of subgenus *Paruroctonus,* stahnkei infragroup (cheliceral fixed digit with inferior carina extending proximally to level of bicusp; pectinal teeth 18-24 in males, 12-17 in females; pedipalp primary denticles, excluding proximal row, 29-34 on fixed finger, 38-44 on movable finger; basitarsus II with mrs seta; dorsal metasomal setae
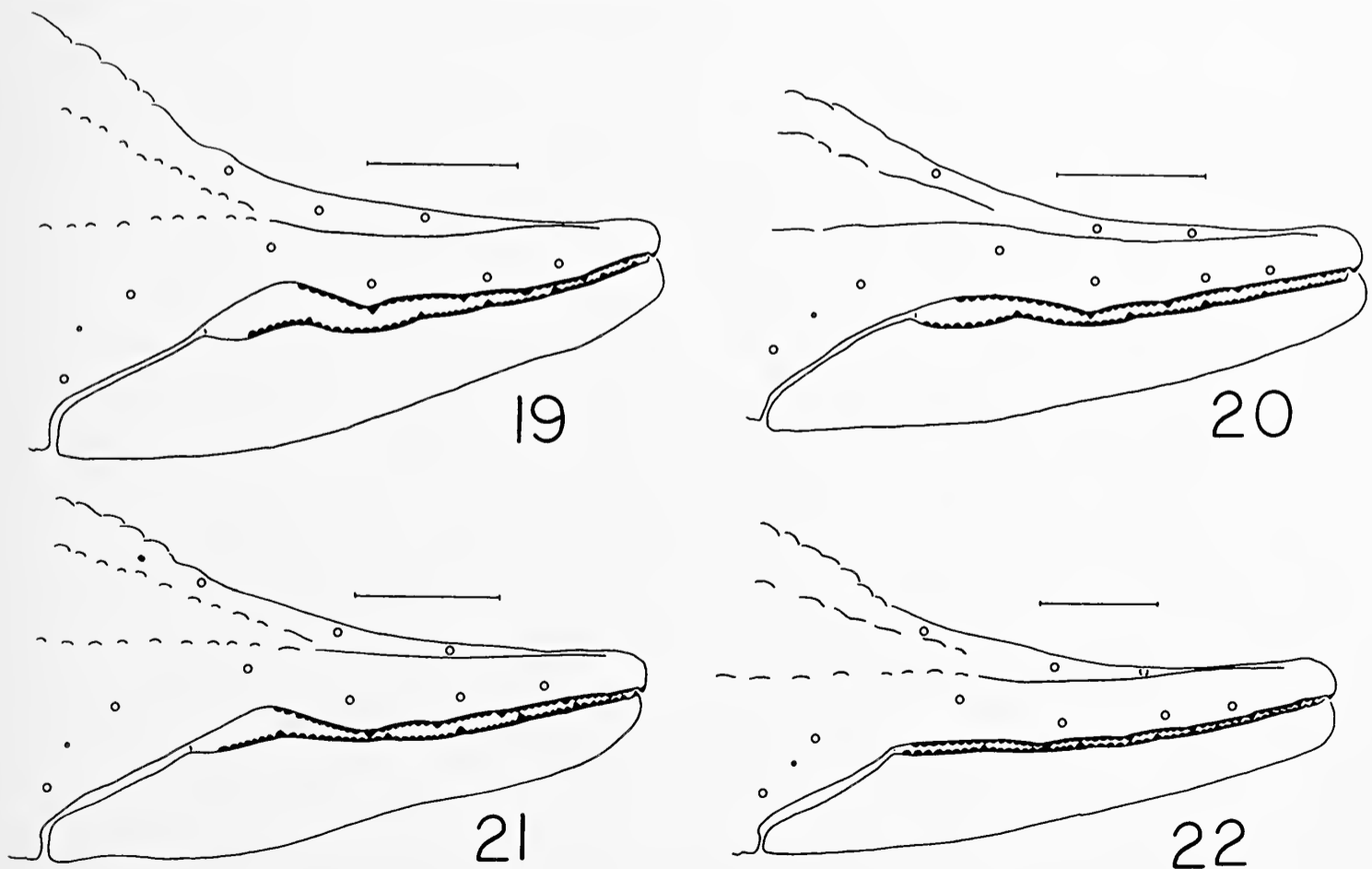
Figs. 19-22.—Right pedipalp fingers, adult state, external views: 19, *P. shulovi,* male; 20, *P. shulovi,* female; 21, *P. simulatus,* n. sp., male 22, *P. simulatus,* n. sp., female. Scale = 1.0 mm.

I-IV 0,1,1,2), and shulovi microgroup (carapace length/cheliceral fixed digit length ratio 7.0-8.0; cheliceral fixed digit with denticles on inferior carina), differentiated by: (1) telotarsi II-IV with one retroinferior terminal seta (Fig. 16); (2) basitarsus III with six (4+2) superior setae (Figs. 13-14); (3) pedipalp fingers in adult male moderately scalloped proximally, closed fingers form moderate gap (Fig. 20), in adult female essentially unscalloped, closed fingers form at most a very narrow gap (Fig. 22); (4) pedipalp palm length/width ratio in adult males 1.5-1.6.

Comparisons: *P. shulovi* (see above) differs in characters 1-4.

Description of male holotype (allotype).—Measurements: Table 4. Pigmentation: pale brownish yellow with fuscous markings on carapace, tergites, pedipalps, legs and ventral surface of metasoma. Carapace: anterior margin straight; surface coarsely (moderately) granular; furrows and carinae well developed. Tergites: I-VII anterior elevated area smooth, posterior area finely granular in anterior half and coarsely (sparsely) granular in posterior half; median carina I-II weakly developed (obsolete), III-VII moderately developed, granular (weak, lightly granular); VII with two pairs granular lateral carinae. Sternites: III-VI very finely granular (smooth), VII moderately (finely) granular with one pair weak carinae. Chelicera: fixed digit with one denticle on inferior carina, subdistal tine meets third superior tine of movable digit; movable digit with superior distal tine elongate and curved, about 1/3 as long as inferior distal tine. Trichobothria typical of genus in number and distribution. Humerus: all carinae well developed, granular; intercarinal surfaces lightly to moderately (lightly) granular; macrosetae include three internal inframedials on proximal 3/5, one internal supramedial, four dorsals, two external medials on distal 3/5. Brachium: all carinae well developed, granular; intercarinal surfaces finely granular; four internal macrosetae. Chela: eight major carinae well developed, granular (lightly to moderately granular); intercarinal surfaces concave, finely granular; macrosetae include two on internal carina (both long), two on ventrointernal carina (proximal long, distal short), none on internal surface of fixed finger, one long internal proximal on movable finger; supernumerary denticles well developed, six on fixed finger, seven on movable finger; primary denticles on fixed fingers 4,6-5,8-7,7-6,7,13-11, movable fingers 5,7-8,8,8,10-11,8-9. Basitarsi I-III: not compressed laterally; superior setae on I 2+2, or 2+3 including mrs seta, II and III 4+2; mrs seta only partially differentiated from superior setae on I, distinctly offset from superior setae on II and III. Telotarsal setae I-IV: proinferiors 1,2,2,2; two each promedials, prosuperiors, retrosuperiors, retromedials; one each retroinferior; one each retroinferior terminal, one extraneous very slender seta on III right and IV left. Ungues I-IV about half as long as telotarsus. Pectines extend to distal margin of trochanter IV (slightly beyond coxa IV). Metasomal carinae: dorsals I-IV serrate (crenulate); dorsolaterals I-IV serrate (crenulate), V granular; laterals I crenulate to serrate, II granular posterior 1/3 (few posterior granules), III with few posterior granules, IV obsolete, V granular anterior 1/2 (1/3); ventrolaterals well developed, I-II granular posterior 1/3 (few posterior granules), III with few posterior granules, IV irregularly crenulate to serrate posterior 1/2, V granular to dentate; ventrals I moderately (weakly) developed, smooth, II-III moderately to well developed, smooth, IV irregularly granular to strongly granular, V dentate; intercarinal surfaces very finely granular except V with scattered coarser granules ventrally. Metasomal setae: long; dorsals 0,1,1,2; dorsolaterals 0,1,1,2; laterals 1,0,0,0,2; ventrolaterals 2,3,3,3,6; ventrals 3,4,4,4-5. Telson: ventral and lateral surfaces granular (with few vestigial granules); nine pairs long ventral and lateral setae.

Variation.—Total adult length of males 32-40 mm, females 36-50 mm. Adult carapace length of males 3.4-4.6 mm, females 4.0-5.6 mm (except one specimen 6.6 mm). Pedipalp palm length/width ratio in adult males 1.5-1.6 (1.51 ± 0.03, n = 13), adult females 1.5-1.6 (1.55 ± 0.04, n = 12). Pectinal tooth counts varied as in Table 3. Pedipalp primary denticles, excluding proximal row, total 29-34 (31.53 ± 1.54, n = 19) on fixed finger, 38-44 (41.33 ± 1.97, n = 18) on movable finger. Ventral metasomal setae varied 3,4,4-5,4-5, usually 3,4,4,5; ventrolateral setae on segment V (sample n = 27) varied as follows. 6/6 (20), 6/7 (6), 7/8 (1); seventh and eighth setae on V usually smaller than and offset from other six.

Etymology.—The name "simulatus" refers to the close similarity of this species to its apparent sister species, *P. shulovi.*

Distribution.—Western Nevada and northern Inyo County, California.

Specimens examined.—Paratypes. U.S.A.: NEVADA; *Mineral County,* 7 mi. N Hawthorne, sand dunes SE Walker Lake, 15 August 1974 (R. M. Haradon, W. E. Savary), 6 males, 2 females, allotype (CAS); *Esmeralda County,* 5 mi. NW Coaldale, 17 December 1972 (collector unknown), 1 male (CAS); CALIFORNIA; *Inyo County,* Eureka Valley, sand dunes, 4 September 1975 (D. Giuliani), 1 male, 1
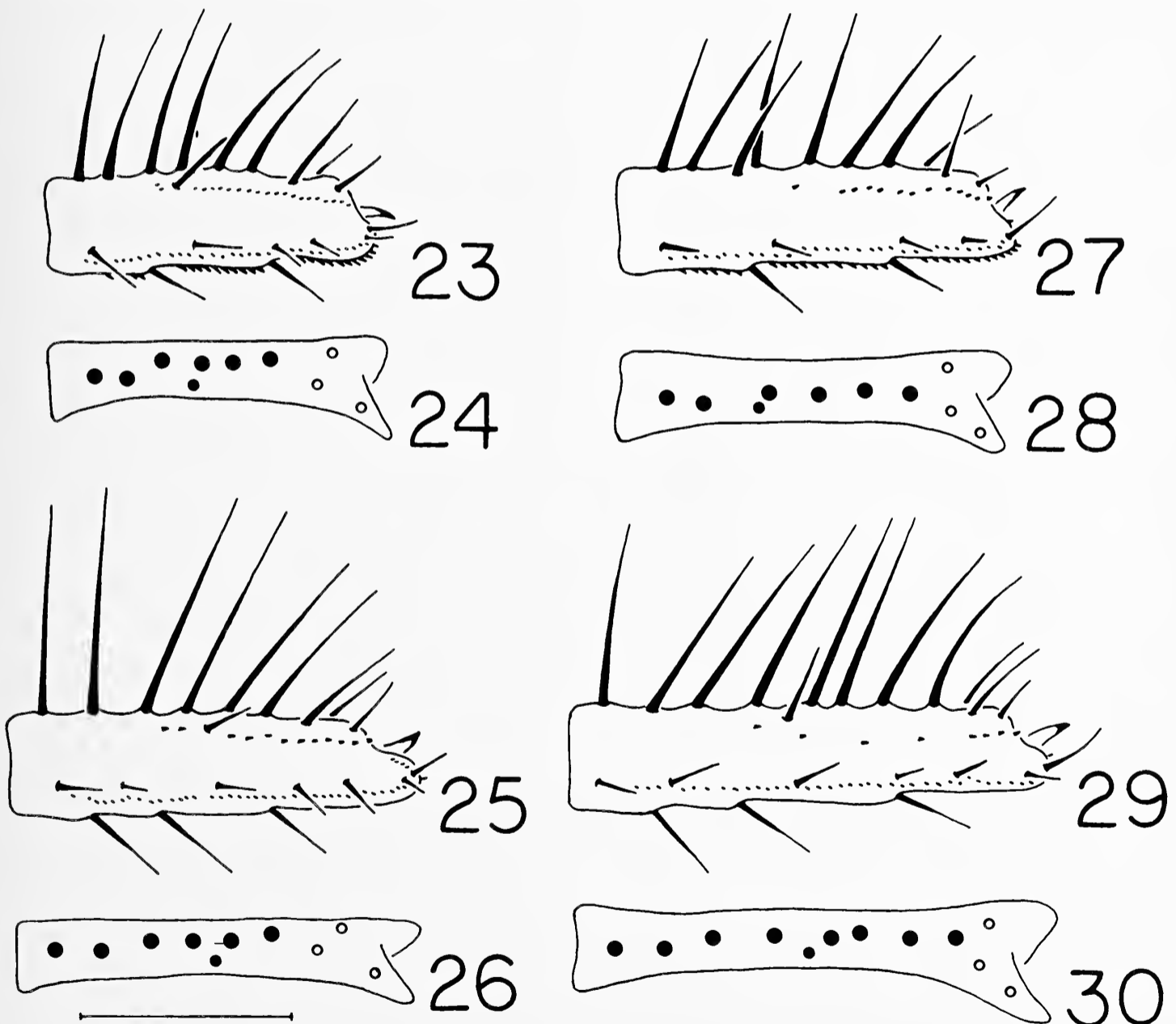
Figs. 23-30.—Right basitarsi. Figs. 23-26, *P. pecos:* 23, basitarsus II, retrolateral view; 24, basitarsus II, superior view; 25, basitarsus III, retrolateral view; 26, basitarsus III, superior view. Figs. 27-30, *P. coahuilanus,* n. sp.: 27, basitarsus II, retrolateral view; 28, basitarsus II superior view; 29, basitarsus III, retrolateral view; 30, basitarsus III, superior view. Key to setae: large solid circles = diagnostic superior setae; small solid circle = mid-retrosuperior (mrs) seta; small open circles = landmark setae. Scale = 1.0 mm.

female (CAS), Saline Valley, Racetrack Valley Rd. (1950-2100 feet), 27 November 1959 (B. Banta), 2 males, 1 female (CAS), Saline Valley, Grapevine Canyon Rd. (2300-3400 feet), 27 November 1959 (B. Banta), 1 male, 2 females (CAS), Death Valley Natl. Mon., along Grapevine Canyon Rd., 32 mi. NW jct. Hwy. 190, 13 October 1977 (J. Hjelle, W. E. Savary), 3 males, 4 females (CAS).

Paruroctonus coahuilanus, new species
Figs. 27-30

Type.—*Paruroctonus coahuilanus:* Holotype male (adult) from Mexico, Coahuila, Cuatro Cienegas basin, 14 August 1968 (S. C. Williams, M. A. Cazier, J. Bigelow). Depository: California Academy of Sciences, Type No. 15059.

Diagnosis.—Female unknown. A species of subgenus *Paruroctonus*, stahnkei infragroup (cheliceral fixed digit with inferior carina extending proximally to level of bicusp; pectinal teeth 18-22 in males; pedipalp primary denticles excluding proximal row, 25-28 on fixed finger, 32-38 on movable finger; basitarsus II with mrs seta; dorsal metasomal setae I-IV 1,1,1,2), and williamsi microgroup (carapace length/ cheliceral fixed digit length ratio 4.8-5.6; telotarsi II-IV with two retroinferior terminal setae; cheliceral fixed digit without denticles on inferior carina), differentiated by: basitarsus III (Figs. 29-30) with six distal plus two proximal (6+2) superior setae (occasionally 5+2 on one leg only).

Comparisons: *P. williamsi* and *P. pecos* differ in having four distal plus two proximal (4+2) superior setae on basitarsus III (Figs. 25-26); *P. williamsi* differs further in having 1,3,3,3 dorsal metasomal setae on I-IV.

Description of holotype male.—Measurements: Table 4. Pigmentation: uniformly pale yellow, except fuscous markings about median ocular tubercle. Carapace: anterior margin protrudes slightly medially; surface granular; furrows and carinae well developed. Tergites: I-VII anterior elevated area smooth, posterior area finely granular in anterior half and coarsely granular in posterior half; median carina I-II weak, III-VII moderately developed, granular; VII with two pairs granular lateral carinae. Sternites: III-VI very finely granular, VII finely granular with one pair weak lateral carinae. Chelicera: fixed digit without denticles on inferior carina; similar to *P. williamsi* and *P. pecos* (see Sissom and Francke 1981:figs. 27-28, 31-32). Trichobothria typical of genus in number and distribution, as in *P. williamsi* and *P. pecos* (see Sissom and Francke 1981:figs.13-26). Humerus: all carinae well developed, coarsely granular; intercarinal surfaces lightly granular; macrosetae include one internal supramedial, two internal inframedials on proximal 3/5; four dorsals; three external medials on distal 3/5. Brachium: all carinae well developed, coarsely granular; intercarinal surfaces finely granular; four internal macrosetae. Chela: eight major carinae moderately developed; external carina irregularly and weakly granular, other carinae irregularly to moderately granular; intercarinal surfaces finely granular, moderately concave; supernumerary denticles well developed, six on fixed finger, seven on movable finger; primary denticles on fixed finger 3-2,4,5,5-6,6-7,13-12, movable finger 3,6-7,7,7,9-10,9-8; macrosetae include one long on internal carina, two on ventrointernal carina (proximal long, distal short), one long internal proximal on movable finger. Basitarsi I-III: moderately compressed laterally; superior setae on I six, irregularly distributed, on II 4+2, on III 6+2; mrs seta on I not clearly differentiated from superior setae, on II moderately off set from superior setae (Figs. 27-28), on III considerably off set (Figs. 29-30). Telotarsal setae I-IV: proinferiors 1,2,2,2; two each promedials, prosuperiors, retrosuperiors, retromedials; retroinferiors 1,1,2,2; retroinferior terminals 1,2,2,2. Ungues about 3/5 as long as telotarsus. Pectines extend to about mid-length of trochanter IV. Metasomal carinae: dorsals well developed, strongly crenulate; dorsolaterals I-IV

strongly crenulate, V coarsely to moderately granular; laterals I crenulate, II-III with few posterior granules, IV obsolete, V present and granular anterior 1/4 only; ventrolaterals I-IV well developed, granular, V dentate; ventrals I-II moderately developed, lightly granular, III-IV well developed, granular, V dentate; intercarinal surfaces finely granular, except scattered coarser granules ventrally on V. Metasomal setae: all long; dorsals 1,1,1,2; dorsolaterals 2,3,3,3,; laterals 2,0,0,0,2; ventrolaterals 2,3,4,4,8; ventrals 3,3-4,4, 5. Telson: smooth; 11 pairs ventral and lateral setae.

Variation.—Total adult length 35-43 mm. Carapace length of adult males 4.2-5.1 mm. Pectinal teeth in males 18-22 (see Table 3). Three specimens (out of 13) each had on one basitarsus III seven (five distal, two proximal) superior setae instead of the normal eight (6+2). Pedipalp primary denticles (three specimens only), excluding proximal row, total on fixed finger 25-28, movable finger 32-38. Metasomal setae: dorsals 1,1,1,2, except for an occasional loss; ventrolaterals I-IV normally 2,3,3,4; ventrolaterals V with seven to 10 (95% with eight or nine); ventrals normally 3,4,4,5, except for loss or presence of individual extraneous seta.

Distribution.—Known only from the Cuatro Cienegas basin, Coahuila, Mexico.

Etymology.—The name "coahuilanus" refers to the state of Coahuila.

Remarks.—The difference in fuscous pigmentation between *P. williamsi* and *P. pecos* reported by Sissom and Francke (1981:107) appears to reflect a difference in intensity of a basically similar but highly variable pattern. The virtual absence of fuscosity in *P. coahuilanus* is very likely only a local edaphic characteristic and not of fundamental taxonomic importance (see *P. gracilior* Remarks above).

Some males of *P. pecos* (CAS) from southern New Mexico are very similar to *P. coahuilanus* in the development of the ventral metasomal carinae, and therefore any apparent distinction in this character that might be inferred from the description of *P. pecos* by Sissom and Francke (1981:103) seems, rather, to be obscure. This character is subject to considerable sexual dimorphism in the williamsi and especially the borregoensis microgroups (i.e., males have well developed granular carinae, and females have weakly developed smooth carinae).

The three allopatric species constituting the williamsi microgroup are very similar, differing significantly only in the two diagnostic characters used to separate them, and possibly in the tendency of *P. coahuilanus* to have a longer mrs seta on basitarsus II (compare Figs. 23 and 27). Therefore, they might be regarded as subspecies of a single species. That they are currently isolated from one another is indicated by the fact that they have so far been found only in, and are probably restricted to, sand dunes. This would explain, also, why the less restricted species, *P. gracilior*, though sympatric with the williamsi microgroup and showing considerable local variation throughout that region, has remained, in contrast, a single species.

The holotypes of *P. williamsi* and *P. pecos* (AMNH) and paratypes of each (OFF, WDS) were examined, in addition to the following *P. coahuilanus* material.

Specimens examined.—Paratypes. MEXICO: COAHUILA; Cuatro Cienegas basin, 14 August 1968 (S. C Williams, et al.), 12 males (CAS).

PARTIAL KEY TO THE GROUPS AND SPECIES IN
THE NOMINATE SUBGENUS *PARUROCTONUS*

1. Cheliceral fixed digit inferior carina extends proximally at least to level of bicusp; carapace length/cheliceral fixed digit length ratio 4.2 or more 2
   Cheliceral fixed digit inferior carina does not extend proximally to level of bicusp; carapace length/ cheliceral fixed digit length ratio 4.1 or less . . . .
   . . . . gracilior infragroup, *P. gracilior*

2. Pectinal teeth 24/24 or more in males and 17/18 or more in females and 37 or more primary denticles (less proximal row) on pedipalp movable fingers, or if fewer pectinal teeth then either (1) dorsal metasomal setae I-IV 0,0,0,1, or (2) no mrs seta on basitarsus II . . . . boreus infragroup, 3
   Pectinal teeth 23/24 or fewer in males and 17/17 or fewer in females and 36 or fewer primary denticles (less proximal row) on pedipalp movable fingers, or either (1) more pectinal teeth, or (2) more primary denticles but dorsal metasomal setae I-IV 0,1,1,1 or more and mrs seta on basitarsus II. . . . . stahnkei infragroup, 6

3. Basitarsus II with mrs seta. 4
   Basitarsus II without mrs seta 5

4. Carapace length/cheliceral fixed digit length ratio 7.0 or more . . . .
   . . . . boreus microgroup, 9
   Carapace length/cheliceral fixed digit length ratio 6.5 or less . . . .
   . . . . becki microgroup, *P. becki*

5. Telotarsus III with six or seven retrosuperior setae. . . . .
   . . . . xanthus microgroup, *P. xanthus*
   Telotarsus III with two to four retrosuperior setae. . . . .
   . . . . baergi microgroup (see Haradon, 1984a)

6. Basitarsus II with mrs seta. 7
   Basitarsus II without mrs seta . . . . . borregoensis microgroup (see Haradon, 1984b)

7. Carapace length/cheliceral fixed digit length ratio 7.0 or more; cheliceral fixed digit with denticles on inferior carina . . . . shulovi microgroup, 13
   Carapace length/cheliceral fixed digit length ratio 5.8 or less; cheliceral fixed digit without denticles on inferior carina. 8

8. Telotarsi II-IV with one retroinferior terminal seta; primary denticles (less proximal row) 37 or more on pedipalp fixed finger. . . . . . . stahnkei microgroup, *P. stahnkei*
   Telotarsi II-IV with two retroinferior terminal setae; primary denticles (less proximal row) 34 or fewer on pedipalp fixed finger . . . . williamsi microgroup, 15

9. Metasomal setae: ventrals I-IV 3,4,4,5; ventrolaterals 4 on IV and 7 on V. 10
   Metasomal setae: ventrals I-IV 3,3,3,3-4; ventrolaterals 3 on IV and 4 or 6 on V . 11

10. Pedipalp fingers in adult male deeply scalloped proximally, in adult female weakly scalloped . . . . *P. arnaudi*
    Pedipalp fingers in adult male weakly scalloped proximally, in adult female essentially unscalloped. . . . . *P. silvestrii*

ACKNOWLEDGMENTS

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EXPERIMENTAL STUDIES OF THE INTERACTIONS BETWEEN A WEB-INVADING SPIDER AND TWO HOST SPECIES

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ABSTRACT

Field experiments were conducted to uncover the effects of a web-invading spider, *Argyrodes trigonum* (Hentz), on two spider species that serve as its host, *Neriene radiata* (Walckenaer) and *Metepeira labyrinthea* (Walckenaer). A series of short-term experiments, each lasting one to three days, investigated (1) the effect of host-*Argyrodes* size differentials on the rate of host emigration and mortality, (2) the effect of additional food on host and *Argyrodes* emigration, (3) the rate of immigration to, and emigration from, host-occupied and host-unoccupied webs by *Argyrodes*, and (4) the use of host webs by *Argyrodes*.

The presence of *Argyrodes* resulted in significant host emigration when host-*Argyrodes* weight ratios were below 10:1. In some invasions *Argyrodes* killed the resident spider. Additional prey did not prevent the host from leaving webs containing adult *Argyrodes*, nor did added prey affect *Argyrodes* emigration from webs. *Argyrodes* invaded host-occupied and host-unoccupied webs with equal frequency and captured prey when occupying both types of webs. These latter results suggest that *A. trigonum* may often inhabit and use empty webs for prey capture, as well as webs occupied by the original resident.

Thus, in its interactions with *N. radiata* and *M. labyrinthea*, the web-invading *A. trigonum* behaves perhaps as a commensal, and certainly as a predator, a thief of prey, a web-thief, and perhaps a web-scavenger. The nature of the interaction between *A. trigonum* and its hosts appears to vary primarily as a function of the relative size of host spider and *A. trigonum*.

INTRODUCTION

Spiders of the genus *Argyrodes* are often described as commensals that inhabit the webs of other spiders, consuming prey neglected or undetected by the host [Exline 1945, Archer 1946 (1947), Comstock 1948, Kaston 1978, Gertsch 1979]. Studies of *Argyrodes* spp. have revealed that they also behave as kleptoparasites by stealing prey previously captured by the host [Wiehle 1928, 1931, Thomas 1953, Kullman 1959 (all cited by Kaston 1965); Robinson and Olazarri 1971, Robinson and Robinson 1973]. Kleptoparasitism can be detrimental to the host. Rypstra (1981) showed that prey consumption by the host *Nephila clavipes* (Linnaeus) was significantly reduced with each additional kleptoparasite in the web. Once prey consumption declined below a critical rate, *N. clavipes* abandoned its web site.

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Argyrodes spp. can also prey on their host. Exline (Exline and Levi 1962) discovered *A. fictilium* (Hentz) eating *Araneus.* Lamore (1958) observed *A. trigonum* (Hentz) eating the basilica spider *Mecynogea lemniscata* (Walckenaer), and Archer [1946 (1947)] reported that *A. fictilium* would kill and eat *Frontinella pyramitela* (Walckenaer). *Argyrodes* spp. have also been found feeding on *Neriene radiata* (Walckenaer) and *Metepeira labyrinthea* Hentz (Wise 1982; J. Martyniuk, pers. comm.). *A. baboquivari* was observed to feed on the eggs, juveniles, and adults of the uloborid *Philoponella oweni* (Chamberlin) [Smith-Trail 1980 (1981)]. In an experimental study, Wise (1982) showed that *A. trigonum* can cause significant mortality in populations of *M. labyrinthea.* He also suggested that web invasions by *Argyrodes* may lead *M. labyrinthea* to abandon their webs. This is consistent with the observation that the webs of *N. radiata* and *M. labyrinthea* are often found containing only *Argyrodes* (pers. ob.).

Argyrodes apparently can behave towards its host as a commensal, a kleptoparasite, or a predator. Responses by the host range from apparent tolerance, through loss of prey, loss of web as a result of emigration, to loss of life. The outcome of a particular interaction between an *Argyrodes* species and its host may be determined by combinations of variables including species and size of the host, species and size of *Argyrodes,* morphology of the host web, food intake of the host and *Argyrodes,* and energy investment by the host and *Argyrodes.* Wise (1982) has suggested that interactions between temperate *Argyrodes* species and their hosts may vary from commensal to predatory as a function of variables such as host feeding rate and relative size of host and *Argyrodes.*

Evidence suggests that the size ratio of host to *Argyrodes* may be particularly important. In situations where the host is very large relative to the web-invading *Argyrodes,* the latter may be incapable of injuring the host, or may risk injury to itself if it attacks the host. In such cases *Argyrodes* may assume the role of commensal or kleptoparasite. Commensal and kleptoparasitic interactions appear to be particularly common between *Argyrodes* and *Argiope* and *Nephila,* hosts which are generally large relative to *Argyrodes* (Robinson and Olazarri 1971, Robinson and Robinson 1973, Vollrath 1979a, Rypstra 1981). When host size approximates that of *Argyrodes,* predation on the host can occur or the host may emigrate soon after *Argyrodes* has invaded its web [Smith-Trail 1980 (1981); Wise 1982].

The level of prey consumption by host or *Argyrodes* may also determine the type of interaction. The host is likely to remain in the web if its food consumption is above a certain level, but will leave the web site if stealing of prey by *Argyrodes* decreases the rate of prey capture below a threshold value (Rypstra 1981). Prey densities might also influence *Argyrodes'* behavior. If the capture rate of small insects by *Argyrodes* is high, it may be less likely to kleptoparasitize or attack its host, particularly if risk to the *Argyrodes* exists.

Invasion of a web by *Argyrodes* may be a quest for a web as well as an opportunity to capture the host. Since *Argyrodes* has been observed in webs without hosts, possibly *Argyrodes* utilizes the web even in the absence of the host. Remaining in the web after the host has emigrated may be beneficial to *Argyrodes* if it can use the empty web to capture prey. The assumed danger of predation while moving to a new web and the complications of finding a suitable host are reduced if more time can be spent in a given web. Apparently to date no one has compared the growth, survival and reproduction of *Argyrodes* in webs with a host to these parameters for *Argyrodes* in vacated webs.

The particular questions addressed by this research are the following: (1) Does comparison of the size of the host relative to that of *Argyrodes* reveal a critical size ratio

where one interaction is more likely than another? (2) Do combinations of particular developmental stages (e.g., adult host with juvenile *Argyrodes*) result in a particular interaction? (3) Does *Argyrodes* of a particular size or developmental stage exhibit different behaviors towards different host species? (4) Does the presence or absence of the host affect the rate of immigration, rate of emigration, and use of the web by *Argyrodes*? (5) Does additional prey affect the rate of host or *Argyrodes* emigration?

Most of the experiments focused on the questions relating to effects of size differences between host and *Argyrodes*. A series of experiments was performed in which a range of host-*Argyrodes* ratios was created. *Argyrodes* of a particular size class were introduced into occupied host webs and observed at three-hour intervals over a 24 hour period. The rate of emigration of those hosts was compared to that of host spiders whose webs were kept free of *Argyrodes*. Two spider species which have only partially coincident life histories (i.e., juveniles and adults of both species do not occur at the same time) were used as hosts so that the behavioral flexibility of *Argyrodes* towards hosts of different developmental stages could be observed.

Experiments to study rates of immigration and emigration involved allowing *Argyrodes* to enter or leave webs with the hosts present or absent over a period of several days. In several experiments of similar design, food was added to some webs and *Argyrodes* movement was compared between supplemented and unsupplemented webs. *Argyrodes* behavior while in host webs was noted; thus, the results of the experiments can be interpreted in the context of specific behaviors of both host and the web-invader.

Argyrodes trigonum (Hentz) (Theridiidae) overwinter as juveniles and are commonly found in antepenultimate or penultimate stages before June. During June and early July mature spiders are present. By late June gravid females and females accompanying egg sacs are abundant. At this time females are sometimes found in small tangles of their own construction as well as webs of other species. In July the spiderlings emerge from the egg sac and early-stage spiders are common. Later-instar *Argyrodes* are commonly found in September, but numbers begin to decline in October.

The life histories of the two host species used in this study, the filmy dome spider *Neriene radiata* (Walckenaer) (Linyphiidae) and the labyrinth spider *Metepeira labyrinthea* (Walckenaer) (Araneidae), contrast with that of *A. trigonum*. Evidence indicates some *N. radiata* complete two generations per year (Wise 1976, in press). Juveniles overwinter and appear in webs in late March or early April. They undergo several molts and reach maturity in May-June. These adults reproduce and spiderlings appear in June-July. Spiderlings that hatched early in the season reach maturity by August or September and produce another generation of overwintering juveniles. Later-emerging spiderlings may overwinter as late-stage juveniles before maturing the next spring. *N. radiata* abundance declines in October and no mature spiders overwinter (Wise 1976). The web of the filmy dome spider is a fine-meshed dome with an extensive tangle above. The spider hangs inverted beneath the center of the dome and captures prey that has entered the tangle by shaking the tangle and pulling the fallen prey through the dome.

Metepeira labyrinthea hatchlings overwinter in the egg sac and emerge in May. Maturity is reached by late July - early August. Females produce egg sacs through October but males disappear in September. The web of *M. labyrinthea* is a composite consisting of a protective tangle and a typical, vertically oriented araneid orb. Within the tangle *M. labyrinthea* builds a protective retreat that often includes web debris or an egg sac. A signal line runs from the center of the orb to the retreat. *M. labyrinthea* generally remains in the retreat and advances to the orb on the signal line to capture prey that has hit the orb.

METHODS

Experiments were conducted in mixed deciduous-pine woods on the Patuxent Wildlife Research Center, Prince Georges Co., Maryland, USA, on natural vegetation and on artificial web sites. The artificial units consisted of a wooden frame 4 m long, 2 m high, and 1.6 m wide. Galvanized wire fencing (5.1 cm mesh chicken wire) composed two 1-meter high rows of undulating waves. These rows were separated by a 1.6 x 4 m horizontal piece of fencing and a similar piece was secured to the top of the unit. The units were distributed approximately 10 m apart on a grid. Host spiders that had colonized or had been introduced onto the artificial web sites were used for the experiments. Spiders on these units were easier to locate and generally easier to remove from their webs than were spiders found on natural vegetation. Removal of spiders found on natural vegetation was difficult because movement of small branches often disturbed the web and webs were often very close to the ground. Webs found on natural vegetation were used when webs located on artificial web sites provided an inadequate sample size. For all experiments 1-8 spiders were added to each of several units. Only 50-60% of these spiders colonized the units, so that at the start of an experiment each unit contained approximately three spiders spaced .5 m to > 3 m apart. For all experiments each web was treated as an individual replicate, since treatments were assigned at random to individual webs, not to units.

Effect of Relative Size of Host and *Argyrodes*.—During the summer of 1982, webs containing adult females or juveniles of the host species were located on the units or, when necessary, on natural vegetation. These spiders were removed from their webs, measured and weighed, then returned to their original locations. These webs were randomized into control (without *Argyrodes*) and experimental (*Argyrodes* added) treatments. *Argyrodes* from host webs on the units or in the surrounding vegetation were then collected, measured, weighed, and introduced into the host webs selected for the experimental treatment.

This type of introduction was conducted several times during the season and encompassed a range of host-*Argyrodes* size combinations: (a) juvenile *Argyrodes* with both juvenile and adult *Neriene* and adult *Metepeira,* and (b) adult *Argyrodes* with juvenile and adult *Neriene* and juvenile *Metepeira* (Tables 1, 2). The different phenologies of *Argyrodes* and the host species prevented all possible permutations from being used.

The number of *Argyrodes* added per web depended upon its size relative to that of the host spider at the time the experiment was conducted. Adult *Argyrodes,* which were always females, were added one to a web for all stages of host spider that were used. Only

Table 1.—Outline of the life history phenologies of the spiders used in this study. The term "spiderlings" is used for animals that have recently emerged from the egg sac. Additional details are found in the text.

	Argyrodes	*Neriene*	*Metepeira*
May	Juveniles	Juveniles & Adults	Spiderlings
June	Adults	Adults & Spiderlings	Juveniles
July	Adults & Spiderlings	Juveniles	Juveniles
August	Juveniles	Adults & Juveniles	Adults
September	Juveniles	Adults, Spiderlings & Juveniles	Adults
October	Juveniles	Juveniles	Adults

Table 2.–Stage, average size and weight of spiders in experiments designed to test interactions at different host-*Argyrodes* size ratios. Sample sizes are the number of spiders upon which the means (± s.e.) are based. Two numbers beneath sample size represent the number of tibia and weight measurements, respectively, where they are different. Numbers of spiders actually used in the experiments appear in Table 3.

	ARGYRODES				HOST				
DATE	N	STAGE	TIBIA (mm)	WT. (mg)	SPECIES	N	STAGE	TIBIA (mm)	WT. (mg)
June 8-9	18	Adult	1.18±0.03	7.42±1.02	*Neriene*	28, 29	Adult	2.32±0.03	14.38±0.65
15-16	14, 16	Adult	1.15±0.02	7.21±0.02	*Neriene*	23, 12	Adult	2.38±0.04	11.83±0.61
27-28	31	Adult	1.23±0.02	5.06±0.35	*Metepeira*	16	Juvenile	0.61±0.02	4.28±0.24
July 8-9	19	Adult	1.21±0.03	5.69±0.65	*Metepeira*	38, 37	Juvenile	0.92±0.03	8.36±0.63
13-14	12	Adult	1.20±0.04	5.90±0.84	*Neriene*	42	Juvenile	1.61±0.03	4.86±0.22
25-26	25	Juvenile	0.29±0.01	0.29±0.01	*Neriene*	65, 66	Adult	2.31±0.02	12.02±0.41
Sept. 6-7	48	Juvenile	0.47±0.01	0.79±0.03	*Metepeira*	53	Adult	1.55±0.02	45.05±2.00
18-19	25	Juvenile	0.51±0.01	1.10±0.04	*Neriene*	50	Juvenile	1.30±0.03	2.72±0.13
25-26	49, 32	Juvenile	0.52±0.01	1.48±0.04	*Metepeira*	6	Adult	1.55±0.06	43.36±6.18

one experiment was performed with single juvenile *Argyrodes* and an adult host; this experiment, with adult *Neriene* females, demonstrated the difficulty of working with juvenile *Argyrodes*. Small *Argyrodes* were difficult to manipulate and appeared frequently to move on and off the webs. By introducing more than one juvenile *Argyrodes* the probability of having at least one remain in the web was increased. Non-experimental webs often have more than one juvenile *Argyrodes* per web. Following the preliminary experiment, three juvenile *Argyrodes* were introduced to adult *Neriene* webs to investigate the effect of several small *A. trigonum* on a single mature host. Two juvenile *Argyrodes* were added to webs containing mature *Metepeira*. In the *Neriene* - *Argyrodes* experiment (September 6-7) that involved juveniles of both species, only one *Argyrodes* was introduced per web because of the similarity in size of *Argyrodes* and juvenile filmy dome spiders.

Argyrodes was added to the support tangle of *Neriene* webs and to the barrier tangle of *Metepeira* webs. Following *Argyrodes* introduction each web was censused and the presence or absence and the location of the host or *Argyrodes* was noted. Censuses were conducted every three hours for 24 hours. *Argyrodes* found in control webs were removed. Adult males of the host species that entered webs were ignored because males visit different female webs and it is difficult to control their presence in the web.

Net Colonization of Host Webs by *Argyrodes*.—During September 1981, *Argyrodes'* preference for webs with a host versus webs without the host was tested. Sixty-two *Neriene* webs were divided into host-present and host-absent treatments. All *Argyrodes* found in the webs were removed. *Argyrodes* from the surrounding vegetation were allowed to invade these webs for the following three days, and the number of webs of each treatment that contained *Argyrodes* was noted. The preference of *Argyrodes* for host-occupied versus host-unoccupied *Metepeira* webs was tested in a similar manner in two separate runs.

In August 1982, the effect of web occupancy by the host on the net colonization by *Argyrodes* was tested by direct introduction of *Argyrodes*. Fifty *Neriene* webs were marked, and the host spider was removed from 25 webs. Two juvenile *Argyrodes* were introduced into all webs. The number of webs containing *A. trigonum* was noted in each of 1-3 censuses conducted each day over the next 72 hours. Two runs of this same experiment were conducted with mature female *Metepeira* and two juvenile *A. trigonum*. Following the first run of the experiment, treatments were reversed so that all webs previously designated as controls had the host removed and the original residents of the removal treatment were returned to their webs.

***Argyrodes* Colonization of Food-Supplemented *Neriene* Webs.**—Studies of the effect of food supplementation on the net colonization by mature female *Argyrodes* of webs of mature female *Neriene* were conducted with host-unoccupied and host-occupied webs in separate experiments during May and June, 1982.

The use of host-unoccupied webs uncovers the effects of supplemental food on *Argyrodes* neglecting any effects due to the host. A single female *Argyrodes* was introduced into each of 50 webs from which the host had been removed. Twenty-six of these webs received supplemental prey. Each feeding round involved introducing a termite larva to the tangle and noting whether the *Argyrodes* responded to the prey (defined as increased activity when prey was introduced), captured the prey, or did not respond. Termite nymphs, found within rotting logs in nature, are not natural prey of web-building spiders. However, termite nymphs were used because they could be captured easily, remained in the tangle after being introduced, continued to move for long periods of time once in the

tangle, and *A. trigonum* would feed on them. Feeding rounds were performed for three days and a final census was taken on the fourth day. A single feeding round was conducted on day one and two rounds spaced 2.5 hours apart were conducted on day two and three. It was considered that only two feeding rounds were necessary on these days because *Argyrodes* usually were feeding on termites from previous rounds or did not respond to prey introduced in the second round. The experiment was terminated when 50% of the *Argyrodes* had abandoned the web. Data collected included presence/absence of *Argyrodes*, response to the prey, and a subjective evaluation of web quality.

The experiment with host-occupied webs uncovered the effect of supplemented prey on *Argyrodes* colonization with the host present, and also provided additional information on the emigration rate of the host from an *Argyrodes*-occupied web. Before an *Argyrodes* was introduced, a single termite was added to each of 51 webs occupied by a mature female *Neriene*. It was thought this preliminary addition of food might decrease the tendency of *Neriene* to emigrate when an *A. trigonum* was introduced. A mature female *Argyrodes* was added to each web, and prey were added to 26 webs in two feeding rounds spaced two hours apart. Each feeding round consisted of adding two termites to the tangle, separated by a 5-10 min. interval.

By the following day 43 of the hosts had abandoned their webs. *Argyrodes* had also emigrated from six of these webs. The experiment was continued with the 37 webs that contained only *Argyrodes*. Over the next three days 19 of the webs (all from the original food-supplemented treatment) received four termite nymphs. The same data were collected as in the experiment involving host-unoccupied webs.

Behavioral Observations of *Argyrodes*.—Throughout the course of these studies, behaviors of *Argyrodes* and its hosts were noted. These observations include capture of the host spider by *Argyrodes*, the behavior of *Argyrodes* in the web with the host present, kleptoparasitism by *Argyrodes*, and the behavior of *Argyrodes* in a web without a host. These observations will be described in conjunction with the results of the experiments.

RESULTS

Effect of Relative Size of Host and *Argyrodes*.—A significant proportion of adult filmy dome spiders left their webs in response to adult *Argyrodes* (Table 3). Juvenile *Neriene* also abandoned their webs when paired with adult *Argyrodes*, as did smaller *Neriene* in response to juvenile *Argyrodes*. The only *Neriene* - *Argyrodes* combination that did not result in significant host emigration is that in which very small *Argyrodes* were introduced into adult filmy dome webs (Table 3). The additional experiment in which three small *Argyrodes* were introduced to each host web also did not result in significant host emigration (χ^2 = 0.004, df = 1, p > 0.90; based on emigration of 3/21 control *Neriene* and 3/22 *Neriene* with *A. trigonum*).

Results of the introductions (Table 3) were also analyzed as a 2 x 2 x 5 contingency table in order to determine whether the effect of *Argyrodes* on its host varied significantly as a function of the stages paired. The three-way interaction term is significant (χ^2 = 14.19, df = 4, p = 0.013), confirming that *Argyrodes* had a varying effect on *Neriene*.

Some combinations of *Argyrodes* and *Neriene* were not studied or observed. Large *Argyrodes* were not usually observed in the webs of extremely small filmy dome spiders, perhaps because their webs are too small to support large *Argyrodes*. Combinations of very small *Argyrodes* and the earliest instar *Neriene* were not studied because of the difficulty of working with first and second instar *Neriene*. Removal of these stages from their webs could not be accomplished without extensive damage to the web.

Table 3.—Results of experiments testing outcome at different host-*Argyrodes* size ratios. All probabilities are presented for one-tailed statistics with d.f. = 1. (Rem. = remain; Prop. = proportion).

NERIENE

| | STAGE | | no ARGYRODES | | | with ARGYRODES | | | | |
Date	Neriene	Argyrodes	N	Rem.	Prop.	N	Rem.	Prop.	χ^2	p
June 8-9	Adult	Adult	27	23	0.85	31	6	0.19	25.02	0.001
June 15-16	Adult	Adult	25	16	0.64	26	7	0.27	7.08	0.005
July 13-14	Juvenile	Adult	14	9	0.64	12	2	0.17	6.00	0.012
July 25-26	Adult	Juvenile	27	22	0.82	30	25	0.83	0.04	N.S.
Sept 18-19	Juvenile	Juvenile	25	16	0.64	23	4	0.17	10.71	0.002

METEPEIRA

| | STAGE | | no ARGYRODES | | | with ARGYRODES | | | | |
Date	Metepeira	Argyrodes	N	Rem.	Prop.	N	Rem.	Prop.	χ^2	p
June 27-28	Juvenile	Adult	21	19	0.90	21	3	0.14	24.44	0.001
July 8-9	Juvenile	Adult	19	16	0.84	18	1	0.06	23.03	0.001
Sept 6-7	Adult	Juvenile	24	24	1.00	24	24	1.00	0.0	N.S.
Sept 25-26	Adult	Juvenile	25	25	1.00	25	24	0.96	1.02	N.S.

Adult *Argyrodes* increased the emigration rate of juvenile *Metepeira* (Table 3). Small and intermediate-sized juvenile *Argyrodes* had no effect on adult *Metepeira* emigration. It should be noted that in the latter experiments two small *Argyrodes* were introduced into the webs because it was assumed *a priori*, based on the previous results obtained from adding single *Argyrodes* to mature *Neriene* webs, that single small *Argyrodes* would not affect adult *Metepeira*. The differential response of *Metepeira*, which varied with the relative size of host and *Argyrodes*, was statistically significant (χ^2 of three-way interaction term from 2 x 2 x 4 table = 10.48, df = 3, p = 0.03). The relative size of the host and invading *Argyrodes* was quantified by calculating the weight ratio of host to *Argyrodes*. Low ratios correspond to a high emigration rate for both host species (Fig. 1).

Certain size combinations of these species do not occur. Adult *Argyrodes* do not coincide with adult *Metepeira*. There may be some overlap between very small *A. trigonum* and large juvenile *Metepeira*, but these combinations were not studied because *Metepeira* populations were lower during 1982 than previous years (unpubl. data) and we were unable to locate enough host spiders for an adequate sample size.

Predation on the host spider was observed only early in the season, when mature *Argyrodes* were introduced to the host webs containing mature *Neriene* or juvenile *Metepeira* (Fig. 2). *Argyrodes* that were feeding on a host spider at the first census the predation was observed were still feeding on the host at the next census 93% (12/14) of the time. Therefore it appears that most required a minimum of three hours to complete feeding on a captured host. Because webs were censused every three hours, it is reasonable to assume that predation by *Argyrodes* was rarely mistaken for emigration of the host. Possibly a captured host may have been discarded or lost for some reason before the capture had been recorded, but this seems to have been an infrequent event.
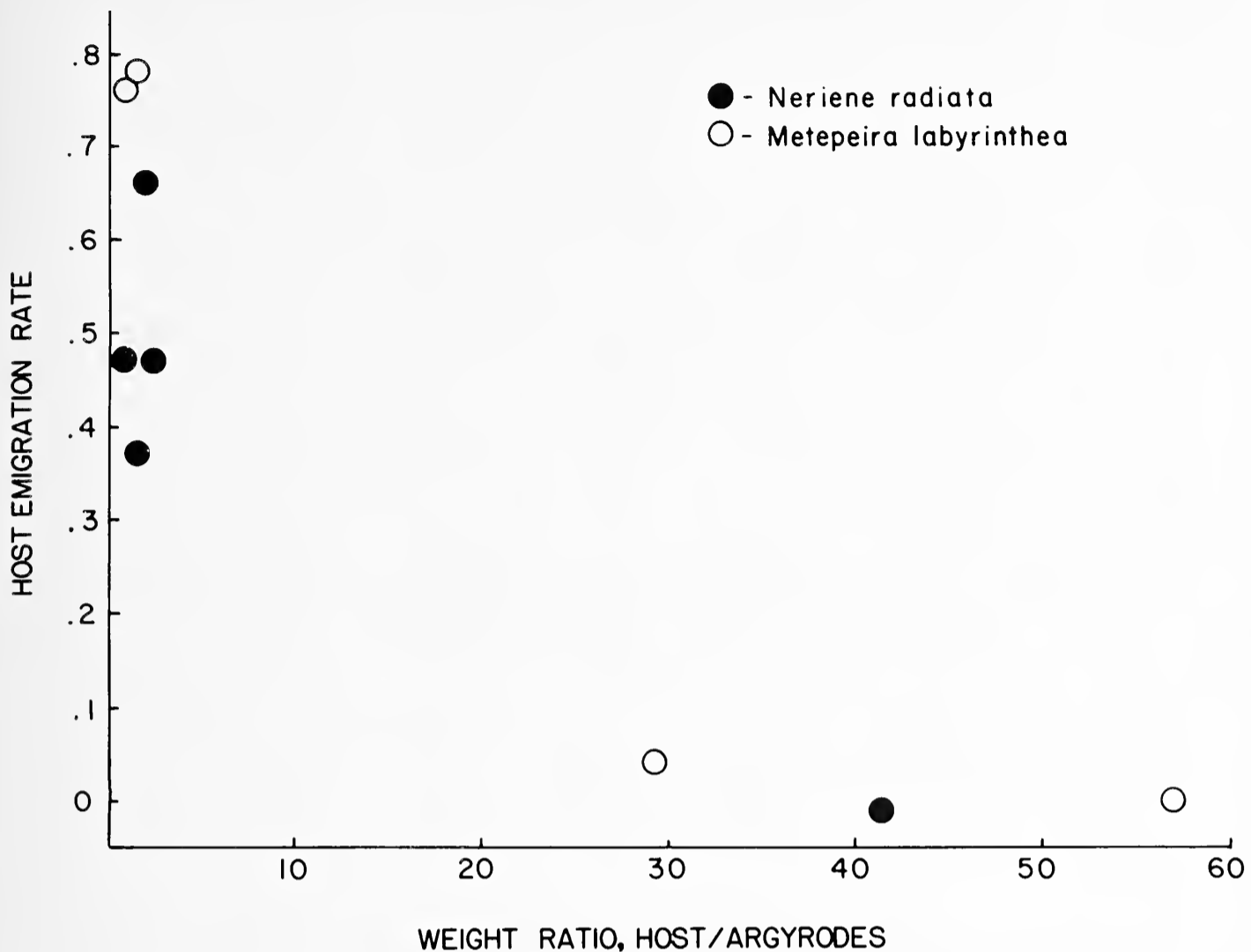
Fig. 1.–The effect of increasing host-to-*Argyrodes* weight ratio on host emigration. Host emigration due to the presence of *Argyrodes* was estimated by subtracting emigration rate in the control from that in the experimental treatment.

Net Colonization of Host Webs by *Argyrodes*.–Two experiments conducted in 1981 indicate that web invasion by *Argyrodes* is not affected by the presence of the host. *Argyrodes* were allowed to invade host-occupied and host-unoccupied *Neriene* or *Metepeira* webs. *Argyrodes* invaded 48% (15/31) of the occupied and 39% (12/31) of the unoccupied *Neriene* webs (χ^2 = 0.59, df = 1, p > 0.25; 2 x 2 contingency table). Pooled data for two runs of the same experiment using *Metepeira* hosts reveals that 35% (13/37) of host-occupied webs and 43% (16/37) of host-unoccupied webs were invaded by *A. trigonum*. As with the *Neriene* experiment, there is no statistically significant difference between invasion rates of each type of web by *Argyrodes* (χ^2 = 0.51, df = 1, p > 0.25).

Argyrodes that were introduced into host webs during the experiments investigating the effects of relative size of host and *Argyrodes* on host emigration did not necessarily remain in the web (Fig. 3). The proportion of *Argyrodes* that abandoned the experimental webs appears relatively constant for *Neriene* but somewhat erratic for *Metepeira*. It was hypothesized that *Argyrodes* would be more likely to abandon the host web when the host is relatively large and *Argyrodes* has no effect on host emigration. Two juvenile *Argyrodes* were introduced to each of 25 host-occupied and 25 host-unoccupied *Neriene* webs. These *Argyrodes* were allowed to emigrate from the webs for approximately 72 hours. Presence of the host had no significant impact on the emigration rate of *Argyrodes*. Four left from 25 occupied webs, and none left the empty *Neriene* webs (p = 0.11, df = 1; Fisher's Exact Probability Test). Two runs of a similar experiment with *Metepeira* webs yielded similar results, though overall emigration rates were higher. Data for these runs were pooled because there was no discernible difference between the size of *Argyrodes* or size of *Metepeira* used in each run. Thirty-six percent (17/47) of the *Argyrodes*

left the *Metepeira*-occupied webs whereas 22% (11/50) left the host-unoccupied webs. There is no indication of a preference by *Argyrodes* for either occupied or vacant webs (χ^2 = 2.40, df = 1, p > 0.10; 2 x 2 contingency table).

Argyrodes **Colonization of Food-Supplemented** *Neriene* **Webs.**—*Argyrodes* placed in webs from which the host had been removed did not differentially abandon webs in response to food supplementation (Fig. 4a; χ^2 = 0.002, df = 1, p > 0.90; 2 x 2 contingency table). When food was introduced into webs containing mature *Argyrodes* and mature *Neriene*, web abandonment by *Neriene* over the next 24 hours was high and did not differ between treatments (Fig. 4b; χ^2 = 0.004, df = 1, p > 0.90). In the same time period few *Argyrodes* left the webs, and their rate of emigration did not differ between food treatments (Fig. 4c; χ^2 = 0.60, df = 1, p > 0.25). Feeding rounds were continued using webs that contained only *Argyrodes*. Their disappearance was analyzed between treatments. Following six feeding rounds (3 days), rates of web abandonment by *Argyrodes* did not differ between experimentals and controls (Fig. 4d; χ^2 = 0.249, df = 1, p > 0.50).

Observations of *Argyrodes* **Behavior in Host Webs.**—(1) Occupation of Web Space by *Argyrodes*. *Argyrodes* that occupy an abandoned *Neriene* web are often found in the dome in the location previously occupied by the host. A sample of 52 webs derived from the seventh or eighth census of the host-*Argyrodes* relative-size experiments that contained only *Argyrodes* revealed that in 75% (39/52) of the webs, *Argyrodes* was in the dome. *Argyrodes* was in the dome in only 35% (6/17) of the webs that contained the host. *Argyrodes* always occupied the barrier tangle of *Metepeira* webs, regardless of host presence (based on 36 host-occupied and 15 host-unoccupied webs).

(2) Prey Capture by *Argyrodes* in Host-Unoccupied Webs. *Argyrodes* captured introduced prey when occupying a web abandoned by the host. Termites were introduced into 41 *Neriene* webs containing only *Argyrodes*. Fifty-four percent (22/41) captured the
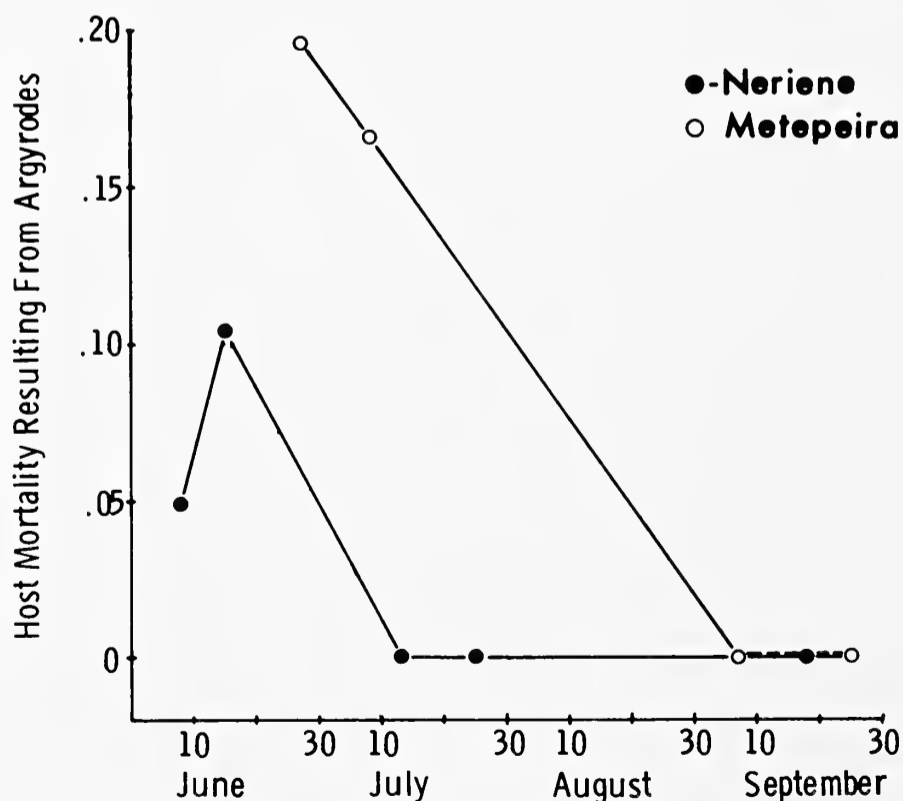
Fig. 2.—Host mortality resulting from *Argyrodes*. Data are derived from the experimental treatments of host-*Argyrodes* relative size experiments.
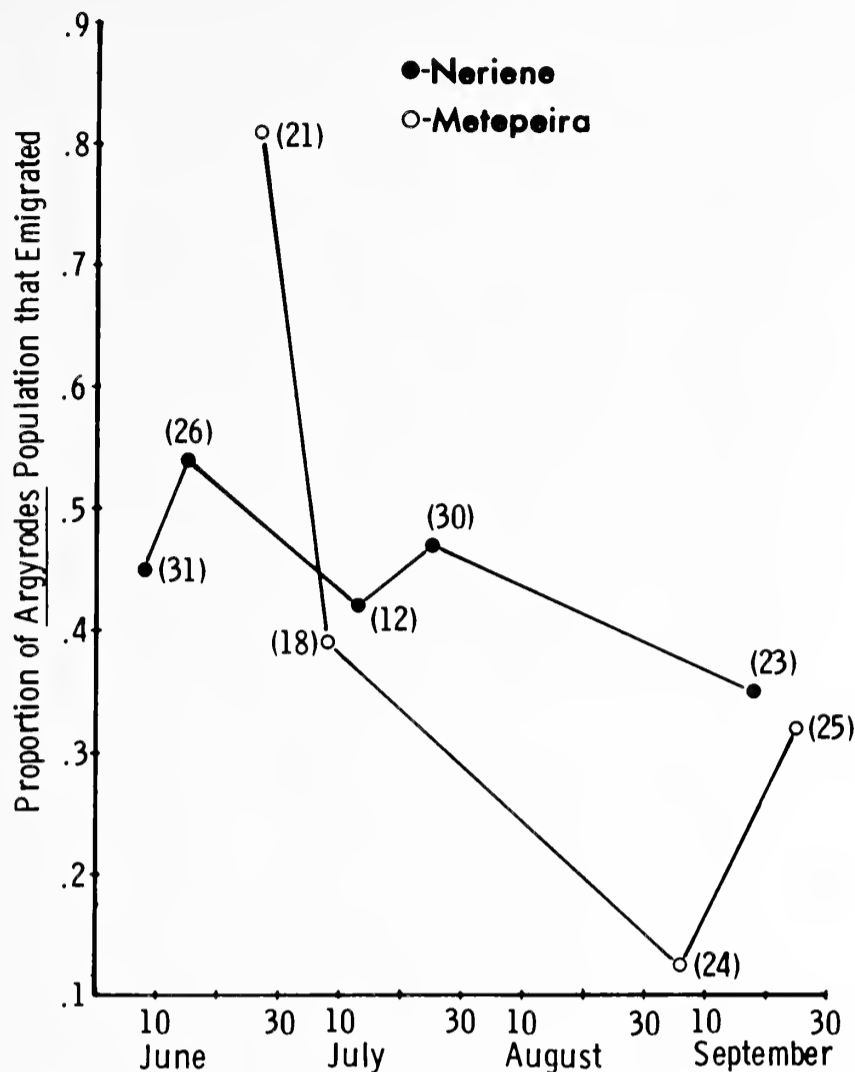
Fig. 3.–Emigration of *Argyrodes* from host webs during host-*Argyrodes* relative size experiments. Sample size is in parentheses.

prey. These data agree with a preliminary experiment in which *Drosophila* were introduced to *Argyrodes*-occupied *Neriene* webs. Fifty-three percent (9/17) of the *Drosophila* was captured by the *Argyrodes*.

Argyrodes that occupy webs containing the host appear to be aware of host movements. During June 1981 *Argyrodes* were introduced into host-occupied webs and observed for periods up to one hour. *Argyrodes* responded to movement in the dome by outstretching their legs and rotating one leg of the first pair in an apparently searching manner. *Argyrodes* sometimes moved towards the host when the host was wrapping prey and moved away if approached by the host. On one occasion the *Argyrodes* dropped to a lower portion of the web when chased by the host *Neriene*. In another instance a labyrinth spider approached the *Argyrodes*, made contact with the invader, and retreated across the web while being followed by *Argyrodes*. Observations of host-*Argyrodes* combinations throughout this study produced several generalizations: (a) *Argyrodes* movement in the tangle or dome of the *Neriene* web or near the retreat of the *Metepeira* web caused the host to stop its own movement or to retreat from the area of the *Argyrodes*, and (b) all host spiders that moved away from an *Argyrodes* later abandoned their webs.

Two observations of kleptoparasitism by mature *Argyrodes* were noted. In the first example the host *Neriene* was wrapping a prey item in the dome. The *A. trigonum* moved into the dome and approached within 3 cm of the host and prey. The *Argyrodes* was

chased by the host and dropped to a lower portion of the dome. The host retreated to the opposite side of the dome, leaving the wrapped prey in the upper portion of the dome. The *Argyrodes* returned to the prey and began to wrap and feed on the prey. The *Neriene* did not return to the upper dome and later abandoned the web. In the second example an *Argyrodes* was in the tangle above a *Metepeira* retreat. The host was in the retreat feeding on a coleopteran. The *Argyrodes* approached the tent and touched the beetle. The host immediately left the retreat and web. The *Argyrodes* began to feed on the abandoned prey. In both of these examples the host made no attempt to reclaim the prey and, instead, retreated from the web once it was aware of *Argyrodes'* presence.

(3) Capture of the Host by *Argyrodes*. Mature *Argyrodes* were commonly found feeding on females and males of the host species. We never observed the actual capture of a *Neriene* female, but have witnessed the capture of a male *Neriene* and a juvenile *Metepeira* by a mature *A. trigonum*.

An *Argyrodes* was in the dome of a *Neriene* web, with the displaced female in the lower portion of the dome. A *Neriene* male entered the web and was approached and touched by the *Argyrodes*. The male did not retreat and the *Argyrodes* bit the first right leg. This leg was then wrapped with silk and the *Argyrodes* bit the third right leg. All right legs were wrapped and then the entire spider was wrapped. Approximately 30 minutes later the *Argyrodes* began to feed on the dead *Neriene*.

In the other instance an *Argyrodes* was introduced into a web containing a juvenile *Metepeira* that was wrapping a prey in its retreat. The labyrinth spider appeared aware of the *Argyrodes* but did not retreat as the *Argyrodes* approached it by climbing the signal line that runs from the orb to retreat. The *Argyrodes* bit the *Metepeira*, which appeared to die within a minute.

In both cases of an observed capture of a host species by *Argyrodes*, wrapping of the prey was not observed until after a bite had occurred. This differs from situations in which *Argyrodes* catches small insect prey by using a wrap-bite behavioral sequence. An observation of a very small *Argyrodes* attempting to capture a large host indicates that the bite-wrap sequence might regularly be employed when *Argyrodes* is attempting to capture large prey. A small *A. trigonum* was observed to approach an adult *Neriene* and bite its fourth leg. The *Argyrodes* made no obvious attempt to restrain the host and no obvious damage to the host resulted from the attack.

DISCUSSION

Argyrodes trigonum causes web abandonment by *Neriene* throughout a large portion of the season that these spiders occur together. The only combination that does not result in significant host emigration (juvenile *Argyrodes* and adult *Neriene*) represents a period of 3-4 weeks. Significant impact of *Argyrodes* on *Metepeira* occurs in June and July (adult *Argyrodes* and juvenile *Metepeira*) but not in September when *Argyrodes* are very small relative to the adult *Metepeira*. One can tentatively predict that weight ratios of host to *Argyrodes* below approximately 10:1 will result in significant host emigration. This value is only an approximation, since some host-*Argyrodes* ratios were not studied. Unfortunately, *M. labyrinthea* populations were low during 1982, and no data for combinations common during late July and August were collected. Consequently, it is unknown if there is a transition in *Argyrodes'* impact as juvenile *Argyrodes* enter the webs of late-stage *Metepeira* juveniles. A prediction could be made that *Argyrodes* would have little effect on larger juvenile *Metepeira* if the weight ratio of host-to-invader is greater than 10:1.

Apparently the critical weight ratio of approximately 10:1 is similar between host species, which suggests that weight ratios might be applied as a predictor of the outcome of host-*Argyrodes* interactions. Previous studies have shown that spiders monitor vibrations in the web to locate the position of other organisms (Witt 1975, Suter 1978, Vollrath 1979b). Weight is an indicator of size; and if the host is large enough, *Argyrodes* may not attempt to oust the host because of the threat of injury. Studies have shown that weight is an important determinant of outcome in intraspecific contests for web occupancy for an agelenid (Riechert 1978) and the labyrinth spider (Wise 1983). Predation by the conspecific appears to be relatively rare for these species. If, as these studies indicate, the heavier spider frequently gains control of the web site, then one might expect *Argyrodes* to rarely displace the host since *Argyrodes* is usually the smaller of the two. However, *Argyrodes trigonum* clearly has evolved the specialized behavior of preying upon the original occupant of the web, which no doubt explains the readiness of large residents to vacate their webs when invaded by *Argyrodes*.

In situations where a single *A. trigonum* does not force the host from the web, it was found that several small *Argyrodes* also did not cause host emigration. The total weight of several small *Argyrodes* does not reach the critical ratio that might lead to host abandonment. Also, these small *Argyrodes* do not seem capable of injuring the host. It is rare to see more than three *Argyrodes* in either *Metepeira* or *Neriene* webs.

Fewer than 20% of the adult *Neriene* were captured by introduced adult *Argyrodes*. No juvenile *Argyrodes* was found with a captured *N. radiata*, and no juvenile *Neriene* was found dead with any stage of *Argyrodes*. Perhaps juvenile *Neriene* are more likely to abandon their web than mature females because juveniles are smaller and more vulnerable to predators such as *Argyrodes*. Since only 4.9% (6/122) of all *Neriene* were captured by *Argyrodes* in the five experiments investigating the role of size differences, it appears that *Argyrodes* is not an important direct source of *Neriene* mortality. *Argyrodes* may, however, be a source of indirect mortality, since displaced *Neriene* may suffer higher mortality from a variety of sources while off the web.

Metepeira were also not often captured by *Argyrodes*. Only adult *Argyrodes* were observed capturing juvenile *Metepeira*. The overall rate of successful attacks by *Argyrodes* on *Metepeira* was approximately 8.0% (7/88). Thus it appears mortality rates from *Argyrodes* may be of similar importance for *Metepeira* and *Neriene*. These rates for both host species measure the outcome of introduced interactions, and are most valuable for comparing interactions between different size classes. These measured mortality rates provide no direct indication of the role or importance of *Argyrodes* mortality in the population dynamics of the filmy dome and laybrinth spiders. These experiments give no indication of how frequently a host spider is exposed to *Argyrodes* invasions during its life, nor do they indicate whether mortality from *Argyrodes* web invasions, either direct or indirect, is density-dependent.

Predation by *Argyrodes* cannot necessarily be assumed when an *Argyrodes* is found feeding on a dead host spider, particularly when the host spider is over 10x the size of the *Argyrodes*. A demonstration in which 15 dead *N. radiata* were introduced into the tangle of webs containing only *Argyrodes* resulted in three of these dead spiders being eaten by *A. trigonum* within three hours of introduction. This is evidence that *Argyrodes* will scavenge dead prey; thus, observations of juveniles feeding on host spiders should not be unexpected. For instance, towards the end of the season, *Metepeira* reaching the end of

their life are often found dead in their webs. If the web is inhabited by juvenile *A. trigonum* at the time of the host's death, it would not be unlikely to find the *Argyrodes* feeding on the dead host.

Argyrodes occupying *Neriene* webs abandoned by the host are often found in the dome as well as the tangle. From either of these locations *Argyrodes* can successfully capture prey that enters the web. *Argyrodes* do not appear to differentially abandon webs with or without hosts. This suggests that *Argyrodes* can benefit from a host web regardless of presence or absence of the host, and that the multiple benefits of a potential meal or a web for catching prey are available to the *Argyrodes*. Rates of immigration of *Argyrodes* into host-occupied and host-unoccupied webs do not differ for both the filmy dome and laybrinth spiders. This suggests that the presence of the host is not the principal attraction to the *Argyrodes*. If host presence was important in terms of being a potential food source, or as a source of prey capture for the kleptoparasite, the net colonization of *Argyrodes* should have been higher in host-occupied webs. The primary factor limiting the use of the web by *Argyrodes* appears to be the web's structural integrity. The *Neriene* web is not particularly sturdy and *Argyrodes* do not appear to substantially reinforce the structure. *Argyrodes* has been observed to strengthen the tangle of a *Metepeira* web with additional silk. This silk could serve the dual functions of additional support or creating denser mesh for increased capture efficiency.
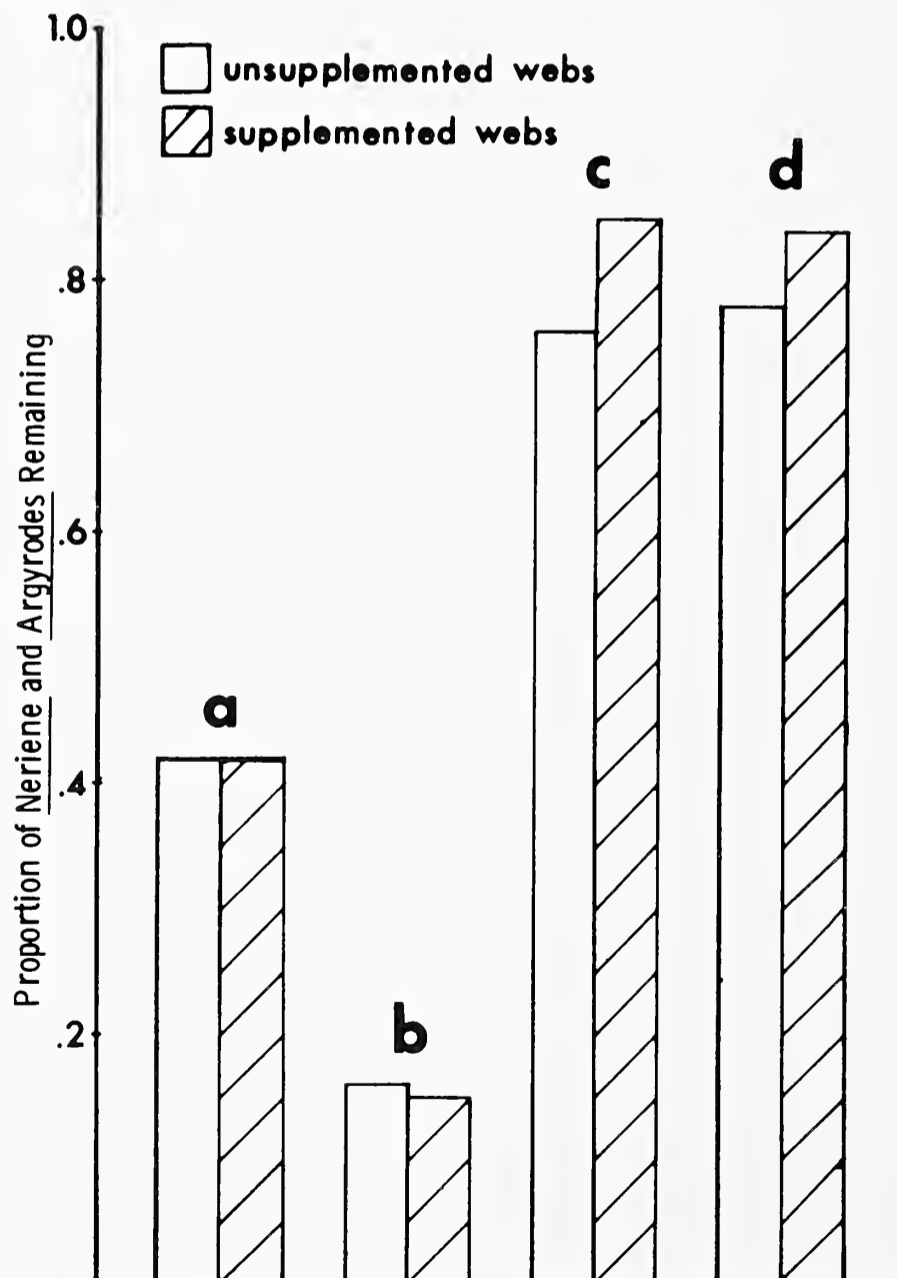
Fig. 4.–Effect of food supplementation on proportion of *Neriene* and *Argyrodes* remaining in the web. Details appear in the text.

Food supplementation did not improve the probability that a mature *Neriene* would remain in a web occupied by a mature *Argyrodes,* nor did supplemental prey increase the probability of *Argyrodes* remaining in the web, whether occupied by the host or not. This suggests that additional food will not influence *Neriene* to risk staying in the web with *Argyrodes,* nor will additional food influence emigration of *Argyrodes.* Because of the limited number of such experiments in this study, interpretations must remain tentative. Prey may not have been in short supply in 1982 for *Neriene* or *Argyrodes.* However, lack of an effect of added prey on the tendency of *Neriene* to vacate the web more likely reflects the fact that *Argyrodes'* major potential impact upon the adult filmy dome spiders is that of a predator, not a prey kleptoparasite. Added prey may not have reduced the emigration rate of *Argyrodes* because it does not repair the empty filmy dome web, and thus web-site quality is more a function of web integrity than short-term prey capture rates. These questions require further study.

Prey kleptoparasitism may play a minor role in *Neriene-Argyrodes* interactions, since the filmy dome spider abandons its web when all but the smallest *Argyrodes* enter the web. Kleptoparasitism may play a more important role for *Argyrodes* that inhabit the webs of mature labyrinth spiders, since this host and invader coexist in the web for the latter 2-3 months of the season (Aug.-Oct.). During periods when *Argyrodes* and its hosts coexist in the web, there is no indication that prey stealing by *Argyrodes* leads to the increased web abandonment that was found in the *Nephila-Argyrodes* system studied by Rypstra (1981). If one defines commensalism in terms of the net fitness of both species, then possibly the cohabitation of small *Argyrodes* and either host is a commensal relationship, since there is no apparent damage to the host spiders. Longer-term experiments are needed, however, to establish conclusively that the presence of even small *Argyrodes* does not lower the fitness of the host. Parameters such as net fecundity of the host with and without the presence of *A. trigonum* should be studied before all possibilities of detrimental effects to the host resulting from *Argyrodes* presence are ruled out.

The term "kleptoparasitism" is usually used to describe a specialized type of competitive behavior, in which one species steals another's prey. The theft of the host's web by *Argyrodes* can be viewed as an example of web kleptoparasitism. This behavior of *Argyrodes* fulfills the definition of kleptoparasitism for several reasons. First, the loss of the web represents an energetic loss to the original owner, since it must build a new web, using energy that could have been applied to future growth or egg production. Also, the act of moving to a new web site may increase the probability of being preyed upon. Either result would reduce fitness. Secondly, the theft of the web represents an energetic gain by the thief. *Argyrodes* captures prey in the stolen web, and on occasion produces an egg sac in the web. *Argyrodes* will inhabit the dome of the *Neriene* web as did the host or will reinforce the tangle of the *Metepeira* web, thereby possibly increasing the web's capture efficiency. Habitation of the web may also improve *Argyrodes'* chances against predators during times when it is not feeding. These points suggest that the net fitness of *A. trigonum* is improved when inhabiting a web abandoned by its host. Further evidence that *Argyrodes* views the web of other species as a resource is the fact that *Argyrodes* are equally attracted to webs with and without hosts. Finally, this specialized behavior towards other species is a one-way competitive interaction—*Argyrodes* does not build a web for other species to capture. Hence the specialized term of "web kleptoparasitism" appears appropriate.

Argyrodes may experience disadvantages to inhabiting an empty web. If the host were to remain and continue normal web maintenance in the presence of *Argyrodes,* the

amount of time that *Argyrodes* could remain at the web site should increase, since apparently *Argyrodes* does not have the ability to spin the variety of webs spun by the species it parasitizes. Also, *Argyrodes* might conserve energy by not being required to perform web maintenance. However, these disadvantages may be outweighed by gains accrued by not behaving as a commensal. The energy provided to the *Argyrodes* by the capture of the host may be more than the energy conserved by continued presence of the host in the web. Also, kleptoparasitism of prey may not be more efficient than capturing live prey, particularly since possible risk of capture by the host exists.

The lifestyle of *Argyrodes* is characterized by an ability to generalize its behavior when invading the webs of different host species. *Argyrodes'* flexible behavior makes possible the exploitation of different species with nonsynchronous phenologies. Assuming *Argyrodes* moves from web to web in a largely random manner, the species of potential host next encountered should primarily be a function of that species' relative frequency in the habitat. *Argyrodes'* quest for a habitable web is made more successful by not having to search for a single host species, or a particular size class of host.

A. trigonum possibly is a commensal, and certainly behaves as a prey kleptoparasite and host-predator. Which alternative behavior *A. trigonum* exhibits appears to depend primarily upon its stage of development and the size of the host spider. Our research suggests that, in addition to exhibiting these behaviors, *A. trigonum* spends considerable time searching out the web of its host species, independently of whether or not the host spider is present. We propose that *A. trigonum* and possibly other *Argyrodes* spp., behave as web kleptoparasites in addition to being web commensals, prey kleptoparasites, and predators on their hosts.

ACKNOWLEDGMENTS

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INTERSEXUAL COMPETITION FOR FOOD IN THE BOWL
AND DOILY SPIDER, *FRONTINELLA PYRAMITELA*
(ARANEAE, LINYPHIIDAE)

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ABSTRACT

Among web-building spiders, bowl and doily spiders *(Frontinella pyramitela)* are unusual because adult males feed frequently. The males rarely build webs, however, and so depend upon females' snares for foraging. In field and laboratory experiments I assessed the impact of male competition on female foraging success and growth rate. During periods when males are abundant, a female is likely to have a male on her web 22% of the time. These cohabiting males capture about 32% of the prey that hit the web despite the female's efforts to capture the same prey. As a result, males decrease female foraging success by about 7% during periods of male abundance. Adult females grow at a rate that increases linearly with increased food consumption—thus the presence of cohabiting males causes a corresponding 7% decrease in female growth rate when males are abundant. The literature on spider foraging and fecundity permits us to calculate that the resultant impact on female fecundity is between 6.1% and 7.0% depending upon what proportion of growth in adult females is attributable to maternal biomass increase and what is attributable to egg production. This detriment to the female is probably outweighed by the high cost of dislodging the male and by a reduction in the probability that the female will be killed by spiders that mimic prey.

INTRODUCTION

Several taxa of insects and spiders effectively reduce the availability of food for host spiders by web parasitism or commensalism (see references in Barth 1982 and Krafft 1982) and some adult female spiders suffer a further effective reduction in food supply because adult males compete for food while in residence on the females' webs (Rovner 1968, Robinson and Robinson 1978, and see references in Kraft 1982). This situation, male use of the female's web for predation, is rare among spiders because in most species the males take no food during adulthood (Bristowe 1958, Savory 1977; in contrast, see Eberhard et al. 1978).

The bowl and doily spider, *Frontinella pyramitela* (Walckenaer), is one species in which the influence of male competition on female growth and fecundity may be particularly severe. This is because 1) males live with females on the females' webs for long periods of time and 2) males capture and feed on prey on those web despite attempts by the females to prevent such activities. This paper describes some aspects of the feeding ecology of bowl and doily spiders and assesses the effect of male competition on female growth and fecundity.

MATERIALS AND METHODS

Spiders.—*Frontinella pyramitela* is a common inhabitant of low vegetation throughout much of temperate North America. Its non-viscid web consists of a bowl-shaped horizontal sheet, an underlying flat sheet, and a barrier or knock-down meshwork of silk that is above the bowl and "doily." The spider lives on the underside of the bowl, dorsal surface downward, and captures prey that are deflected onto the bowl by the barrier silk. The webs are approximately circular when viewed from above and those of adult females have a diameter of about 8 cm. The female spiders are small (4 mm long, 6 mg) and the males are smaller still (3 mm, 3 mg). Mating in this species occurs on the underside of the bowl of the female's web and is preceded by a complex vibration- and chemical-mediated courtship (Suter and Renkes 1982, 1984).

Field Procedures.—Prey capture rates by adult female *F. pyramitela* were assessed in the field (Poughkeepsie, NY, USA) by observations at one-hour intervals at marked web sites. The time of capture, size of prey, and web site were recorded for each captured prey item. More frequent visits to webs were not possible because of the large number of webs that were under observation at a given time. I found that little inaccuracy in quantification of capture rates resulted from hourly observations because spiders fed on most prey items for more than one hour. Prey capture rates were assessed once in 1981 (July) and twice in 1982 (May and July) for a total of 1093 web-hours. Observations spanned all hours of the day and night but periods of inclement weather (during rain, or ambient temperature less than 10°C) were avoided because the spiders temporarily abandoned their webs or were unresponsive to prey at those times.

I performed censuses of occupied *F. pyramitela* webs 16 times during the 1982 season. All adults and late-instar juveniles (greater than 2.5 mm long) were counted and adults' sexes were recorded. The presence of a common theridiid inhabitant of bowl and doily webs, *Argyrodes trigonum* (Hentz), was also recorded. I confined my censuses to a single unmanipulated study area and, within the confines of that area, tried to achieve sample sizes of at least 80 spiders. When the population in the study area was very low, I could not always achieve that sample size.

I measured male-female cohabitation times (the total consecutive time spent by a male on a female's web) both in the field and in the laboratory (see below). In the field, both marked (fluorescent tempera paint on the dorsal surface of the abdomen) and unmarked males were used at marked web sites. Each male was swung by its dragline onto the periphery of a web occupied by a solitary female. There the male would usually begin courtship immediately (Suter and Renkes 1982), mate, and remain with the female for some time. Timing began as the male first contacted the web and continued until he could not be found on the web. Though the initiation of timing was precise, its termination could have been off by 0.5 hour for marked individuals because they were checked each 0.5 hour, and by 0.5 minutes for unmarked individuals because they were checked each 0.5 minutes.

Vestigial-winged (Vg) *Drosophila melanogaster* were used as experimental prey to assess competition for prey between male and female spiders. These flies were used because many similarly sized prey are encountered by *F. pyramitela* in nature (see results) and because they cannot fly and so are readily captured by the spiders. Naturally formed cohabiting pairs of spiders that were neither actively courting nor feeding on prey were presented with a single fruit fly dropped so that it would land approximately midway between the spiders on the bowl of the web. The spider that ultimately fed on the fly was designated the winner despite occasional changes of possession during the frequent

stereotyped contests that preceded feeding. I presented a second fly about 1.5 hours later, after the first fly had been entirely consumed and its carcass discarded.

Laboratory Procedures.—Adult female spiders captured on hedges near Poughkeepsie, New York, were placed on glass or wooden hexapods and enclosed in 3.8 l plastic aquaria. Because adult males rarely build webs, males were enclosed in 10 ml test tubes stoppered with cotton. Both aquaria and test tubes contained wet sand which kept the air near 100% RH. I fed vinegar flies to females on their own webs and to males on webs vacated by females. The temperature in the laboratory varied between 21°C and 23°C.

I measured cohabitation times in the laboratory via continuous visual monitoring of unmarked males on females' webs. Methods were identical to those used in the field (above) except that the webs were on wooden or glass hexapods and were continuously lighted. The cohabitation times of 40 pairs were measured in the laboratory and 17 were measured in the field. Because there were no statistically significant differences between field and laboratory results, both sets of results were pooled.

I assessed the relationship between food consumption and growth rate in 30 adult female spiders by feeding the spiders different numbers of Vg vinegar flies each day for eight days. Spiders were weighted to the nearest 0.01 mg at the beginning and end of the study and the weights of egg masses produced during the study were added to the weights of the responsible females. The flies had a group mean weight of 0.96 mg.

The mortality rates of adult male spiders are usually insensitive to food supply because adult males don't eat (see introduction). *F. pyramitela* males do eat, however, and so may suffer increased mortality when food is scarce or unavailable due to competition. To check the relationship between feeding history and mortality rates, I fed variable numbers of vinegar flies to 33 adult males and then withdrew all food. All of the spiders were maintained at 100% RH until their deaths.

RESULTS

Prey-capture Rates.—During 1093 web-hours of observation, *F. pyramitela* females captured 149 prey that varied in length from 0.5 mm to 11 mm. The mean rate of prey capture (0.14 prey per hour or 1 prey every 7.3 hours) did not vary systematically with the hour of the day or with the date during the adults' foraging season. Because many of the hours of observation were not contiguous, I could not directly derive a frequency distribution of times between prey captures from the field data. However, because webs encounter prey randomly with respect to time of day, the distribution of times between prey captures can be approximated from the exponential distribution with μ = 7.3 hours (Schaeffer and Mendenhall 1975). The distribution indicates that 50% of the time a lone female spider will have to wait less than six hours between prey captures, that 75% of the time she will wait less than 12 hours, and that about 10% of the time she will have to go without food for over 25 hours.

Of course, not all captured prey are equally valuable. The insect prey of *F. pyramitela* vary considerably in mass and consequently in nutrient content. Figure 1 shows how prey length varied among prey captured by spiders in the field. More than 80% of all prey captures were smaller than 3 mm—that is, about the size of a female *D. melanogaster* or smaller, and more than half of all prey captures were smaller than 1.5 mm. At the other extreme, the largest prey was an 11 mm beetle.

The prey lengths shown in Fig. 1 are readily converted into mass units using the empirically derived conversion formula given by Suter (1977). I converted the frequency

distribution of prey lengths into a frequency distribution of prey masses and then built a
two-dimensional matrix whose elements were the products of those mass frequencies and
the exponential frequencies (above) of times between captures. The resulting frequency
distribution of rates of prey capture (in mg/h) reveals that the median prey capture rate is
0.13 mg/h, that 25% of the time the spiders capture at a rate greater than 0.39 mg/h, and
that 25% of the time they capture prey at a rate less than 0.05 mg/h.

Male impact on the female.—The time spent by males on females' webs in the labora-
tory and in the field varied between 0.37 and 50 hours and showed no systematic differ-
ences between the two sites. The frequency distribution of cohabitation times of 57 pairs
from both field and laboratory sites is shown in Fig. 2. The distribution has a median of
7.8 hours with more than 20% of the males leaving the webs in less than 2 hours and a-
bout 25% remaining on the webs longer than 12 hours. Two of the males were still on
webs after 50 hours.

An assessment of the impact of cohabitation on female foraging depends on informa-
tion about the prevalence of males in a spider population and on the foraging success of
the males. Web censuses throughout the bowl and doily spider's active season revealed
only one period when males were present (Fig. 3) though in previous years I had seen a
second but smaller pulse of males during September. During the peak period of male
abundance (May 25 to June 9, 1982), males could be found on 21.9 ± 0.6% (mean ± S.D.,
N = 3 samples days) of all *F. pyramitela* webs. That apparently skewed sex ratio could
have been underestimated because males wander between females' webs and might remain
off webs for many hours. To test that possibility I performed a removal experiment. All
males (N = 13) were removed from webs in a small population (48 webs) of spiders, and
the appearance of additional males was monitored over the succeeding three days. Over
those three days, only four males appeared on the 48 female-occupied webs. Thus it is
likely that, in a population of bowl and doily spiders, more than 80% of all males in the
population can be found on female webs at any given time. (I could not eliminate immi-
gration of males into the test population, so any or all of the males that appeared during
the experiment could have been immigrants). I conclude that the sex ratio is only slightly
underestimated by counts of spiders on webs.

Also present on *F. pyramitela* webs were both sexes of the theridiid *Argyrodes tri-
gonum*. The mean frequency of web occupancy by *A. trigonum* on three days in late May
was 0.19 ± 0.04 (SD); of 487 webs checked, 94 harbored at least one *A. trigonum*.

F. pyramitela males captured 32% (24/75) of all test prey *(Drosophila)* given them in
field studies of male-female competition for prey. When the first fly was presented to
a cohabiting pair, 37% (20/54) of the time the male captured the fly. Second fly presenta-
tions resulted in only 19% (4/21) capture success by males. The difference between first-

Fig. 1.—Frequency distribution of sizes of
prey captured by bowl and doily spiders during
1093 web-hours. N = 149, median = 1 to 1.9 mm
(vertical dashed line).

Prey Size Category (mm)
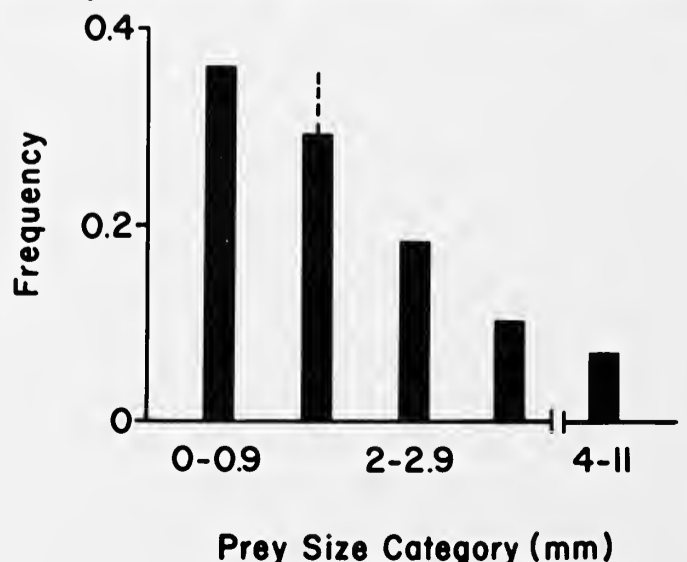
and second-presentation capture success is not significant (χ^2 = 1.50). However, a comparison of the success of males capturing both first and second prey (0/11, 0%) with females capturing both (11/22, 50%) revealed that males are significantly less likely than females to capture two prey in a row when the second prey comes soon after the first (binomial test, P < 0.001). During 35 of the presentations of test prey, I noted not only which spider eventually captured the prey but also which spider contacted the prey first. Males were the first to contact the prey 46% of the time (16/35).

Growth rates of females and starvation morality of males.—Figure 4 shows the results of a eight day laboratory study in which I fed vinegar flies to female bowl and doily spiders and measured the spiders' growth rates. The two spiders that received no food during the study lost only 14% of their original mass after eight days. Over the 0 to 0.23 mg/h range of capture rates, spider growth rates increased linearly with capture rates. The linearity of the data indicates that neither satiation nor decreased nutrient utilization occurred at high feeding rates.

Figure 5 shows the frequency distribution of deaths of male spiders as a function of time since the last feeding. Starved males died within 34 days of their last vinegar fly meal if kept at approximately 22°C. Time of death was neither related to the date (i.e. the age of the spider) (runs test, P > 0.1) nor to the number of flies consumed prior to withdrawal of food (r_s = 0.08, P > 0.1) nor to the mass of the spider at the beginning of the study (r^2 = 0.01, P > 0.1). Only the time spent fasting was strongly related to time of death (runs test, P < 0.025).

DISCUSSION

Impact of male competition for prey.—In spiders, as in many other invertebrate groups, fecundity is directly proportional to the mass of the female and to her foraging success (Turnbull 1962, Kessler 1971, Riechert and Tracy 1975, Wise 1975, Van Wingerden 1978). Any limitation of a female spider's food supply, then, results in a limitation of
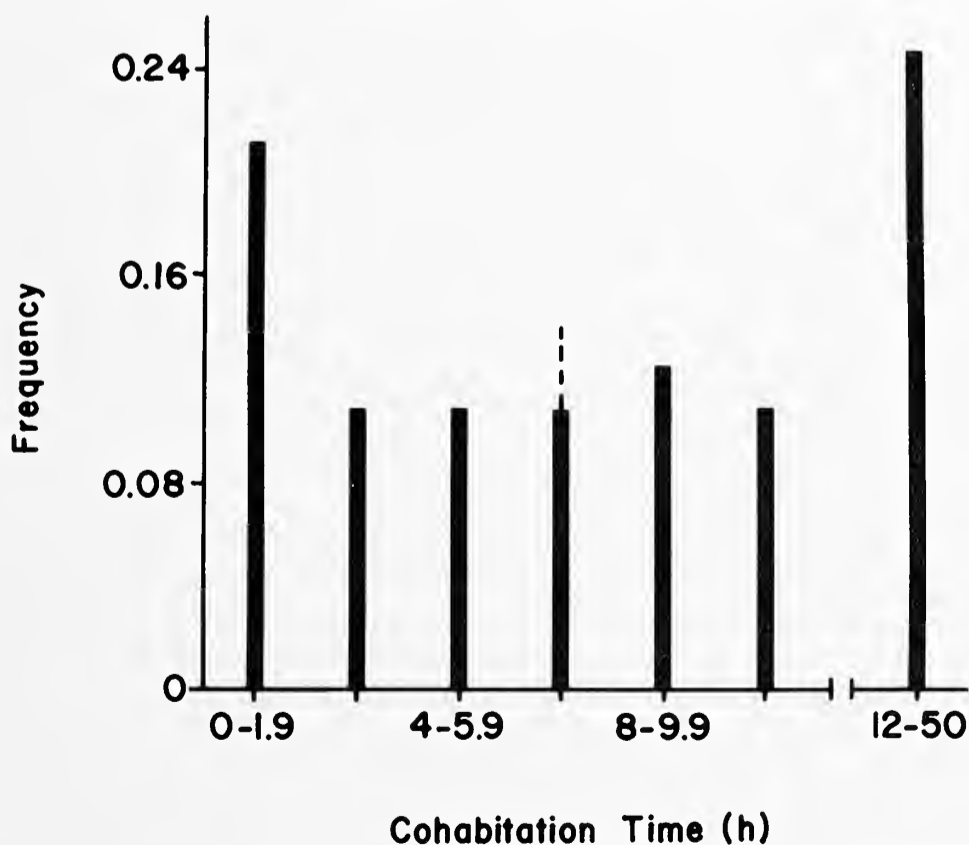
Fig. 2.—Frequency distribution of cohabitation times of pairs of spiders from both field and laboratory observations. N = 57, median = 7.8 hours (vertical dashed line).

her fecundity and a consequent limitation of her fitness. The data presented herein show that male bowl and doily spiders cause a considerable decrease in female foraging success by competing with them for prey items. The competition must also cause a decrease in the females' fecundity and, if females are not all equally tolerant of male cohabitation, a decrease in their fitness.

The impact of male competition on *F. pyramitela* females can now be estimated. During periods of high male:female ratio, a female is likely to have a male on her web about 22% of the time (assuming that cohabitation times are approximately evenly distributed across females). The cohabiting male captures about 32% of the prey that hit the web despite the female's efforts to capture those same prey. Thus during periods of male abundance, males decrease female foraging success by about 7.0% (0.32 X 0.22 X 100).

Though a 7% decrease in prey capture constitutes a major effect of competition, the impact must be much greater for many females in a population of bowl and doily spiders. The number of visits of males to a particular female's web, the time between prey captures at the web, and the sizes of prey are all highly variable, apparently random parameters. And the tenacity of the visiting males, though sensitive to female reproductive status (Austad 1982) and to several identifiable male attributes (Suter, unpublished), is not entirely under the female's control. Some females will therefore lose considerably more than 7% of their food to males during periods of male abundance because they cohabit with more males who stay longer and are more successful at competing for prey. During the remainder of the reproductive lives of the female spiders, male impact is low or nil because males are scarce.

Adult female bowl and doily spiders grow at a rate that depends linearly on the amount of food they consume (Fig. 4). Turnbull (1962), in studies of the fecundity of another linyphiid spider, *Linyphia triangularis,* showed that growth in his mature females was entirely composed of increase in total egg mass rather than increase in maternal tissue biomass. Assuming that is also the case for *F. pyramitela,* the impact of the male competition is then as great on fecundity (or mean egg mass) as it is on the "growth" rate in Fig. 4. In contrast, Kessler (1971) showed that in four species of wolf
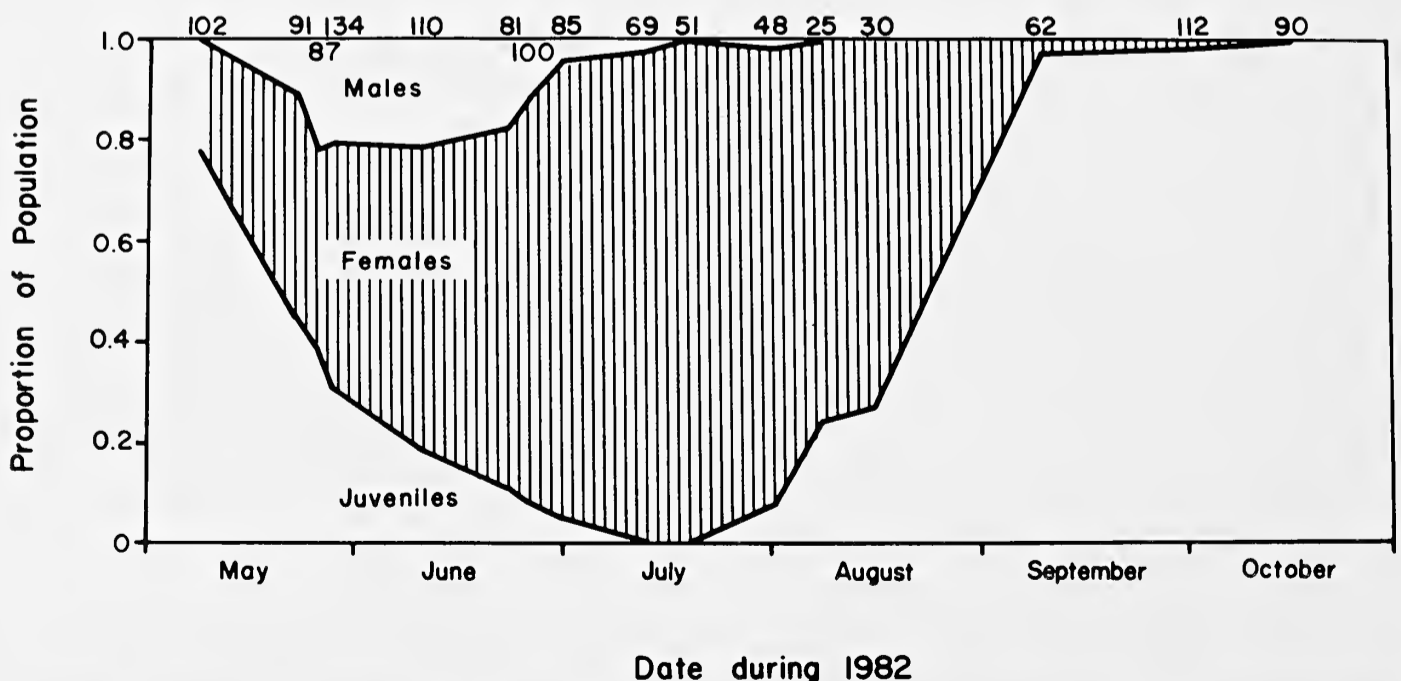
Fig. 3.—Relative abundances of male, female, and immature spiders inhabiting webs during the 1982 season. Numbers at the top of the graph indicate the total number of *F. pyramitela* counted on each census date.

spiders (Lycosidae) about 13% of adult female growth was increase in maternal biomass and the remaining 87% was egg production. If bowl and doily spiders are very similar to the wolf spiders in their reproductive ecology, then 87% (rather than 100%) of the growth deficit would be subtracted from the female's current reproductive effort. In either case, the fecundity deficit caused by the male competition for prey is large— between 7.0% (all growth is egg production) and 6.1% (87% of growth is egg production) during the period when males are most abundant. Figure 3 shows that males are common for about four weeks early in the summer, time enough for the female to produce at least two, perhaps three clutches of eggs (Kessler 1971, Eberhard 1979, Austad 1982) and time enough to encompass a majority of the reproductive life of most females (Austad 1982a). Because the aggregate impact of males varies with their abundance, the 6-7% estimate of their impact at peak abundance overestimates the impact of males during an entire season.

Benefit (to males) of competition for prey.—In most spider species, the males apparently do not feed as adults (see introduction) but rather wander from female to female, from web to web, consuming stored nutrients. If male mortality is high while searching
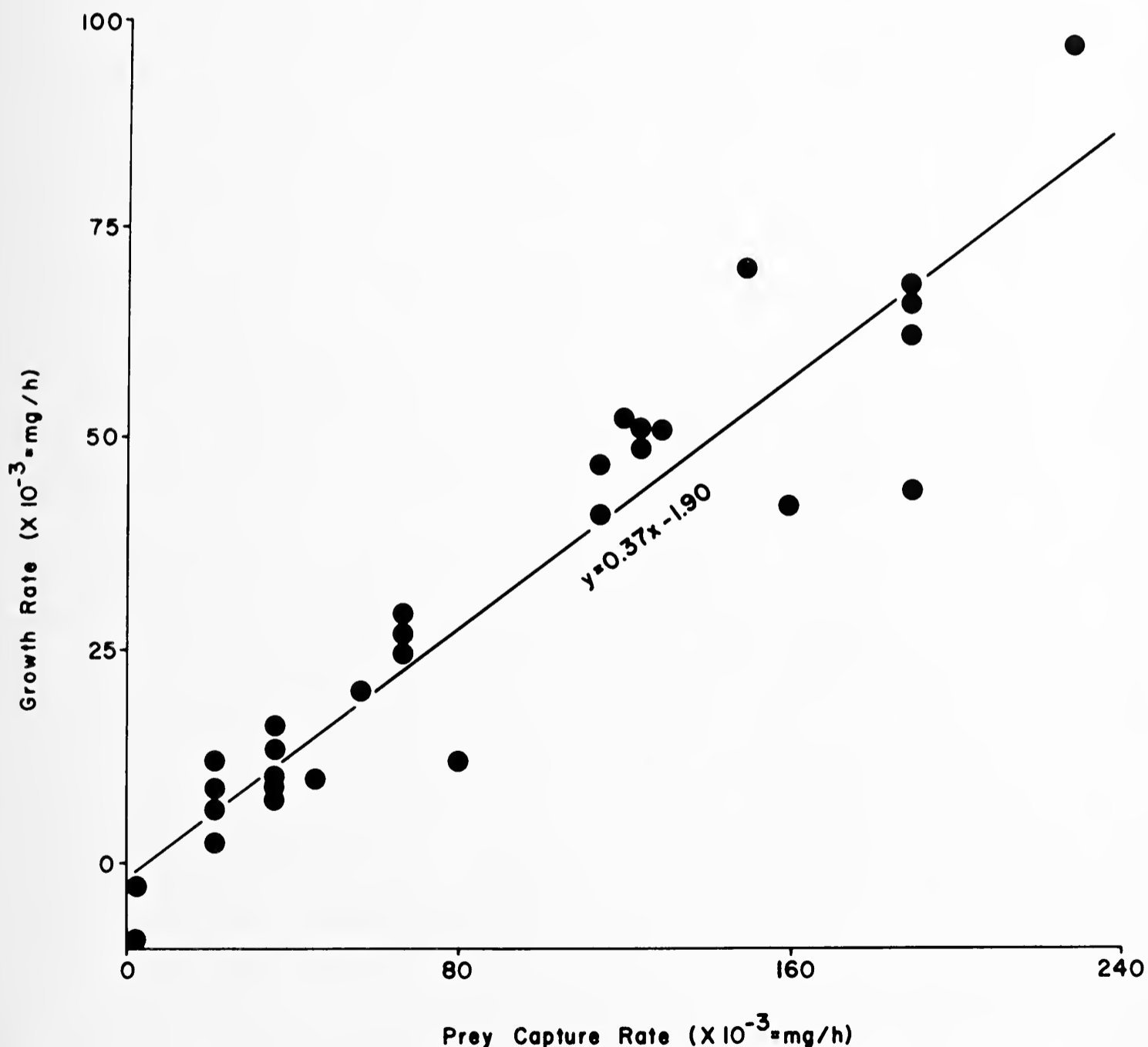
Fig. 4.—Growth rates of adult female bowl and doily spiders as a function of the rate of prey capture. The solid line indicates the best fit to the data (r = 0.947) for the growth of the 30 spiders in the study.

for females, then male foraging would confer no nutritional advantage because the spiders, with their comparatively low metabolic rates (Anderson 1970), would die of other causes before they died of starvation. Thus high off-web mortality is an adequate explanation for the absence of feeding by males in some species of spiders. What explanations can be offered for the existence of vigorous foraging by adult male bowl and doily spiders? 1) Off-web mortality from predators may be low due to crypsis, small size, unpalatability, location of search, etc.; 2) desiccation may be a primary source of male mortality in dry habitats and thus feeding may more appropriately be considered drinking; or 3) intrasexual competition for scarce resources may favor heavier spiders and males can become heavier by eating.

Neither I nor the literature have information on mortality in vagabond male spiders although Robinson and Robinson (1978) suggest that such mortality may be relatively low for small male spiders because of their inconspicuousness. Desiccation certainly is a problem for both sexes of *F. pyramitela* during periods when there is neither rain nor dew formation, and both sexes can be observed to drink as dew forms or when it rains. However, males kept at high relative humidity still feed readily when placed on female webs and this feeding, in the absence of desiccation, prolongs their lifetimes under laboratory conditions (Fig. 5). Thus the threat of desiccation is not a sufficient explanation of male feeding in the bowl and doily spider. Several authors have shown that the results of intrasexual competition among male spiders are biased by mass: the heavier male has a higher probability of winning an encounter (Rovner 1968, Dykstra 1969, Christenson and Goist 1979; in contrast, see Aspey 1977). Austad (1983) and Suter and Keiley (1984) have shown the same mass bias in *F. pyramitela*. It may be, then, that increase in mass

Time from Last Food to Death (days)
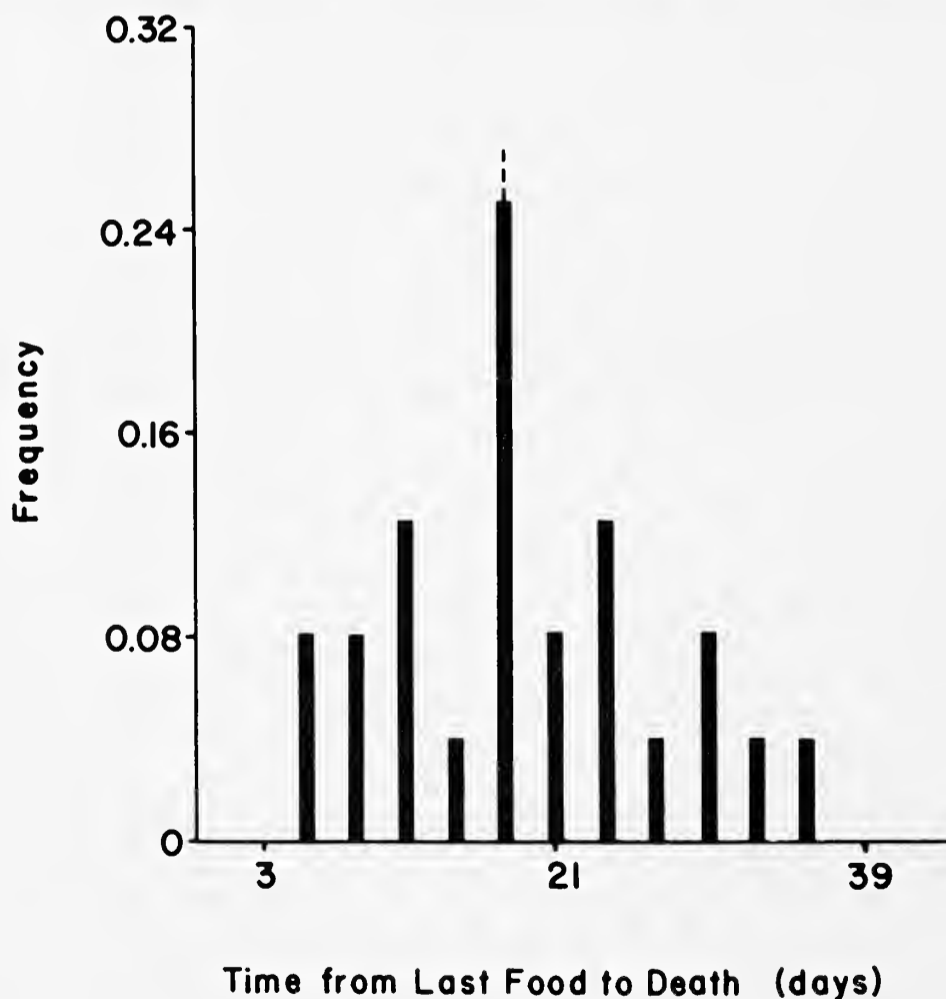
Fig. 5.—Male morality due to starvation. Twenty three males kept at high RH and at approximately 22°C died within 34 days after their last meal (median = 17 days, dashed line). Time of death was neither related to the age of the spider nor to the number of flies consumed prior to withdrawal of food nor to the initial mass of the spider. The time spent fasting was significantly related to time of death (runs test, P < 0.025).

through opportunistic feeding is adaptive for males both because it prolongs their lives (above) and because it makes them more formidable opponents during agonistic encounters. Both prolongation of life and success in agonistic encounters would allow a male to inseminate more females than if he was short-lived and a frequent loser.

Benefit (to females) of male cohabitation.—*F. pyramitela* males cohabit with females far longer than is necessary for insemination of the females (Austad 1982) and yet far shorter than is necessary to guard the female and thereby ensure paternity. Indeed, Austad has shown that first male sperm priority is so complete in this species that first males have no need to guard and subsequent males have no paternity to ensure. Those conclusions and our data indicate that the males remain in webs to feed.

A female's tolerance of such prolonged male cohabitation is difficult to understand, then, because her interests are apparently in direct conflict with his. Austad (1984) argues that, at least with respect to multiple matings, the costs of compliance with the male are less than the costs of resistance. His argument was tenable for multiple matings because all known costs to the female were small. The nutrient cost of lengthy periods of cohabitation with males, however, is high.

I propose two explanations for female tolerance of male cohabitation. 1) Males are probably expensive to dislodge. Observations of males and females both during courtship (Suter and Renkes 1984) and during competition for prey indicate that the two sexes are equally agile on the female's web. Thus, though the female is heavier than her mate, she is unlikely to be able to throw him off without expending considerably time and energy in prolonged chase. In this respect, the male's behavior contrasts sharply with his behavior when confronted with another male: when confronted by an aggressive female, the male avoids direct contact by fleeing from the female but remaining on the web; when confronted by another male, the resident male promptly engages in display and fighting behavior that ends when one male flees from the web altogether (Austad 1983, Suter and Keiley 1984). 2) The presence of the male decreases by approximately 50% the probability of female mortality caused by predation by other spiders. Several spiders in the Theridiidae and Mimetidae prey upon bowl and doily spiders. Typically the bowl and doily spider senses the presence of the intruding predator, mistakes it for prey, and rushes to the attack only to be attacked and consumed itself (pers. obs.). When males share females' webs, males and females are equally likely to rush at prey and thus equally likely to rush at predators that mimic prey. In my study areas, *Argyrodes trigonum,* known to be a predator on other spiders (Wise 1982) is very common during the period when male *F. pyramitela* are also abundant and may therefore contribute strongly to mortality during that period. Indeed, I have frequently observed *A. trigonum* feeding on both sexes of bowl and doily spiders. I hypothesize, therefore, that a major benefit to the female of prolonged male cohabitation is the deflection of predation from female to male. I am currently testing this hypothesis in field populations.

ACKNOWLEDGMENTS

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AGGREGATIONS OF *NEPHILA CLAVIPES* (L.) (ARANEAE, ARANEIDAE) IN RELATION TO PREY AVAILABILITY

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ABSTRACT

Females of the species, *Nephila clavipes* (L.), sometimes build their webs in interconnected clusters. Aggregations in a Peruvian population of this spider were located in areas of high insect activity. This locale enabled individuals in aggregations to capture more prey than solitary individuals. Experiments with prey removal and prey supplementation verified that a high prey capture rate was essential in maintaining such groups. Agonistic interactions frequently preceded departure of a spider from a cluster. These data imply that high prey availability is a prerequisite for the evolution of more complex sociality in *Nephila* and other similar spider species.

INTRODUCTION

The evolution of sociality in various groups of animals has received much attention in light of the theory of natural selection (Wilson 1975, Maynard-Smith 1983 and references therein). Spiders are an unlikely recipient of this attention since they are voracious predators that frequently recognize conspecifics as prey. Nevertheless three levels of social interaction have been described for spiders based on some degree of tolerance, interattraction and cooperation (Shear 1970, Kullmann 1972). These social types include (1) colonial spiders that forage in interconnected webs, (2) spiders that aggregate only for the protection and rearing of young, and (3) spiders that share a common web in which they cooperate both in prey capture and in the rearing of young. Aggregate behavior in arachnids increases foraging efficiency, habitat exploitation, ease of mate location, and offers protection from predators and parasites (Buskirk 1975, Lubin 1974, Brach 1977, Rypstra 1979).

There appear to be two evolutionary pathways capable of producing some form of aggregation in spiders (Shear 1970, Kullmann 1972, Krafft 1979, Buskirk 1981). Along one route sociality results from an extension of parental care and the family unit. In the second pathway communal habits are the result of opportunism: selection favoring those individuals able to reap some ecological advantage from unintentional contact with conspecifics. In the study presented here, I focus on the evolution of intraspecific tolerance via that second pathway.

High prey availability is a likely prerequisite for the formation of aggregations in spiders. In spider species that maintain well-defined territories, field-measured nearest neighbor distances are smaller in populations that live in areas with high prey densities (Riechert 1978, 1981, Uetz et al. 1982). In situations where prey abundances are artificially maintained at exceptionally high levels territories disappear and both inter- and intraspecific tolerance appear in species that are normally solitary (Rypstra 1983). These factors make it tempting to hypothesize that occurrences of very high natural prey abundances make intraspecific competition for resources less necessary and allow the evolution of more amicable interactions between individuals.

The golden-web spider, *Nephila clavipes* (L.), is the focal species of this study. *Nephila* females build large webs in the open forest or edge habitats of tropical and subtropical America (Gertsch 1949, Peters 1954). The webs are fine-meshed circular orbs with varying amounts of barrier webbing surrounding them. An insect, detained by the sticky orb area, is usually subdued, wrapped and transported to the center of the web. Prey can either be cached or consumed immediately (see Robinson and Merick 1971, Moore 1977 for more details). Smaller spiders, called kleptoparasites, frequently occupy the barrier webbing and steal captured prey from the host spider (Vollrath 1976, Rypstra 1981).

I selected *N. clavipes* for this investigation of the relationship between food availability and sociality in spiders for two reasons. (1) Although adult females are usually solitary, in some habitats, individuals build webs adjacent to or intertwined with the webs of others (Shear 1970, Robinson and Merick 1971, Farr 1977). Understanding the circumstances when members of this species tolerate conspecifics in close proximity should provide insight into the factors that make possible the evolution of more advanced sociality. (2) Individuals of this species respond within one or two days to low prey consumption rates by relocating their webs (Rypstra 1981). Since long-term web site tenacity is apparently a reflection of an adequate prey supply, one would predict that webs remaining in close proximity are gathered around a favorable prey source.

METHODS

Aggregations of *Nephila clavipes* were studied in an area of subtropical moist forest in the Tambopata Reserve Zone, 29 km SSW of Puerto Maldonado, Department of Madre de Dios, Peru. Data were collected during June and July 1983. This time is the beginning of the dry season. Searches were made of all areas associated with major paths of the reserve. Each *N. clavipes* female found was marked with a drop of acrylic paint on her abdomen. If the barrier silk of two or more webs was contiguous the spiders were considered aggregated. Solitary spiders had webs with no silk connections to the webs of others.

I observed natural spider webs for two-hour periods at some time between 0900 and 1500 h. I recorded all activities of spiders and of insects that moved within ten cm of the webbing. Specific attention was paid to insect activity, prey capture rates, aggressive interactions in complexes, and kleptoparasite actions. Ten periods (20 hours) were spent with solitary individuals and 11 periods (22 hours) were spent with web complexes of four or more spiders. On three occasions I attempted to transfer kleptoparasites from the barrier webbing of one web to another.

An independent measure of prey availability was obtained via adhesive traps. Sheets of plastic (10 x 10 cm) covered with Tack Trap[TM] (Animal Repellents, Inc., Griffin, Georgia) were strung in the forest undergrowth for four-hour intervals. Sixty-four samples

were taken within a seven-day period. Thirty-two sheets were positioned 50 cm away from the capture surface of an individual in an aggregate and 32 sheets were placed 50 cm away from solitary webs. At the end of four hours the traps were collected and the captured insects were counted and categorized by order and size.

These observations allowed simple comparisons between the webs of solitary and aggregated individuals. In an attempt to reinforce any conclusions made about the formation and maintenance of aggregations, I conducted two experiments.

Experiments 1: Prey Removal.—A natural aggregate of six *N. clavipes* females located near a small stagnant stream was selected. Normal prey activity around this complex was determined by observation for four hours prior to manipulation. For ten consecutive days I visited this complex at 14:00 h. At that time I removed prey items, both living and dead, contained in the webbing. The diffuse nature of the barrier webbing made it possible to remove approximately 80-90% of the insects with little or no damage to the structure. I also noted changes in position or number of *N. clavipes* while observing the group for one hour. Prey removal was terminated after ten days. I returned to the complex on six subsequent days to determine if any other changes in the colony occurred. On these visits I plucked the webs near each prey item without removing them. This procedure should control for effects of web disturbance on colony integrity.

Experiment 2: Prey Supplementation.—*Nephila* females that have been starved for 48 hours will usually spin a web where they are released. Using this technique I created an aggregate of three spiders in an area for which both adhesive traps and insect observations indicated low prey activity. I visited this group daily at 10:30 h. for ten consecutive days. Ten to 15 live fruit flies (*Drosophila* spp.) were gently placed onto the capture surface of each *N. clavipes* web. I recorded the number and position of the spiders and observed their actions for one hour after prey addition. Supplementation was terminated after ten days. I returned to the site for six days to monitor the fate of this artificial aggregate. On these occasions I carefully touched the webbing in 10 places with a live insect but did not leave any additional prey in the trap.

RESULTS

Thirty-two *N. clavipes* females were located in the study area. Four natural aggregates accounted for 17 of these spiders (one with three members; two with four; one with six). The remaining 15 spiders were solitary.

During my observations *N. clavipes* spent about four percent of its time in web maintenance activities (clearing debris and repair). No difference is evident between solitary and aggregated webs (Table 1). Since all observations were of foraging spiders in completed webs no overall time/energy budget budget was determined.

Seventy-seven percent of the prey captured by *N. clavipes* in the Tambopata forest were small dipterans and hymenopterans (1-5 mm in total length). Many larger insects seemed to be capable of either avoiding the web or escaping before they were attacked. Overall, the webs captured 79% of the insects that contacted them (Table 1). The activity of insects in the small size range was significantly higher near aggregated webs than it was near solitary webs (Table 1). Individuals in aggregations captured more prey than did those in solitary webs (Table 1).

Two species of kleptoparasites in the genus *Argyrodes* Simon (Araneae: Theridiidae), occupy the barrier webbing of *N. clavipes* web in the Tambopata forest. From 0-12 *Argyrodes* fed on the prey of each host spider (Table 1). Similar numbers of *Argyrodes*

Table 1.—Comparative data collected for solitary (20 observation hours) and aggregate (22 hours) webs of *N. clavipes*. The presence of a * means there is a significant difference between the two groups using the Mann-Whitney U-test, p < 0.05.

	Solitary Webs X̄ ± S. D.	Aggregated Webs X̄ ± S. D.
Prey Activity/h (adhesive traps)*	3.9 ± 2.2	10.2 ± 3.4
Prey Activity/h (observed)*	7.6 ± 2.4	11.6 ± 3.8
Prey Captured/spider/h*	5.5 ± 1.4	10.3 ± 3.1
Capture Efficiency (captures/prey in web)	77.1 ± 7.5	82.5 ± 9.1
Web Maintenance (min/h)	2.6 ± 1.7	2.3 ± 2.0
Total Number of Kleptoparasites	3.2 ± 1.4	3.6 ± 1.9
Kleptoparasites/*Nephila**	3.2 ± 1.4	1.2 ± 0.9
Prey Lost to Kleptoparasites/*Nephila*/h	2.2 ± 1.7	1.4 ± 1.2
Prey Captured by Each Kleptoparasite/h*	2.2 ± 1.7	4.2 ± 1.4

occupied solitary and aggregated webs (Table). Consequently those individuals in colonies acquired significantly more prey (Table 1). *Nephila* females gave no indication that they were aware of the other spiders in the web. In no instance did they move into the barrier webbing or recover an item. Prey losses per *Nephila* individual were not significantly different between solitary and grouped spiders (Table 1). Kleptoparasite transplants were unsuccessful. *Argyrodes,* when introduced, retreated to a remote position or dropped out of the webbing entirely.

Aggressive interactions between *N. clavipes* females consisted of a rapid exchange of web jerks. During interactions individuals would orient toward the other spider with the anterior legs nearly straight out. In no instance did one female move onto the capture surface of the other. The spider would, however, move into the barrier webbing within three to four cm of another before either retreated. Only four interchanges were observed in natural aggregates. All of these were initiated by the same individual in one four-member colony. That individual had a capture rate of 5.5 prey per hour, which was the lowest recorded for any colony member.

Experiment 1.—The prey activity around this six-member colony was 15.4 insects/h which was the highest measured. Between six and 28 prey items were removed from each web surface daily during the experimental period (Table 2). On the third day of removal,

Table 2.—Data for individuals involved in prey removal experiment (exp. 1) including: prey capture prior to manipulation, average number of prey removed during the ten day experimental period, the day on which that individual departed from the colony, and whether that spider returned in six days after removal procedures were stopped.

Spider	Initial Capture Rate/ spider/hour	Number of Prey Removed X̄ ± S. D.	Day Left	Return?
1	7.5	9.0 ± 0.0	3	no
2	8.0	9.3 ± 2.5	4	yes
3	8.5	14.0 ± 3.5	5	no
4	12.0	20.4 ± 4.6	8	yes
5	13.0	21.6 ± 7.4	>10	–
6	13.5	22.0 ± 5.4	>10	–

Nephila individuals began to relocate away from the group (Figure 1). There is a correlation between the amount of prey captured by a spider in a given position and the time at which it relocated (Kendall's Tau = 0.933, p < 0.05) (Table 2). On days nine and ten a total of eight aggressive interactions took place between the two remaining females in the complex. After prey removal attempts were terminated, three *Nephila* females joined the aggregation (Figure 1). Two of the three were former residents of the colony (Table 2). The third previously occupied a solitary web about 12 m away. The number of *Argyrodes* in the aggregate declined form 12 to six during the experimental period.

Experiment 2.—The natural activity of prey around the artificially created aggregate was relatively low at 3.9 insects/h. During the period in which prey were added to the webs no *Nephila* females left and one previously unidentified female joined the group (Figure 1). After supplementation ceased, spiders began to disperse out of the area (Figure 1). Three aggressive interactions were observed on day 11. The initiator of these encounters was absent from the complex on day 12. Two acts of aggression were observed on day 13 and followed with the departure of the intiator by day 14. No kleptoparasites colonized these webs during this experiment.

DISCUSSION

Web construction constitutes a large energy investment on the part of a spider (Ford 1977, Prestwich 1977). Therefore it is essential that the web provide the spider with a suitable return in the form of insect prey. Many spiders, including *N. clavipes,* appear to make decisions about relocating their web based on their prey consumption rates (Turnbull 1964, Gillespie 1981, Rypstra 1981). Thus, it is not surprising that clusters of *N. clavipes* females should be associated with patches of prey. Even with this small sample size, the prey distributions, capture rates, and aggression levels recorded for the Peruvian population support this contention. Further evidence is provided by the relatively rapid dispersal of group members when food consumption was experimentally lowered (Figure 1). Similar results were obtained for the colonial orb-weaver *Metapeira spinipes* (Araneae; Araneidae) in Mexico. Uetz et al. (1982) found both the number of individuals remaining in a colony as well as the nearest neighbor distances within the group related to prey availability.

Agonistic interactions between *N. clavipes* females appear to be related to their prey consumption rate and to precede departure form a colony. Aggression between conspecifics at low prey levels is a likely factor operating to break apart aggregates. The metabolic cost of interactions coupled with a marginal prey capture rate could hasten the need for web relocation of juxtaposed individuals. At high prey levels aggression was not observed, presumably because competition for prey is reduced. One hypothesized prerequisite for a complex social existence to evolve is consistently high prey levels. Interestingly enough most social spiders live in tropical regions which typically have higher overall insect abundances than do comparable habitats in the temperate zone (Janzen 1973, Janzen and Pond 1975).

It has been suggested that spider's silk is a preadaptation for the evolution of social behavior in arachnids (Shear 1970). The silk acts as a communication network that precludes the need for physical or even visual contact during information transfer. The reactions of *N. clavipes* females to conspecifics in their web is clearly distinct from their reaction to potential prey items. During such agonistic encounters genuine communication occurs via an exchange of signals (Krafft 1982). Discrimination of web signals is key

to the development of any more complex social structure (Krafft 1982). However, the precise structure of an orb web seems to set limits on the amount of communal behavior that can evolve in a species such as *N. clavipes* (Burgess and Witt 1976, Burgess and Uetz 1982). The vibratory information that is transmitted in the circular capture surface of the web is focused on a single central point where there is only room for one spider (Burgess and Witt 1976). For this reason gregarious orb-weavers are usually colonial, maintaining individual webs within a matrix of interconnected webs (Buskirk 1981, Burgess and Uetz 1982, Krafft 1982).

It was not the purpose of this paper to evaluate if *N. clavipes* reaps any advantages directly form group participation. There is no difference in web maintenance expenses or capture efficiency between solitary and communal webs evident in the data presented here. No predation attempts were observed. Farr (1977), working with a population of *N. clavipes* in Florida, concluded that clumping was a stochastic phenomenon influenced by population density and the availability of suitable web sites. My data do not negate that contention in so far as a suitable site is one with a high prey yield for the spider. Farr (1977) also cited two disadvantages to colony formation in this species; lowered feeding efficiency and increased direct competition for mates. Prey capture rates did vary among the positions in Peruvian colonies (Table 2), however, all webs in the complexes were more productive than solitary webs (Table 1). In addition, experiments suggest that high prey capture rates are essential for continued group existence. This study generated no data on the mating hierarchies that might exist within *N. clavipes* colonies. However in
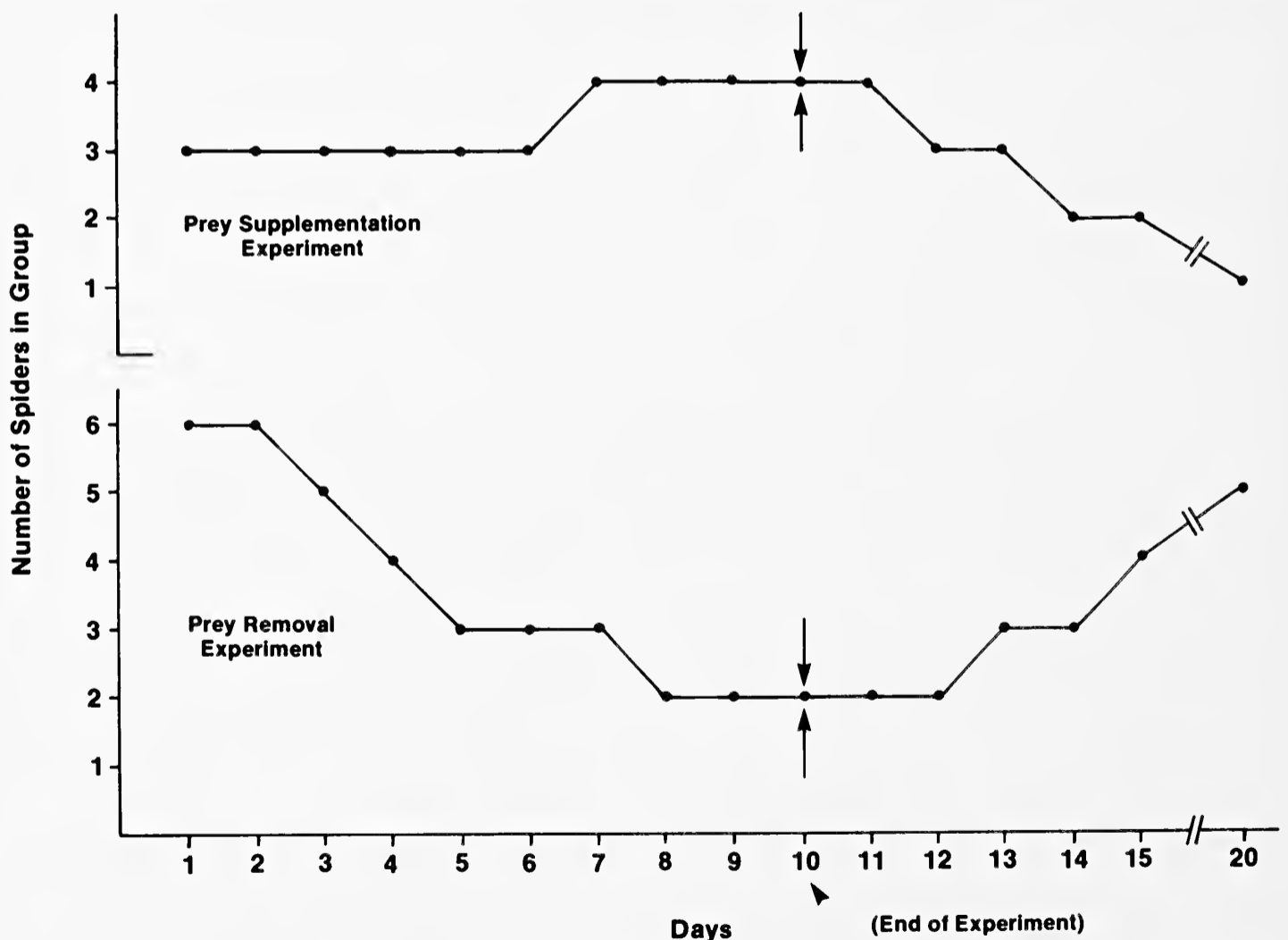
Fig. 1.—Number of *N. clavipes* in aggregations during experiments. In the prey removal experiment (bottom line) prey were removed from the webbing once a day for the first ten days. In the prey supplementation experiment (top line) 10-15 fruit flies were provided daily for each spider during the first ten days.

other studies of communal spiders, facilitation of sexual encounters was suggested as an advantage to group living (Lubin 1974, Valerio and Herrero 1977). The resolution of this question requires comparable data concerning the fitness of solitary females vs. the fitness of low-ranking females within an aggregation.

In a previous study on *N. clavipes,* the activity of kleptoparasites had a substantial affect on web site tenacity (Rypstra 1981). However in the few webs available for study here similar numbers of kleptoparasites occupy web complexes as live in single webs (Table 1). Based on that piece of information one would predict that aggregated individuals should loose fewer prey because the stealing events are spread over all of those in the group ("selfish herd effect" Hamilton 1971). No difference in prey losses to kleptoparasites by individual *Nephila* females were revealed between the two web situations (Table 1). Alternatively, if these few data reflect actual trends, kleptoparasites are experiencing significantly higher prey levels in *Nephila* aggregations (Table 1). The *Argyrodes* may be limiting their own density within webs in order to increase their food intake. My inability to alter *Argyrodes* densities in host webs made it difficult to test any of this more specifically.

Regardless of the actual position of *N. clavipes* in the evolutionary progression to spider sociality, the role of prey consumption in maintenance of aggregations in Peru has been established. The variability in spacing patterns that this species displays make it a valuable model system with which the situations that might allow for the appearance of more complex social interactions can be clarified.

ACKNOWLEDGMENTS

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GNAPHOSID SPIDERS OF NORTH-CENTRAL TEXAS
(ARANEAE, GNAPHOSIDAE)

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ABSTRACT

Thirty-two species representing 11 genera of Gnaphosidae are recorded from north-central Texas.
The study has extended the ranges of *Callilepis chisos* Platnick and Shadab, *Gnaphosa altudona*
Chamberlin, *Haplodrassus chamberlini* Platnick and Shadab, *Herpyllus hesperolus* Chamberlin, *Nodo-
cion rufithoracicus* Worley, *Rachodrassus captiosus* (Gertsch and Davis), and *Sergiolus angustus*
(Banks). Habitat and natural history data for species are presented.

INTRODUCTION

North-central Texas includes, as used here, Wilbarger, Wichita, Baylor, Archer, Clay,
and Montague counties. The eastern portion of the area is included in the Cross Timbers
and Prairies, whereas the western portion is within the Rolling Plains (Gould 1975). The
study area is included in the Texas and Kansan biotic provinces of Blair (1950).

Five araneid studies have confined themselves to the north-central Texas area. Carpen-
ter (1972) conducted a survey of the Salticidae of Wichita County; and Cokendolpher,
Horner, and Jennings (1979) reported on the Philodromidae and Thomisidae. Zaltsberg
(1977) and Salmon and Horner (1977) studied aerial movements of spiders in Wichita
Falls, and Matelski (1982) investigated *Peckhamia* (Salticidae). Other information on
spiders from this area appears as locality records in revisionary works or checklists. The
lack of information concerning gnaphosid spiders from this area prompted this study.
This paper describes the gnaphosid fauna of north-central Texas and presents natural
history data and range extensions for species.

METHODS AND MATERIALS

The collection of gnaphosid spiders at Midwestern State University was examined,
checked for proper taxonomy and habitat, and locality records recorded. Intensive field
work was conducted in Wichita County from July 1981 to September 1982. The primary
method of collection was overturning ground cover. Large to small stones, logs, card-
board, lumber, sheet metal, and cow manure all harbored gnaphosids. Fallen bark, leaves,

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and other ground litter were placed in a sifter with a 1 cm mesh screen and shaken over a white cloth. Any spiders present were easily seen and captured in snap-top plastic vials. A sweep net was employed where the vegetation permitted. The outer bark of trees was stripped away with a metal probe and examined for gnaphosids. Twenty-one pitfall traps were employed in Wichita County. Each trap consisted of a 1500 ml can dug flush into the ground and filled 2/3 full with a 1:1 mixture of water and ethylene glycol.The trapping periods were July 12-19, August 9-16, September 13-20, and October 11-18, 1981. At the end of each trapping period the traps were removed from the ground and the contents poured through a fine-meshed strainer and sorted. This method was abandoned when only three adult gnaphosids were collected.

Immature specimens were reared to maturity in the laboratory. Rearing chambers were made of glass or plastic tubes measuring 1 x 9, 2 x 10, or 3.5 x 10 cm. Spiders were offered food three times a week, principally termites and adult fruit flies (*Drosophila melanogaster* Meigen). Cotton stoppers were wetted once a week for five weeks but the spiders shunned the moist sides of their tubes and were not observed drinking. The practice was discontinued with no ill effects. Each tube contained a strip of heavy paper to provide cover and a molting surface. The tubes were cleaned after each molt and as prey debris accumulated.

Adult spiders collected in the field and those matured in the laboratory were killed and preserved in 70% ethanol and have been added to the Department of Biology Invertebrate Collection at Midwestern State University.

RESULTS AND DISCUSSION

Suitable ground cover seemed to be a major requirement for gnaphosids in this region. Localities with abundant cover often harbored 10 or more species within a small area. Notable exceptions were areas with sandy soil; these yielded very few spiders even if ground cover was present. The majority of the adult and penultimate specimens were collected from February to May, after which the variety and number of species declined significantly.

The accounts that follow include natural history data such as behavior, habitat, and egg sac contents.

(1) *Callilepis chisos* Platnick.—Two females were collected in May and September; one was found indoors and the other in bark debris along a small lake. These specimens, from Wichita County, extend the known range approximately 300 miles eastward from San Miguel County, New Mexico (Platnick 1975).

(2) *Cesonia sincera* Gertsch and Mulaik.—Eight of the nine specimens collected were found under rocks along the margins of two reservoirs and a pond. Similar habitat a few hundred yards from the collection sites yielded no additional specimens. Seven of the nine spiders were immature and were reared to adults in the laboratory. Two immature males collected on 26 March matured in 11 and 14 days. The five immature males collected in late March and April reached maturity between 25 April and 1 July.

(3) *Drassodes gosiutus* Chamberlin.—Only females were collected, mostly in March. Of the 16 specimens, 14 were found under rocks in broken country. Twelve of the spiders were guarding single egg sacs within their hibernacula. The hibernacula consisted of silken tubes stretched across the undersides of rocks, or of silk-lined burrows extending straight down into the ground. The female would not leave her hibernaculum until it was broken open; she would then seize the egg sac in her chelicerae and attempt to drag or push it to

safety. The 12 egg sacs contained 60, 63, 82, 83, 95, 98, 105, 105, 106, 116, and 147 eggs; one egg sac held 101 deutova. A mature female collected 26 March deposited an egg sac on 11 April. She carried the sac in her chelicerae but dropped it on 12 April to feed. Three days later she opened the egg sac and scattered the eggs. Although Platnick and Shadab (1976a) state that mature males may be found from late June to late December, none were collected by us.

(4)   *Drassodes saccatus* (Emerton).–This species was more common than *Drassodes gosiutus*. All 65 specimens were found under some type of ground cover, usually stones. Gertsch (1979) states that the males of some species of *Drassodes* enclose immature females in hibernacula adjacent to their own. Thirteen males were found sharing hibernacula with females. Of these, 12 mature males were found cohabiting with penultimate females and one mature male was found in a hibernaculum with a mature female. The hibernacula varied from a sac just large enough to enclose the two spiders to silken tubes 12 cm or longer. The spiders would usually exit from opposite ends of their retreat when disturbed. Most of the specimens were collected between 18 March and 13 April. All the males found during this period were mature. Six penultimate females molted between 1 April and 22 April. A female caught on 19 May had an egg sac which contained 111 first instar spiderlings.

(5)   *Drassyllus aprilinus* (Banks).–Platnick and Shadab (1982) list this species from Montague and Wichita counties and state that mature spiders have been collected year-round. The species was not encountered in this study.

(6)   *Drassyllus dromeus* Chamberlin.–This spider does not appear to favor a particular habitat. Sixteen specimens were found from March to June under rocks, boards, bricks, sheet metal and willow tree bark; indoors, and by sweeping grass. Two penultimate females collected 18 March and 16 April molted 21 March and 24 April.

(7)   *Drassyllus lepidus* (Banks).–This was the most common *Drassyllus* collected. Twenty-seven specimens were found from May to October under rocks, concrete, boards, sheet metal, and indoors. Eight immatures (seven males and one female) collected in April reached maturity by 30 May. An immature female collected on 30 October molted by 27 November and to an adult on 24 December.

(8)   *Drassyllus notonus* Chamberlin.–Three females and one male were collected from May to June. One of the females was found under a stone, another under a board and the third indoors on a garage floor. The male was collected in June by sweeping vegetation.

(9)   *Drassyllus orgilus* Chamberlin.–Nine female specimens were collected in Wichita and Clay counties during February and March. Spiders were found under rocks and boards, in grass and other vegetation, and indoors.

(10)   *Drassyllus texamans* Chamberlin.–Four specimens were taken from collection sites in Wichita County on the sandy terraces along the Red River. This species seems to prefer loose, sandy soil. A female from Hardeman County was found on the silty floor of a cave (Platnick and Shadab 1982). A penultimate male collected on 20 May molted after five days.

(11)   *Drassyllus* species.–A single unidentified male *Drassyllus* was found under a stone in a pasture in Wichita County. Return trips to the same locality failed to yield additional specimens. This may be a species of which only the female has been described.

(12)   *Gnaphosa altudona* Chamberlin.–Five of the six specimens collected were males found under stones. All the spiders were found during June and July in rough, eroded country dominated by stones and bare ground. A female collected on 15 July had an egg sac which contained 27 first instar spiderlings. Two immature males reared in the

laboratory reached maturity on 2 and 16 August. The present record extends the range approximately 400 miles north from Brewster, Presidio, and San Patricio counties of Texas (Platnick and Shadab 1975a).

(13) *Gnaphosa clara* (Keyserling).—A single female collected on 10 June was found with two egg sacs. The first sac had already been vacated and contained only exuviae where as the second sac held 59 eggs.

(14) *Gnaphosa fontinalis* Keyserling.—Two specimens were collected in Wichita County on 6 May. No specific habitat data were recorded.

(15) *Gnaphosa sericata* (L. Koch).—The four specimens collected were found in areas with sandy soil and little available ground cover, a niche that other gnaphosids seemed to avoid. Spiders were taken from under small bits of wood, cow manure, and in a pitfall trap. Of two immature females caught on 20 May, one molted to maturity on 8 June and the second molted on 13 June (penultimate) and 24 July.

(16) *Haplodrassus chamberlini* Platnick and Shadab.—Twenty individuals were found from March to May, eighteen under stones in grassy pastures and rough, eroded areas. Six penultimate spiders (four females and two males) collected on 16 March all molted to adults by 27 March. This is a new state record for this species: the closest previous records are Roosevelt County, New Mexico, and Texas County, Oklahoma (Platnick and Shadab 1975b). Its presence in north-central Texas extends the range 270 miles to the southeast.

(17) *Haplodrassus signifier* (C. L. Koch).—Forty-one specimens were found from March to June, most of them under stones. Three females were collected on 19 May, each protecting one large and one small egg sac. The large sacs were drab and dirty while the small sacs were obviously newer because they were whiter. Each female, when exposed, tried to move the large egg sac to safety by carrying it in her chelicerae. The large sac of one female contained 232 second instar spiders and the small sac had 50 first instar spiderlings. The egg sacs of the second female held 94 first instar spiders and 24 eggs. The sacs of the third female contained 160 second instar spider and 26 first instar spiderlings. Three penultimate spiders molted on 21 February (female), 21 March (male), and 24 March (female). A late instar spider, probably *H. signifer*, was parasitized by the acrocerid fly *Ogcodes eugonatus* Loew. The larva ruptured the abdomen of the spider, pupated on 18 April, and the adult female emerged on 29 April.

(18) *Herpyllus bubulcus* Chamberlin.—A single female was collected on 3 March from a rock pile in Hardeman County by an araneology student.

(19) *Herpyllus ecclesiasticus* Hentz.—This widespread species is opportunistic as to habitat. Fourteen specimens collected from February to August were found indoors, under tree bark, on trees, and in grass. A penultimate female found 11 July molted on 3 August.

(20) *Herpyllus hesperolus* Chamberlin.—Two females were collected on 20 March along a rocky, eroded hillside. This discovery extends the range approximately 400 miles east of a line from Pecos County, Texas, to the Big Meddy Valley in Saskatchewan (Platnick and Shadab 1977).

(21) *Micaria.—Micaria* is present in the area. This genus is currently under revision and is not dealt with within this paper.

(22) *Nodocion floridanus* (Banks).—Only four specimens have been recorded from this area. The single specimen examined was a male collected from a wasp nest in Wichita County. Records indicate another male from Wichita County was found under tree bark and two males were found in a tamarisk bower in Baylor County (Platnick and Shadab 1980a).

(23) *Nodocion rufithoracicus* Worley.—Eight spiders (4 males and 4 females) were found from March to August in Wichita County under rocks in broken eroded country. A penultimate male collected on 18 March molted on 23 March. This material extends the range 320 miles east of a line extending from Eddy County, New Mexico, to Divide County, North Dakota (Platnick and Shadab 1980a).

(24) *Rachodrassus captiosus* (Gertsch and Davis).—A single male was found in June under a piece of railroad tie at the base of a high bluff. Previous specimens are known only from San Luis Potosi, Mexico, and Cameron and San Patricio counties of the south Texas coast. This is a range extension of over 400 miles to the north.

(25) *Sergiolus angustus* (Banks).—A single female was collected along a rocky hillside in March. The only other Texas record for the species is Kleberg County on the coast of south Texas. This is a range extension of approximately 100 miles east of a line from northern Colorado to Kleberg County, Texas (Platnick and Shadab 1981).

(26) *Sergiolus bicolor* Banks.—Two males collected in June were found, one under a stone and the other indoors.

(27) *Sergiolus lowelli* Chamberlin and Woodbury.—This form is found throughout the area and is variable in habitat. Nine specimens were collected from March to October in grass, indoors, from a bird's nest, a tamarisk bower, and a tarpaulin.

(28) *Sergiolus stella* Chamberlin.—A female was collected on 19 May along a stony, eroded hillside. The spider molted on 2 June and 28 June. The record extends the range 100 miles west northwestward from Denton County, Texas (Platnick and Shadab 1981).

(29) *Zelotes aiken* Platnick and Shadab.—Four specimens were taken during March and April from Clay, Montague, and Wichita counties. The spiders were found along a lake shore, under rocks, and in Bermuda grass. A penultimate male caught 31 March molted that day.

(30) *Zelotes anglo* Gertsch and Riechert.—A single male was found in Wichita County and Platnick and Shadab (1983) record a male from Wilbarger County. The Wichita County specimen was taken in September from a pitfall trap set in an open pasture.

(31) *Zelotes gertschi* Platnick and Shadab.—This was the most common *Zelotes* detected. Forty specimens were collected from Archer, Clay, and Wichita counties, mostly between March and July under stones, boards, railroad ties, and cardboard. Eighteen laboratory reared spiders molted one to four times between 24 March and 4 August. Six were males and all had matured by 13 June, with most maturing in April. The maturity dates of the females were much later: two matured in April, six in May, two in June, one in July and one in August.

(32) *Zelotes pseustes* Chamberlin.—Two males (collected 10 January and 28 February) and two females (collected 24 April and 16 August) were found under a rock and a board, in dead leaves, and in a pitfall trap set in sand.

(33) *Zelotes tuobus* Chamberlin.—A single male was taken on 28 April, 1975, from under a rock in Wichita County.

(34) Addendum.—Dr. Norman Platnick has recently (personal communication March 30, 1984) identified two European species that were collected from north-central Texas. Two males of *Urozelotes rusticus* (Koch L.) were collected in homes in Wichita County in June 1976 and May 1977. A single female of *Trachyzelotes lyonneti* (Audouin) was collected in May 1975 from the ground in Baylor Co.

In addition to the confirmed gnaphosid fauna, based on records from surrounding counties, range maps, and habitat data, an additional two genera and nine species are

believed to occur in north-central Texas. *Callilepis imbecilla* (Keyserling) is present in Comanche County, Oklahoma, and has been found under leaf litter and boards (Platnick 1975) and under stones in pastures and dry, sandy areas (Kaston 1981). *Cesonia bilineata* (Hentz) ranges from New Mexico to the Atlantic coast and has been collected in open and tall grass prairies, mesquite woods, and Bermuda grass (Platnick and Shadab 1980b). *Drassodes auriculoides* Barrows is known from Comanche County, Oklahoma. Platnick and Shadab (1976a) list leaf litter and a pasture as habitats and Kaston (1981) reports this species can be found under stones and logs. *Rachodrassus exlineae* Platnick and Shadab (female) is known from Comanche County, Oklahoma. *Sergiolus montanus* (Emerton) is found across the contiguous states and has been collected from under rocks, bark, dry cow dung, and indoors (Platnick and Shadab 1981). *Sosticus insularis* (Banks) is known from Comanche County, Oklahoma, and Dallas County, Texas, and has been found under bark and indoors (Platnick and Shadab 1976b). *Synaphosus syntheticus* (Chamberlin) has been recorded from Dallas County, Texas; it has been found indoors and in salt cedar, cottonwood, and mesquite litter (Platnick and Shadab 1980a). *Zelotes hentzi* Barrows ranges across the United States except for the Southwest and has been collected from under rocks, boards, logs, and in cottonwoods, cotton fields, pecan groves, prairies, and meadows (Platnick and Shadab 1983). *Zelotes lasalanus* Chamberlin is present in Tarrant County, Texas, and has been found under debris, dung, and stones, and in grass, mesquite, meadows, and prairies (Platnick and Shadab 1983).

Of the 32 species that have been reported from north-central Texas, 16 are represented by four or less specimens taken in 14 months of intensive collecting. Further collecting may be expected to produce additional species records and natural history data.

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THE NATURAL HISTORY AND TAXONOMY OF
CICURINA BRYANTAE EXLINE (ARANEAE, AGELENIDAE)

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ABSTRACT

Since its description in 1936 *Cicurina bryantae* Exline has been rarely collected. The recent discovery of the microhabitat preference of this spider has allowed the observation and collection of substantial numbers of specimens. The following account is compiled from these data. The natural history of the species is discussed (including the interesting tubular retreat constructs inhabited by immatures and adults). Both sexes are described and figured (the male for the first time).

INTRODUCTION

In 1936 Harriet Exline described a new species in the genus *Cicurina* Menge, 1869 on the basis of female specimens collected at Newfound Gap on the Tennessee-North Carolina border in 1930 by Nathan Banks. She named the species *bryantae* in honor of Elizabeth Bangs Bryant who was at that time working at the Museum of Comparative Zoology where the specimens were deposited. Since that date, *Cicurina bryantae* has rarely been collected, its behavior and life history have not been recorded, and the male has not been described.

Chamberlin and Ivie (1940) redescribed the female and mentioned two more females captured by Ivie in 1933 in East Tennessee. Apparently no other specimens were collected until 1972 when J. O. Howell found an undescribed *Cicurina* male in a pitfall trap set in Union County, Georgia. Vincent Roth tentatively identified it as the male of *C. bryantae* but no effort was made to describe it at that time as no other males were found (Howell 1972, pers. comm.).

During the late fall of 1982 I began finding populations of *C. bryantae* living within a fairly specific microhabitat in and around Jackson County, North Carolina. From then until January 1984 substantial numbers of males, females and immatures were observed and collected. The resultant data are presented in this paper; both sexes are described and figured (the male for the first time) and a general account is given of the life history. Specimens collected during this study have been deposited in the American Museum of Natural History (AMNH), Dr. N. I. Platnick; the Museum of Comparative Zoology (MCZ), Dr. H. W. Levi; the Canadian National Collection of Insects, Arachnids and Nematodes (CNC), Dr. C. D. Dondale; and the Florida State Collection of Arthropods (FSCA), Dr. G. B. Edwards; and in my private collection (RGB).

Since my acquaintance with some agelenid taxa is limited, I have here conservatively retained the classical placement of *Cicurina* within the Agelenidae. However, I do believe that the Agelenidae as it is usually envisioned is probably a polyphyletic assemblage and tentatively concur with Lehtinen's transfer of *Cicurina* to the Dictynidae: Cicurininae (1967:222-223) as catalogued recently by Brignoli (1983:518).

NATURAL HISTORY

Specimens of *C. bryantae* have been collected at elevations of 300-1350 meters (1000 to 4400 ft.) above sea level in the Blue Ridge and Great Smoky Mountain regions of the Southern Appalachians (Fig. 6). The true southern and south lateral boundaries of its range probably correspond closely to the southerly collection locales. The more northerly limits of its range are not known because of a lack of collection data from northwestern North Carolina and adjacent areas of Tennessee. It is possible that this spider ranges well into the Appalachians of Virginia.

Populations are most common in mixed deciduous forests (dominated by oak, hickory and tulip poplar) and are encountered less frequently in deciduous woods mixed with conifers such as white pine and hemlock. Within a suitable wooded habitat *C. bryantae* is usually found within retreats constructed on the undersurface of rotting wood well settled in the leaf litter of the forest floor. Retreats are never found on substrates other than rotting wood. Gryllacridid crickets, cryptocercid roaches and large numbers of collembolans as well as spiders of the genera *Antrodiaetus, Calymmaria, Coras, Wadotes, Liocranoides* and other species of *Cicurina* commonly occupy the same microhabitat as *C. bryantae*. Unidentified pseudoscorpions have been collected from otherwise empty retreats.

Eugène Simon (1898:265) observed that *Cicurina cicurea* (Fabricius) "file une toile très légère et horizontale, sous les pierres ou au milieu des mousses. . ." (Spins a very slight and horizontal web, beneath stones or within mosses. . .). Exline (1936) reported that the delicate webs of *Cicurina* species can be found in rotting logs or under rocks or boards and that no retreat is built. Although the observations of Simon and Exline may apply to most species of *Cicurina, C. bryantae* is an exception; it builds no fine horizontal sheet web but does construct an interesting retreat (Figs. 7, 8).

The retreats are built in natural cavities on suitable wood surfaces or wherever there is sufficient space between the wood and the ground. The retreat is a tube with twin, often turret-like openings at either end. The tube consists of very fine and delicate silk coated on the outside with organic debris derived from the rotting substrate or the ground beneath. The wooden substrate forms the ceiling of the retreat and is covered only lightly with silk. The openings normally point downwards and are never closed by the spider as are the similar appearing (although normally larger) entrances to the subterranean burrows of *Antrodiaetus* spiders (see Coyle 1971). The turrets are often connected to the surrounding substrate with short silk threads which may possibly function as trip wires to aid in the detection of prey.

Males, females and immatures build retreats similar in all respects except size, although male retreats occasionally exhibit a slight but pronounced lateral widening between the twin openings. Adults of both sexes occupy retreats measuring 12 to 15 mm between the inner edges of the openings (Fig. 8). Immatures build retreats (Fig. 7) ranging from about 2 mm in length (as measured above) to adult size. It is not known whether immatures

expand their retreats as they grow or simply move out and construct new larger retreats. A number of adult and immature-sized retreats can often be found in close proximity.

In an effort to observe aspects of their behavior I placed five females in an observation chamber containing a piece of rotting wood. Five others were placed in a similar chamber with a clean, unrotted piece of wood. The atmosphere was kept humid and there were ample suitable sites for retreat construction in both chambers. Overnight, spiders in the first group all built retreats on the undersurface or sides of the rotting wood. These retreats seemed quite typical although they lacked turrets and were rather sparsely coated with debris. Over a period of weeks these spiders successfully maintained themselves on a diet of cricket nymphs. The spiders of the second group built no retreats or obvious webbing of any kind and did not feed on the cricket nymphs which were introduced into the chamber. It seems evident from this that the presence of a suitable substrate and/or debris particles is a necessary prerequisite to normal retreat construction and prey capture.

Cicurina bryantae retreats are remarkably similar to those built by several species of Japanese cavernicolous cybaeinine agelenids (Komatsu 1961). Komatsu describes the cybaeinine retreats as being pipe-like in construction and usually coated with sand grains. The openings lie at the extreme ends of the tubes rather than at right angles to the tube axis, as do the entrances to the retreats of *C. bryantae.* From each opening a pair of long silk tripwires extends to the surrounding substrate. Some retreats may have as many as three openings. The retreats are encountered in open locations within caves but insofar as these areas are dark and of relatively constant humidity, they resemble the dwelling sites of *C. bryantae.*

Immatures and adult females of *C. bryantae* can be collected year round, but adult males have been collected only from late August to late January suggesting that mating occurs in the fall. Additional support for this idea is the observation that females collected during the fall, winter and early spring often have one or both passages leading from the copulatory opening blocked with what is apparently a copulatory plug of unknown composition.

Females begin producing egg cases in late spring (May). These flattened lenticular structures are composed of two silken half shells and are attached to the inner surface of the ventral-most wall of the retreat. Cases typically are filled with from three to ten eggs, each roughly spherical and approximately 0.9 mm in diameter. As the summer progresses additional egg cases are constructed and attached to any already present. Normally each succeeding egg case will have fewer eggs than its predecessor. One retreat, examined in early October 1983, contained nine egg cases in a stratified lump coated with substrate debris. Eggs in five of these had already hatched and the spiderlings had dispersed. Two contained small numbers of spider nymphs and two were parasitized. No eggs were present in any of these cases. Out of a total of 43 egg cases examined during 1983, four were parasitized. In each of these four cases a single ichneumon wasp pupa (*Gelis* sp.) was found.

Dispersal of the immatures from the maternal retreat commences during the summer. Since very small retreats are commonly found in late summer clustered near the retreats of adults, it is likely that most spiderlings simply leave the mother's retreat and build their own retreats at the first suitable location they come upon. Often these immature constructs will be built upon the surface of the presumed parental retreat (which may or may not be occupied).

Observations made over 16 months of study of *C. bryantae* populations suggest that there may be a two year or longer life cycle involved. Maturation may occur when the spiders are one year old (teneral adults have been collected regularly and only in the late summer and early fall) but there is a strong possibility that the immatures take more than one year to reach maturity as a wide range of sizes of immature retreats may be observed at any one point in time.

That a female may pass more than one winter as an adult is intimated by the collection in the early spring of 1983 of a female from a retreat containing three empty egg cases. This capture was made at a high altitude (1350 m) and sometime before any new egg cases for that year had been observed. The presence of a plug in only one of the two copulatory tubes of some females collected with egg cases suggests that if females are capable of surviving to a second breeding season, they may be able to mate again successfully.

TAXONOMY

Methods.—All measurements and counts were made with a Leitz stereomicroscope fitted with 10x eyepieces and a micrometer reticle. Measurements are accurate to 0.025 mm. Abbreviations are as follows: CL, carapace length; CW, carapace width; SL, sternum length; SW, sternum width; ALE, anterior lateral eyes; AME, anterior median eyes; PLE, posterior lateral eyes; PME, posterior median eyes; MOQ, median ocular quadrangle. Statistics are presented as follows: sample range (mean ± standard deviation). All measurements are in millimeters.

Macroseta counts for all legs are presented either literally or through the use of a standard macroseta formula where for a particular face of a leg segment a series of three numbers separated by hyphens represents the number of macrosetae on the proximal, medial, and distal portions respectively.

A 10x10 squared grid reticle and 16x Zeiss wide field eyepieces were used with the Leitz stereomicroscope to make drawings. Male palps were examined and drawn whole in 80% ethanol. Epigyna were treated likewise and also dissected out of the abdomen and cleared in clove oil or hot 10% KOH for study and drawing internal sclerotized characters.

Cicurina bryantae Exline
Figs. 1-11

Cicurina bryantae Exline 1936:13, figs. 4, 14 [female holotype from Newfound Gap on the Tennessee (Sevier County)-North Carolina (Swain County) border, 9 July 1933 (W. Ivie), in MCZ, examined]; Chamberlin and Ivie 1940:25, fig. 12; Bonnet 1956:1087.

Diagnosis.—Specimens of *C. bryantae* can be separated from the morphologically similar species *Cicurina pallida* Keyserling and *Cicurina breviaria* Bishop and Crosby, and from all other species of *Cicurina,* by the following series of characters: abdomen and cephalothorax unmarked; copulatory tubes smoothly curving to slightly sinuous and leading to undivided spermathecae (Figs. 3-5); embolus short and thick, terminating bluntly on distal end of short conductor; conductor with small retrolateral accessory projection originating from base of hook (Figs. 1, 2); distal retrolateral tibial apophysis short, shallowly bifurcate distally and slightly cupped dorsally.

Description.—Small to medium size spiders. Sexes similar morphologically except for sexual characteristics; males slightly larger than females. Cephalothorax and legs uniform light reddish brown (darkening with age), with dark longitudinal streak demarking position of thoracic groove. Carapace glabrous except for a few lines of sparse setae radiating from thoracic groove primarily towards and around eye region. Abdomen light colored, unmarked and lightly clothed with short setae. Chelicerae robust, each with single strong macroseta dorsally on prolateral face (Fig. 9). Retromargin of cheliceral fang furrow with 3 or 4 teeth and 2 to 5 denticles; promargin with 3 or occasionally 2 teeth. Sternum approximately as wide as long, roughly heart-shaped, with short projection extending between hind coxae. Colulus indicated by 2 to 4 setae. Spinnerets closely grouped, with
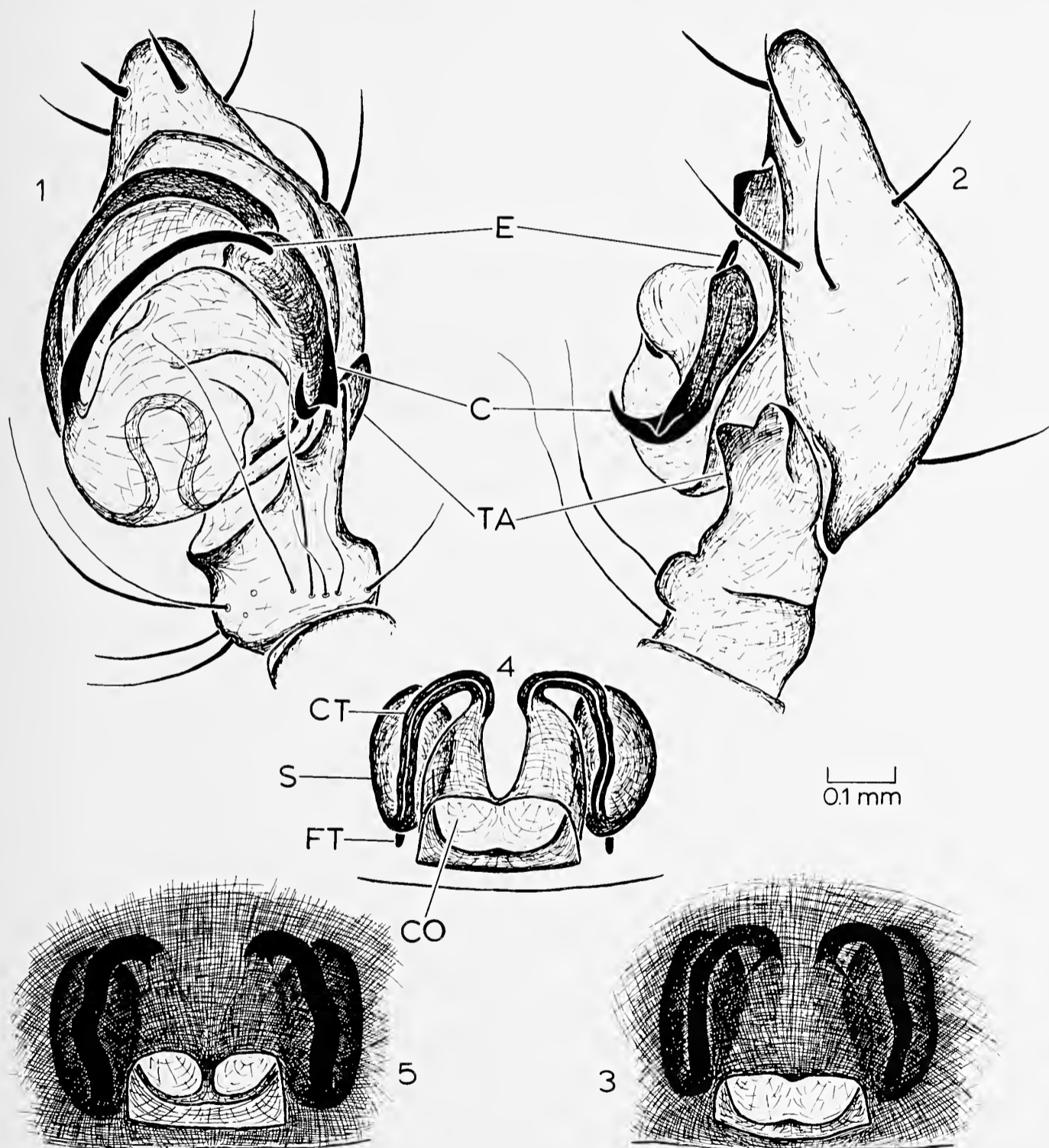
Figs. 1-5.—Genitalia of *Cicurina bryantae* Exline; 1, left palpal tibia and tarsus of male, ventral view, specimen from Cane Creek, Cullowhee; 2, same, retrolateral view; 3, epigynum, ventral view, specimen from Cane Creek, Cullowhee; 4, same cleared to show internal sclerotization; 5, variation of epigynum, ventral view, specimen from Cataloochee Valley. Abbreviations: C, conductor; E, embolus; TA, tibial apophysis; CO, copulatory opening; CT, copulatory tube; S, spermatheca; FT, fertilization tube.

median pair smallest; anterior pair close together and relatively stout; posterior pair
longer, thinner and more widely spaced than anterior spinnerets. AME alone dark, others
light (Fig. 9). AME smallest, slightly smaller than PME. PLE largest but only slightly
larger than ALE. MOQ wider behind and slightly higher than wide. Height of MOQ about
1.5 times height of clypeus. Legs with numerous macrosetae. All femora with 3 macro-
setae dorsally along midline, with a pair of lateral macrosetae bracketing the terminal
dorsal macroseta except for femur I which normally bears a retrolateral pair of offset
macrosetae distally. Ventrally on all femora a double row of relatively small thin macro-
setae, ventral retrolateral row heavier than ventral prolateral row, and macrosetae decreas-
ing in size to status of setae from femur I to femur IV. Macrosetation of tibia I and
metatarsus I complicated and somewhat variable (Figs. 10-11). Tibia I normally with row
of 5 macrosetae originating on ventral prolateral surface and terminating prolaterally; two
other macrosetae along ventral retrolateral surface and a pair of small macrosetae distally
on ventral surface; one additional macroseta prolaterally above second and third ventral
prolateral macrosetae; dorsally one small macroseta near proximal end. Ventral surface of
metatarsus I with similar macroseta pattern but three macrosetae each on prolateral,
ventral prolateral and ventral retrolateral surfaces. Tibia II 2-2-2 ventrally, with distal pair
of macrosetae and ventral prolaterals reduced; prolaterally two strong macrosetae; two
weak macrosetae dorsally. Metatarsus II 2-2-3 ventrally and 3 macrosetae along prolateral
surface. Tibia III 2-2-2 or 1-2-2 ventrally, and two macrosetae each on prolateral, retro-
lateral and dorsal surfaces. Metatarsus III 2-2-3 ventrally, one macroseta each on pro-
lateral and retrolateral faces and 2-2-2 dorsally with the median pair staggered. Tibia IV
normally 1-2-2 ventrally, otherwise similar to tibia III. Metatarsus IV 2-2-1 ventrally, with
2 macrosetae on retrolateral surface and 2-2-2 dorsally. Metatarsal and tarsal trichobo-
thria patterns typical, arranged in single longitudinal row dorsally and increasing in
length distally along both segments on each leg. Tarsi and metatarsi each with 4 or 5
trichobothria; metatarsi II and III often with 4 and metatarsi I and IV with 5. Legs
arranged in order of decreasing length: IV-I-II-III.
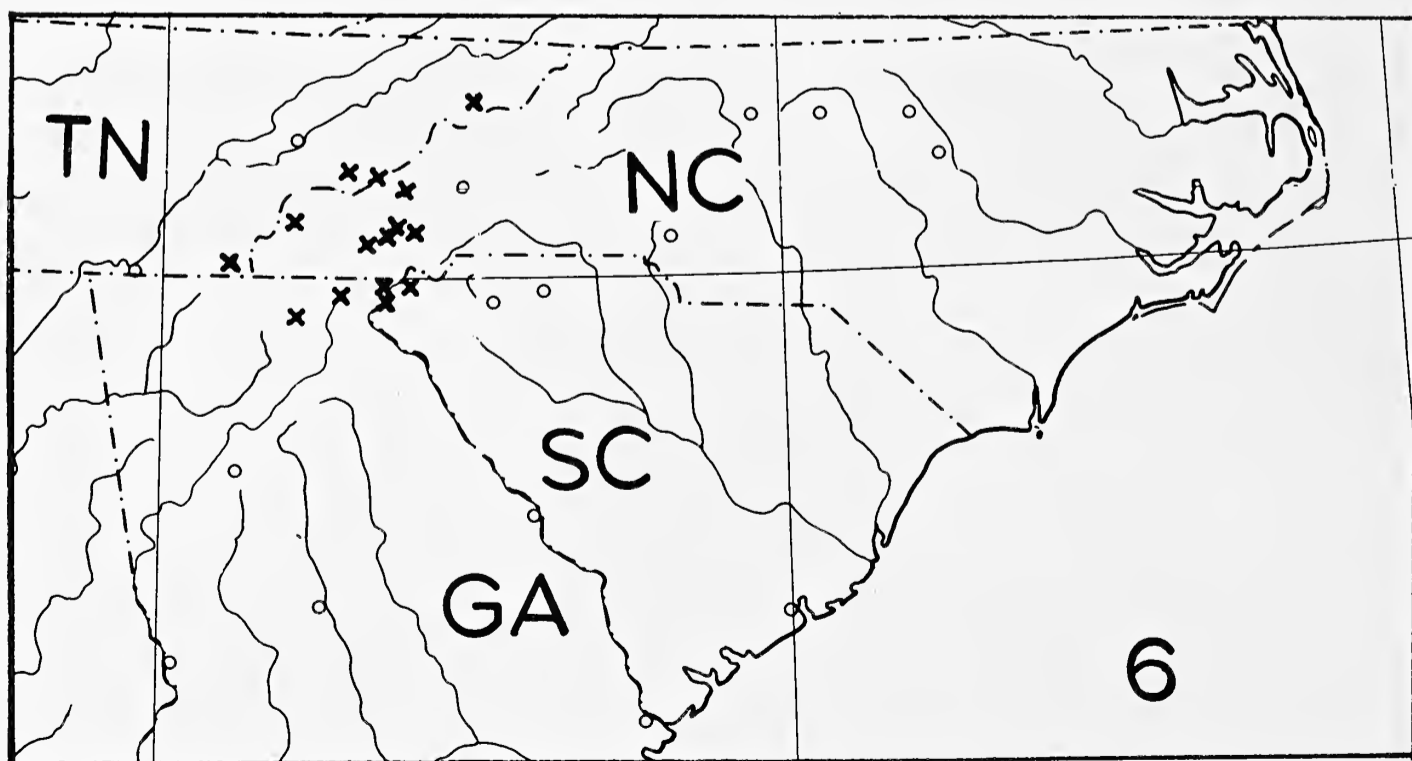
Fig. 6.—Known geographic distribution of *C. bryantae.*

Figs. 7-8.—Retreats of *C. bryantae*, specimens from Cullowhee: 7, retreats of immature specimens, both approximately 5 mm between inner edges of entrances. Lower entrance of right hand burrow blurred due to momentary presence of occupant in entrance during time exposure; 8, retreat, 12 mm between inner edges of entrances, with mature female at one entrance.
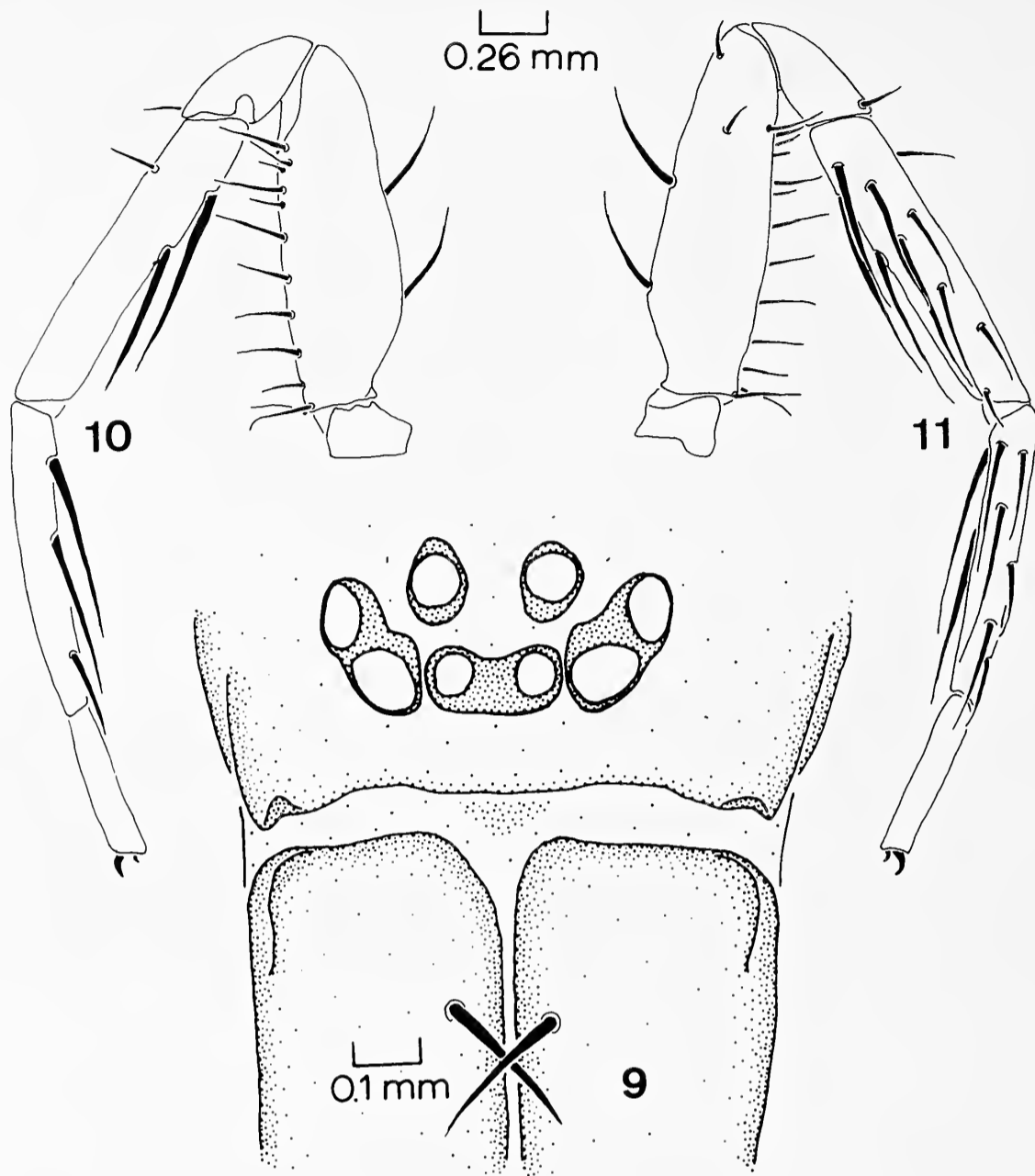
Fig. 9—Frontal view of eyes and cheliceral bases of *C. bryantae.*
Figs. 10-11.—Left leg I of male, 10, retrolateral aspect; 11, prolateral aspect.

Male: Figs. 1, 2. 26 specimens measured. CL 1.78-2.45 (2.09 ± 0.16), CW 1.38-1.73 (1.57 ± 0.11), SL 0.88-1.1 (0.99 ± 0.06), SW 0.85-1.08 (0.96 ± 0.06). Palpus very simple in comparison to most *Cicurina* males. Cymbium short and stubby. Terminal conductor hook short and smoothly curved ventrally. Other characters as in diagnosis.

Female: Figs. 3-5. 30 specimens measured. CL 1.73-2.35 (2.06 ±0.17), CW 1.25-1.63 (1.45 ± 0.12), SL 0.8-1.08 (0.97 ± 0.07), SW 0.83-1.03 (0.92 ± 0.07). Epigynum very simple. Copulatory opening usually appearing single and dividing into two funnel shaped bursae just inside opening (Figs. 3, 4). In some specimens, particularly those from the Cataloochee Valley, Haywood County, North Carolina, the copulatory opening itself appears to be divided (Fig. 5). This is because the internal division into the pair of bursae is more ventrally placed within the mouth of the copulatory opening. (No concommitant variation has been detected in males from the Cataloochee Valley.) A single, short sclerotized fertilization tube exits each spermatheca dorsocaudally and proceeds for a short distance anteriorly and dorsally in a tight arch before sclerotization becomes weak and tubes become invisible. Copulatory tubes thick-walled with a thin canal visible within. Other characters as in diagnosis.

Specimens examined.–(Collected by author unless otherwise noted.) U.S.A.: GEORGIA; *Rabun County,* W of Chatooga R. on Highway 708, 11 January 1984, 1 male, 1 female (FSCA), intersec. of St. Rds. 76 and 197, 12 miles W of Clayton (2160 ft.), 12 January 1984, 3 males, 8 females, 4 immatures (AMNH); *Union County,* Vogel St. Pk. (2750 ft.), 17 January 1972 (J. O. Howell), 1 male (JOH), south end of Vogel St. Pk. (2300 ft.), 12 January 1984, 4 immatures (FSCA); *White County,* Unicoi St. Pk., Ana Ruby Falls (1800 ft.), 12 January 1984, 2 females (FSCA). NORTH CAROLINA: *Graham County,* Stratton Meadows (4400 ft.), 4 April 1983, 5 females, 5 immatures (MCZ); *Haywood County,* Pinnacle Ridge, Blue Ridge Parkway (4400 ft.), 31 May 1983, 1 female (AMNH), Great Smoky Mtn. Nat. Pk., Cataloochee Valley (2700-3200 ft.), 7-9 October 1983, Caldwell Fork, 1 male (MCZ), near Caldwell House, 2 males, 1 female (AMNH), above Rough Fork, 2 males, 7 females (FSCA), above Beech Grove school, 4 males, 6 females (RGB), Hannah Cabin, 2 males, 4 females (MCZ), near Palmer Cemetery, 1 male, 4 females (AMNH); *Jackson County,* N slope Little Panther Knob, Long Branch Rd., Cullowhee (2600 ft.), 5 November 1982, 1 male, 9 females, 16 immatures (AMNH), 17 May 1983, 3 females, 3 immatures (AMNH), Cane Creek Valley, Cullowhee (2200-3200 ft.), 7 November 1982, 2 males, 11 females, 9 immatures (MCZ), 31 December 1982, 1 female (RGB), 15 March 1983, 3 females (RGB), 16 June 1983, 5 females, 3 immatures (RGB), 25 August 1983, 4 females, 1 immature male, 1 immature (AMNH), 5 September 1983, 1 female (MCZ), 13 September 1983, 4 males, 10 females, 2 immatures (MCZ), 30 September 1983, 2 females (FSCA), 19 October 1983, 5 males, 8 females (RGB), Owens Gap, intersec. of Co. Rd. 1763 and Highway 281 (3600 ft.), 22 November 1982, 1 male, 3 females (FSCA), Tuckaseegee River at 40 mile bend, Cullowhee (2050 ft.), 30 September 1983, 6 males, 10 females, 4 immatures (MCZ), Fall Cliff, WCU Preserve, Cullowhee Mtn. Rd., 4 July 1983, 4 females, 1 immature male, 6 immatures (MCZ), Mull Creek, Cullowhee (3000 ft.), 27 August 1983, 1 female (MCZ), 5 September 1983, 1 male (MCZ), Webster, Morgan Farm, 27 April 1983, 3 females, 1 immature (FSCA); *Swain County,* Newfound Gap near Cherokee, 3 August 1930 (N. Banks), 1 female (MCZ). SOUTH CAROLINA: *Oconee County,* N side of Highway 76 at Chatooga River (1240 ft.), 11 January 1984, 4 immatures (FSCA). TENNESSEE: *Polk County,* Goforth Creek at Highway 64 (1000 ft.), 1 female (AMNH); Sevier County, Laurel Falls Trail, Little River Rd., Great Smoky Mtn. Nat. Pk., 8 May 1983, 1 female, 1 immature (MCZ).

Additional Records.–TENNESSEE: *Unicoi County,* Erwin, 8 July 1933, (W. Ivie), 1 female; *Sevier County,* Little Pigeon Creek, Great Smoky Mtns., 9 July 1933, (W. Ivie), 1 female.

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PRELIMINARY SURVEY OF WANDERING SPIDERS OF A MIXED CONIFEROUS FOREST

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ABSTRACT

This study of nomadic riparian ground-surface inhabiting spiders was made at the Los Alamos National Environmental Park, Mew Mexico. Spiders constituted about 10% of this mixed coniferous forest community. They were widely distributed in all samples, as the frequency of occurrence was high (mean for year was 85%). The mean relative densities of spiders, however, was low, ranging from less than 2% in winter to about 15% in summer. There is a seasonal shift of relative densities indicating that this population of carnivores may increase proportionately faster than its prey from winter to summer. Actual numbers of spiders trapped seasonally ranged from 102 individuals at all sites in late winter to over ten times as many (1140) in early summer. This mean number of species per season per site ranged from eight in winter to nearly 22 in early summer. The four sites were not significantly different from each other in total number or mean number of species, number of individuals or relative densities. Only frequencies show any differences and as indicated they are suspect especially in this preliminary study where samples are shown to be inadequate in most cases in numbers and length of time in operation.

INTRODUCTION

This study was part of a more extensive pitfall sampling of the wandering invertebrates of the ground surface in a streamside coniferous forest community. The sites sampled were located in Mortandad canyon at the Los Alamos National Laboratory in New Mexico. The study of spiders was made to determine what the species and populations of spiders were, what their relative abundances were, their abundances relative to all other invertebrates at the sites, what the seasonal and habitat preferences were and whether there was a single or more than one community in the transect studied and what modifications of techniques might be done to more accurately and definitely assess the characteristics of the spider community (ies). It was a preliminary study in the National Environmental Research Park. Four sites were sampled. The site at the highest altitude (site I) had constantly running water but no radionuclide contamination from fluid radioactive wastes whereas the other sites had varying degrees of minor contamination. An assessment of the affects of the radionuclide contamination was also an object of the study. Trapping was done at five different times of the year (late winter, midspring, early

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summer, midsummer and midfall), based on manpower, climatic and other mainly practical considerations.

This part of the study analyzes the spider portion of the carnivore trophic level. Only part of the ground inhabitants were sampled; the mobile portion. It did not include all spiders of the ground surface. Many of the web builders, none of the less mobile spiders, often only one sex, and often none of the immature portion were collected. Pitfall samples are selective and need to be supplemented by quadrat or "zeitfang" (equal effort) samples to census all of the ground dwelling spiders.

MATERIALS AND METHODS

Site Descriptions.—Four sets of ten pitfalls each were placed along the upper elevations (about 2200 m) of Mortandad Canyon. Each site was located 1000 m down the canyon from the previous site. Traps were ten meters apart alongside the meanderings of the stream. Elevation differences between sites were slight, ranging from 5 to 75 m. These four sites appeared different enough to be different communities.

The canyon extends mainly from west to east and empties into the Rio Grande, although only severe flash floods actually drain any water into the river. More detailed descriptions of the soils, contamination, etc. of the canyon are available elsewhere (Hakonson et al. 1973; Miera et al. 1977). The features of the sites which seem to be important are summarized in Table 1.

The canyon was a dry canyon which had water in it only at periods of rainfall. Over 15 years ago a cooling tower was installed at the head of the canyon and began releasing water into the streambed. Later, liquid effluent from a disposal plant began to be released into the stream about 100 m below the cooling tower. This is released suddenly, creating a rush of water at Site II which continued for as long as half an hour once or twice a day, except on weekends. Aquatic forms occur in the stream, and waterside spiders have become established. Site III commonly is affected by the daily surge of water although even here its onset is quite gentle. The traps at the sites, however, are set 6-9 cm above the stream channel and hence are not directly subjected to the effects of the surge. Site IV seldom receives water from the liquid disposal. The water has usually sunk into the ground somewhere in Site III. Summer storms still occasionally flood this part of the streambed.

As may be seen from these descriptions each site differs in several features although most of them are not sharp and distinct either quantitatively or qualitatively. Absolute differences occur between Sites I and IV, mainly in some plant occurrences, probably in soil moisture, soil texture and chemical composition (although not measured), winter and summer precipitation and streamside slope. However, no close correlation with any of these features has been made with the spider species occurring at each site. Generally, shade, soil moisture and density of vegetation is highest at Site I and least at Site IV. The canyon floor is greatest in area at Site IV and much more dry, level, and sandy than at Site I, where there is more humus but a much smaller and more rocky and irregular surface.

Methods.—A pitfall trap was designed so that it could be placed in position and easily removed with only slightly disturbing the vegetation and soil surface.

Alcohol (75% ethanol) was placed in the bottom to preserve the trapped animals. Pitfalls were placed in position in the morning and collected one to five days later, again in the morning. Initial trapping (midsummer and midfall) varied in duration, as indicated,

Table 1.–Characters of invertebrate trapping sites in Mortandad Canyon.

SITE	I	II	III	IV
Mean elevation	2190 m	2165 m	2090 m	2085 m
Rainfall Aug. 1975-Aug. 1976	42.5 cm	41.3 cm	43.6 cm	38.9 cm
Water flow of stream	constantly running water up to 25 cm deep in places	constantly running water with periodic surges of greater volume	usually daily surges of water with no flow in between	seldom any water except during rainstorm
Winter - water and snow	heavy snow cover surface stream water frozen most of winter	heavy snow cover water usually frozen	light snow cover heavy - up to 0.5 m deep ice	mostly snow and water free except for short period after storms
Insolation	sun irregular - much ground surface in shade	same or less sun reaching ground mostly sun flecked	some direct sun - ground mostly in shade except at midday	direct sun on ground much of day limited sun in late afternoon
Soil	moist to wet and marshy with much humus and few dry areas	moist to dry with humus and much sand	moist to dry with sand and much less humus	usually dry - sandy with least humus of all sites
Slope of stream	stream dropping most steeply of all sites	stream slope much less than I	less slope but much like IV	hardly any slope to stream
Stream banks	scarcely any banks pitfalls about same level as stream	streambed sides steep and up to 2 m deep abrupt drop to streambed	banks quite steep but less than 1 m deep. Abrupt drop to streambed.	banks shallow and less than 0.5 m deep and sloping to streambed
Streamside dominant plants	grasses, barberry, cattails, willows, mountain mahogany, Gambel's oak	boxelder, barberry, cliffbush, Douglas fir, Gamble's oak	grasses, clematis, yellow pine	grasses (Poa) currants, yellow pine

mainly to determine the efficacy of one or two days versus longer trapping periods. The winter, spring and early summer trapping was established at two sets of three days each (except for one period when pitfalls were accidentally left for four days). Catch numbers were adjusted (multiplying or reducing numbers actually caught) to make them all as though six days of trapping had been done at each site each season. Although this adjustment is not statistically valid or as valid as if all data had been collected the same number of days, it is more comparable than actual numbers since sampling times did vary. I did not know before making the samples whether the number of specimens would be too great for identifying and counting in a reasonable period of time. Also, too few samples might easily be too small to generate any dependable data if they were too variable, for example. The results will show my conclusions about these methods.

The animals from a bottle at a single pitfall were examined with a dissecting microscope. Each specimen was identified to species, or genus in some immatures, and the number of individuals for each taxon enumerated. I identified most of them but sent various groups with which I was not sufficiently familiar to the specialists indicated. Some have still not been identified as to species and there was one new species (Millidge 1981), and several others not yet described. Micryphantids and small linyphiids were not all identified to species and exact records as to site and season were not kept because so many were unidentifiable immatures or females. Voucher specimens of most species collected have been deposited in the general collection of the American Museum of Natural History.

The following data were recorded and/or calculated: numbers of species, numbers of individuals, sex, frequency of occurrence (Ashby 1935, Cox 1967, Curtis and McIntosh 1950), relative density (Cox 1967), site of occurrence and season of occurrence. Most of these terms are self-explanatory or in common usage and will not be defined. A few terms unique to this study, or which are not always used uniformly, are the following:

The mean number of individuals, or species, per site per three days of pitfall use have been recorded (or calculated) from the data. Various factors of the environment, mainly climatic (rainfall, temperature, wind, etc.) were seldom the same from day to day. Therefore, as shown by the two sets of three day samples taken successively, the samples were seldom without great variability.

Frequency (or percent frequency) is a widely-used easily determined ecological statistic which is commonly defined, and so used here, as the percent of the samples in which a species is found (Cain 1932, Cox 1967, Hoel 1943, McGinnies 1934). However, it is a poorer statistic than most because it depends upon a number of factors such as size of the organism, size of the sample, number of samples taken, density of the population, etc., instead of only a single factor such as density (number of individuals) or dominance (size, weight, volume or the like of individuals). Specifically in pitfall trapping there is the problem of the length of time a pitfall is in operation at any one period of sampling. In addition there is the problem of whether there are enough samples to get a "true" statistic representing the ubiquity of the population being sampled. The less common species, more so than the common ubiquitous species, will have larger frequencies if the sample is in operation for a longer period of time because that gives the individual of the population a longer time to fall into a trap. I know of no way to determine the amount of time a trap should operate to give a "true" value for that population's "actual" frequency.

Theoretically, the larger the frequency the more widespread and/or common a species is. To be an adequate sample of the actual population the number of pitfalls in use must be large enough to sample the less ubiquitous species as well as the wide ranging species.

What skewness occurs in this sampling is on the side of making frequencies lower than they would actually be if a larger number of samples had been taken. One way to judge the adequacy of the sample is to determine the distribution of species according to Preston's octaves of abundance (Preston 1948). When these data are plotted, it is apparent that there are too few rare species (those represented by one or a few individuals) as well as not enough individuals of common species, those with large numbers of individuals. This is aside from the environmental affects upon the community. Many more samples would give a more nearly complete sampling of the total species in the community. Nevertheless, a number of the common species have frequencies that are above 20% which has been determined to be an adequate percentage for most of the calculations (Ashby 1935, Cox 1967, McGinnies 1934, Morris 1960). However, this statistic is less reliable than others used here.

Relative densities (RD) are percentages (also called relative abundance. Uetz and Unzicker 1975) that indicate the proportion of the catch (pitfall, or group of pitfalls) that consists of a certain species (Cox 1967). The number of individuals of each species in the catch is divided by the total number of individuals of all species and multiplied by 100. Ideally, and theoretically, this is proportional to the actual numbers of individuals of the species in the total community but it is affected by the mobility, or nomadism of the species in the total community, the weather (Lowrie 1971), size, number and placement of samples, and other factors. However, it is one of the best statistics available and at least is more valid in comparing species abundance in a single study, like this, where samples are all the same, taken in the same way.

Catch (or sample) is used here for the number of species, or individuals, collected in a sample (pitfall or group of pitfalls). The community of spiders is used to encompass all the individuals and/or species caught in the pitfalls. The population of species inhabit a basically mixed coniferous forest with the plant species present as indicated in Table I.

Some of the limitations of sampling should be mentioned, as well as specific problems peculiar to this study. Immatures in most studies of invertebrates are difficult to identify and with spiders this is also a problem. However, in a specific localized area when many adults have been captured and there are no, or few closely related species, the immatures of that genus are the species which has been identified by the adults.

The pitfall technique, as has not been too clearly or generally emphasized in the literature, samples only moving individuals. It seems better than the quadrat method for sampling this roving population (Uetz and Unzicker 1975). However, any stage of development of a species which is relatively sedentary will only rarely be sampled, so it does not sample roving and stationary ground species equally. Most ground level species probably do move at some time during their life cycle, although for each species these values would be different. They are certainly not trapped always in the same proportion that they occur in an area. This gives relative densities and numbers per pitfall that must be markedly different from, usually below, and at least not always in proportion to their actual numbers. Quadrat sampling can compensate for this to a great extent but the amount of field work necessary to get an equal amount of information is several times as great and in addition will not sample the tiny species very well unless it is combined with the Tullgren Funnel extraction or other methods.

Variability between samples is great. This is at least partly due to the differences in the weather (rain, snow, temperature and wind mainly) on the sampling days. These data from this preliminary sampling show that this variability can be smoothed out or dampened by more days of sampling at any one sampling period. The two sets of three day

samples or the three sets with a total of nine days of sampling in this study give better, more nearly average representative counts of the wandering spiders of an area than a short, one or two day, sample.

Finally, there is probably a lack of sampling of some species and " overcatching" of others because their vision allows them to avoid the trap or they may be attracted to it as a possible retreat to avoid rigorous weather, predators, or other features of the environment. However, there is no way to determine the extent of these effects on numbers caught—it must simply be recognized that the sampling is biased.

RESULTS AND DISCUSSION

Frequency and Relative Density.—Spiders average nearly 10% of the invertebrate mobile ground populations of Mortandad Canyon for the entire year.

Relative density figures show that Acarina had an RD of 35%, Collembola 28%, Formicidae 17%, Diptera 3.6%, Coleoptera 2.4%, Homoptera 1.8%, Heteroptera 1%, Thysanoptera 0.9%, Hymenoptera (mainly wasps) 0.8%, Orthoptera 0.5% and the remaining insects (Psocoptera, Lepidoptera, Thysanura, Mecoptera, Neuroptera, Siphonaptera) the remaining 1%.

In considering the spiders as a whole, we find the following frequencies and relative densities by sites and seasons (Table 2). Although the relative densities are low the frequencies are quite high most of the year. In other words, spiders are found in most of the pitfalls most of the time, that is, spiders are quite ubiquitous. Throughout the year they are found in 85% of the pitfalls. Late winter occurrence was significantly lower than any other time with a mean frequency of 55%. At other seasons all four sites had similar frequencies.

Early summer contrasted markedly with winter in that every pitfall had at least one spider (frequency 100%). This is true even if the great number of active males of *Pardosa yavapa* which were in their courtship stage of life, searching for females, were eliminated form the analysis. Eliminating this species could only change two sets of pitfalls dropping the F to 90%. Midspring was also high with a mean of 94%. The other seasons were lower but high also.

The frequency of finding spiders at each site was high and about equal each season although winter, as might be expected, was lower. The relative density of spiders fluctuated much more than did the frequency (Table 2). Relative densities for spiders ranged from a low of 2.4% in winter at Site I (they were a small proportion of the total community) to a high of 25% at Site II in early summer, nearly eleven times as great. However, this high value is greatly inflated since over 75% of the catch was of the one species, *Pardosa yavapa*, most of which were males in search of females with sex, not food, as the stimulus for movement.

I am at a loss to explain these data as far as density analyses are concerned because of the large number of *P. yavapa*. Similar increases in abundances of some other species probably occur at mating time although not in all species to the same degree. It is possible also that the absolute density of this species is greater than that of any others in this community but this one set of early summer samples can only hint at such a possibility. More extensive sampling seems called for to better analyze this species' abundance and its relationship to the other species in the community.

Table 2.–Spider distributions by seasons and sites (for six trap days).

		Sites					
		I	II	III	IV	Mean	Total
Late	No. of species	6	4	6	16	8	25
Winter	No. of individuals	13.7	6.9	22.0	59	25	101.6
	% Mean frequency	50	50	50	85	59	
	% Mean relative density	1.4	3	0.8	2.6	1.9	
Mid	No. of species	13	11	16	26	16.5	30
Spring	No. of individuals	70	45	89	53	64	257
	% Mean frequency	100	90	100	85	94	
	% Mean relative density	8.6	5	4.75	3.05	5.4	
Early	No. of species	19	19	22	26	21.5	45
Summer	No. of individuals	242	418	319	161	285	1140
	% Mean frequency	100	100	100	100	100	
	% Mean relative density	15.3	25.45	14.45	7.95	15.8	
Mid	No. of species	18	15	10	14	14.25	32
Summer	No. of individuals	60	43	25	81	52	209
	% Mean frequency	87	83	71	93	84	
	% Mean relative density	12.4	10.2	4.35	9.3	9.5	
Mid	No. of species	9	12	8	11	10	21
Fall	No. of individuals	43	41	61	57	50.5	202
	% Mean frequency	83	90	87	93	88	
	% Mean relative density	11.1	7.5	11.9	2.1	8.1	
Yearly	No. of species	31	32	26	43	33	78
Means	Mean no. of species	13.0	12.2	12.4	18.6	14	
and	No. of individuals	429	554	516	411	476	1910
Totals	Mean no. of						
	Individuals per site	85.8	111	103	82	95-97	382
	% Mean frequency	84	83	82	91	85	
	% Mean relative density	9.8	10.2	7.25	5.0	8.1	

The mean yearly RDs of spiders at Sites I, II and III were 7% to 10% whereas at IV the RD was only about half that, 5%. The variability in relative density from site to site and season to season was similar. Sites I and II were about twice as high in RD as III and IV. Most seasons showed lowest RDs about half that of the highest, except in midfall.

Statistically significant relative densities between sites and seasons were few as determined by using the arc-sine conversion of RD figures. However, there is no clear trend or clue as to what the causes of these differences might be (and for this reason I'm not presenting these data). There were significantly higher RDs for early summer, but definite conclusions must be avoided at this time because they are due to the larger number of *Pardosa yavapa* as indicated earlier. All other seasons are not statistically significantly different from one another. More samples at each site might show significant differences. At present it would seem that the only certain conclusion is that the relative density of spiders in winter is significantly low while for the rest of the seasons the proportion of the community that is spiders remains high and about the same.

The RDs of spiders and the actual numbers of all invertebrates (all potential prey) per pitfall or site are related as follows. Discounting early summer for the reasons already noted, only Site IV shows RDs that are significantly lower from season to season. When more than about 50 individuals invertebrates are collected in a pitfall the RDs of spiders are usually less than 10%. Conversely, when spider RDs are high (more than 20%) then

the numbers of individuals per pitfall are less than about 40. This is not applicable to the early summer figures. The added numbers of male *P. yavapa* produce higher RDs. When both values (numbers of individual invertebrates and RD of spiders) are low there are neither positive nor negative correlations. And, finally, there are no cases where numbers of individuals and RDs are both high. This seems to mean that when the numbers of individuals of all species in the environment are high, then the numbers of spiders are not increasing as rapidly to avail themselves of the added prey. Conversely, when the proportion of spiders is high it might be because the prey have died and left proportionately more spiders alive. This condition applies (except for the unusual summer condition) almost exclusively during midfall (about 20 pitfalls out of the 120 censused). Only five of nearly 200 pitfalls produced over 25% RD (except for early summer).

Finally it must be acknowledged that these are possible conclusions only as many prey species were probably not sampled in the pitfalls and features such as life cycle durations and mobility patterns of the insects and spiders were not known or taken into consideration. The collecting may average out differences or even skew them one way or another, but I present them here as giving some evidence that predator-prey relationships may show the lag indicated, and should be investigated in any subsequent study of this sort.

Numbers of Individuals.—In this discussion I am eliminating the early summer collections (Table 3). The number of individuals for that period is significantly higher than for any of the other collecting periods. But this is due to the large number of *Pardosa yavapa.* Of 1140 individuals collected during this period, 819 were *P. yavapa,* and over 80% of these were males. Collecting was apparently done at or near the peak of their period of search for females. This was corroborated by some collecting done at the same time the following year, although the numbers were only about half as large.

Finally, I am not considering this summer collection in detail also because it was taken at the beginning of the summer season and comparable collections at the beginning of each season were not made. Although it was a valid collection in general it seems to me that because of these factors (including the overwhelming numbers of *P. yavapa*) it is reasonable to consider these data as atypical. I will only point to the actual figures and not compare them with the other collection figures.

In general the number of individual spiders per pitfall, regardless of the species, was low. Means ranged from 0.4 spiders per trap to 4.45 while actual numbers went as high as 13. Finally, only 34 of 379 traps for the year had six or more spiders in them. The overall mean for the four seasons was 2.5 spiders per pitfall. The data in Table 2 indicates that few of the pitfall means were different from one another, except for the winter sampling

Table 3.—Number of individuals of *Pardosa yavapa* (adjusted to 10 traps totals for six days).

	Sites				Season Total
	I	II	III	IV	
Late Winter	0	0	0	1	1
Midspring	27	4	8	7	46
Early Summer	177	362	184	99	822
Midsummer	4.5	0	0	11.3	15.8
Midfall	.7	0	0	7.3	8
Totals	209.2	366	192	125.6	892.8

at Sites I, II and III. Some were statistically significant, but no trend is obvious enough to make the data reportable. They were all significantly lower in spider catches from nearly all other sites and seasons of collecting (except early summer).

Dispersion of Spiders.—An attempt was made to determine whether the spiders were dispersed in a random, clumped or uniform fashion (Cole 1945). Using analyses relative to the Poisson distribution (variance equal to the mean in randomly dispersed populations and variance greater than the mean in clumped populations) all seasons show clumped figures. Even when considering one set of pitfalls placed at a site for one, three or five days only three samples of ten pitfalls showed a dispersion that was not clumped.

All indications in this study are that the spiders are dispersed in a somewhat clumped fashion. The difference in conclusions between this analysis and Cole's is presumable due to the differences in the habitat. The wooded area in which Cole sampled was a rather homogeneous habitat without marked differences in moisture, litter, temperature or other ecological factors to which the spiders might react. Although each of the sites in Mortandad Canyon did not have a great deal of difference between pitfalls, nevertheless, there were differences in moisture, temperature due to insolation, degree of shade, etc. These were probably enough to cause spiders to aggregate in certain pitfalls and not so much in others. This created a tendency to clump because of the environment and not because of the behavior of the spiders to the presence of other spiders (or other small carnivores) and/or prey.

Number of Species.—The total number of species of spiders collected at a site seasonally ranged from four (late winter at Site II) to 26 (early summer at Site IV—Table 2), about seven times as great. During any season the differences between sites were not as great, ranging from four to only 1.4 times as many species at the site with the greatest number of species as the one with the least number. This means that there were about the same number of active species at any of the sites at any particular season.

The greatest variation in numbers of species is seasonal. Site II and III show the greatest variation with early summer showing between four and five times as many species as the low winter numbers. Site IV is more uniform, with numbers of species varying from a low of eleven to a high of 26, only 2.4 times as great. (This mean number of species per season per site varied from eight in late winter to 2.7 times as great (21.5) in early summer). Consistent with this is the fact that the range in total numbers of species collected at all sites per season was also great, varying from 21 in midfall to 45 (2.14 times as many) in early summer.

Site IV has the greatest variety of species; more species occurred there in most seasons than at any other site. From a general assessment of the sites this would seem due to the site being less extreme, or at least less variable, in temperature, precipitation and moisture. The site would seem to have a greater variety of microhabitats also. Both the total number of species found here (43) and the mean number per six pitfall days (19) was over 1.5 times as great as at the lowest site (Site III). At the same time the community of spiders at Site IV was more stable, showed less variation in numbers, than at the other sites. This generally coincides with our knowledge of more complex communities such as rain forests versus less complex communities such as deserts and tundra. It is also an expression of the fact that the physicochemical parts of the environment (temperature, winds, humidity, moisture, etc.) are more variable and affect the biotic community more in a less protected environment than in a more complex community in which the biotic affects control the organisms mostly (Odum 1971).

Seasonally, the late winter is most variable in number of species (from site to site: four to 16) whereas summer is least variable (14 to 26). Mean seasonal variations are of greater magnitude (eight to 21.5—seven times greater) than mean site variations (26 to 43—1.65 times greater). Only winter shows a range between sites (four times as great) that is greater than the magnitude of the range between seasons (eight to 21.5—only 2.7 times as great). This again illustrates the possibility that physicochemical factors control the environment in winter.

In summary, the range in numbers of species between sites was never great at any one season except in late winter. That is, at any season but winter, the number of species at each site was not significantly different.

Phenology—Seasonal Distribution.—The patterns of seasonal activity shown by the common species (Appendix) are as follows. Only *Hahnia cinerea* is active equally, or nearly so, at all seasons. Most species are active in spring, often in greater numbers at certain sites. *Pardosa yavapa* is abundant at all sites in early summer but significantly less so at IV and with a definite preference for site I. *Agroeca pratensis* is more common at Sites I and III whereas *Zelotes subterraneus* is more common at III and IV. In terms of the moisture gradient the *Cicurina* and the *Gnaphosa* may be tolerant of a wide range of moisture whereas *P. yavapa* and the *Agroeca* prefer moist sites.

Most common species show preference for two sites rather than a single site. The following distributions can be inferred from this study, but only future replication can establish them as true consistent generalizations for the species involved. *Pardosa sierra*, a typical streamside species (Lowrie 1973) and *Hahnia cinerea* prefer Sites I and II. *Titanoeca silvicola* and *Micaria montana* are more abundant at Sites II and III and *Neo-antistea gosiuta* at Sites III and IV. *Schizocosa mccooki* and *Trochosa gosiuta* show a strange abundance at the extremes, I and IV. What the explanation of this is cannot be determined for certain but does seem to correlate with the species preference for drier habitats: Site I does have some dry areas. Only one genus, *Haplodrassus,* is commonly at one site only, III. The two species of the genus do occur at other sites but only as one or two individuals. However, this may be an artifact of collecting and identifying as most specimens were immature, or it may be just the situation this year.

At each site we can say there are about the same number of common species. It is suggested that this may be due to the carnivorous habits of spiders and the tendency for carnivores to be evenly or randomly distributed (Cole 1945), in a uniform habitat.

A cluster analysis of the common spiders at each site was also done, but not presented here because no significance can be attributed to it since they were not consistent and no field data or information on the species would give a reason for such correlations. Seventeen species of spiders were involved with an unweighted pair-group method used to produce a dendrogram. This dendrogram showed Sites I and II to be very similar and Sites III and IV likewise, with a greater distance between II and III. This could fit in with the evaluation of the situation from year long observation although other evaluations may be equally plausible, such as that Site I is different from II and III, and III is different from IV or I. There is little justification for any conclusion of differences between sites. A much more extensive and intensive sampling would be necessary to determine whether there were any differences.

CONCLUSIONS AND SUMMARY

1. Spiders constitute about 8% of the wandering streamside ground-inhabiting invertebrates of this mixed-conifer biotic community, in Mortandad Canyon.

2. Spiders' frequency of occurrence (measure of their ubiquity) is high with a mean for the year of 85%, winter was significantly low (59%) and summer was high (100%).

3. Spiders occurred about equally at the four sites with frequencies from 82% to 91% for the year. Site IV showed higher frequencies than other sites, but in light of the unreliability of this statistic do not seem to warrant conclusion of a difference at Site IV from this study.

4. The mean relative densities of spiders were low, ranging from less than 2% (late winter) of the invertebrate population to over 15% (early summer). Their relative densities were highest (about 10%) at Sites I and II and lowest (5%) at Site IV.

5. At Site IV the RDs were most stable (varied less) throughout the year (2.1% to 9.3%). Site III was most variable ranging from a low of 0.8% to a high of 14.45%. The seasonal shift in relative densities of spiders indicates that this carnivorous population increases proportionately more than its prey population from winter into summer. It then regresses during the rest of the year to a low proportion when prey seems to be correspondingly low.

6. The actual densities of spiders (the numbers of individuals per pitfall or site) throughout the year were about equal at each of the sites (low mean of 82 individuals per site at IV to a high mean of 111 at Site II). Seasonally, their abundance ranged from a total of 102 individuals from all four sites in late winter to over 200 in the other seasons, with a high in early summer of 1140. Thus densities were lowest in late winter (mean of 25 individuals per site) increasing to a high in early summer (mean of 285 individuals per site) and then back down to a low in winter.

7. The mean numbers of species per season range from eight per site in winter to nearly 22 per site in early summer and then declined to the near low of ten in midfall. There was an overall mean of 14 species per site for the year. The mean number of species per site for the year ranged from lows slightly over 12 at the 3 higher sites to a high of 19 species at IV. The number of species (species diversity) was greatest at Site IV most of the year, and was more variable at the other sites.

8. The dispersion of spiders was clumped. This may be due to the habitats being relatively heterogeneous with a variety of micro-environments although no analysis of this factor was made. If that is the case then the spiders would clump in microhabitats that they prefer, and avoid those not suitable.

9. This study shows no effect of the contaminating radionuclides introduced into the stream at Site II. That is, the sites of contamination did not show significantly greater or fewer numbers of individuals, number of species, relative densities, frequencies or other measurements than any other site. It is concluded that this study shows no effect of the radioactive material on the spider population.

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Appendix

Wandering Spiders of Mortandad Canyon collected in pitfalls. Numbers for commonest species (more than 10 specimens) in parentheses: 1 = Rank (16 most common), 2 = Number of individuals captured.

Agelenidae	1. *Cicurina robusta* Simon (4 - 60)
Amaurobiidae	2. *Titanoeca silvicola* Chamberlin and Ivie (10 - 20)
Anyphaenidae	3. *Anyphaena marginalis* (Banks)
	4. *A. pacifica* (Banks)
Clubionidae	5. *Agroeca pratensis* Emerton (2 - 142)
	6. *Castianeira cingulata* (C. L. Koch)
	7. *C. descripta* (Hentz)
	8. *Clubiona* sp?
	9. *Phrurotimpus* nr. *woodburyi* Chamberlin and Gertsch
	10. *Trachelas deceptus* Banks
Dictynidae	11. *Dictyna apacheca* Chamberlin and Ivie
	12. *D. completa* Chamberlin and Gertsch
	13. *D. terrestris* Emerton
Gnaphosidae	14. *Callilepis eremella* Chamberlin
	15. *Drassodes neglectus* Keyserling
	16. *Drassylus* nr. *argilus* Chamberlin
	17. *Gnaphosa muscorum* (L. Koch) (12 - 14)
	18. *Haplodrassus chamberlini* Platnick and Shadab
	19. *Haplodrassus bicornis* (Emerton) (11 -17)
	20. *Micaria montana* Emerton (3 - 98)
	21. *Nodocion* nr. *florissantus* (Chamberlin)
	22. *Zelotes subterraneus* (C. L. Koch) (5 - 57)
Hahniidae	23. *Hahnia cinerea* Emerton (7 - 42)
	24. *Neoantistea gosiuta* Gertsch (16 - 11)
Linyphiidae	25. *Helophora* sp?
	26. *Lepthyphantes subalpina* Emerton
	27. *Lepthyphantes* sp?
	28. - 31. *Meioneta* sp?
	32. *Neriene radiata* (Walckenaer)
	33. *Wubana drassoides* (Emerton)
Lycosidae	34. *Arctosa* sp?
	35. *Pardosa montgomeryi* Gertsch
	36. *P. orophila* Gertsch
	37. *P. sierra* Banks (13 - 12)
	38. *P. sternalis* (Thorell)
	39. *P. yavapa* Chamberlin (1- 919)
	40. *Schizocosa mccooki* (Montgomery) (9 - 21)
	41. *Alopecosa kochi* (Keyserling)
	42. *Trochosa gosiuta* (Chamberlin) (6 - 47)
Micryphantidae	43. *Ceraticelus crassiceps* (Chamberlin and Ivie)
	44. *Ceraticelus* sp?
	45. *Ceratinella* sp?
	46. *Ceratinops* n. sp.
	47. *Collinsia perplexa* (Keyserling)
	48. *C. plumosa* (Emerton)
	49. *Disembolus anguineus* Millidge

	50. *Eperigone taibo* Chamberlin and Ivie
	51. *E. trilobata* (Emerton)
	52. *Eperigone* sp?
	53. *Grammonota gentilis* Banks
	54. *Islandiana flaveola* (Banks)
	55. *Pocadicnemis pumila* (Blackwell) (8 - 22)
	56. *Spirembolus pallidus* Chamberlin and Ivie (14 - 14)
	57. *S. vallicolens* Chamberlin
	58. *Walckenaera directa* (O. P.-Cambridge)
	59. *W. spiralis* (Emerton (15 - 12)
	60. *Walckenaera* n. sp.
	61. - 63. Three species not placed as to genus
Oonopidae	64. *Orchestina saltitans* Banks
Philodromidae	65. *Thanatus coloradensis* Keyserling
	66. *T. formicinus* Clerck
Pholcidae	67. *Pholocophora americana* Banks
	68. *Psilochorus imitatus* Gertsch and Mulaik
Salticidae	69. *Pellenes* sp?
Tetragnathidae	70. *Tetragnatha laboriosa* Hentz
Theridiidae	71. *Euryopes* sp?
	72. *Theridion murarium* Emerton
Thomisidae	73. *Ozyptila sincera canadensis* Dondale and Redner
	74. *Misumenops* or *Misumenoides* sp?

SIZE AND PHENOLOGY OF BALLOONING SPIDERS AT TWO LOCATIONS IN EASTERN TEXAS[1]

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ABSTRACT

The aerial dispersal of spiders at two locations in eastern Texas was studied using a Johnson-Taylor suction trap. A total of 17,596 spiders were collected at College Station, Texas during a one year period, and 6248 spiders at the Ellis Unit from April to August. Nineteen families were found including Uloboridae and Hahniidae. The greatest numbers of spiders were collected during May and June at College Station with immatures representing 94% of total spiders collected during the year. The families Erigonidae, Araneidae, and Oxyopidae comprised ca. 74% of all spiders collected at College Station. The size class 1-2 mm represented 64% of all spiders collected at College Station with those < 1 mm in length next in abundance with 28%.

INTRODUCTION

Suction traps have been used to study the monthly dispersal of spiders in Oklahoma and Texas (Horner 1975, Salmon and Horner 1977). Ballooning spiders, captured in a Johnson-Taylor suction trap, peaked during June and September (Salmon and Horner 1977) and spiders in the family Erigonidae were reported to be the most numerous. Horner (1975) studied the dispersal of salticids in Oklahoma and found immatures peaking in July. Adult spiders were also observed to balloon.

Other workers used different methods to study dispersal. Glick (1939) collected ballooning spiders at different heights by airplane in Louisiana. The number of spiders collected was highest near the ground and lowest at 5000 ft. elevation. Freeman (1946), at a height of 3 m, used nets attached to masts to observe that spiders actively ballooned at all wind velocities ranging from 6-35 mph. More ballooning male spiders were present in September and October than any other month in England (Duffey 1956). Ballooning females were abundant over a longer period of time, from September to March. Bristowe (1929) observed that immatures of several families balloon in late summer and early autumn in England but as winter approaches, the proportion of linyphiids increases and the other families decrease.

Spiders are known to be predaceous and McDaniel and Sterling (1982) and McDaniel et al. (1981) determined those species of spiders which are predaceous on *Heliothis* spp. eggs and larvae in a cotton field in eastern Texas. Dean et al. (1982) listed the species of

spiders collected from the same cotton field. To eventually predict the phenology and abundance of spiders colonizing cotton fields, the seasonal profile of potential colonizing species should be known. The current study was conducted to determine the seasonal phenological profile of each spider family and the size most likely to balloon in eastern Texas. The dispersal of adults identified to species will be presented in a separate paper.

METHODS AND MATERIALS

A Johnson-Taylor suction Trap (Johnson and Taylor 1955) was used to study the aerial dispersal of spiders in eastern Texas. The cylindrical trap is 2.5 m tall and 55.8 cm in diameter. A cone-shaped fine mesh screen located in the trap funnels the spiders into a one pint jar of either 70% ethyl alcohol or 50% ethylene glycol. A 0.33 h.p. electric motor driven fan pulls air and spiders into the trap.

Two locations were used for sampling: at College Station, Texas from 26 March 1979 to 25 March 1980 and at the Ellis Unit of the Texas Department of Corrections from 3 April to 31 August 1980 (through the growing season). The College Station site was located next to the Entomology Research Laboratory on the Texas A&M University campus. The area is surrounded by paved streets, buildings, small cotton plots, natural vegetation, and trees. The Ellis Unit is located 8 km northeast of Huntsville, Texas. This site is on a flood plain of the Trinity River and surrounded predominantly by pinewoods. The trap was located in an area surrounded by pastures, silage, sorghum, and corn; the nearest cotton was ca. two km away. The trap was set at ground level at each location, and spiders ballooning at ca. 2.5 m in elevation were captured. Jars containing the samples were changed daily at College Station and daily when possible at the Ellis Unit. It is possible that large adult salticids may have crawled into the trap since a nest was occasionally seen near the top of the trap. However, adults [e.g. *Phidippus audax* (Hentz)] were observed attached to a drag line and being blown about by the wind.

Identification to the family level was recorded along with the life stage (adult/immature). No attempt was made to determine the instars, but each spider was assigned to an arbitrary size class (< 1 mm, 1-2 mm, etc.). The size was measured from the anterior of the carapace to the posterior of the abdomen, excluding the spinnerets.

RESULTS

A total of 17,596 spiders in 19 families were captured in the suction trap at College Station (hereafter, abbreviated as C.S.) during a one year period (Table 1). Most of the families have previously been reported to balloon. The Mysmenidae were included in the Theridiidae but are currently considered to be a separate family (Platnick and Shadab 1978).

Spiders were captured in the trap every month of the year, but the highest catches were recorded in June and September. Most of the spiders were immature (94.0%). More adult males (4.4%) were captured than adult females (1.6%). The size class 1-2 mm represented 64.1% of all spiders collected. Other size classes included < 1 mm (28.1%), 2-3 mm (6.1%), 3-4 mm (1.0%), 4-5 mm (0.3%), and > 5 mm (0.4%).

Most (84%) of the spiders at C.S. were captured between May and October. Salmon and Horner (1977) found a similar pattern at Wichita Falls, Texas. Collections made during the winter months of January through March comprised 2.7% of the total yearly collection at C.S. compared to 1.7% at Wichita Falls.

Table 1.—Ballooning spiders collected at College Station, Texas (26 March 1979-25 March 1980).

	Month												Total	% of Total
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.		
Erigonidae	29	24	80	276	723	1277	803	587	1187	623	274	92	5975	34
Araneidae	7	12	39	216	947	1051	625	726	735	112	99	49	4618	26
Oxyopidae	16	16	25	4	37	137	74	268	927	361	394	148	2407	14
Tetragnathidae	18	19	10	204	448	369	226	93	208	129	73	26	1823	10
Lycosidae	17	11	8	13	19	40	65	110	392	46	63	30	814	5
Theridiidae	2	8	8	7	29	43	55	86	169	58	63	30	558	3
Salticidae	2	9	6	7	13	52	30	40	67	22	27	14	289	2
Thomisidae	3	8	14	10	14	34	13	16	33	47	48	39	279	2
Philodromidae	13	16	24	9	17	12	29	36	33	11	20	49	269	1
Dictynidae	2	1	2	1	—	5	16	35	32	26	25	14	159	<1
Linyphiidae	5	1	12	5	9	17	10	14	33	13	20	6	145	<1
Clubionidae	1	1	3	—	5	5	8	16	25	6	28	2	100	<1
Anyphaenidae	1	1	2	3	2	6	6	13	27	6	8	3	78	<1
Mysmenidae	—	—	—	—	1	2	—	10	5	2	3	—	23	<1
Mimetidae	—	—	—	—	—	—	1	4	9	1	6	1	22	<1
Gnaphosidae	—	1	2	8	6	—	3	—	—	—	—	—	20	<1
Uloboridae	—	—	—	—	—	—	1	2	5	3	2	—	13	<1
Pisauridae	1	—	—	—	—	—	—	—	1	—	—	1	3	<1
Hahniidae	—	—	—	—	—	1	—	—	—	—	—	—	1	<1
Total	117	128	235	763	2270	3051	1965	2056	3888	1466	1153	504	17596	

At the Ellis Unit 6248 spiders were captured during the growing season (April-August). The same families found at C.S. were also found at Ellis (Table 2). A lower number of immatures was found at this location (83.0%) and adult males (9.3%) slightly outnumbered adult females (7.7%). The distribution of size classes was as follows: < 1 mm (21.8%), 1-2 mm (66.4%), 2-3 mm (6.5%), 3-4 mm (2.5%), 4-5 mm (1.4%), and > 5 mm (1.4%). Peak dispersal occurred during May.

In the < 1 mm size class, the three most abundant families at each location were the Araneidae, Erigonidae, and Tetragnathidae. The Erigonidae and Araneidae were among the most abundant families in the 1-2 mm class (Fig. 1). The most abundant families in the 2-3 mm and > 5 mm classes varied between locations. Although not shown in Fig. 1, the 3-4 mm and 4-5 mm size classes were dominated by the Salticidae.

Spiders captured in the suction trap may not accurately represent the total ballooning fauna since it collected only those ballooning at the 2.5 m altitude. However, Glick (1939) reported that spiders were most abundant close to the ground. Other factors such as amount of silk, wind, habitat, and time of day may affect the ballooning fauna so to sample the entire spider fauna may require the use of several sampling techniques simultaneously.

The Erigonidae and Tetragnathidae are subfamilies of the Linyphiidae (Millidge 1980) and Araneidae (Levi 1980), respectively, but are raised to the family level here for greater detail and for comparisons to the study by Salmon and Horner (1977).

Family Dispersal at C.S.—*Erigonidae:* One-third (34%) of the spiders collected belong to this family (Table 1). The size class < 1 mm comprised 17.3% of the erigonids and peaked in June whereas those > 1 mm (1-2 mm, 80.8%) remained abundant from May to October. Males peaked in September (20.1% of male erigonids) and females peaked in August (17.0%). Adults comprised 12.2% of total erigonids.

Araneidae: The most numerous size class of araneids was < 1 mm (57.0%) which peaked in June. Spiders > 1 mm (1-2 mm, 41.7%) remained abundant from May to September.

Oxyopidae: This family was most abundant during the fall. Most of the specimens collected were < 2 mm (86.7%) and were captured in September. A peak occurred in November for those > 2 mm. The 2-3 mm class contained 11.8% of the oxyopids and < 1 mm with 2.3%.
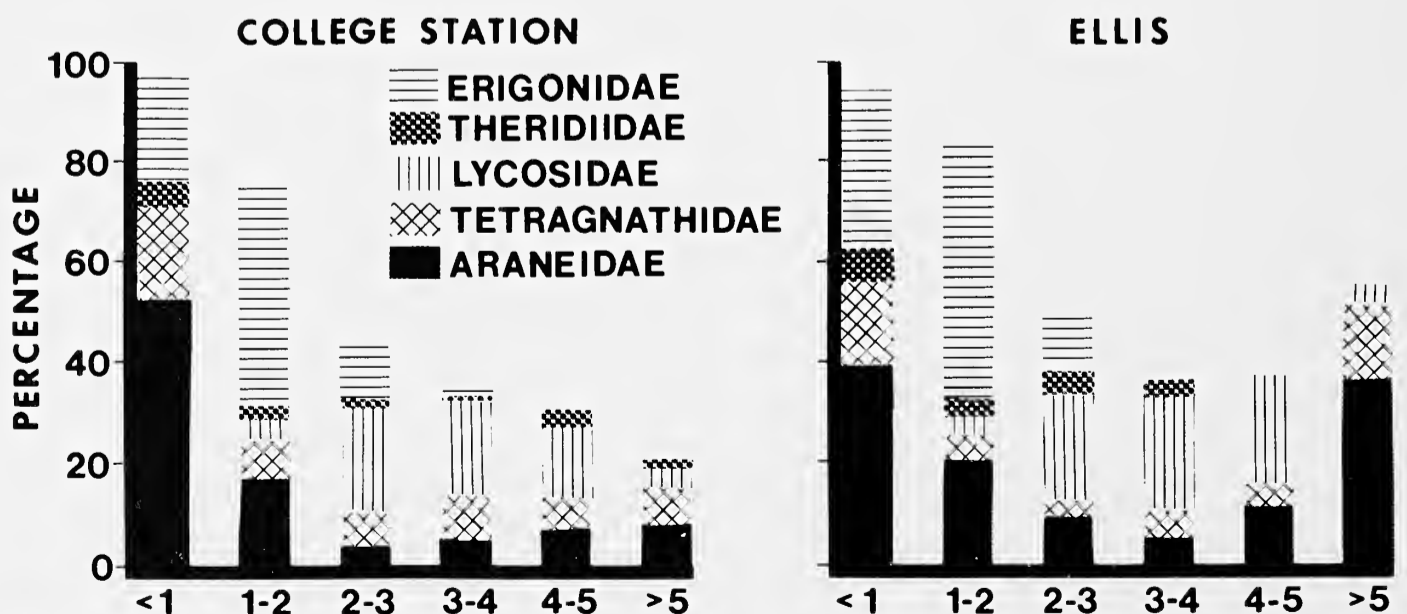
Fig. 1.—Percentages of the most abundant families of spiders collected in a suction trap at College Station and the Ellis Unit in Texas.

Tetragnathidae: This family was the fourth most abundant. Those spiders < 1 mm (49.9%) were the most numerous and peaked in May and June. Those > 1 mm (1-2 mm, 45.1%) also peaked in May.

Lycosidae: Nearly half (48%) of the lycosids captured ballooned in September. The size class 1-2 mm (66.3%) was most abundant in September. Those > 2 mm (2-3 mm, 27.9%) also peaked in September.

Theridiidae: The peak month was September for the size class < 1 mm (39.2%). Theridiids > 1 mm (1-2 mm, 56.8%) also peaked in September. Adults were most numerous in the trap in September with more males being captured than females.

Salticidae: The salticids 1-2 mm in length (46.0%) were most numerous in June. September was the peak month for the size class 2-3 mm (31.2%). The 3-4 mm class comprised 14.5%.

Thomisidae: Thomisids peaked during the fall months as did those in the size class 1-2 mm (77.4%) in October and November. The other classes were similar in abundance: < 1 mm (5.4%), 2-3 mm (7.5%), 3-4 mm and 4-5 mm (4.3% each).

Philodromidae: Like the previous family, the philodromids also peaked during the fall. The peak month for those < 2 mm (45.4%) was August, whereas December was the peak month for those > 2 mm (2-3 mm, 45.3%) in length.

Dictynidae: Dictynids were most numerous form August to November. Most of those 1-2 mm (73.0%) ballooned in August. The size classes < 1 and 2-3 mm comprised 13.8% and 13.2%, respectively.

Linyphiidae: September was the peak month for the 1-2 mm size class (89.0%) and for total linyphiids. The < 1 mm class represented 9.6%. Males and females were captured in similar numbers with a peak in September.

Table 2.—Ballooning spiders collected at Ellis (3 April-31 August 1980).

	Month						% of Total
	Apr.	May	June	July	Aug.	Total	
Erigonidae	380	1173	719	247	50	2569	41
Araneidae	111	483	297	516	79	1486	24
Tetragnathidae	37	173	90	119	38	457	7
Lycosidae	35	92	81	86	11	305	5
Thomisidae	19	21	53	152	19	264	4
Theridiidae	14	35	53	88	48	238	4
Dictynidae	3	8	9	119	98	237	4
Oxyopidae	15	22	38	81	27	183	3
Salticidae	79	32	12	27	19	169	3
Anyphaenidae	14	11	26	32	11	94	1
Linyphiidae	23	34	19	14	3	93	1
Philodromidae	8	10	16	9	7	50	1
Clubionidae	2	6	5	7	16	36	<1
Gnaphosidae	2	12	7	3	2	26	<1
Mysmenidae	–	10	3	2	–	15	<1
Mimetidae	–	1	1	6	6	14	<1
Pisauridae	–	6	2	1	–	9	<1
Uloboridae	–	1	–	1	–	2	<1
Hahniidae	--	1	–	--	–	1	<1
Total	742	2131	1431	1510	434	6248	

Clubionidae: The clubionids tended to be more numerous during the fall. The most individuals were in the size class 1-2 mm (34.0%) which peaked in September. The second largest grouping were those > 5 mm (32.0%), peaking in November. The 2-3 mm class comprised 25.0%.

Anyphaenidae: August and September were the peak months for total anyphaenids and also for the size class 1-2 mm (50.0%). Other size classes included: 2-3 mm (19.2%), 3-4 mm (14.1%), 4-5 mm (5.1%), and > 5 mm (11.6%).

Mysmenidae: All mysmenids captured were < 1 mm. Most were collected during the fall.

Mimetidae: In this study, 22 mimetids were collected from July to December. Salmon and Horner (1977) reported finding only one mimetid. The size class 1-2 mm contained 63.6% of the total. The other size classes were ca. evenly distributed. No males were captured but females were collected in September, November and December.

Gnaphosidae: Gnaphosids were captured mainly in April and May with the 2-3 mm size class containing 80.0% of the total (1-2 mm, 20.0%).

Uloboridae: This may be a new record, as we have not seen a previous report of this family ballooning. Thirteen specimens were collected from July to November. One male was captured in September. The most individuals were in the 1-2 mm class (61.5%).

Pisauridae: Three pisaurids were collected.

Hahniidae: This also appears to be a new record for ballooning activity. One specimen was taken in June. Duffey (1956) reported that *Hahnia nava* Bl. was common in England but did not disperse by aerial means.

Size Dispersal.—The percentages by size of six of the most common spiders (where the immatures could be identified) collected in a suction trap (adults and immatures included) are presented in Figure 2. The most individuals of *Acanthepeira stellata* (Walckenaer) (As) at C.S. were in the size class 1-2 mm which peaked in September. Those > 5 mm (all males, x̄ = 6.9 mm) were captured in September. The size class 1-2 mm at Ellis included the most individuals in July. This was also the peak month for those > 5 mm (all males, x̄ = 8.4 mm). Over 85% of the total at each location were in the 1-2 mm size class.

Gea heptagon (Hentz) (Gh) was not very numerous at C.S. but the size classes < 1 and 1-2 mm included the most individuals which were collected mostly from August to
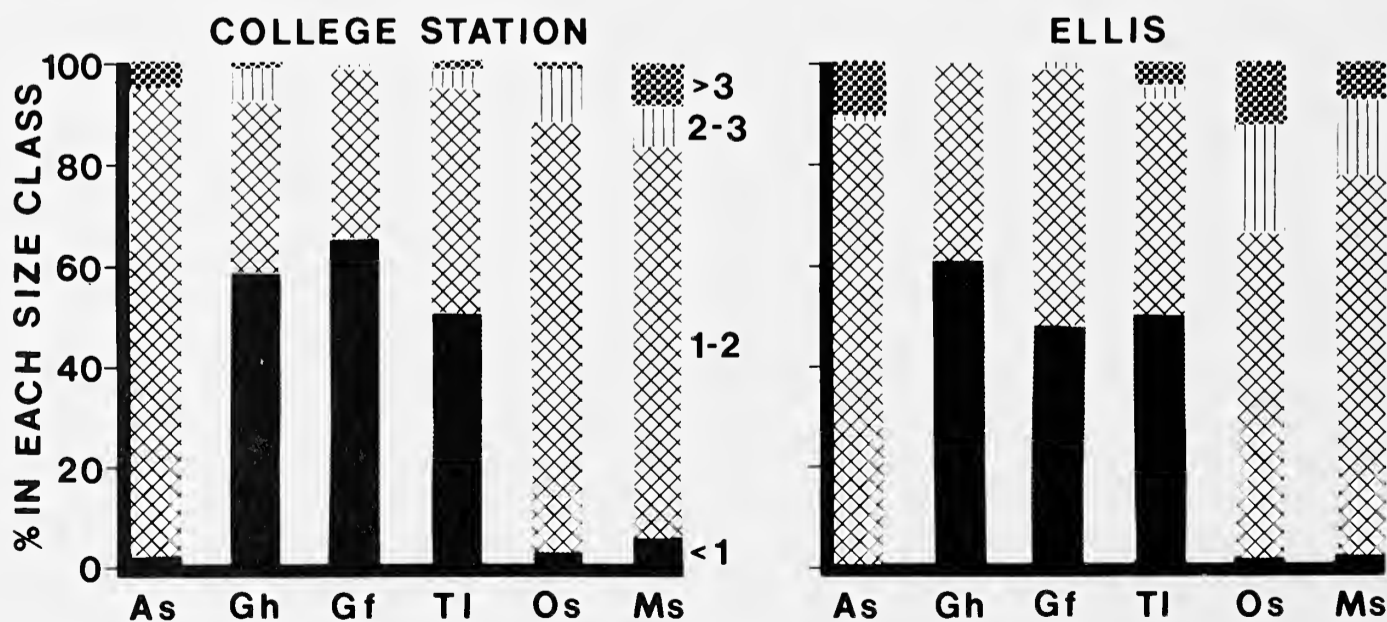
Fig. 2.—Distribution of the most abundant species by size class at College Station and the Ellis Unit in Texas. (As = *Acanthepeira stellata,* Gh = *Gea heptagon,* Gf = *Glenognatha foxi,* Tl = *Tetragnatha laboriosa,* Os = *Oxyopes salticus,* and Ms = *Misumenops* spp.).

December. More individuals were collected at Ellis where these two size classes peaked in July. About 60% of the total at each location were < 1 mm in size. Most of the remaining spiders were in the 1-2 mm size class.

The most numerous species at C.S. was *Glenognatha foxi* (McCook) (Gf) with most individuals in the smaller size class, < 1 mm, being captured in May and June. August and September was the peak period for the 1-2 mm size class. June was the peak month at Ellis for these size classes. Most of the individuals of *G. foxi* belonged in these two size classes. Adult males ($\bar{x}$ = 1.7 mm) were most abundant in September at C.S. and May at Ellis. One adult female ($\bar{x}$ = 2.2 mm) was collected in April at each location.

Tetragnatha laboriosa Hentz (Tl) was the third most abundant species at C.S. The size classes < 1, 1-2, and 2-3 mm peaked in May and June. May was also the peak month at Ellis for the size classes < 1 and 1-2 mm. About 50% of the total at each location were < 1 mm. This size class corresponds to the second instar stage that emerges from the egg sac ready to disperse (LeSar and Unzicker 1978). Few adults were collected ($\bar{x}$ of males = 5.5 mm at C.S. and 8.0 mm at Ellis; $\bar{x}$ of females = 9.2 mm).

Oxyopes salticus Hentz (Os) was the second most abundant species at C.S. with the size classes < 1 and 1-2 mm peaking in September. Those 2-3 mm in size peaked in November. The numbers at Ellis were much lower with the size classes 1-2 mm to 4-5 mm peaking in July. Several males were collected with a $\bar{x}$ of 4.4 mm at C.S. and 4.7 mm at Ellis.

Misumenops spp. (Ms) were collected in similar numbers at each location with those spiders 1-2 mm in size the most numerous (ca. 75% of the total). The 1-2 mm size class peaked in October. The size classes 1-2 mm to 3-4 mm at Ellis peaked in July. Four males were collected at each location ($\bar{x}$ = 3.5 mm). Two females at Ellis measured 7.2 mm in length.

DISCUSSION

It is well known that immature spiders disperse when they emerge from the egg sac, primarily to avoid the cannibalistic tendencies of their siblings and to increase survival chances by avoiding overcrowding (Turnbull 1973). "It is usually, but not invariably, very young spiders that exhibit the aeronautic habit" (Comstock 1948). Horner (1975) reported that 88% of the salticids collected in a Johnson-Taylor suction trap were immature (mostly early instar). Salmon and Horner (1977) stated that size is one of the major restrictions to ballooning. Richter (1970) observed that aerial dispersal occurs generally in young instars of eight *Pardosa* species, though different species have different dispersal capacities.

These observations suggest that smaller species of spiders tend to balloon more frequently than larger species and that early instars balloon more than later instars. Smaller spiders, such as the erigonids, are caught ballooning more frequently than larger spiders in other families. However, without knowing the relative abundance of individuals in these families, the conclusion that small spiders balloon more readily than large spiders is questionable. Obviously, we see a dramatic reduction in numbers of individuals correlated with increasing size classes (Fig. 3). But, do spiders in earlier instars within a taxon balloon more often than later instars?

We suggest that in nature some species exhibit little or no difference in the ballooning rates of the various sizes and the difference in numbers of individuals in the various size classes may largely represent normal mortality; i.e. mortality of the young result in fewer

Fig. 3.—Numbers of spiders in their respective size ranges captured in a suction trap at College Station and the Ellis Unit in Texas.
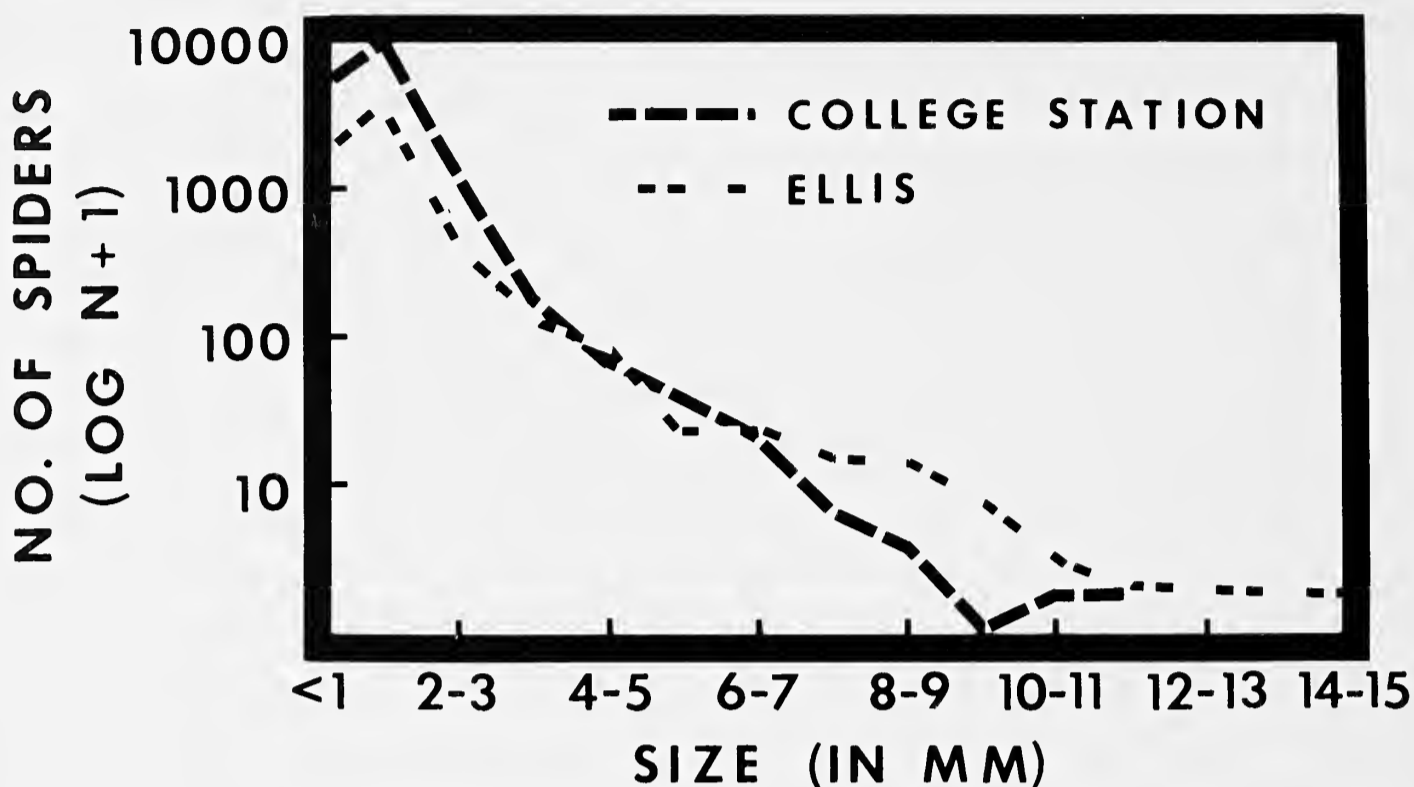
large individuals rather than reduced ballooning behavior in these later instars. In Table 3 we suggest that the number collected in each size class compared to the class with the most individuals may represent percent survival. For example, at C.S. from the class containing the greatest number of individuals of a species to the 4-5 mm class the survival of *Tetragnatha laboriosa* would be 0.4%, *Oxyopes salticus* 0.3%, *Chiracanthium inclusum* (Hentz) 12.0%, and *Misumenops* spp. 5.9%. In the long term the average number of adults which must survive from the eggs deposited by a single female must be two (1 male and 1 female) for the population density to remain stable from year to year. Thus, for *C. inclusum*, which averages ca. 76 eggs per female (Peck and Whitcomb 1970), survival of 12.0% of the ballooning stages to the 4-5 mm size class leaves ca. 9.1% additional generation mortality which can take place before 2.9% of the generation remains. This lower survival rate is equal to 1 male and 1 female or an Ro (increase per female per generation) of one. However, Peck and Whitcomb (1970) found ca. 10% mortality form egg to first instar. This results in an Ro of ca. 4.1. *Misumenops* spp. was calculated to have an Ro of 14.0 based on data from Muniappan and Chada (1970). Early mortality of *O. salticus* and *T. laboriosa* would leave them with an Ro of ca. 1.0. Since *O. salticus* and *T. laboriosa* appear to have a lower survival rate but are more abundant in the suction trap and in cotton (Dean et al. 1982) than *C. inclusum*, numbers in the trap in this study do not appear to indicate equal ballooning rates among size classes.

Definitive tests of a hypothesis that instars balloon at equal rates should be based on field collections by species and by classifying individuals into instars. Then with season-long suction trap samples the yearly survival rates could be estimated and year to year trends in population dynamics of various species could be more accurately determined.

Other factors that could influence the results of this experiment are: (1) the efficiency of the suction trap in collecting various sizes of spiders, (2) elevation preference of ballooning individuals of the various instars within a species, (3) ballooning time of individuals in different size classes, and (4) actual mortality in the field.

Table 3.–Percentage survival from the size class with the most individuals to the other size classes captured in a suction trap at College Station, Texas.

	Size		class in mm	(n)	% survival
Tetragnatha laboriosa	<1	(909) to	1-2	(823)	90.5
			2-3	(66)	7.3
			3-4	(16)	1.8
			4-5	(4)	0.4
			>5	(5)	0.5
Oxyopes salticus	1-2	(2022) to	2-3	(257)	12.7
			3-4	(23)	1.1
			4-5	(6)	0.3
			>5	(2)	0.1
Chiracanthium inclusum	1-2	(25) to	2-3	(24)	96.0
			3-4	(4)	16.0
			4-5	(3)	12.0
			>5 imm.	(19)	76.0
			>5 ad.	(13)	52.0
Misumenops sp.	1-2	(186) to	2-3	(18)	9.7
			3-4	(7)	3.8
			4-5	(11)	5.9
			>5	(3)	1.6

However, for certain species of spiders, the catch-frequency may represent expected abundance due to natural mortality rather than higher ballooning rates of smaller individuals. If this size frequency is due to natural mortality, then continuous suction trapping throughout the year may be used to obtain data useful in developing life tables and predicting the dynamics of spider populations.

Of the most abundant species collected during this study, most ballooned in more than one size class and many ballooned as adults. Thus, Comstock (1948) may be correct in stating that it is usually young spiders that exhibit the aeronautic habit. However, our data provide evidence that two other factors should be considered: (1) differential rates of ballooning between instars and (2) age dependent survivorship.

ACKNOWLEDGMENTS

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MERMITHID (NEMATODA) PARASITES
OF SPIDERS AND HARVESTMEN

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ABSTRACT

Nematode parasites of spiders and harvestmen are restricted to members of the family Mermithidae. A literature review shows that nematode parasitism of arachnids is worldwide and at least 51 species of spiders and harvestmen have been recorded as hosts of mermithid nematodes. Infected spiders have varied habits and it is postulated that two types of parasite life cycles probably exist and that the indirect life cycle (involving a paratenic host which falls prey to the arachnid) is probably the common type.

INTRODUCTION

Representatives of the family Mermithidae are the only nematodes known to parasitize spiders. Their effect on spiders is similar to that on other arthropod hosts, namely host mortality at the time of parasite emergence.

The difficulty in rearing adult mermithids from postparasitic juveniles that have emerged from parasitized spiders has prevented a systematic assessment of spider mermithids. However, it is apparent that mermithid parasitism of spiders is widespread and occurs in various habitats. The present work tabulates previous instances of these associations, adds some, and discusses the host parasite relationship. Reports of spider parasitism by horsehair worms are not discussed here. The latter, commonly referred to as *Gordius*, are not nematodes and belong to a separate phylum, the Nematomorpha. Early reports of spiders parasitized by the horsehair worms may actually have involved mermithid nematodes and vice versa. The adult forms of both groups are similar superficially and may have the same type of life cycle.

RESULTS AND DISCUSSION

Parasite identification.—Records of spider parasitism by mermithid nematodes are summarized in Table 1. E. Schlinger gave me mermithids that emerged from spiders in New Guinea and New Zealand but they have not been included in the Table since the hosts were not identified. Such is the case for a parasitized male clubionid from Papua, New Guinea, that L. N. Sorkin had in his collection.

Table 1.—Records of mermithid nematode parasitism in spiders and harvestmen.

Host	Parasite identified as	Reference
Argyoneta aquatica (Clerck)	*Mermis albicans* von Siebold	Menge, 1866
Atypoides riversi O. P.-Cambridge	unknown	Vincent, in press
Cesonia bilineata (Hentz)	*Aranimeris aptispicula* Poinar and Benton	Poinar and Benton, in press
Coelotes inermis (L. Koch)	unknown	Müller, 1983
Combridgea sp. [New Zealand]	unknown	Lowe (pers. comm.)
Diaea dorsata Fabricius	*Arachnomermis dialaensis* Rubtsov	Rubtsov, 1980
Drassodes sp. [Canada]	unknown	Holmberg (pers. comm.)
Lycosa riparia sphagnicola Dahl.	*Mermis* sp.	Holm, 1941
Lycosa sp. [Argentina]	unknown	Doucet (pers. comm.)
Drassus lucifugus (Walckenaer)	unknown	von Siebold, 1843
Epeira diadema Clerck	unknown	Walckenaer, 1883
Geolycosa patellonigra Wallace [U.S.A.]	unknown	Miller (pers. comm.)
Gnaphosa sp. [U.S.A.]	unknown	Sorkin (pers. comm.)
Homolophus biceps (Thorell) [Canada]	unknown	Holmberg (pers. comm.)
Lycosa saccata Latreille	*Mermis* sp.	Holm, 1941
Lycosa scutulata Hentz	*Filaria lycosae* Haldeman	Haldeman, 1847, 1851
Lycosa sp.	*Mermis* sp.	Bristowe, 1941
Lycosa sp.	*Filaria*	Kryger, 1910
Lycosa sp.	*Mermis robusta* Leidy	Leidy, 1856
Lycosa tarsalis Thorell	*Mermis* sp.	Holm, 1941
Lycosa verisimilis Montgomery	*Mermis* sp.	Montgomery, 1903
Lycosa vorax Walckenaer	unknown	von Siebold, 1854
Micryphantes bicuspidatus C. L. Koch	unknown	von Siebold, 1848
Miranda ceropegia C. L. Koch	unknown	Hoppe, 1796
Misumenops sp.	*Aranimeris aptispicula* Poinar and Benton	Poinar and Benton, in press
Mitopus morio (Fabricius)	*Agamermis incerta* (Steiner)	Stipperger, 1928
Opilio sp.	*Hexameris* sp.	Unzicker and Rotramel, 1970
Opilio sp.	*Mermis* sp.	Kästner, 1928
Paecilaemana quadripunctata Goodnight & Goodnight	unknown	Goodnight and Goodnight (pers. comm.)

Table 1.—Continued

Host	Parasite identified as	Reference
Pardosa glacialis (Thorell)	*Hexameris* sp.	Leech, 1966
Pardosa hortensis (Thorell)	unknown	Parker and Roberts, 1974
Pardosa lugubris (Walckenaer)	*Amphimermis(?) pardosensis* Rubtsov	Rubtsov, 1977
Pardosa nigropalpis Emerton	*Mermis* sp.	Montgomery, 1903
Pardosa riparia (C. L. Koch)	*Amphimermis pardosensis* Rubtsov	Rubtsov, 1977
Pardosa scita Montgomery	*Mermis* sp.	Montgomery, 1903
Pardosa sp.	*Agamermis decaudata* C. S. C.	Kaston, 1945
Pardosa sp.	*Arachnomermis araneosa* Rubtsov	Rubtsov, 1978
Pardosa vancouveri Emerton [Canada]	unknown	Holmberg (pers. comm.)
Peucetia viridans (Hentz) [U.S.A.]	unknown	Landau (pers. comm.)
Phalangium cornutum Linn.	*Filaria phalangii* Haldeman	Haldeman, 1851
Phalangium opilio Linn.	unknown	Pfeifer, 1956
Phalangium opilio Linn.	*Filaria truncatula* Rudolphi	Rudolphi, 1819
Phidippus borealis Banks [U.S.A.]	unknown	Cutler (pers. comm.)
Phidippus clarus Keyserling	*Agamermis decaudata* C. S. & C.	Kaston, 1945
Phidippus putnamii (Peckham & Peckham) [U.S.A.]	unknown	Cutler (pers. comm.)
Phidippus sp.	*Aranimeris aptispicula* Poinar & Benton	Poinar and Benton, in press
Pseudicus sp. [U.S.A.]	unknown	Sorkin (pers. comm.)
Salticus formicarius Latreille	unknown	Bertkau, 1888
Schizocosa saltatrix (Hentz)	*Mermis* sp.	Montgomery, 1903
Schizocosa sp. [U.S.A.]	unknown	Sorkin (pers. comm.)
Sosippus floridanus Simon	unknown	Kaston, 1945
Tarentula inquilina Thorell	*Mermis* sp.	Bertkau, 1888
Tetragnatha sp. [Canada]	unknown	Sorkin (pers. comm.)
Tetragnatha sp.	unknown	Sorkin (pers. comm.)
Theridion ovatum (Clerck)	*Mermis* sp.	Bristowe, 1931
Tibellus oblongus (Walckenaer)	unknown	Holmberg (pers. comm.)
Tmarus sp.	*Aranimeris aptispicula* Poinar & Benton	Poinar and Benton, in press
Verrucosa arenata (Walckenaer)	*Aranimeris aptispicula* Poinar & Benton	Poinar and Benton, in press
Wadotes sp.	*Aranimeris aptispicula* Poinar & Benton	Poinar and Benton, in press
Wulfila alba (Hentz)	*Aranimeris aptispicula* Poinar & Benton	Poinar and Benton, in press
Xysticus deichmanni Soerensen	*Hexameris* sp.	Leech, 1966
Xysticus funestus Keyserling	*Hexameris* sp.	Kaston, 1945
Zora maculata O. P.-Cambridge	*Filaria* sp.	Kryger, 1910

The earliest reported incidence of mermithid parasitism of spiders was by Hoppe in 1796. No attempt was made to describe the parasite. In 1833, Walckenaer cited a *Filaria* from *Aranea diadema*. At that time, the name *Filaria* was used as a collective genus name for representatives of various groups, especially the larger parasitic worms, such as representatives of the Mermithidae. It had no taxonomic significance. Kryger (1910) also cited *Filaria* from *Lycosa* sp. and *Zora maculata*. In 1819, Rudolphi described mermithids he obtained from *Phalangium cornutum* and *P. opilio* as *Filaria truncatula*. However, his description was very brief and based on general characters found in the postparasitic juveniles. Since adult characters are needed for proper taxonomic placement, this must be cited as a species inquirenda. Also included in this category are *Filaria phalangii* Haldeman 1851 and *Filaria lycosae* Haldeman 1847.

Later, the genus *Mermis* was used in a broad sense to represent members of the family Mermithidae. It and the frequently used binomial, *Mermis albicans*, were assigned to a range of species collected from arthropods. However, as in the case of *Filaria*, these names were used in a collective sense and either lacked a description or the description was so general that it was useful only to family level. Thus the citations listed in Table 1 for Menge (1866), Holm (1941), Bristowe (1931; 1941), Montgomery (1903), Kästner (1928) and Bertkau (1888) when *Mermis* sp. or *Mermis albicans* is mentioned must stand as species inquirendae. Kaston (1945) cited *Agamermis decaudata* as a parasite of *Pardosa* sp. and *Phidippus clarus*. Those nematodes were identified by G. Thorne, basically a plant nematologist. Since he was probably examining juveniles, it is doubtful that a specific designation could have been possible. Also, *A. decaudata* is a parasite of Orthoptera and has not otherwise been reported from spiders. It is my contention that this was a misidentification.

Reports of a *Hexameris* sp. parasitizing *Xysticus deichmanni*, *X. funestus* and *Pardosa glacialis* (Kaston, 1945) (Leech, 1966) are also not exact since postparasitic juveniles were examined and only rarely can a genus be determined from these stages. More recently, Rubtsov described *Amphimermis pardosensis* from *Pardosa riparia* (1977), *Arachnomermis araneosa* from *Pardosa* sp. (1978) and *Arachnomermis dialaensis* from *Diaea dorsata* (1980). The descriptions of these species are based on postparasitic juveniles and again, their true identity remains unknown. From what we now known about mermithid morphology and systematics, all of the above mentioned mermithids from spiders have no systematic position in the classification of the Mermithidae and might well be placed in the collective genus, *Agamomermis*, erected to receive mermithids that could not be placed in existing genera (Poinar and Welch, 1981).

The only completely described mermithid parasite of spiders is *Aranimeris aptispicula* Poinar and Benton (in press). The description is based on adult characters comparable with those of existing genera.

Effects of parasitism.—External symptoms of mermithid parasitism of spiders usually are associated with the size and shape of the host's body. A swollen abdomen is a common symptom and Leech (1966) noted that parasitized *P. glacialis* had a lopsided or greatly enlarged opisthosoma, an altered epigynum, malformed palpi, legs that were shorter and thicker than normal and poorly developed or absent male secondary sexual characteristics. It is possible to see the coils of the parasite through the host's integument since the mermithid usually occupies the entire abdomen and occasionally the cephalothorax. Parasitic castration was noted by Bertkau (1888) in a *Tarentula inquilina* attacked by a mermithid.

Infection signs generally start with a reduction or absence of the digestive gland. In extreme examples, other organs may also be reduced. Leech (1966) commented that

parasitism of *P. glacialis* resulted in the loss of the main prosomatic muscles, the entire digestive system and the entire reproductive system.

Behavioral changes in parasitized spiders have also been noted. Leech (1966) (and personal correspondence) mentioned that some infected individuals of *P. glacialis* were sluggish and did not attempt to escape when approached. During the week before the
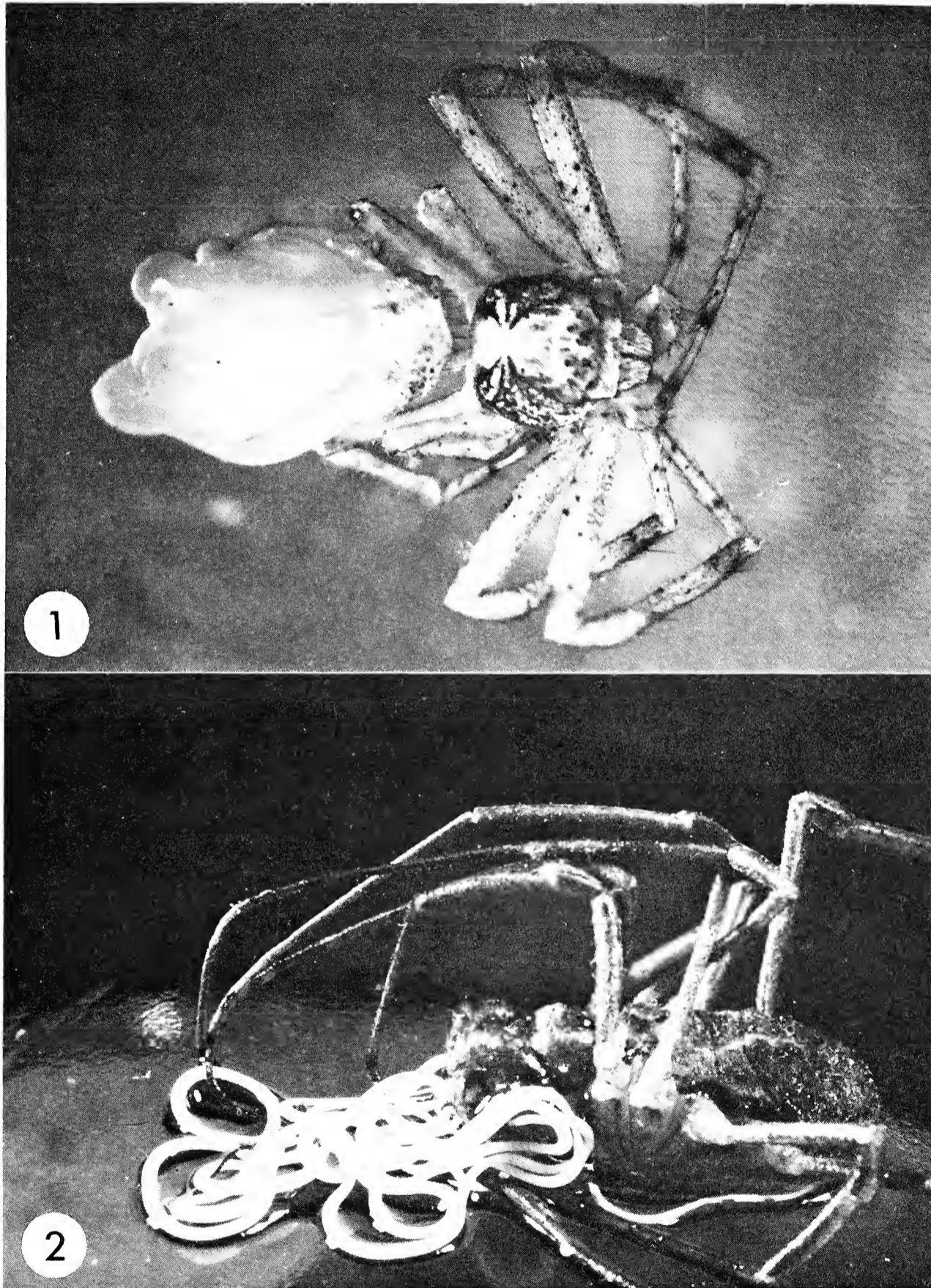
Fig. 1.--Coils of *Aranimeris aptispicula* Poinar and Benton filling the abdominal cavity of the spider, *Tmarus* [probably *angulatus* (Hentz)]. (Photo by the author; specimen from C. Benton). (Mag. x 10).

Fig. 2.--A postparasitic juvenile mermithid that has just emerged from its phalangid host, a male *Protolophus* sp. (Photo by Pat Craig). (Mag. x 5).

parasites emerged the spiders ceased feeding but drank a lot of water. This attractiveness to water was noted in infested *A. aptispicula* which would come out of neighboring woods and fields to find a source of water.

Kaston (1945) presented some evidence that mermithids retard the development of their spider hosts.

Incidence of infection.—Most of the reports of mermithid parasitism of spiders mention only a single incidence of infection. Leech (1966) noted that 1% of the *Pardosa glacialis* he collected were parasitized and that most were females. He mentioned that the rate might have been higher since the infection is very hard to detect in young spiders.

Color of parasites.—Certain species of mermithids can be recognized by their color and both Haldeman (1851) and Leidy (1856) mentioned that upon emergence, the nematodes were pale pink to reddish. The former author noted that the color changed to yellowish after the specimen was heat-killed. This color change was also noted by Poinar and Benton (in press) in *A. aptispicula*. Emerging individuals were pinkish, yellowish and occasionally green, but all became white after some days in water. The initial color may have been acquired from the host.

Life cycle of mermithids attacking spiders.—Although the life history of no spider mermithid is completely known, *Aranimeris aptispicula* is one that probably possesses an indirect life cycle. Its occurrence in a wide range of spiders suggests this. In this type of development, the females deposit eggs in an aquatic habitat. The eggs are ingested by immature insects and the infective stage mermithid hatches, penetrates the gut wall, invades the parenteral tissues of the host and then enters dormancy. Thus when the host matures, it carries the parasite. When one of these paratenic hosts falls prey to a spider and is eaten, the nematode becomes active, enters the spider's hemocoele and resumes development. Such a life cycle has been shown to occur in *Pheromermis pachysoma*, a parasite of yellowjackets (Poinar et al. 1976).

However, from the descriptions of some postparasitic juvenile mermithids that emerged from spiders, it is obvious that at least one other mermithid species attacks spiders in North America. This species could well have a direct cycle, that is, one where the infective stage emerging from the egg enters a young spider by direct penetration through the integument and initiates development. A second host is not involved in such a cycle.

Type of spiders attacked.—Spiders that are attacked by mermithids demonstrate a wide range of behavior and habitat preference. Thus, it is not just ground-stratum hunters that show mermithid parasitism but also orb web weavers, aquatic forms, plant climbers, and even crab spiders that catch insects attracted to flowers. Food preference for parasitized spiders is not restricted to any particular group of insects. It is interesting to note that all spiders found parasitized would have an opportunity to feed on adult insects which possess an aquatic larval stage (e.g. Chironomidae, Culicidae, Trichoptera). Such insects would make ideal paratenic hosts.

Recommended handling of mermithids.—Upon noticing the emergence of a mermithid from a spider host, the investigator should place the parasite in a small amount of water in a glass container with a layer of sand in the bottom. It should be left until it has molted (a single molt composed of the final two shed cuticles) to the adult stage which normally occurs within a month. During this time, the water should be changed daily to avoid the accumulation of fungi which can kill the parasite. Adult stages can be recognized by the appearance of the vulva in the female and the spicules (copulatory organs) in the male [see Poinar (1983) for figures of the appearance and location of these structures].

The adults should be killed by placing them in water heated to 50-60°C. After death, they can be fixed in 3% formalin or 70% alcohol for taxonomic studies. If the living worms are placed directly into fixative when they emerge from the spiders, further taxonomic studies will be prevented.

ACKNOWLEDGMENTS

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LOW TEMPERATURE ACCLIMATION IN THE DESERT SPIDER, *AGELENOPSIS APERTA* (ARANEAE, AGELENIDAE)

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ABSTRACT

Agelenopsis aperta (Gertsch) inhabits desert grasslands and lava beds in the southwestern U.S.A. The capacity of this species to cold-harden was assessed by exposing second generation laboratory-reared specimens to an artificial low temperature cycle simulating the "summer-autumn-winter" transition. Low temperature acclimation had no effect on whole body supercooling points, freeze tolerance or rates of oxygen consumption. Elevated levels of cryoprotectants were not detected using high performance liquid chromatographic techniques. Cold tolerance was similar between males, females and immatures. Exposure to temperatures immediately above the whole body supercooling point caused no apparent injury. It is hypothesized that movement into protected overwintering microhabitats may obviate the necessity for the evolution of seasonal mechanisms of cold-hardening in *A. aperta*.

INTRODUCTION

Cold-hardening refers to physiological mechanisms by which organisms acquire enhanced tolerance to low temperature. Few workers have examined the overwintering biology of arachnids, despite the fact that for temperate species winter represents a significant portion of the life span.

Comparable studies with terrestrial insects have revealed two basic patterns of cold-hardening (Salt 1961). One group tolerates the formation of extracellular ice within the body, whereas, other species are freeze susceptible or freezing intolerant. The latter avoid the lethal effects of freezing by lowering the temperature at which the spontaneous freezing (nucleation) of body water occurs. This value is termed the supercooling point and is experimentally determined by detecting the released latent heat of fusion as body water freezes. For intolerant species, the supercooling point represents the temperature at which body tissues freeze and the lower lethal limit.

Exposure to low environmental temperatures often serves as a proximal cue triggering the seasonal acquisition of increased cold tolerance (Baust 1981, Baust and Lee 1982). For both freeze susceptible and freeze tolerant arthropods cold-hardening is often associated with the accumulation of low molecular weight sugars (glucose and trehalose) and polyhydric alcohols (glycerol, sorbitol and mannitol). These cryoprotectants are believed

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to afford protection in a number of ways including the colligative depression of super-cooling and melting points, a reduction in the rate and amount of tissue ice formation and by the prevention of injurious levels of cellular dehydration (Meryman 1974).

The purpose of this investigation was to assess the capacity of *Agelenopsis aperta* (Gertsch) to cold-harden. This species is a funnel-web weaver of the family Agelenidae. The specimens used in this study were laboratory-reared offspring of spiders collected from desert grassland and lava bed habitats at an elevation of 1600m in south-central New Mexico. In this area winters may be severe with heavy snowfall and extended periods of sub-zero temperatures. Advanced juveniles overwinter from late October until activity resumes in March (S. E. Riechert, pers. comm.; Riechert 1974). This species population has been extensively studied with respect to habitat selection and web-site distribution by Riechert *et al.* (1973), Riechert (1974), Riechert and Tracy (1975), Riechert (1976) and Riechert and Gillespie (in press).

Second generation laboratory-reared specimens were exposed to an artificial "summer-autumn-winter cycle" by gradually exposing them to decreasing temperature during a 72 day laboratory experiment. Periodically low temperature tolerance was evaluated by determining whole body supercooling points, freeze tolerance versus susceptibility, cryoprotectant titers and rates of metabolism.

MATERIALS AND METHODS

Initial stocks of *Agelenopsis aperta* were collected from desert grasslands in south-central New Mexico, U.S.A. (Riechert *et al.* 1973). All specimens used were juvenile second-generation laboratory-reared for their entire lives at temperatures between 24 and 28°C at the University of Tennessee. Their age was similar to those of spiders overwinter-ing in natural habitat. The spiders were mailed to the University of Houston and allowed to acclimate to 26 ± 1°C for three weeks prior to experimentation. Each week 2-3 live *Musca domestica* adults and droplets of water were provided for each spider. However, spiders were not fed for five days prior to supercooling point, cryoprotectant and respira-tion rate determinations. Spiders were fasted to remove potential nucleating agents in the food which might result in artifically high supercooling points.

Spiders were cold-acclimated using 5°C temperature steps decreasing from 20°C to 0°C over a 72-day period. Details of the acclimation schedule are shown in Fig. 1. Groups of 4-6 males and females (e.g. females and immature individuals) were removed periodic-ally and tested for supercooling point, cryoprotectant levels and freeze tolerance using methods described by Lee and Baust (1981). A cooling rate of approximately 1°C/min was used for supercooling point determinations. The cryoprotectant levels were analyzed using high performance liquid chromatography with a radially compressed amine modif-ied silica column (Hendrix *et al.* 1981, Lee *et al.* 1983). Freeze tolerance or susceptibility was assessed by allowing the body temperature of the spider to return to the temperature of its supercooling point after the release of the heat associated with the freezing of body water. Post-freezing survival was evaluated after 24 hr at 5°C.

Oxygen consumption was determined using a microrespirometry system described by Lee and Baust (1982). Each respirometer consisted of a 5cc disposable plastic syringe depressed to 2cc with a 20 μl micropipette. Two groups of eight females were acclimated for 12 days without food at 26 or 10°C prior to oxygen consumption determinations. Each spider was placed in a separate microrespirometer and equilibrated for 30 min at 15°C followed by oxygen consumption measurements during the next two hours. The

same individuals were then transferred to 10°C and respiration measurements were repeated as described above. All determinations were made between 1300-1800 hr. Oxygen consumption is expressed in nanoliters (nl) per mg live weight per hour.

RESULTS

Survival was high (> 90%) during the 72-day period of low temperature acclimation in the laboratory and did not differ between cold-acclimated spiders and ones held continuously at 26°C. Fewer males were available for study and as a result were tested only during the first 30 days of the acclimation schedule. At no time during acclimation did a spider survive freezing of body fluids. However, cooling to temperatures immediately above the supercooling point caused no apparent injury in any spider, including individuals maintained at 26°C without cold acclimation.

Supercooling points of males and females were similar and remained unchanged during the first 30 days of acclimation to low temperature (Fig. 1). The supercooling point represents the lower temperature limit for survival under natural conditions for organisms intolerant of freezing. Therefore, these data indicate that males and females have similar levels of cold tolerance. Although in most samples the supercooling point values were tightly clustered in the -8 to -12°C range, some individuals extended supercooling to as
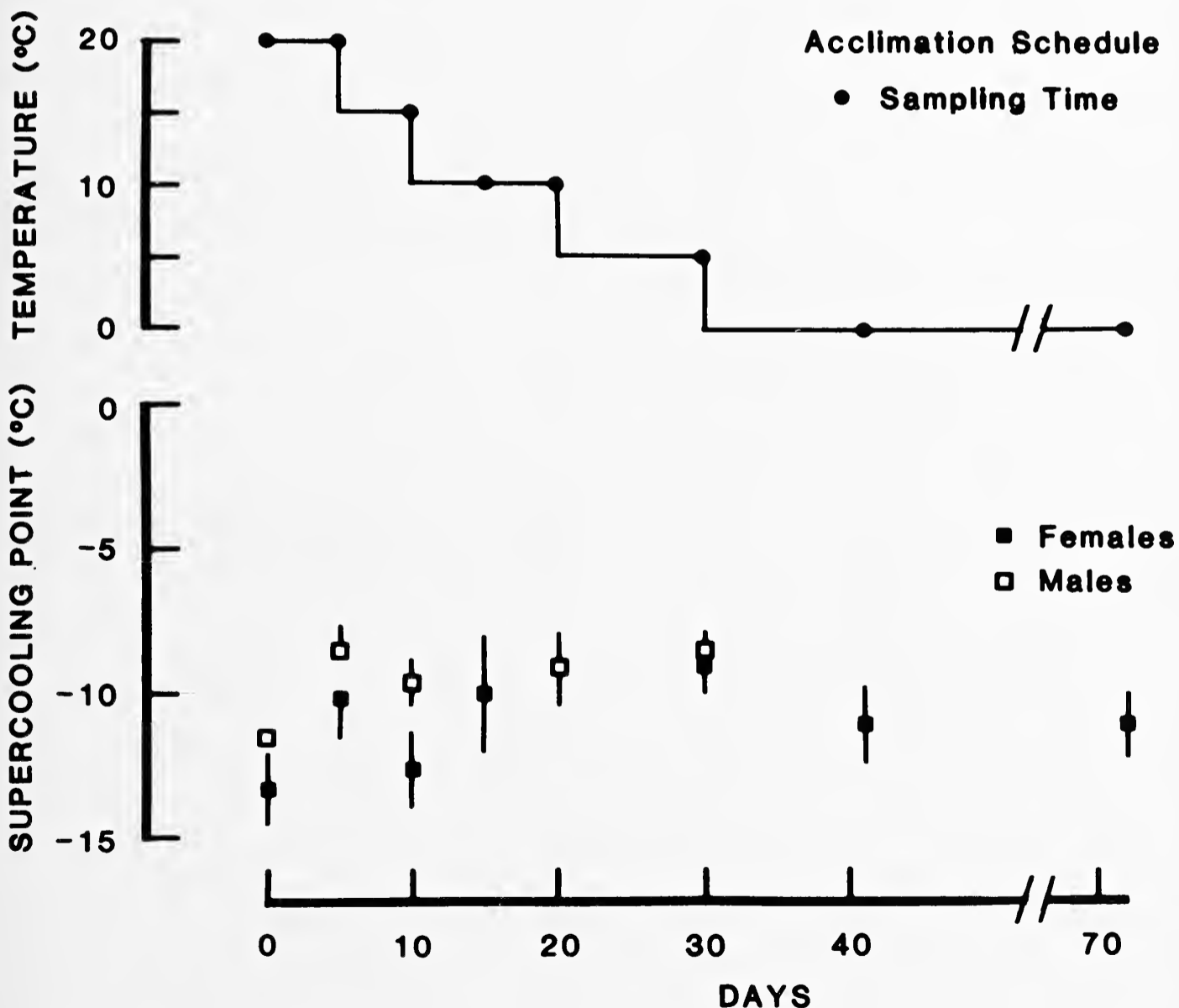
Fig. 1.–Top: Laboratory low temperature acclimation schedule for *Agelenopsis aperta*. Bottom: Comparison of supercooling points for males and females of *A. aperta* determined at intervals during the acclimation schedule ($\overline{X} \pm$ SE).

low as -18.2°C before spontaneous nucleation occurred. Even after 72 days of low temperature exposure, no change in the lower limit of cold tolerance as judged by whole body supercooling points was observed (Fig. 1).

Homogenized spider extracts were analyzed using high performance liquid chromatographic techniques to determine whether low temperature acclimation had an effect on endogenous levels of cryoprotectants. Elevated levels of typical cryoprotectants including glycerol, sorbitol, trehalose, glucose, mannitol and erythritol were not detected. In fact, no glycerol, trehalose or erythritol were identified in chromatograms despite detection limits of greater than 0.05 μg per mg of live weight.

Two groups of eight female *A. aperta* were acclimated to 10 or 26°C for 12 days. Measurement of oxygen consumption at 10 or 15°C revealed no significant differences between the groups. The combined consumption rates ($\bar{x} \pm$ SEM) at 10 and 15°C were, respectively, 112 ± 9 and 171 ± 15 nl/mg/hr.

DISCUSSION

Cold-hardening in spiders appears to be restricted to the avoidance of tissue freezing by depressing the whole body supercooling point. Kirchner (1973) found no evidence for freeze tolerance in studies conducted during the winter with 50 species belonging to 15 families. The data of other investigators are consistent with his observations (Table 1). Regardless of the length of cold acclimation, freeze tolerance was never observed in *A. aperta*. Cooling to temperatures immediately above the supercooling point, however, produced no apparent injury. In general it appears that spiders tolerate exposure to low temperature as long as the limit of supercooling of body fluids is not exceeded. A single exception is the tropical species, *Agelena consociata* which dies after a few hours of exposure to 0°C (Kirchner 1973).

In certain spiders considerable increases in freeze avoidance by supercooling may be observed on a seasonal basis. *Philodromus* immatures lower the supercooling point from -6.2°C in summer to -26.2°C in winter (Duman 1979). Overwintering eggs have the greatest capacity for freeze avoidance with supercooling points extending below -30°C (Table 2). In contrast, overwintering stages of some species lack specific mechanisms of changing cold-hardiness as evidenced by the similarity between summer and winter supercooling points. In Table 2 five species have summer and winter values within one degree of each other and none below -6.8°C.

Supercooling points for *A. aperta* were relatively constant regardless of the temperature or duration of low temperature exposure. Apparently this species lacks the capacity for cold-hardening despite the fact that it is exposed to sub-zero temperatures in the field. A second possibility is that low temperatures alone are not sufficient to induce hardening in this species. For example, seasonal changes in daylength provide a reliable cue for cold-hardening (Duman and Horwath 1983). This alternative is perhaps less likely since the four other agelenids listed in Table 2 apparently, also, lack the capacity for cold-hardening. For phylogenetic reasons the Agelenidae as a group may not have evolved biochemical or physiological mechanisms of seasonally enhancing low temperature tolerance. Seasonal field collections which assess cold tolerance in the natural habitat are needed to definitively resolve this question for *A. aperta*.

Physioloigcal mechanisms regulating the supercooling point are poorly understood. Although glycerol accumulation has been associated with cold-hardening in several species (Kirchner and Kestler 1969, Duman 1979) other common cryoprotectants, such as sorbitol, glucose and trehalose have not been identified in overwintering spiders.

Table 1.—Summary of cold-hardiness in overwintering spiders. Blanks in table indicate that specific information was not provided in the original article or that a given parameter was not investigated. Mean supercooling points are for spiders collected during the winter unless noted otherwise. Unless specifically stated the overwintering stage of spiders studied by Kirchner (1973) were adults or immatures. All species are intolerant of tissue freezing.

Taxon	Study Site	Overwintering Stage	Supercooling Point (°C)	Source
Agelenidae				
Agelenopsis aperta	New Mexico, U.S.A. (Lab reared)	Adult, Immature	-8.0 to -12.0	Present study
Cicurina cicurea	W. Germany		-6.7	Kirchner, 1973
Coelotes terrestris	W. Germany		-6.2 (Winter) -5.3 (Summer)	Kirchner, 1973 Kirchner, 1973
Histopona torpida	W. Germany		-6.5 (Winter) -6.0 (Summer)	Kirchner, 1973 Kirchner, 1973
Tegenaria sp.	W. Germany		-8.0	Kirchner, 1973
Amaurobiidae				
Amaurobius fenestralis	W. Germany		-6.6	Kirchner, 1973
Araneidae				
Araneus cornutus	W. Germany	Adult, Immature	-23 (Winter) -8 (Summer)	Kirchner and Kestler, 1969
Argiope aurantia	Illinois, U.S.A.	Spiderling		Riddle, 1981
Meta menardi	W. Germany		-4.0	Kirchner, 1973
Singa nitidula	W. Germany		-21.4	Kirchner, 1973
Clubionidae				
Clubiona sp. [1]	Indiana, U.S.A.	Immature	-15.4 (Winter) -9.2 (Warm-acclimated)	Duman, 1979
Clubiona phragmitis	W. Germany		-16.1	Kirchner, 1973
Eresidae				
Eresus niger	W. Germany		-16.6	Kirchner, 1973
Linyphiidae				
Bolyphantes index [1]	Norway	Adult	-15.2	Husby and Zachariassen, 1980
Floronia bucculenta	W. Germany	Egg	-30 (Summer and Winter)	Schaefer, 1976
Linyphia sp.	W. Germany	Egg	-25.2 to -33.8	Kirchner, 1973
Lycosidae				
Pardosa lugubris	W. Germany		-6.8 (Winter) -5.8 (Summer)	Kirchner, 1973
Nesticidae				
Nesticus cellulanus	W. Germany		-4.7 (Summer and Winter)	Kirchner, 1973
Philodromidae				
Philodromus sp. [1]	Indiana, U.S.A.	Immature	-26.2 (Winter) -6.2 (Summer)	Duman, 1979
Philodromus sp.	W. Germany		-21.5	Kirchner, 1973
Tetragnathidae				
Pachygnatha clercki	W. Germany		-5.8	Kirchner, 1973
Theridiidae				
Tentana castanea	W. Germany		-9.5	Kirchner, 1973
T. triangulosa	W. Germany		-10.9	Kirchner, 1973
Theridion deuticulatum	W. Germany		-11.4	Kirchner, 1973
T. notatum	W. Germany		-26.1	Kirchner, 1973
T. tepidariorum	W. Germany		-8.2	Kirchner, 1973

[1] Thermal hysteresis factors present.

Thermal-hysteresis factors are present in the hemolymph of several overwintering spiders (Duman 1979, Husby and Zachariassen 1980, Duman and Horwath 1983). These proteins produce a thermal hysteresis between the freezing and melting points and are similar in this respect to antifreeze proteins in polar fishes and some insects. Recently, Zachariassen and Husby (1982) have hyposthesized that these factors may function to enhance supercooling capacity by absorption to the surface of embryo ice nuclei and, thereby, prevent additional growth of the ice crystal. Additional studies are needed in order to determine the general significance of thermal-hysteresis factors in relation to mechanisms of cold-hardening in spiders.

Terrestrial arthropods from thermostable habitats generally lack the capacity for compensatory acclimation of respiration rate, whereas ones from variable habitats may possess considerable potential for adjustment (Hazel and Prosser 1974). Metabolic studies related to overwintering in spiders have produced varying results. A seasonal decrease in oxygen consumption has been reported for *Pisaura mirabilis* (Dondale and Legendre 1971) and *Araneus cornutus* (Kirchner 1973). This decrease may represent a state of winter diapause similar to that commonly observed in insects (Dondale and Legendre 1971). On the other hand, no evidence for seasonal acclimation of respiration rate was observed in spiderlings of *Argiope aurantia*, a species which overwinters in exposed sites above the ground (Riddle and Markezich 1981). However, laboratory studies suggest a potential for metabolic compensation since low temperature acclimation elevated the respiratory rate of spiderlings with respect to animals held at higher temperatures. Several species studied by Anderson (1970) respond to acclimation at 30°C by reducing oxygen consumption, but did not respond to low temperature acclimation at 10°C by increasing the metabolic rate. The results of our study suggest a lack of compensatory change in *A. aperta.*

The capacity for cold-hardening and the limit of cold temperature tolerance are often closely correlated with the overwintering microhabitat. Spiders which overwinter above the ground on vegetation or beneath the bark of dead standing trees possess the greatest cold tolerance (Kirchner 1973). Cave dwelling or species overwintering on the ground or in the soil are less tolerant with supercooling points between -4 and -8°C (Table 2). Furthermore, the lower lethal temperature for these species often remains essentially the same throughout the year. Edgar and Loenen (1974) suggest that the more northerly distribution of *Pardosa lugubris* relative to congeneric species is possible due to its protected hibernaculum in leaf litter.

Agelenopsis aperta is a ground dwelling species whose funnel retreat may extend 25-50cm into cracks in the substrate (Riechert *et al.* 1973). Agelenids, in general, retreat into their funnels during periods of unfavorable environmental temperature (S. E. Riechert, pers. comm.). The scorpion, *Paruroctonus aquilonalis,* also inhabits desert grasslands in New Mexico and similar to *A. aperta,* retreats into burrows in the ground (Riddle and Pugach 1976). In January with low ambient temperatures of -14°C, burrow temperatures for *P. aquilonalis* at 2 and 4 cm depth were respectively -12 and -6°C. These observations suggest that by moving only a few cm into the substrate *A. aperta* would be able to avoid environmental temperatures approaching its supercooling point.

The selection of a protected overwintering microhabitat obviates the need for seasonal mechanisms enhancing cold tolerance. The combination of a normal (i.e. non-cold-hardened) supercooling point of -8 to -10°C and movement into a moderate thermally buffered hibernaculum is likely sufficient protection for a species inhabiting southern temperature regions. In turn, this provides an explanation for the lack of mechanisms of

cold-hardening and metabolic compensation in *A. aperta* and other species overwintering in protected hibernacula.

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RESEARCH NOTES

BALLOONING BEHAVIOR OF *UMMIDIA* SPIDERLINGS (ARANEAE, CTENIZIDAE)

Ever since Baerg (1928, Entomol. News, 39:1-4) described the pre-ballooning behavior of *Ummidia carabivora* spiderlings, it has been assumed that at least some species of *Ummidia* disperse by ballooning, an uncommon mode of dispersal for mygalomorph spiders. Additional observations of pre-ballooning behavior in *Ummidia* spiderlings (J. Ragan, pers. comm.), the widely scattered distribution of *Ummidia* burrows (Coyle, F. A., 1983, J. Arachnol., 11:283-286), and the fact that distribution ranges of some *Ummidia* species bridge water gaps (Yaginuma, T., 1979, Bull. National Sci. Mus., 13:639-701; G. B. Edwards, pers. comm.) provide further support for this conclusion. The purpose of this paper is to describe, for the first time, the ballooning behavior of *Ummidia*, only the second non-araneomorph taxon that has been observed ballooning (Coyle, *ibid.*).

The 100-150 *Ummidia* spiderlings, clustered on top of a 0.9 m tall tombstone, were discovered by Sandra and Matthew Beachy at 1045 hr on 7 April 1984 in a graveyard on a flat grassy knoll just below my home five miles south of Cullowhee, North Carolina. During the period of observation (1100-1345 hr) I was assisted by Lloyd, Phillip, and Matthew Beachy, and my son, Alec. During this period the air temperature rose from 14-20°C, there were no clouds, and there were frequent gusts of light wind, ranging up to perhaps 20 knots and variable in direction (but primarily from the north). A single 2-3 mm wide band of multiple draglines, presumably marking the approach route of the spiderling brood, extended from the base of the tombstone northward through the grass for only 1.5 m before disappearing. Careful searches over a 10 m² area on this side of the tombstone failed to reveal the maternal burrow.

Early in the observation period almost all the spiderlings were clustered at each end of the central apical ridgeline formed at the junction of the two inclined (45°) surfaces that formed the top of the tombstone. As time passed, however, more and more of these spiderlings walked about, primarily along the ridgeline and edges of the top surface of the tombstone, always trailing draglines. Later observation of two of these spiderlings alive under a stereomicroscope confirmed that this dragline is a flat band of numerous fibers issuing from spigots on both sides of the spinning field. During the strongest gusts of wind the spiderlings would stop walking and "hug" the surface of the stone.

Ballooning activity commenced about 1115 hr and continued until the last spiderling departed at 1345 hr. Ballooning was accomplished in the following manner: The spiderling would move to an edge of the tombstone's top surface, tilt its cephalothorax upward, extend its pedipalps and first two pairs of legs off the substrate and out over the edge, and drop (or be blown off) a few to about 30 cm on its dragline (Fig. 1A). The breeze would push and lift the spiderling and its dragline up towards the horizontal and away from the attachment point as the dragline lengthened (Fig. 1B-1C). Eventually, after a few to several seconds, the lengthening dragline would incline slightly above the hori-
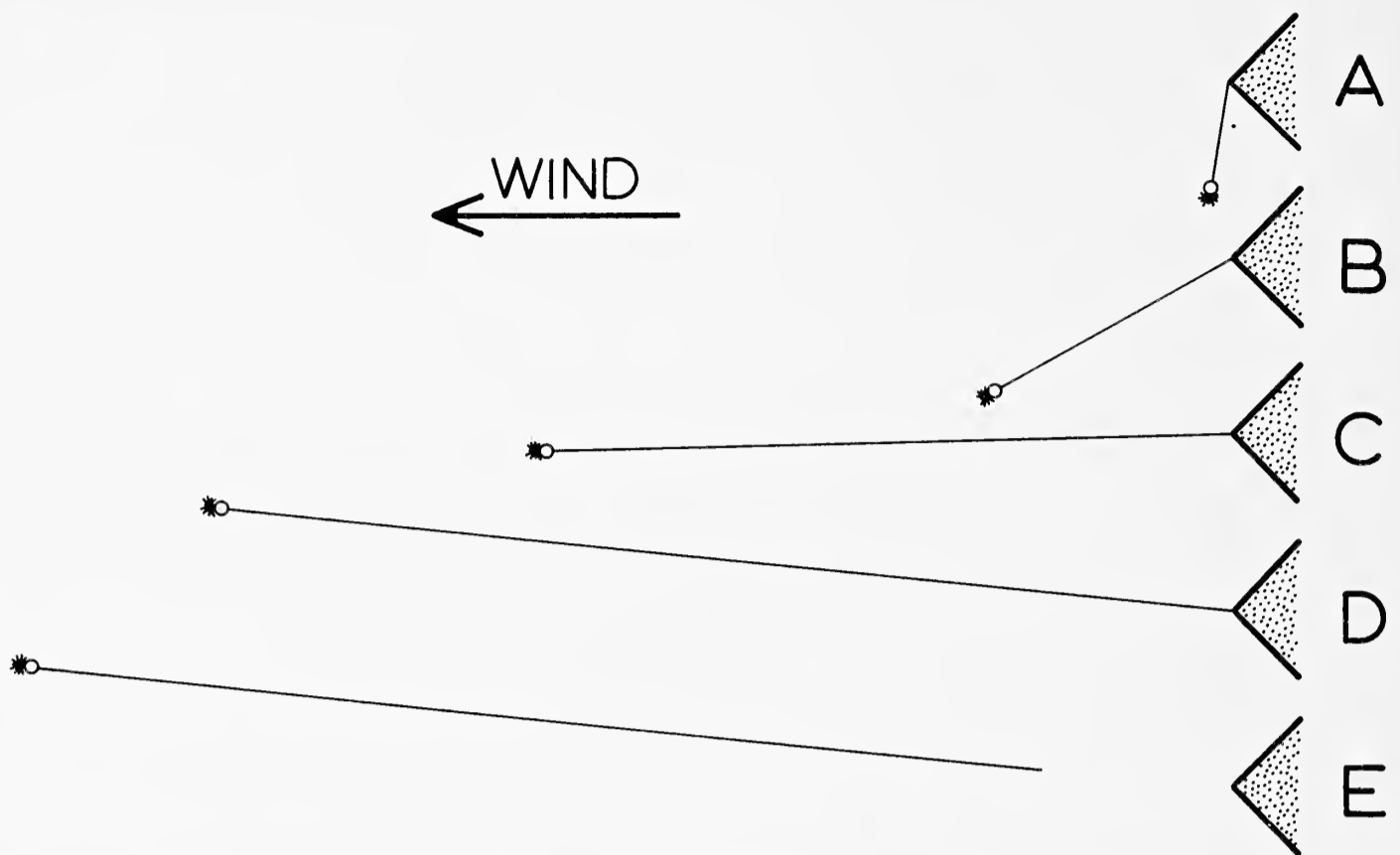
Fig. 1.—Diagrammatic representation of ballooning method of *Ummidia* spiderlings: A, Spiderling drops on dragline from edge of launching surface; B-D, Wind pushes spiderling away from launch point, and, as dragline lengthens, spiderling and dragline are lifted to and then above horizontal; E, Dragline breaks near attachment point and spiderling drifts downwind.

zontal (Fig. 1D) and break at or near the attachment substrate so that the spiderling would be airborne (Fig. 1E), drifting off in a slightly upward trajectory. Close observation failed to reveal any silk fibers issuing from the spinnerets other than those fibers that composed the dragline. Successful launchings like this were observed very infrequently. More commonly, after dropping on a dragline in the manner just described, the spiderling was either blown against the tombstone's surface (after which it ascended to repeat the launching process) or the spiderling drifted to the ground before the lengthening dragline could be lifted to the horizontal.

Although the method of ballooning is the same, the launching success of these *Ummidia* spiderlings was not as great as that of *Sphodros* spiderlings I have observed ballooning (Coyle, *ibid.*). Whether this low launching success is typical of *Ummidia* and is due to a heavier body (Coyle, F. A., M. H. Greenstone, A. L. Hultsch and C. E. Morgan, in prep.), a heavier dragline, some other inherent constraint, or whether it was due to the greater fluctuation in wind velocity and direction, is not clear. *Ummidia* spiderling draglines appear to have a higher tensile strength than those of *Sphodros* since the *Ummidia* draglines tended to become much longer before breaking (one was 6 m long) in spite of the higher wind velocities.

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SPIDERLING SURVIVAL IN A *MANTISPA* (NEUROPTERA, MANTISPIDAE) INFESTED EGG SAC

Larvae of the insect subfamily Mantispinae (Neuroptera, Mantispidae) are obligatory predators on the eggs of spiders (Redborg 1983). A first instar mantispid must gain access to spider eggs by one of two methods; either the larva boards a female spider and descends into the egg sac during construction, or it locates and penetrates an egg sac that has already been formed (Redborg and MacLeod 1984).

The survival of the eggs and subsequent spiderlings would appear to be nonexistent or very limited once a mantispid larva has successfully entered a spider egg sac, as indicated by previous researchers. No spiders survived from three egg sacs of *Scytodes* sp. which were separately preyed upon by larvae of *Mantispa fuscicornis* Banks (Gilbert and Rayor 1983). An egg sac of *Peucetia viridans* found by Killebrew (1981) contained a *Mantispa* cocoon which filled the entire space of the egg sac, and it is therefore assumed no eggs or spiderlings survived. Valerio (1971) studied *Mantispa viridis* Walker preying upon *Achaearanea tepidariorum* and noted that the mantispid almost always devoured all of the spider eggs and only when the number of eggs was sufficiently high, would a few remain intact and survive naturally. Limited spiderling survival was also observed by Capocasale (1971) with 15 juvenile *Lycosa poliostoma* surviving the larva of *Mantispa decorata* Erichson. Within this egg sac, around 300-400 dehydrated eggs were also found.

However, large numbers of spiderlings can survive in an infested egg sac. On September 27, 1983, a female *Lycosa rabida* Walckenaer with an egg sac was collected from a weedy field in Wharton, Texas. The *Lycosa* egg sac was opened on October 5 and contained 367 live spiderlings plus one mantispid cocoon. All spiderlings appeared healthy and scrambled from the egg sac when it was opened. An adult *Mantispa interrupta* Say subsequently emerged from the cocoon on October 8. Measurements were taken of the following structures to indicate adult size: head capsule width 2.8 mm; pronotal length 5.3 mm; and forewing length 17.7 mm.

This contrast between numerous spiderling survival versus minimal or no spiderling survival may be the result of one or a combination of several factors.

It is not known whether *M. interrupta* is an obligate spider boarder, an obligate egg sac penetrator or a facultative spider boarder/egg sac penetrator although larvae will board lycosids (Viets 1941). If the species is an egg sac penetrator, and the larva entered the egg sac an appreciable amount of time after it had been formed, then the failure to consume all of the eggs may be related to embryonic development. Spiderling eclosion may have occurred before some of the embryos could have been eaten (Redborg pers. comm.).

Spiderling survival may also relate to the larva's ability to locate all of the spider eggs. Under laboratory conditions, *Mantispa uhleri* Banks larvae will occasionally end up surrounded by empty, stuck-together chorions from eggs that it has eaten and may be unable to locate more viable eggs (Redborg pers. comm.).

Another explanation of spiderling survival may be based on a density dependent factor. The three *Scytodes* egg sacs studied by Gilbert and Rayor (1983) contained only

31, 37 and 38 eggs, yet that was a sufficient amount of food for *M. fuscicornis* to complete development to the adult stage. The survival of the 367 *L. rabida* spiderlings not fed upon by the *M. interrupta* larva probably represents a surplus of prey not required by the predator during development. A *Mantispa* species may have a prey resource range whereby a minimum-maximum number of spider eggs would fulfill the necessary nutritional requirements for biological development. Based upon the limits of this single observation, it appears plausible that the probability of any spiderlings surviving a *Mantispa* infestation would be dependent upon the total number of eggs within the sac. A spider species producing an egg sac with relative large numbers of eggs should be more likely to produce progeny than a species laying only a few eggs in a sac if both were to become infested.

I would like to thank Dr. William B. Peck for identifying the *Lycosa rabida* and graciously providing English translations from the Spanish manuscripts. A thanks also to Dr. Kurt E. Redborg for confirming the identity of *Mantispa interrupta* and commenting on an early draft of the manuscript.

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THE SYSTEMATICS OF THE FAMILY STERNOPHORIDAE
(PSEUDOSCORPIONIDA)

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ABSTRACT

A systematic revision of the family Sternophoridae is presented. Three genera are recognized: *Garyops* Banks, *Idiogaryops* Hoff and *Afrosternophorus* Beier; the latter is given full generic status. These genera are distinguished solely on the female genitalia. The following generic synonymies are proposed (junior synonym first): *Sternophorus* Chamberlin = *Garyops; Sternophorellus* Beier = *Afrosternophorus; Indogaryops* Sivaraman = *Afrosternophorus*. The following species are synony-mized with *A. ceylonicus* (Beier): *Sternophorus transiens* Murthy and Ananthakrishnan, *S. indicus* Murthy and Ananthakrishnan, *S. montanus* Sivaraman, *S. femoratus* Sivaraman, *S. intermedius* Sivara-man and *Indogaryops amrithiensis* Sivaraman. Four new species are proposed: *Afrosternophorus anabates* (Australia), *A. fallax* (Vietnam), *A. nanus* (Australia) and *A. xalyx* (Australia). *Garyops* contains *depressus* Banks, *sini* (Chamberlin), *centralis* Beier and, possibly, *ferrisi* (Chamberlin). *Idiogaryops* consists of *paludis* (Chamberlin) and *pumilus* (Hoff). *Afrosternophorus* contains *aethiopi-cus* (Beier), *anabates,* new species, *araucariae* (Beier), *cavernae* (Beier), *ceylonicus* (Beier), *chamberlini* (Redikorzev), *cylindrimanus* (Beier), *dawydoffi* (Beier), *fallax,* new species, *grayi* (Beier), *hirsti,* (Chamberlin), *nanus,* new species, *papuanus* (Beier) and *xalyx,* new species. Two species-groups are proposed in each of the two genera *Idiogaryops* and *Afrosternophorus* to accommodate species with differing trichobothrial numbers. Male genitalia was found to be a useful adjunct to traditional charac-ters, and a detailed description of the male genitalia of *A. hirsti* is presented. Post-embryonic develop-ment, biogeography and possible evolutionary pathways are discussed.

INTRODUCTION

Members of the family Sternophoridae are small to medium sized pseudoscorpions that are immediately recognizable by the possession of an extensive pseudosternum, a feature indicated by their family name. Their pale colour and corticolous habits combine to render them comparatively rare in collections.

Six sternophorid genera or subgenera have been described to date, but several inconsis-tencies in the literature indicate that the generic classification is apparently artificial and in disarray. In particular, authors have relied heavily on the number of chelal trichobo-thria and the form of the carapace as generic characters, and ignored genitalic features, even though the latter have proved to be extremely valuable in the delimitation of genera in other pseudoscorpion families, such as the Chernetidae. For example, females of

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the Mexican *Sternophorus sini* Chamberlin (the type species of the genus) have genitalia with two spurred, median cribriform plates (Chamberlin 1923, 1931), whereas *S. hirsti* Chamberlin, and other Australian sternophorids have only one unspurred plate. Likewise, females of *Garyops depressa* Banks (the type species of the genus) have two spurred, median cribriform plates (Hoff 1963), whereas *G. pumila* Hoff and *Idiogaryops paludis* (Chamberlin) have two unspurred plates (Hoff 1963). Thus, the present study was aimed at clarifying the taxonomy of this family which appeared to be unreliable, at least as far as the female genitalic characters were concerned.

MATERIALS AND METHODS

Much of the material used in this study was borrowed from overseas institutions which are listed in the Acknowledgments section of this paper. My own material has been lodged in the following depositories (see Acknowledgments for abbreviations): Australian Museum, Sydney (AM); Australian National Insect Collection, Canberra (ANIC); MHNG; MV; Museums and Art Galleries of the Northern Territory, Darwin (NTM); Queensland Museum, Fortitude Valley (QM); and VAM.

My personal accession numbers (e.g. MH237.01) basically follow the system employed by other workers, and are used to refer to the exact specimen upon which diagrams and observations are made. The number to the left of the decimal point refers to the lot number, and the number to the right of the decimal point refers to each individual specimen.

Specimens were examined in two ways, depending on curatorial preferences. Permanent microscope slides were made as follows: specimens were removed from 75% ethanol, an incision was made along one pleural membrane, and the specimens were then cleared overnight at room temperature in 10% potassium hydroxide, dehydrated through a graded ethanol series, and mounted on microscope slides in Euparal (Chroma-Gesellschaft, Schmid GmbH and Co.). One chela of some specimens was dissected off and mounted on a cavity slide to facilitate the inspection of the trichobothrial pattern. Temporary mounts were made by clearing whole specimens in clove oil or lactic acid and mounting on slides in glycerol.

Each specimen was measured with a micrometer eyepiece in a compound microscope, measurements were made in accordance with those discussed by Chamberlin (1931), except for coxa I length (Harvey 1981a) [the "accessory length" of Chamberlin (1931)]. When appendages, especially chelae, were not lying in a horizontal plane, Pythagoras' theorem was employed to determine their true length (Bird et al. 1979). Appendages were often observed to be slightly larger on one side of the body than the other. Hence, measurements were taken from both sides (to the nearest 0.005 mm, except for body length which was taken to the nearest 0.01 mm) to fully record the range of variation.

Benedict and Malcolm (1977) have recently suggested a modified system of reference lines for obtaining accurate measurements of the pedipalpal chela since they found it "nearly impossible to secure reliable measurements of the chela when it remains attached to the palp." They preferred taking measurements from a lateral aspect, rather than a dorsal or ventral one as suggested by Chamberlin (1931). I had no trouble measuring undissected specimens (including large, heavily sclerotized garypids) and Chamberlin's original reference lines are used here. There seems to be a serious lack of uniformity between different workers, and consequently, this makes the comparison between the

different descriptions very difficult. For example, some authors present chelal measurements including the pedicel, whereas others provide them without the pedicel. Mahnert and Muchmore have obviously tried to rectify this problem by providing measurements of the pedicel, but I have found that this is slightly misleading because adding the length of the pedicel to the length of the chela (without pedicel) does not provide the length of the chela (with pedicel). I have followed Chamberlin's (1947 and subsequent papers) system by providing the length of the chela with the pedicel and without the pedicel. Similarly, the ratios of the chela are given with the pedicel and without the pedicel. For the sake of uniformity, all workers should present both of these measurements.

The number of setae within the male genital atrium is given in brackets (e.g. [4-6]), and the number of setae associated with the spiracular plate is shown in parentheses. The abbreviation for a tergal or sternal tactile seta is T. The dimensions of females are in parentheses and follow those of males. The numerator refers to the length of a segment, and the denominator refers to its width.

Drawings were made with the aid of a Leitz camera lucida attached to a Leitz Orthoplan microscope or with a Leitz Prado photographic slide projector with a Prado microscope slide attachment.

The spelling of various southeast Asian localities was found to vary from atlas to atlas, and to differ from the spelling used by Redikorzev (1938) and Beier (1951). Thus, the spelling advocated by the U.S. Board on Geographic Names was adopted in this study (Table 1).

When portions of the locality data were known from published records, but were not present on locality labels, they are shown in brackets.

Abbreviations for chelal trichobothria and cheliceral setae follow those employed by Chamberlin (1931), and are commonly used in pseudoscorpionid literature. Genitalic abbreviations follow Legg (1974b, 1975a), but are listed here for convenience:

aa	anterior apodeme
da	dorsal apodeme
dag	dorsal anterior gland
dmgs	dorsal median genital sac
ejc	ejaculatory canal
ejca	ejaculatory canal atrium
f	foramen
hp	hyaline plate
la	lateral apodeme
lcp	lateral cribriform plate
lgs	lateral genital sac
lr	lateral rod
mcp	median cribriform plate
mgs	median genital sac
pdg	posterior dorsal gland
pvdv	posterior ventral diverticulum
te	testis
vdv	ventral diverticulum

Two females of *Afrosternophorus hirsti* were critical point dried, mounted on points and gold coated for examination in a JEOL JSM-35C Scanning Electron Microscope.

Table 1.—Gazetteer of southeast Asian localities. The first column depicts the spelling used by Redikorzev (1938) and Beier (1951), and the second column shows those used by the U.S. Board on Geographic Names. The latter are used in this paper.

KAMPUCHEA		
Beng Mealea	Phumĭ Boĕng Méalea	13°28′N 104°14′E
Prah Khan	Prasat Preăh Khăn	13°24′N 104°45′E
Phailin	Pailĭn	12°51′N 102°36′E
Rusei Chrum	Roessei Chrum	11°46′N 103°04′E
Sré Umbell	Srê Āmbĕl	11°07′N 103°46′E
Réam	Phsar Ream	10°30′N 103°37′E
LAOS		
Luang Prabang	Louangphrabang	19°52′N 102°18′E
Paclay	Pak-Lay	18°12′N 101°25′E
Plateau von Boloven	Plateau des Bolovens	15°20′N 106°20′E
VIETNAM		
Plateau von Langbian	Cao Nguyên Lâm Viên	12°00′N 108°25′E
Dalat	Da Lat	11°56′N 108°25′E
Arbre-Broyé	Aṗ Tram Hahn	11°51′N 108°34′E
Krongpha	Thôn Sông Pha	11°50′N 108°42′E
Insel Phu-Quoc	Đảo Phú Quốc	10°12′N 104°00′E

FAMILY STERNOPHORIDAE CHAMBERLIN

Sternophorinae Chamberlin 1923:370.
Sternophoridae Chamberlin 1931:238, 1932a:140; Beier 1932:15, 1954b:136; Hoff 1956:3, 1963:2; Murthy and Ananthakrishnan 1977: 117-118; Sivaraman 1981:313.

Diagnosis.—This family may be easily distinguished from other pseudoscorpion families by the extensive pseudosternum (Fig. 10); other supplementary characters include: carapace posteriorly angulate and eyeless (e.g., Fig. 12); venom apparatus present in both chelal fingers (e.g., Fig. 15); accessory teeth absent from chelal fingers (e.g., Fig. 15); legs monotarsate and homofemorate, the junction of the femora perpendicular to the long axis of the leg (Fig. 11); and pedal tarsi without elevated slit sensilla.

Description.—Pedipalps and anterior portion of carapace red brown, terga with pale fuscous stripes, remainder of body pale. Pedipalps, carapace and often legs with striations and ovoid sculpturing. Cheliceral palm with four setae, *ls* absent, *bs* short and blunt (Fig. 9); moveable finger with one subdistal seta; flagellum of four blades, anterior blade very broad and often with several spinules; galea of male always simple, occasionally with one or two small rami; galea of female always with several distinct rami. Carapace posteriorly angulate, eyeless, without transverse furrows, and with a small cucullus and cheliceral condyle. Pedipalpal femur usually with a single, often subbasal, dorsal tactile seta. Fixed chelal finger with seven trichobothria, moveable chelal finger with two or three trichobothria; *eb* and *esb* basal, adjacent, *est* about halfway between *eb* and *et, et* subdistal, *ib* and *isb* basal, adjacent, opposite *eb* and *esb, ist* about halfway between level of *esb* and *est, it* absent, *b* and *sb* subbasal, adjacent, *t* submedial, *st* absent, *sb* sometimes absent; areole shape not unusual (Fig. 4); a long seta usually present slightly proximal to *t,* approximately three quarters the length of a trichobothrium, not arising from a large areole (Fig. 1). Chelal fingers without accessory teeth; each with a mediolateral row of stout, curved, spatulate setae (Fig. 6) (usually more on moveable finger than on fixed finger); and with
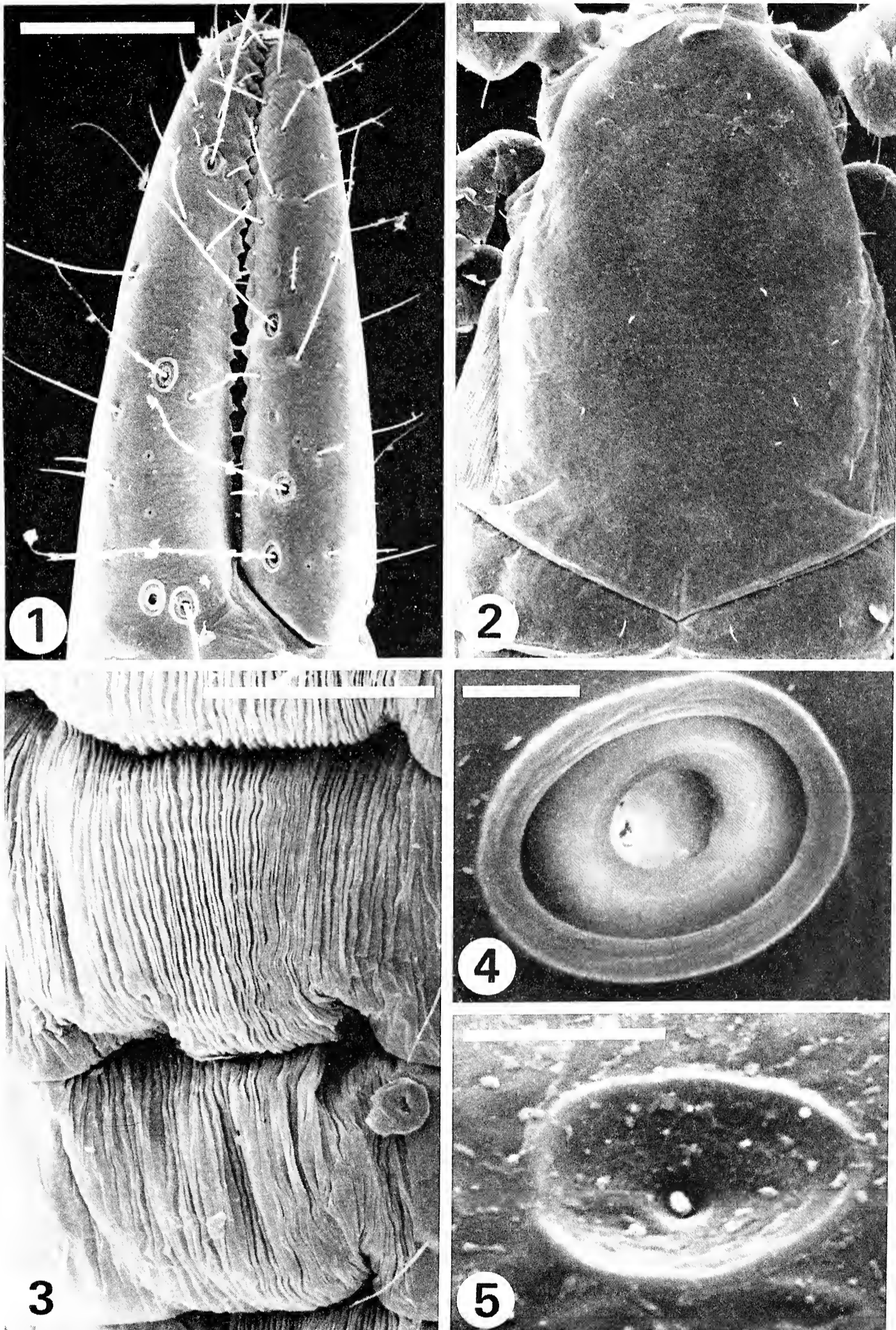
Figs. 1-5.—*Afrosternophorus hirsti* (Chamberlin), scanning electron micrographs, females: 1, lateral aspect of right chela, MH474.18; 2, dorsal aspect of carapace, MH474.17; 3, pleural membrane of segments VII-VIII, MH474.17; 4, areole of trichobothrium *sb*, MH474.17; 5, sensory pit slightly anterior to *sb*, MH474.18. Scale lines = 0.1 mm (Figs. 1-3), 0.005 mm (Figs. 4-5).
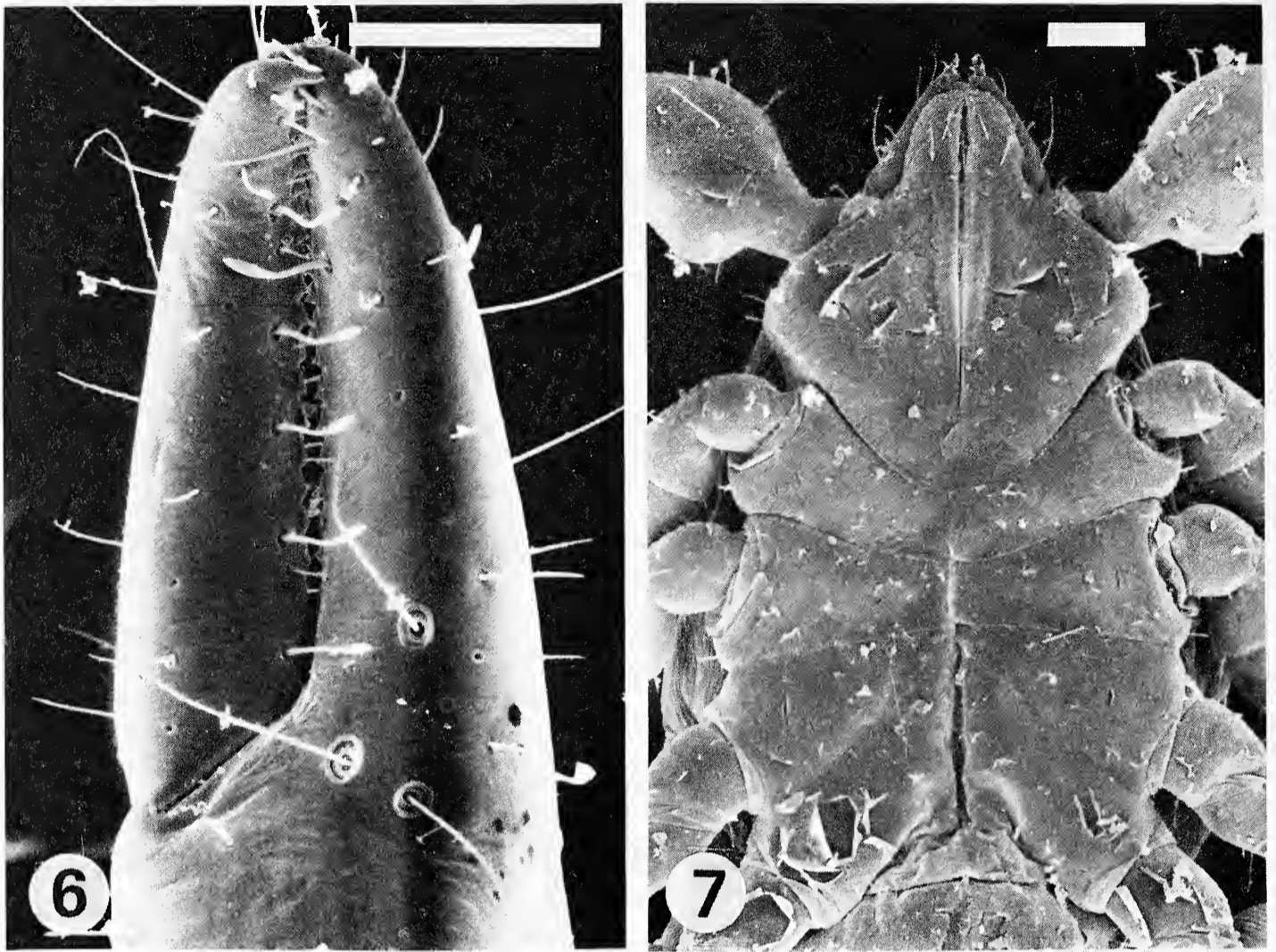
Figs. 6-7.—*Afrosternophorus hirsti* (Chamberlin), scanning electron micrographs, female, MH474.18: 6, lateral aspect of right chela; 7, ventral aspect of coxal area. Scale lines = 0.1 mm.

several sensory pits, each with a small, blunt seta (Fig. 5). Venom apparatus present in both chelal fingers, nodus ramosus midway between *et* and *est* in fixed finger, and slightly proximal to *t* in moveable finger. Pedal coxae touching in midline (Fig. 7), but with a large medial section that is unsclerotized, thus appearing as a 'pseudosternum' (Fig. 10). Legs homofemorate, junction of the femora perpendicular to the long axis of the leg; femur I always shorter than femur II; tarsi unsegmented, much shorter than tibiae; legs III and IV each with a medial, tibial tactile seta and a proximal, tarsal tactile seta (Fig. 11); tarsi without elevated slit sensilla; arolia shorter than claws. Abdominal terga and sterna not medially divided. Pleural membrane longitudinally striate (Fig. 3). Spiracles situated within pleural membrane; anterior pair of tracheae fairly long, ramifying into tracheoles when above the third or fourth coxae; posterior pair of tracheae very short, branching almost immediately (Fig. 10). Male genitalia described in detail below. Female genitalia with one or two median cribriform plates, with or without spurs, and with one pair of lateral cribriform plates. Spermathecae absent. Tergum and sternum X each with two pairs of lateral tactile setae. Tergum and sternum XI fused, with several tactile setae (because of this fusion, these setae are difficult to count with accuracy, and are simply referred to in the species descriptions with '?'). Anus terminal, anal plate oval.

Type genus.—*Garyops* Banks 1909 (= *Sternophorus* Chamberlin 1923).

Remarks.—The Sternophoridae is a remarkably uniform group that presents few characters for its subdivision. Previous authors have utilized only external morphological characters to delimit genera. These characters are insufficient to divide the family into monophyletic genera. They are discussed in detail below:
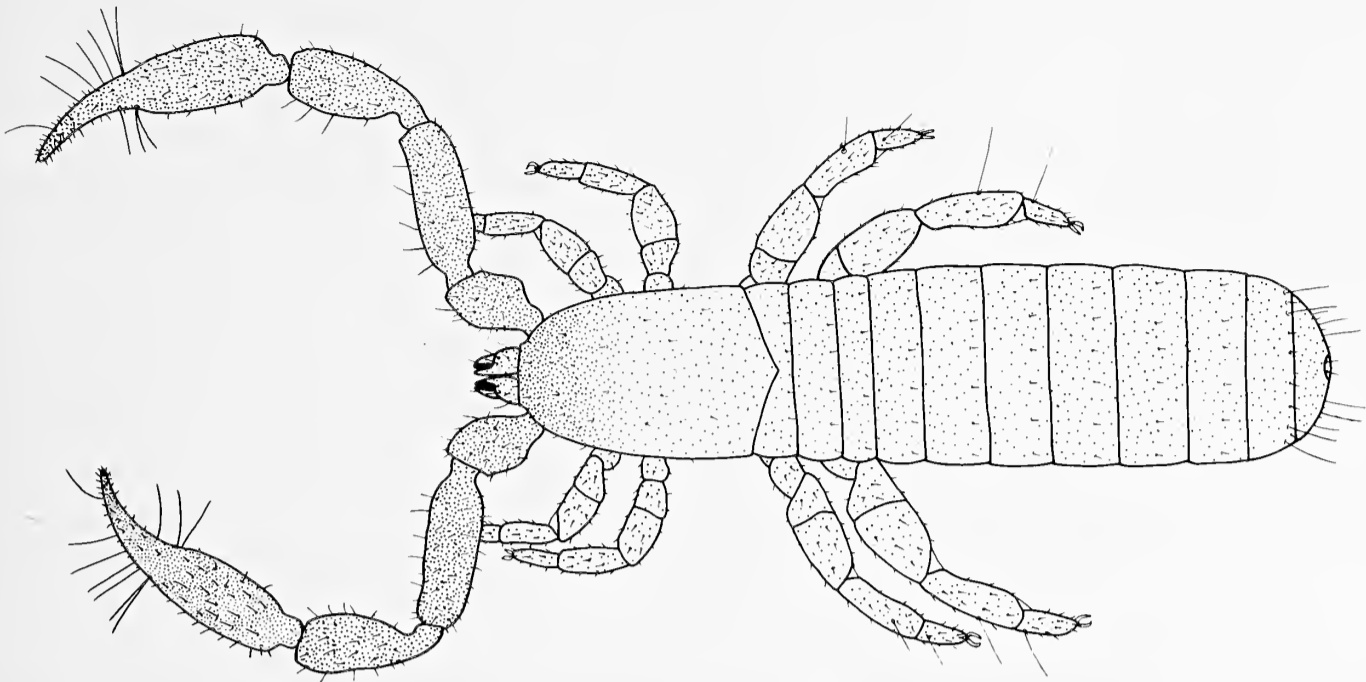
Fig. 8.—Dorsal aspect of *Afrosternophorus anabates,* new species, male holotype.

(1) Anterior constriction of the carapace: The degree of constriction of the carapace has been utilized as a major generic character by previous authors ever since Chamberlin [1931: based on Banks' (1909) misleading description of *Garyops depressus*] separated *Garyops* and *Sternophorus* on the presence or absence, respectively, of this constriction. This study has revealed that a constriction is indeed present in *S. sini* (the type species of the genus) and that the two genera cannot be separated by this criterion. Furthermore, intraspecific variation has been observed in several species, most notably in *Afrosterno-phorus dawydoffi;* some specimens possess no constriction (Fig. 95), others possess a slight constriction (Fig. 96), and others display a distinct constriction (Fig. 97). General-ly, it appears that the degree of constriction is related to the overall size of the animal. The larger species such as *A. dawydoffi, Garyops* spp. and *Idiogaryops pumilus,* and to a lesser extent, *I. paludis, A. anabates* and *A. ceylonicus,* often possess a constriction, whereas the smaller species (the remaining *Afrosternophorus* species) do not possess this constriction. Clearly then, this character is too variable to be given serious consideration as a valid generic character.

(2) Cucullus: The subgenus *Afrosternophorus* and the genus *Indogaryops* were charac-terized by their authors, Beier (1967) and Sivaraman (1981), respectively, as possessing a distinct cucullus. This study has revealed that all sternophorids possess a cucullus, and therefore, it must be rejected as a valid generic or subgeneric character.

(3) Absence of trichobothrium *sb: Idiogaryops* and *Sternophorellus* were separated from other genera by the possession of only two trichobothria on the moveable chelal finger. The type species of these two genera, *I. paludis* and *S. araucariae,* are, in all other respects, very similar to species which possess three trichobothria on this finger. The relative position of *b* and *t* of all species is the same and the only difference that can be found is the absence of *sb.* To retain different genera for species which lack one or more trichobothria has clearly extended the generic system and obscured obvious affinities. Thus, the generic limits of the sternophorid genera are herein extended to include species with either two or three trichobothria on the moveable chelal finger. Nevertheless, in accordance with the importance that is placed on trichobothria in pseudoscorpion taxon-omy, two species groups in each of two genera, *Idiogaryops* and *Afrosternophorus,* have been erected to accommodate species with different trichobothrial numbers.

Many other pseudoscorpion genera are known to include species with varying numbers of trichobothria. These include *Geogarypus* Chamberlin (Chamberlin 1930, Harvey, unpublished observations), *Synsphyronus* Chamberlin (Chamberlin 1943, Harvey, in press), *Larca* Chamberlin (Hoff 1961), *Eremogarypus* Beier (Beier, 1962, 1973a), *Anagarypus* Chamberlin (Muchmore 1982a) and *Thaumastogarypus* Beier (Mahnert 1982b), the vachoniid *Paravachonium* Beier (Muchmore 1982b), the cheiridiid *Neocheiridium* Beier (Mahnert 1982a) and the chernetid *Parachernes* Chamberlin (Muchmore and Alteri 1974). More detailed analyses of other generic complexes may well yield further genera whose trichobothrial numbers vary. Indeed, a perusal of the literature reveals that many African garypid genera are extremely similar, and that the North American garypids *Larca* and *Archeolarca* Hoff and Clawson are probably synonymous. Furthermore, the *Solinus-Aldabrinus* complex (Olpiidae) contains several genera that may eventually prove to be synonymous.

(4) Cheliceral setation: Hoff (1963) stated that the cheliceral seta *sbs* was absent in *Garyops* and *Idiogaryops.* Chamberlin (1931) indicated that *ls* was the missing seta in *Sternophorus,* and Murthy and Ananthakrishnan (1977) utilized this apparent difference to separate *Sternophorus* from the former genera. In fact, the cheliceral setation of all sternophorids is identical, and it is contended here that *ls* is the missing seta.

Thus with all of the traditional characters discarded, only the genitalic characters were found to be of any use at the generic level. Three genera are recognized herein: *Garyops, Idiogaryops* and *Afrosternophorus.* Females of *Garyops* and *Idiogaryops* possess two median cribriform plates and females of *Afrosternophorus* possess only one. Furthermore, females of *Garyops* possess lateral spurs on these plates. The generic synonymies are discussed and justified under the relevant genera.

The genus name *Garyops* has clearly been treated as feminine by Banks (1909) and subsequent authors, but Article 30a(i)(2) of the International Code of Zoological Nomenclature [as amended by the Commission in 1972 (Bull. Zool. Nomen., 29:182)] unequivocally states that a "genus-group name ending in -*ops* is to be treated as masculine regardless of its derivation or of its treatment by its original author." Only two names are affected by this rule in the genera *Garyops* and *Idiogaryops: depressa* and *pumila* are converted to *depressus* and *pumilus,* respectively.

AFFINITIES OF THE STERNOPHORIDAE

Opinions of the taxonomic position of the Sternophoridae have varied over the years. Chamberlin (1931) placed it with the Cheiridiidae and Pseudochiridiidae in the superfamily Cheiridioidea on the grounds that all three possess homofemorate legs. Beier (1954b) transferred it to the Cheliferoidea, allying it to the Goniochernetinae, when he found that *Goniochernes goniothorax* (Redikorzev) possesses not only a posteriorly angulate carapace (Beier 1932), but also a 'pseudosternum', features characteristics of the Sternophoridae. As discussed in the familial description, the 'pseudosternum' of all sternophorids is not a gap between the coxae, but a large unsclerotized region roughly in the center of the coxal area. However, the 'pseudosternum' of the goniochernetines, at least in the Australian representatives that I have examined [*Calymmachernes angulatus* Beier, *Conicochernes brevispinosus* (L. Koch), *C. crassus* Beier, *C. incrassatus* (Beier) and *C.* spp.], is an actual space between the coxae [as described by Beier (1954a) for

Calymmachernes angulatus], there being no translucent cuticle. Other chernetids examined by me, including *Chernes cimicoides* (Fabricius) and *C. hahni* (C. L. Koch), also have a small gap between coxae II and III, which often extends to coxae IV. Thus, the sternophorid pseudosternum and the gap of the Chernetidae are quite different structures and cannot be regarded as homologous.

Where, then, do the relationships of the Sternophoridae lie? The similarity to the goniochernetines can hardly be gainsaid, at least as regards the posteriorly angulate carapace, but I consider that the Goniochernetinae truly belongs in the Chernetidae and is unrelated to the Sternophoridae. Characters supporting this contention include: (1) elevated slit sensillum present on all pedal tarsi (absent in Sternophoridae); (2) venom apparatus present in moveable chelal finger only (present in both fingers in Sternophoridae); (3) chelal fingers with accessory teeth (accessory teeth absent in Sternophoridae); and (4) females with spermathecae (without spermathecae in Sternophoridae). The first three characters are considered by Muchmore (1973) to be diagnostic of the Chernetidae. Other characters include the grouping of the setae on the genital opercula (usually compact in Chernetidae; not so in Sternophoridae), the suture of the pedal femora (oblique in Chernetidae; perpendicular in Sternophoridae), the form of the male genitalia, which, although hard to define, is "chernetid-like" in the Chernetidae, quite unlike the relatively simple genitalia of the Sternophoridae, and the presence (Chernetidae) and absence (Sternophoridae) of a medial division of the abdominal terga and sterna (W. B. Muchmore, pers. comm.).

Therefore, I concur with Heurtault (1983) that the Sternophoridae is not closely related to the Goniochernetinae. This does not solve the problem of which superfamily they belong to, and I consider that the placement of the Sternophoridae into either the Cheiridioidea or the Cheliferoidea is a conjectural matter which cannot be resolved at present. Further research into areas such as male genitalia may lead to a more stable classification.

GENITALIA

Pseudoscorpion genitalia have not been frequently studied, but the recent papers by Legg (1973, 1974a, b, c, 1975a, b, c) have allowed for a comprehensive understanding of the complex morphology of many British species of the order.

As shown in the taxonomic section, the three sternophorid genera are distinguishable by female genitalic characters alone. Furthermore, the male genitalia often delimit taxa at the specific level.

Female genitalia.—The most obvious structures are the cribriform plates, which are porous plates of unknown function (Legg 1974c). All taxa possess one pair of lateral cribriform plates *(lcp)* (e.g., Fig. 16). One genus, *Afrosternophorus,* also possesses one median cribriform plate *(mcp)* (e.g., Fig. 85), whereas *Idiogaryops* and *Garyops* possess two (e.g., Figs. 16, 45). Furthermore, the latter possesses a unique pair of lateral spurs or projections on these plates (e.g., Fig. 16). The significance or function of these spurs is unknown, and the study of them may be of extreme interest.

Spermathecae are present in most "higher" families such as the Cheliferidae, Chernetidae and Atemnidae (Chamberlin 1931), yet are absent or significantly reduced in the Chthoniidae, Neobisiidae and Cheiridiidae (Legg 1975b, c). Detailed examination of all sternophorid genera revealed an absence of spermathecae. The "spermathecae" of *Garyops sini* figured by Chamberlin (1931: Fig. 52o, as *Sternophorus sini*) are, in fact, the median glands (cf. Legg 1974c: Fig. 1).

Male genitalia.—The male genitalia of pseudoscorpions consist of a complex series of sclerotized apodemes and rods, which serve as attachment sites for muscles and as support for the genital atrium (Legg 1975a). As shown in the taxonomic section, the morphology of the male genitalia was often seen to vary significantly at the species level. Given this variation, and the fact that male sternophorid genitalia have not been studied in detail before, a relatively comprehensive account of the armature and glands is presented. Although the genital armature was examined in every species in which males were known, the soft portions were examined only in *Afrosternophorus hirsti* (Chamberlin) (Fig. 51).

Chamberlin (1923) figured the male genitalia of *Garyops sini* (as *Sternophorus sini*), but my observations on material of this species indicate that his diagram is not entirely accurate. Chamberlin (1932a) noted that he could distinguish between the four sternophorid species known to him, but refrained from quantifying these differences.

All nomenclature follows that of Legg (1975a), but is presented in the Materials and Methods for convenience.

(1) Genital opercula and aperture: As with all pseudoscorpions (Legg 1975a), the anterior and posterior genital opercula are formed from the opisthosomal sternites II and III. An invagination between these plates forms the genital atrium. Within this atrium are several (2-8) small setae. The genital aperture is relatively small, as in most of the Monosphyronida.

(2) Genital armature: Associated with the genital atrium are a series of apodemes and rods which constitute the genital armature (Legg 1975a). The lateral apodeme *(la)* extends laterally and sometimes may be curved anteriorly; these apodemes meet in the midline. Arising anteriorly from the dorsal portion of the armature of some species is an anterior apodeme *(aa)*. This varies considerably in shape and size, and in *A. hirsti* it is brush-like (Fig. 56). The paired dorsal apodemes *(da)* are usually elongate and acute, but several species (in two genera) show various modifications in size and shape. Between the dorsal apodeme and the lateral apodeme is a clear area of cuticle, here termed the hyaline plate *(hp)*. It is often difficult to observe except under high magnification and strong illumination. The lateral rod *(lr)* forms a complete circle, and is often broadest ventrally. It possesses a ventral midpiece that is often terminally bifurcate. The lateral rod often may lie anterior to the genital armature, and thus give a totally different appearance to the genitalia. Such a situation occurs in *A. aethiopicus* (Beier) (Fig. 52), *A. ceylonicus* (Beier) (Fig. 53) and *Idiogaryops* sp. (Fig. 33). Although it may represent distortion arising during the slide making process, it appears that this is not the case, because the many spirit preserved specimens of *A. ceylonicus* that I have examined all possess this condition. Often one, or sometimes two, foramina *(f)* occur in the area where the lateral rod and lateral apodeme fuse. Some species of *Garyops* and *Idiogaryops* also possess a foramen where the lateral apodemes join.

(3) Accessory glands, genital sacs and ventral diverticula: Extending posteriorly from the genital armature is the posterior dorsal gland *(pdg)*. As noted by Legg (1975a), it occurs in all pseudoscorpion families that have been examined. Lying anterior to the genital armature is the dorsal anterior gland *(dag)*; this gland is bilobed in most pseudoscorpions, yet is absent in the Cheiridiidae (Legg 1975a). The single lobed structure found in sternophorids may be an intermediate stage, but much more work needs to be completed before such a statement can be verified. Ventral anterior glands are not present.

A pair of lateral genital sacs *(lgs)* originate from the distal ends of the lateral apodemes. A bilobate median genital sac *(mgs)* lies posterior to the genital armature, and is

connected to the posterior ventral diverticulum *(pvdv)* via the long, thin duct of the median genital sac *(dmgs)*. The ventral diverticulum *(vdv)* is semicircular, and the anterior edge is often gently sinuate.

(4) Testis, ejaculatory canal atrium, and ejaculatory canal: The testis *(te)* extends posteriorly into the abdomen and terminates bluntly. The ejaculatory canal atrium *(ejca)* is cup-shaped and lies anterior to the genital armature. It is connected to the genital atrium by the ejaculatory canal *(ejc)*.

POST-EMBRYONIC DEVELOPMENT

Pseudoscorpions characteristically possess four post-embryonic stages, termed protonymph, deutonymph, tritonymph and adult. Apart from the obvious fact that each stage is slightly larger than the preceding one, the only other apparent differences are the increase in the number of setae and the development of genitalia at the final moult. It is the first difference that will be addressed now, since the acquisition of genitalia (or, at least, the sclerotized portions) is apparently confined to the final moult, and does not exhibit sequential development. In particular, the number of cheliceral setae and chelal trichobothria will be examined.

Cheliceral setae.—Little may be said concerning the development of the cheliceral setae, except that protonymphs differ from the adult and remaining nymphal stages by lacking *gs*.

Chelal trichobothria.—The chelal trichobothria of pseudoscorpions are added sequentially during their ontogeny, and provide a means for recognizing the three nymphal stages (Vachon 1934). Vachon (1936) found that for species in which adults possess eight trichobothria on the fixed chelal finger and four trichobothria on the moveable chelal finger (herein abbreviated to 8/4), the nymphal complement was 3/1 for protonymphs, 6/2 for deutonymphs, and 7/3 for tritonymphs. This has subsequently been confirmed for many genera of most pseudoscorpion families, even though different trichobothria may be added at each moult (Mahnert 1981). Furthermore, Vachon (1936) and Nelson (1982) have found that even though adults of *Microbisium dumicola* (C. L. Koch) and *M. confusum* Hoff (Neobisiidae), respectively, possessed a reduced trichobothrial complement of 7/3, the nymphs retained a complement typical of those species whose adults possessed 8/4. [Beier (1963) and Gabbut (1969) have expressed doubt as to the validity of *M. dumicola* and Vachon's material may belong to a different species].

Adults of all known sternophorid species possess a reduced complement of either 7/3 (*Garyops* spp., *Idiogaryops pumilus* species group and *Afrosternophorus aethiopicus* species group) or 7/2 (*I. paludis* species group and *A. araucariae* species group). Unfortunately, the nymphal stages of only four sternophorid species are known. The first observations were made by Murthy and Ananthakrishnan (1977: Fig. 40B), who demonstrated that tritonymphs of *A. ceylonicus* (as *Sternophorus transiens*) possessed 7/2, whereas the adults possessed 7/3. This situation can now be confirmed in three other species of the *aethiopicus* species group, *A. hirsti, A. nanus* and *A. anabates*. Furthermore, the deutonymphs of the former species and the protonymphs of *hirsti* and *anabates* are known. Following the format of Vachon (1936) and Gabbut and Vachon (1965, and subsequent papers), the order in which the trichobothria are added at each moult in *A. hirsti* (the only species for which all nymphal stages are known) is summarized in Table 2. Following the format of Vachon (1973), it may be summarized as follows, where the

Table 2.—The order in which trichobothria are added at each moult in *Afrosternophorus hirsti* (Chamberlin).

	protonymph	deutonymph	tritonymph	adult
moveable finger series	*t*	*b*	–	*sb*
fixed finger, external series	*eb, et*	*est*	*esb*	–
fixed finger, internal series	*ib*	*isb, ist*	–	–

stage at which a certain trichobothrium appears is shown as a subscript (A = adult, N3 = tritonymph, N2 = deutonymph, N1 = protonymph):

$$t_{N1} \; st. \; sb_A \; b_{N2}/et_{N1} \; est_{N2} \; esb_{N3} \; eb_{N1}/it. \; ist_{N2} \; isb_{N1} \; ib_{N2}$$

Notwithstanding the absence of *st* and *it*, this is similar to Mahnert's (1981) pattern for the Cheliferinea (Monosphyronida), to which the Sternophoridae currently belongs.

The reduced trichobothrial complement of all sternophorids makes it difficult to ascertain which trichobothria are absent. My interpretation that *it* and *st* are the missing trichobothria may need modification as our knowledge of pseudoscorpion trichobothriotaxies increases.

Although *A. hirsti* is the only sternophorid species to be studied in detail, there is no reason to assume that the situation will be any different for the other species whose adults possess 7/3. The nymphs of those species which possess a reduced adult complement of 7/2 *(I. paludis, A. araucariae, A. cavernae, A. fallax* and *A. xalyx)* will probably possess a slightly different pattern.

KEY TO GENERA OF STERNOPHORIDAE

1. Females with two median cribriform plates 2
   Females with one median cribriform plate . . . . *Afrosternophorus* Beier

2. Female median cribriform plates with a pair of lateral spurs. . . . . *Garyops* Beier
   Female median cribriform plates without lateral spurs . . . . *Idiogaryops* Hoff

Genus *Garyops* Banks

Garyops Banks 1909:305 (in part); Chamberlin 1931:238 (in part); Beier 1932:18 (in part); Hoff 1963:2-3 (in part). Type species by original designation and monotypy *Garyops depressus* (pro *depressa*) Banks 1909.
Sternophorus Chamberlin 1923:371, 1931:238-239; Beier 1932:16 (in part); Murthy and Ananthakrishnan 1977:18 (in part). Type species by original designation and monotypy *Sternophorus sini* Chamberlin 1923. NEW SYNONYMY.

Distribution.—Dominican Republic; El Salvador; Mexico; Florida, U.S.A. (Map 1).
Diagnosis.—Females with two spurred, median cribriform plates. Fixed chelal finger with seven trichobothria, moveable chelal finger with three trichobothria.
Subordinate taxa.—*Garyops depressus* Banks, *G. sini* (Chamberlin), *G. centralis* Beier, *G. (?) ferrisi* (Chamberlin).
Remarks.—Chamberlin (1931) separated *Garyops* and *Sternophorus* on the presence or absence, respectively, of an anterior constriction of the carapace. The degree of narrowing

Map 1.—North America showing known distribution of *Garyops depressus* Banks (circles), *G. sini* (Chamberlin) (squares), *G. centralis* Beier (triangle) and *G.* (?) *ferrisi* (Chamberlin) (star) (state record only). Open symbols represent literature records only.

in *G. depressus* was unknown to Chamberlin, and he overlooked the slight constriction evident in *S. sini*, the type species of *Sternophorus*. This study has revealed that the form of the carapace of the two genera is not different, and furthermore, that females of both genera possess unique spurs on the median cribriform plates. On this basis, *Garyops* and *Sternophorus* are here synonymized. Hoff (1949, 1963) and Hoff and Bolsterli (1956) suggested that the two genera may be identical, yet refrained from formally synonymizing them.

Garyops depressus Banks
Figs. 9-16, 28, 34, 39; Map 1

Garyops depressa Banks 1909:305-306 (in part); Beier 1932:18; Hoff 1958:19, 1963:4-7, Figs. 1-4; Beier 1976:46; Brach 1979:34-38.
nec *Garyops depressa* Banks: Hounsome 1980:85 (misidentification).

Types.—Lectotype female (designated by Hoff 1963:4), paralectotype male, paralectotype female, Punta Gorda, Charlotte County, Florida, U.S.A., date? [A. T. Slosson], MCZ (slides and spirit).

Distribution.—Florida, U.S.A.; Dominican Republic (Map 1).

Diagnosis.—Female galea with three distal rami. Male genitalia with long, acute, dorsal apodemes. Chela (with pedicel) 0.97 to 1.18 (male), 1.015 to 1.19 mm (female) in length, 3.96 to 4.44 (male), 3.78 to 4.37 (female) times longer than broad.

Description.—Supplementary to Hoff (1963). Chela (with pedicel) 3.96 to 4.44 (male), 3.78 to 4.37 (female) times longer than broad. Carapace (Fig. 12) 1.23 to 1.38 (male), 1.34 to 1.35 (female) times longer than broad. Male genitalia (Fig. 28) with long, acute, dorsal apodemes.
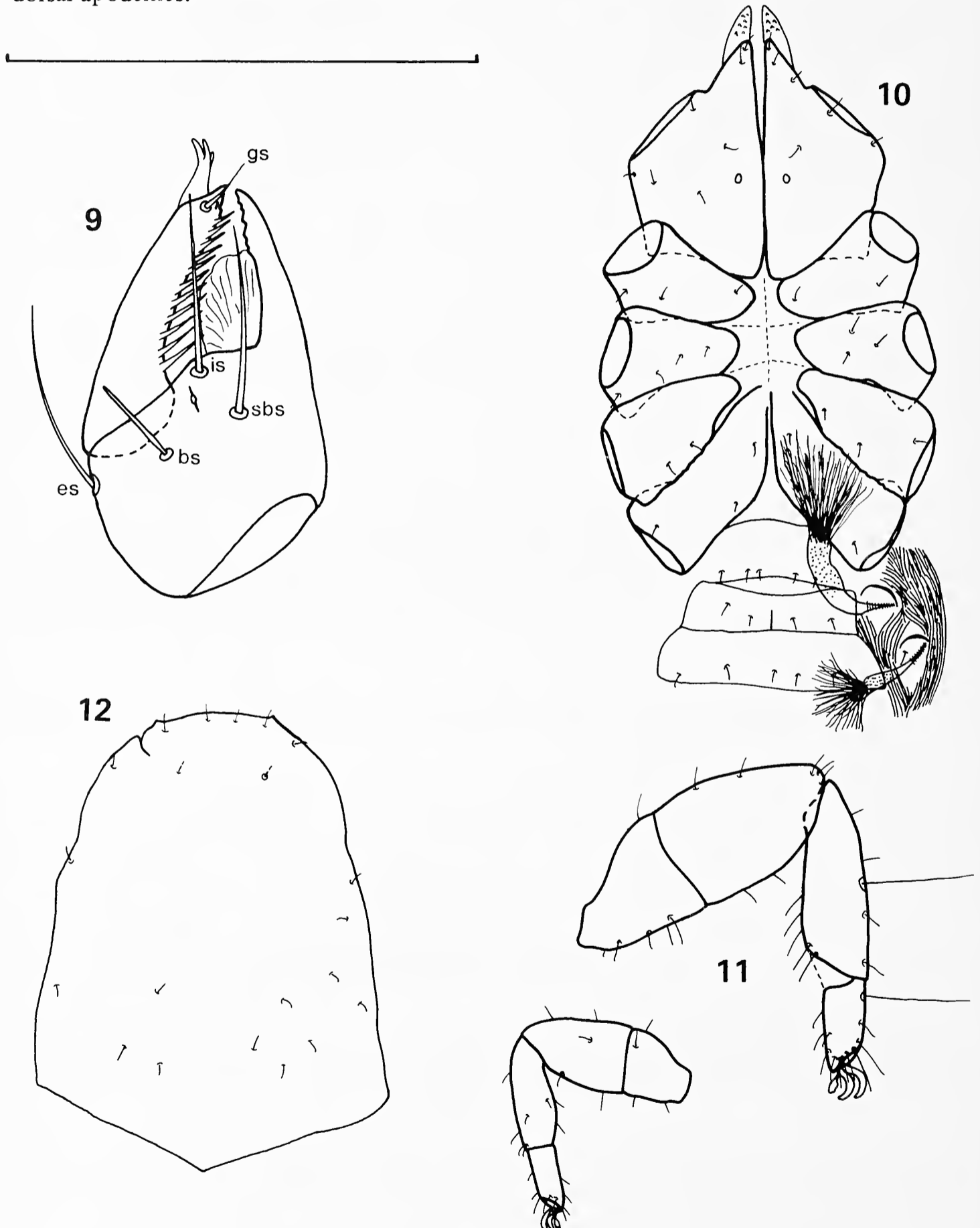
Fig. 9-12.—*Garyops depressus* Banks: 9, dorsal aspect of left chelicera, female, S-2840.1; 10, ventral aspect of coxal area, with left tracheae, male, S-2792.4; 11, leg I and leg IV, male, S-2782.2; 12, dorsal aspect of carapace, male, S-2792.4. Scale line = 1.00 mm (Figs. 10-12), 0.25 mm (Fig. 9).
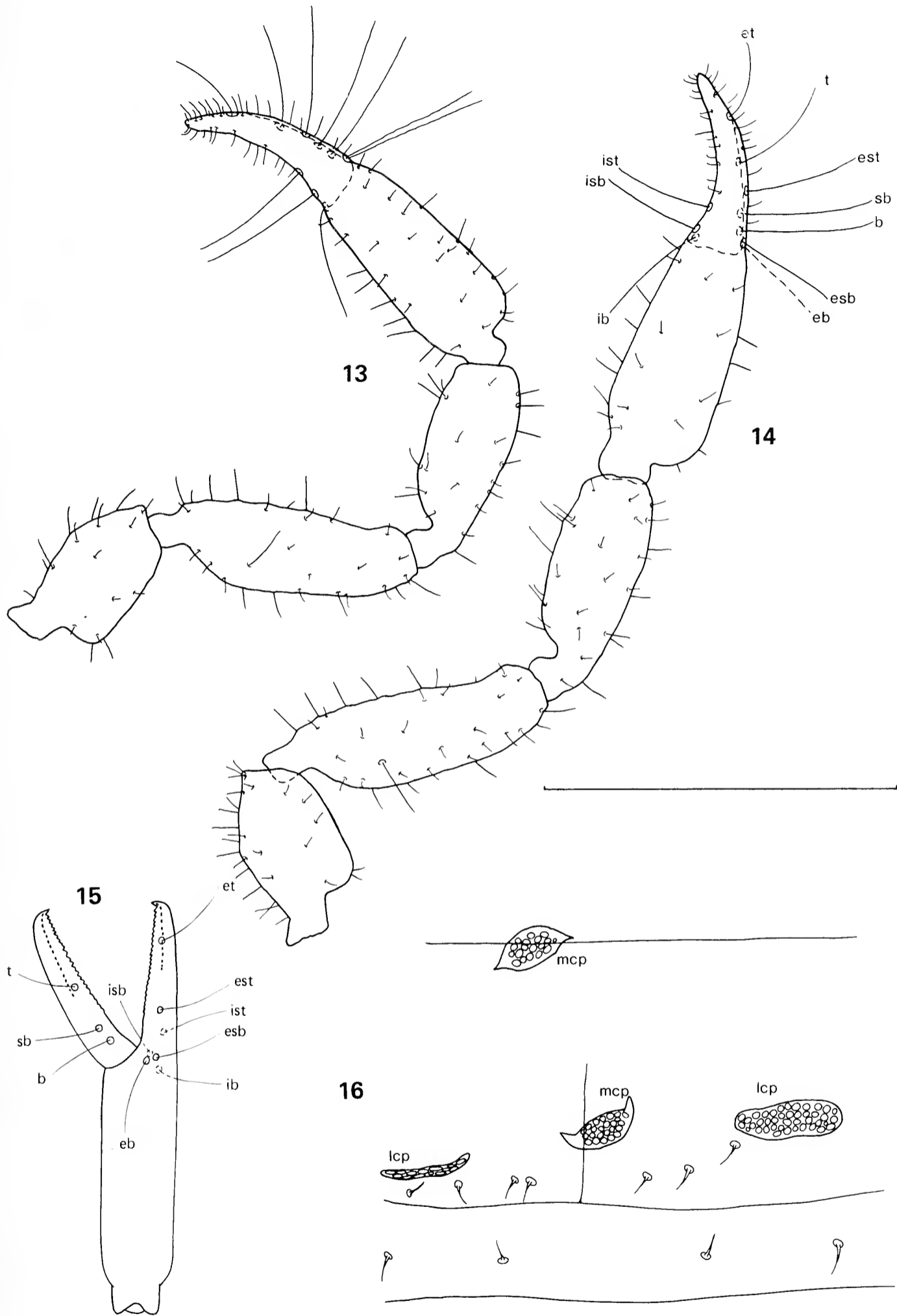
Figs. 13-16.—*Garyops depressus* Banks: 13, dorsal aspect of right pedipalp, male, S-2782.2; 14, same, female, S-2829.2; 15, lateral aspect of left chela, female, S-2829.2; 16, female genitalia and associated sternites, S-2829.2. Scale line = 1.00 mm (Figs. 13-15), 0.25 mm (Fig. 16).

Dimensions (mm): Chela (with pedicel) 0.97-1.18/0.245-0.28 (1.015-1.19/0.26-0.30).

Habitat.—Hoff (1963) and Brach (1979) discussed the habitat preferences of this species, and all the specimens (with known habitat data) have been taken from under bark of *Pinus elliotti.*

Remarks.—Hoff (1963) adequately redescribed this species, and little needs to be added here except for details of the male genitalia, measurements of the chela including the pedicel, and carapaceal ratios, which were omitted in Hoff's paper.

Hoff examined three of Banks' syntypes, and found that two females were referable to *G. depressa,* whereas the third female belonged to his new species *G. pumila* (herein transferred to the genus *Idiogaryops*). I have had the opportunity to examine the other three syntypes and found that one male belongs to *G. depressus,* whereas the other two specimens, a male and a female, belong to *I. pumilus.*

Hounsome (1980) recorded *G. depressus* from Little Cayman Island based upon Prof. Beier's identification. I have been able to examine this material, and it is clearly *I. pumilus.*

Garyops depressus is extremely similar to *G. sini,* and they eventually may be considered synonymous. They are retained here as separate species on the basis of the slightly larger size of *G. depressus,* even though there is considerable overlap (Fig. 39).

Other specimens examined.—DOMINICAN REPUBLIC: Bani (65 m), 24 September 1972 (J. and S. Klapperich), 5 males, 3 females (MHNG) (spirit). U.S.A.: FLORIDA; *Highlands Co.,* Archbold Biological Station, under bark of *Pinus elliotti,* 7 April 1956 (C. C. Hoff), 1 male (AMNH, S-2782.2) (slide). Same data as above except 10 April 1956, 1 male (AMNH, S-2792.4) (slide). Same data as above except 15 April 1956, 1 female (AMNH, S-2829.2) (slide). Same data as above except 16 April 1956, 1 female (AMNH, S-2840.1) (slide).

Garyops sini (Chamberlin), new combination
Figs. 17-21, 29, 35, 39; Map 1

Sternophorus sini Chamberlin 1923:371-372, Plate 1, Fig. 6, Plate 2, Fig. 21, Plate 3, Figs. 6, 15, 22-25, 1931·192, 239, Figs. 4d, 10c, 11z, 20f, 52o-q, 67, 1932a:142; Beier 1932:17, Figs. 11-12.

Types.—Holotype male, paratype female (designated as allotype by Chamberlin), SE corner of Tiburon Island, Gulf of California, Mexico, under bark, 4 July 1921 (J. C. Chamberlin), CAS, Type Nos. 1286, 1287 (slides). Paratype male, paratype female, same data as above except under bark of mesquite, JCC, JC-183.02003-4 (slides). Paratype male, paratype female, same data as above except date? (collector?, presumably J. C. Chamberlin), NHMW, JC-344.01003-4 (spirit). Paratype female, Palm Canyon, Angel de la Guarda Island, Gulf of California, Mexico, 3 May 1921 (J. C. Chamberlin), JCC, JC-167.02001 (slides). Paratype male, paratype female, Los Angeles Bay, Baja California, Mexico, 25-27 June 1921 (J. C. Chamberlin), JCC, JC-176.04001-2 (slides). Paratype male, paratype female, Las Animas Bay, Baja California, Mexico, 8 May 1921 (J. C. Chamberlin), JCC, JC-714.01001-2 (slides). The type series also included many other specimens which were not examined.

Distribution.—Baja California, Gulf of California, Sonora, Mexico (Map 1).

Diagnosis.—Female galea with three distal rami. Male genitalia with long, acute dorsal apodemes. Chela (with pedicel) 0.835 to 0.935 (male), 0.86 to 1.14 mm (female) in length, 3.80 to 4.00 (male), 3.54 to 3.81 (female) times longer than broad.

Description.—Pedipalpal trochanter large and inflated, 1.95 to 2.05 (male), 1.79 to 2.10 (female), femur 2.77 to 3.05 (male), 2.68 to 3.05 (female), tibia 2.31 to 2.45
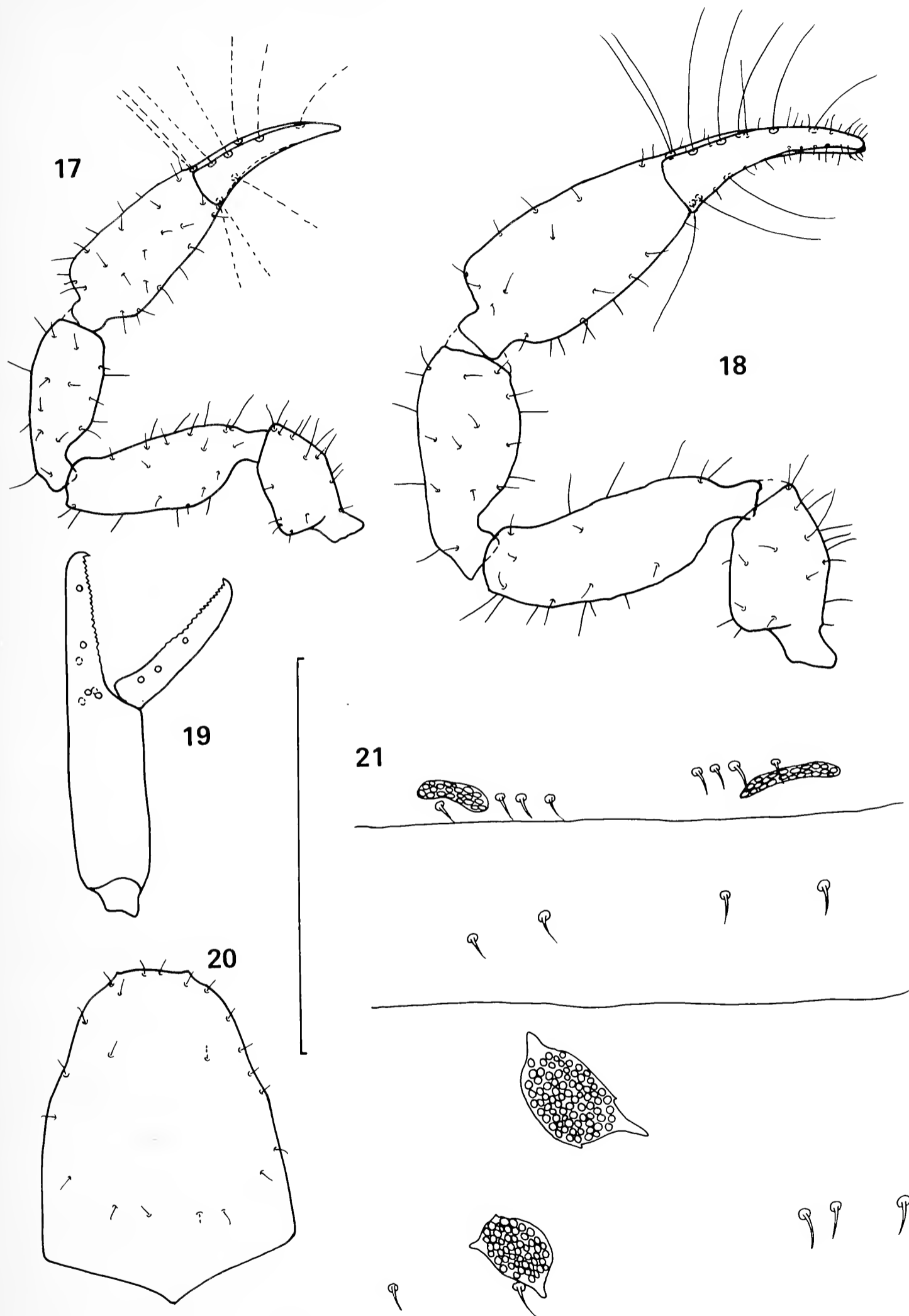
Figs. 17-21.—*Garyops sini* (Chamberlin): 17, ventral aspect of right pedipalp, male paratype, JC-176.04001; 18, same, female paratype, JC-167.02001; 19, lateral aspect of right chela, female paratype, JC-714.01002; 20, dorsal aspect of carapace, female paratype, JC-176.04002; 21, female genitalia and associated sternites, paratype, JC-167.02001. Scale line = 1.00 mm (Figs. 17-20), 0.25 mm (Fig. 21).

(male), 2.11 to 2.35 (female), chela (with pedicel) 3.80 to 4.00 (male), 3.54 to 3.81 (female), chela (without pedicel) 3.59 to 3.84 (male), 3.35 to 3.61 (female) times longer than broad. Trichobothria as for genus, in usual position (Figs. 17-19). Serrula exterior of chelicera with 10 to 12 (male, female) lamellae. Two males (JC-176.04001, JC-714.01001) possess an extra gs on the moveable fingers of their chelicerae. Galea of male simple, of female with three distal rami, one usually smaller than the others (Fig. 35). Carapace anteriorly constricted (Fig. 20) with 25 (male), 20 to 32 (female) setae; 1.34 to 1.41 (male), 1.35 to 1.48 (female) times longer than broad. Male genitalia with long, acute dorsal apodemes (Fig. 29). Female genitalia as for genus (Fig. 21); some females possess extra, smaller projections on the median cribriform plates. Tergal chaetotaxy: male, 6:5-6:4-5:5:4-6:5:5-7:5-6:6:T1T4T1T:?:2; female, 6-7:5-6:3-6:4-6:4-6:4-6:4-8: 5-7:5-6:T1T3-4T1T:?:2. Sternal chaetotaxy: male, 0:4-7:(0)4[2](0):(1)3-6(1):6-7:5-8: 5-6:6:6:T1T4T1T:?:2; female 0:3-9:(0)3-4(0):(1)4-7(1):4-8:5-8:5-8:6-8:5-8:T1T4T1T: ?:2. Coxal chaetotaxy: male, 4-5:3-5:3-5:3-5; female, 3-6:3-6:2-5:3-4.

Dimensions (mm): Body length 2.1-2.4 (2.4-3.8); pedipalps: trochanter 0.36-0.40/ 0.18-0.20 (0.34-0.49/0.185-0.245), femur 0.545-0.625/0.195-0.205 (0.54-0.74/0.19-0.25), tibia 0.44-0.49/0.185-0.205 (0.435-0.60/0.20-0.26), chela (with pedicel) 0.835-0.935/0.22-0.24 (0.86-1.14/0.23-0.31), chela (without pedicel) 0.79-0.885 (0.82-1.075), moveable finger length 0.40-0.43 (0.39-0.515); chelicera 0.16-0.17/0.085-0.095 (0.16-0.20/0.09-0.115), moveable finger length 0.11-0.13 (0.115-0.14); carapace 0.75-0.83/ 0.50-0.60 (0.795-1.02/0.56-0.72); leg I: coxa 0.215-0.24/0.23-0.27 (0.23-0.29/0.265-0.34), trochanter 0.11-0.125/0.09-0.095 (0.13-0.16/0.09-0.115), femur I 0.10-0.14/ 0.105-0.12 (0.105-0.15/0.115-0.15), femur II 0.16-0.195/0.105-0.12 (0.165-0.24/0.115-0.15), tibia 0.19-0.215/0.07-0.075 (0.18-0.265/0.075-0.095), tarsus 0.115-0.14/0.05-0.055 (0.115-0.17/0.05-0.065); leg IV: coxa width 0.225-0.28 (0.27-0.29), trochanter 0.16-0.185/0.11-0.125 (0.165-0.21/0.125-0.15), femur I 0.195-0.23/0.17-0.19 (0.205-0.28/0.18-0.22), femur II 0.23-0.28/0.175-0.195 (0.23-0.32/0.18-0.225), tibia 0.34-0.365/0.10-0.11 (0.33-0.45/0.105-0.155), tarsus 0.17-0.19/0.07-0.075 (0.13-0.235/ 0.07-0.105).

Habitat.—Specimens have been taken from under the bark of several species of trees, including mesquite (*Prosopis* sp.), palo tinto (the scientific name of this tree could not be located) and *Sideroxylon* sp. (Chamberlin 1923).

Remarks.—As discussed above, this species may eventually prove to be identical with *G. depressus*. The male genitalia of these species show no constant differences. The only real differences appear to be the disjunct distributions (Map 1) and the slightly smaller size of *G. sini* (Fig. 39). More specimens must be collected and examined before any definitive statement may be made about the status of *G. sini*.

Other specimens examined.—MEXICO: BAJA CALIFORNIA: Los Angeles Bay, 5-6 May 1921 (J. C. Chamberlin), 4 females (JCC, JC-119.03001-4) (slides): Gulf of California; San Gabriel Bay, Espiritu Santo Island, 1 June 1921 (J. C. Chamberlin), 1 female (JCC, JC-361.03001) (slide): SONORA; San Carlos Bay, under bark of palo tinto, 8 July 1921 (J. C. Chamberlin), 1 female (JCC, JC-687.02001) (slide).

Garyops centralis Beier
Figs. 22-24, 36, 39; Map 1

Garyops centralis Beier 1953:15-16, Figs. 1-2.

Types.—Paratype female, La Union, Cutuco, El Salvador, 19 April 1951 (A. Zilch), SM, 7682, (spirit). Paratype female, same data as above, NHMW (spirit).

Distribution.—El Salvador (Map 1).

Diagnosis.—Female galea with five distal rami and one subbasal ramus. Chela (with pedicel) 1.31 to 1.43 mm (female) in length, 4.09 to 4.15 (female) times longer than broad.

Description.—Female only. Pedipalpal trochanter large and inflated, 1.97 to 2.03, femur 2.95 to 3.25, tibia 2.52 to 2.70, chela (with pedicel) 4.09 to 4.15, chela (without pedicel) 3.86 to 3.95 times longer than broad. Trichobothria as for genus, in usual position (Fig. 23). Serrula exterior of chelicera with 13 lamellae. Galea with five distal and one subbasal rami (Fig. 36). Carapace anteriorly constricted (Fig. 22), with 34 to 35 setae; 1.30 to 1.33 times longer than broad. Genitalia as for genus (Fig. 24). Tergal chaetotaxy: 6-7:6:4:6-7:6-7:6-8:7-8:7-8:6:T1T4T1T:?:2. Sternal chaetotaxy: 0:9:(0)4-5(0):(1)5-6(1):7:6-7:7:8:6:T1T4T1T:?:2. Coxal chaetotaxy: 4-5:4-5:4-5:5-6.

Dimensions (mm): Body length 3.6; pedipalps: trochanter 0.59-0.635/0.195-0.32, femur 0.90-0.96/0.28-0.325, tibia 0.72-0.78/0.27-0.31, chela (with pedicel) 1.31-1.43/
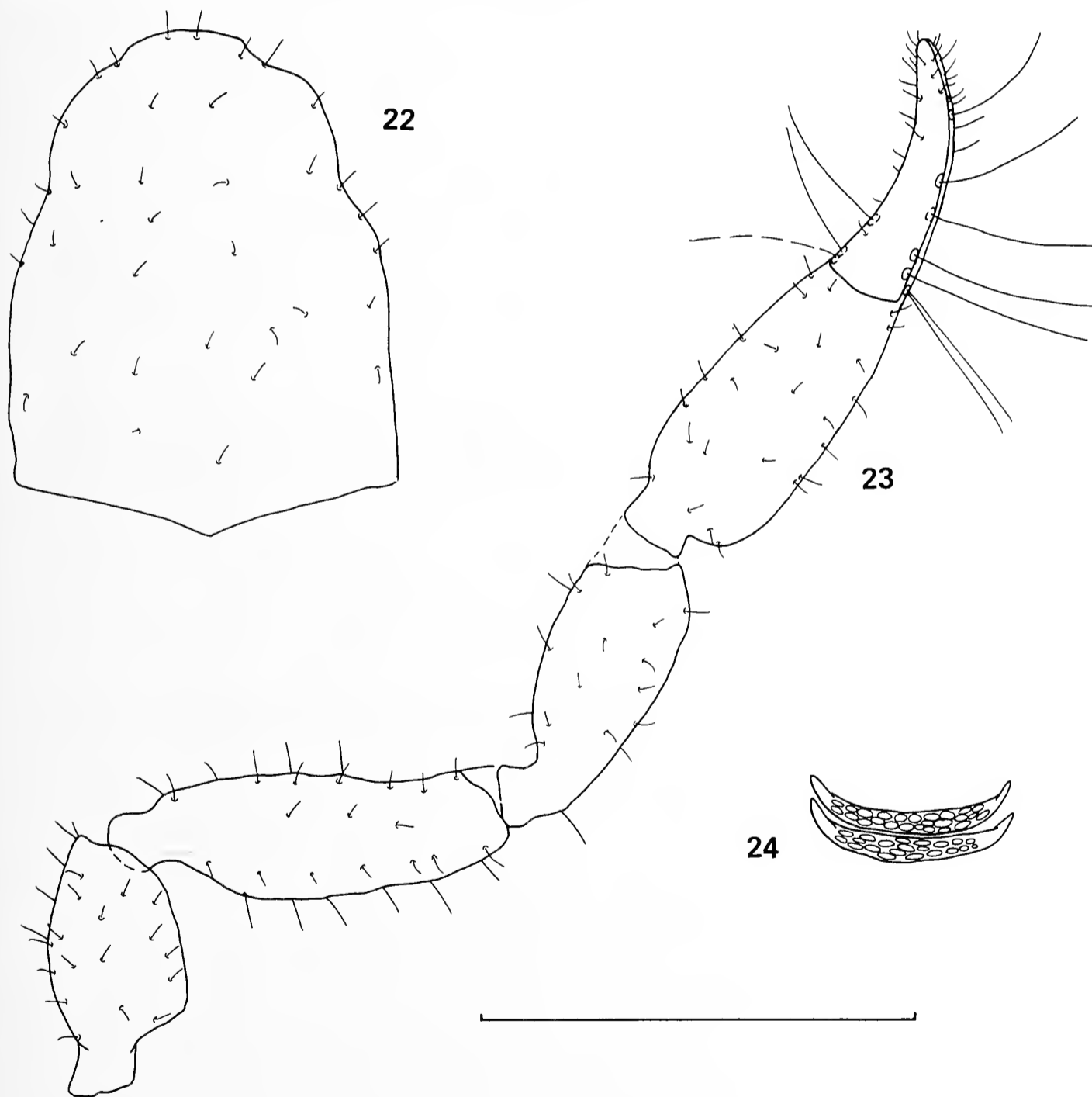
Figs. 22-24.—*Garyops centralis* Beier, female paratype: 22, dorsal aspect of carapace; 23, ventral aspect of left pedipalp; 24, median cribriform plates. Scale line = 1.00 mm (Figs. 22-23), 0.25 mm (Fig. 24).

0.32-0.35, chela (without pedicel) 1.265-1.35, moveable finger length 0.61-0.65; chelicera 0.22-0.255/0.12-0.135, moveable finger length 0.05-0.065; carapace 1.16-1.21/0.87-0.93; leg I: coxa 0.32-0.36/0.40-0.43, trochanter 0.185-0.21/0.21-0.13, femur I 0.19-0.22/ 0.145-0.155, femur II 0.28-0.295/0.15-0.16, tibia 0.28-0.31/0.10, tarsus 0.14-0.165/0.07; leg IV: coxa width 0.39-0.44, trochanter 0.23-0.26/0.155-0.17, femur I 0.33-0.375/ 0.22-0.265, femur II 0.445-0.48/0.23-0.275, tibia 0.51-0.56/0.14-0.155, tarsus 0.26-0.27/ 0.105-0.11.

Habitat.—No habitat data accompanied the specimens.

Remarks.—Beier (1953) erroneously referred to the NHMW specimen as a male, and labelled it as such. Furthermore, he stated that the holotype male and a paratype female were deposited in SM; the former specimen is apparently not housed in this institution (Dr. Grasshoff, pers. comm.), but a lectotype female has not been designated in the hope that the male might eventually reappear.

Garyops centralis may be a junior synonym of *G.* (?) *ferrisi*, but the paucity of specimens precludes any definite statements. They are virtually identical in size (Fig. 39), but since males of *centralis* and females of *ferrisi* are not yet known, the final decision must await further collecting.

Females of *G. centralis* possess spurred median cribriform plates which justifies its inclusion in this genus. These plates (Fig. 24) appear to be different to those of the other species of the genus, but this is simply due to the mode of preservation of the specimens. Females of *G. depressus* and *G. sini* were eviscerated and mounted on microscope slides; this tends to push the cribriform plates so that they lie flat. Females of *G. centralis* were not eviscerated (due to curatorial preferences) and the cribriform plates were lying in a slightly different plane. Several non-eviscerated specimens of *G. depressus* and *G. sini* were examined, and their plates also lay at a different angle, as shown by Chamberlin (1931: Fig. 52o) for the latter species.

<center>

Garyops (?) *ferrisi* (Chamberlin), new combination
Figs. 25-27, 30, 39; Map 1

</center>

Sternophorus ferrisi Chamberlin 1932a:143; Beier 1932:18.

Type.—Holotype male, no exact locality, Michoacan, Mexico, under bark of tree, date? (G. F. Ferris), JCC, JC-275.01001 (slide).

Distribution.—Michoacan, Mexico (Map 1).

Diagnosis.—Male genitalia with long dorsal apodemes. Chela (with pedicel) 1.425 to 1.45 mm (male) in length, 4.25 (male) times longer than broad.

Description.—Male only. Pedipalpal trochanter large and inflated, 2.05 to 2.08, femur 3.33 to 3.36, tibia 2.76 to 2.86, chela (with pedicel) 4.25, chela (without pedicel) 4.01 times longer than broad. Trichobothria as for genus, in usual position (Figs. 26-27). Serrula exterior of chelicera with 12 to 13 lamellae. Galea simple. Carapace anteriorly constricted (Fig. 25), with 23 setae; 1.27 times longer than broad. Male genitalia (Fig. 30) with long dorsal apodemes, and apparently with a large, median foramen. Tergal chaetotaxy: 6:6:4:5:6:6:6:5:?:T1T4T1T:?:2. Sternal chaetotaxy: 0:7:(0)3[3](0):(1)6(1):8: 8:6:6:6:T1T4T1T:?:2. Coxal chaetotaxy: 4-5:5-6:4-5:5.

Dimensions (mm): Body length 3.8; pedipalps: trochanter 0.665-0.675/0.325, femur 0.99-1.00/0.295-0.30, tibia 0.80/0.28-0.29, chela (with pedicel) 1.425-1.45/0.335, chela (without pedicel) 1.34-1.345, moveable finger length 0.59-0.62; chelicera 0.27/0.16-

0.165, moveable finger length 0.17-0.175; carapace 1.205/0.95; leg I: coxa 0.32-0.33/ 0.40-0.41, trochanter 0.18-0.19/0.125-0.145, femur I 0.165-0.17/0.185-0.195, femur II 0.28/0.185-0.195, tibia 0.315-0.32/0.10-0.105, tarsus 0.20/0.07-0.075; leg IV: coxa width 0.37-0.38, trochanter 0.235-0.24/0.165-0.17, femur I 0.31/0.265-0.27, femur II 0.42-0.43/0.28, tibia 0.54/0.15, tarsus 0.275-0.28/0.105.

Habitat.—No habitat data accompanied the specimen, yet Chamberlin (1932a) noted that it was "collected under bark of a tree".

Remarks.—Since females of this species are unknown, the generic position of *ferrisi* is uncertain. It is tentatively placed in *Garyops* because of its similarity with *G. centralis*, with which it may be conspecific (see above).

The apparent lack of setae on one side of the pedipalpal tibia and chela (Fig. 27) is an artifact which probably occurred during preparation of the slide.

The exact collection site of the holotype is unknown, and Map 1 shows the state record only.
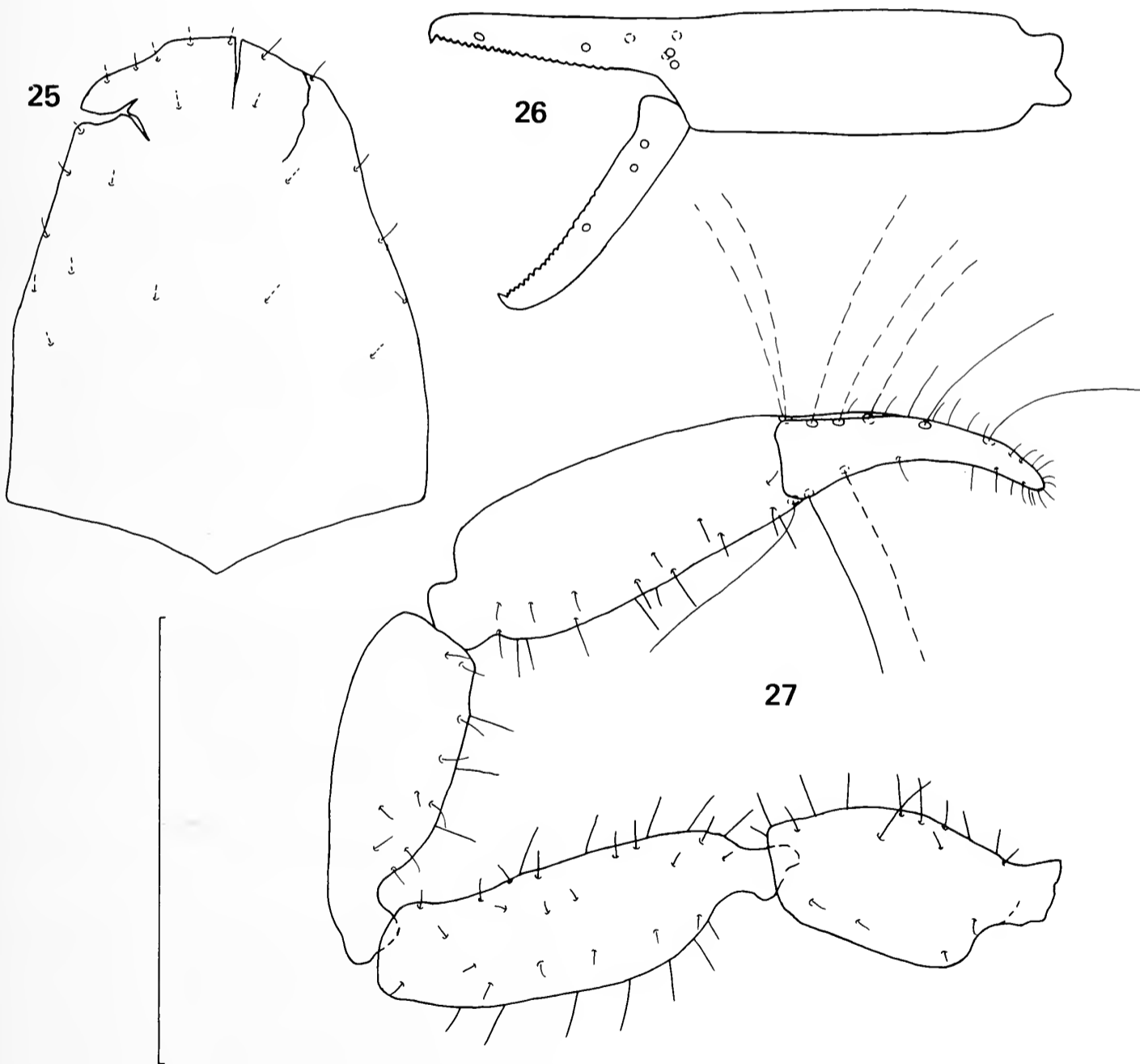
Figs. 25-27.—*Garyops* (?) *ferrisi* (Chamberlin), male holotype: 25, dorsal aspect of carapace; 26, lateral aspect of left chela; 27, ventral aspect of right pedipalp. Scale line = 1.00 mm.
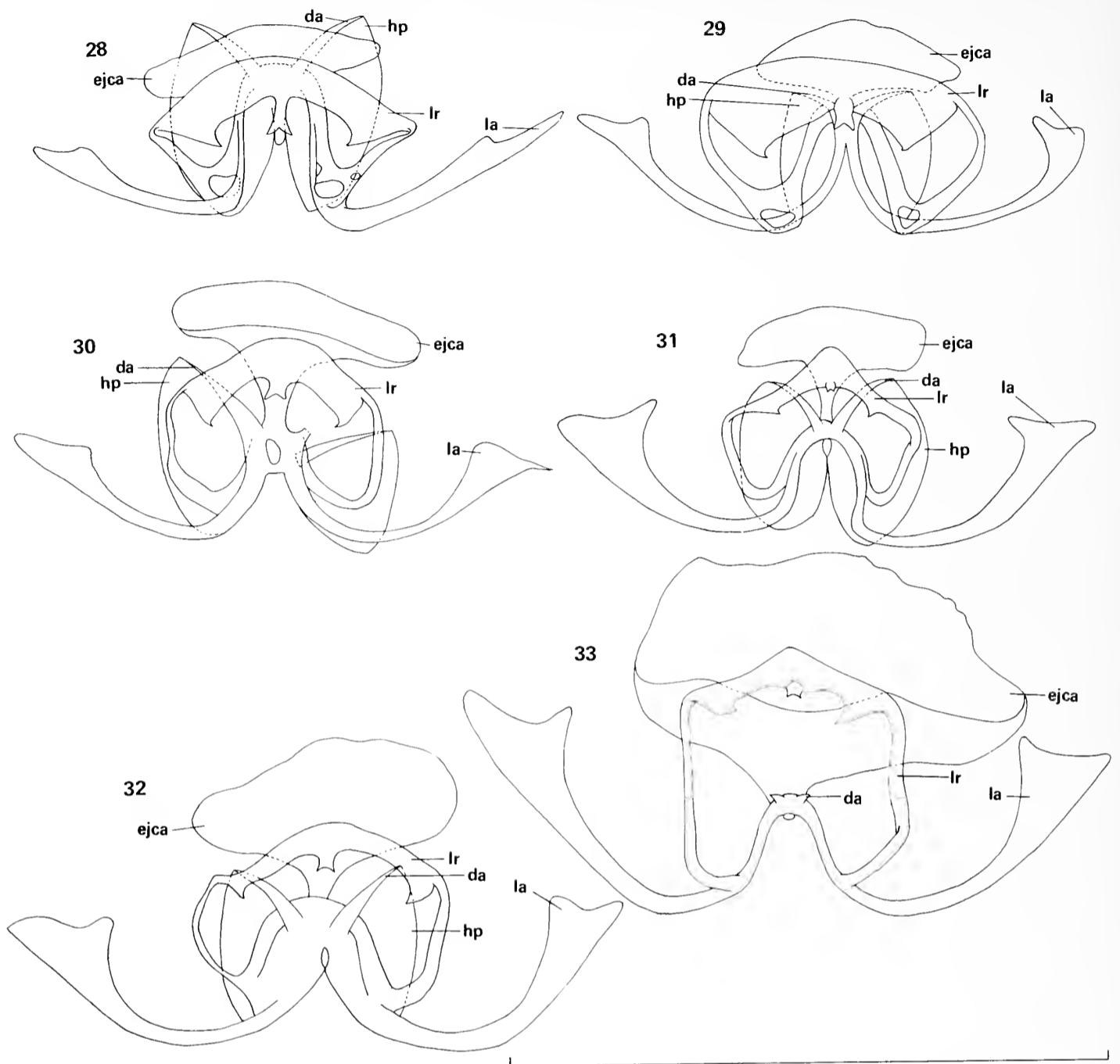
Figs. 28-33.—Anterior portion of male genitalia, ventral aspect: 28, *Garyops depressus* Banks, S-2782.2; 29, *G. sini* (Chamberlin), paratype, JC-176.04001; 30, *G.* (?) *ferrisi* (Chamberlin), holotype; 31, *Idiogaryops paludis* (Chamberlin), S-2887.?; 32, *I. pumilus* (Hoff) from Little Cayman Island; 33, *I.* sp., S-2886.2. Scale line = 0.25 mm (Figs. 28-29), 0.33 mm (Fig. 30), 0.167 mm (Figs. 31-33).

Genus *Idiogaryops* Hoff

Garyops Banks 1909:305 (in part); Chamberlin 1931:238 (in part); Beier 1932:18 (in part); Hoff 1963: 2-3 (in part).
Sternophorus Chamberlin: Beier 1932:16 (in part); Murthy and Ananthakrishnan 1977:16 (in part).
Idiogaryops Hoff 1963:10-11. Type species by original designation and monotypy *Sternophorus paludis* Chamberlin 1932a.

Distribution.—Little Cayman Island; Arkansas, Florida, Georgia, Illinois, Mississippi, North Carolina, Texas, U.S.A. (Map 2).

Diagnosis.—Females with two (occasionally three) unspurred, median cribriform plates. Fixed chelal finger with seven trichobothria, moveable chelal finger with two or three trichobothria.

Subordinate taxa.—*Idiogaryops paludis* (Chamberlin), *Idiogaryops pumilus* (Hoff).
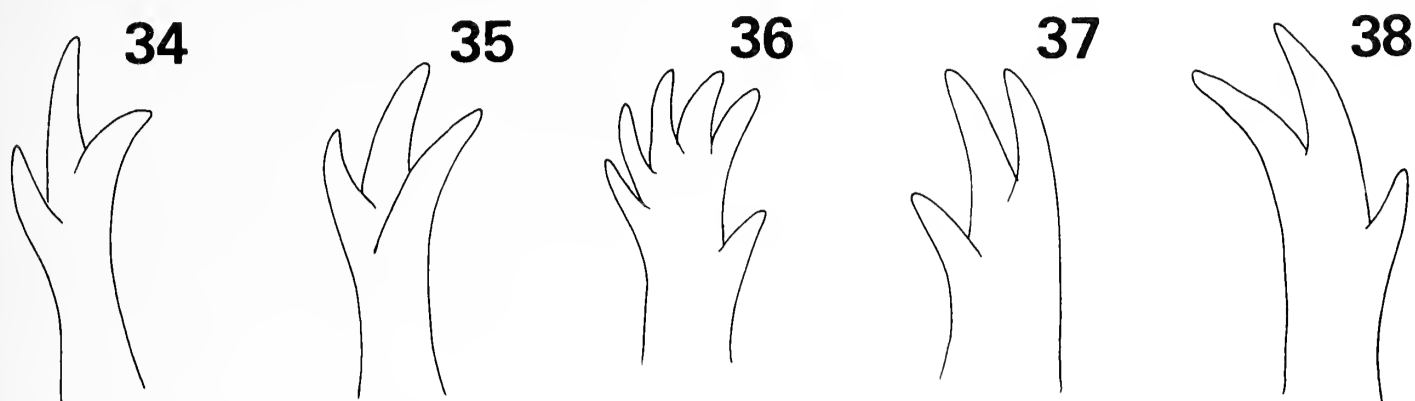
Figs. 34-38.—Female galeae: 34, *G. depressus* Banks, S-2840.1; 35, *G. sini* (Chamberlin), paratype, JC-714.01002; 36, *G. centralis* Beier, paratype; 37, *Idiogaryops paludis* (Chamberlin), S-2826.2; *I. pumilus* (Hoff), paratype, S-3782.3. Not to same scale.

Remarks.—*Idiogaryops* is here redefined to include all sternophorids with two unspurred, median cribriform plates, even though it was originally restricted by Hoff (1963) to include only *I. paludis,* on the basis of it possessing only two trichobothria on the moveable chelal finger. As discussed above, to give generic status to species which lack individual trichobothria has extended the generic system and has obscured obvious relationships between species. Therefore, this genus, as here interpreted, contains species with two or three trichobothria on the moveable chelal finger. Those with two trichobothria are placed in the *paludis* group, and those with three trichobothria are placed in the *pumilus* group.

Map. 2.—North America showing known distribution of *Idiogaryops paludis* (Chamberlin) (circles) and *I. pumilus* (Hoff) (squares). Open symbols represent literature records only.
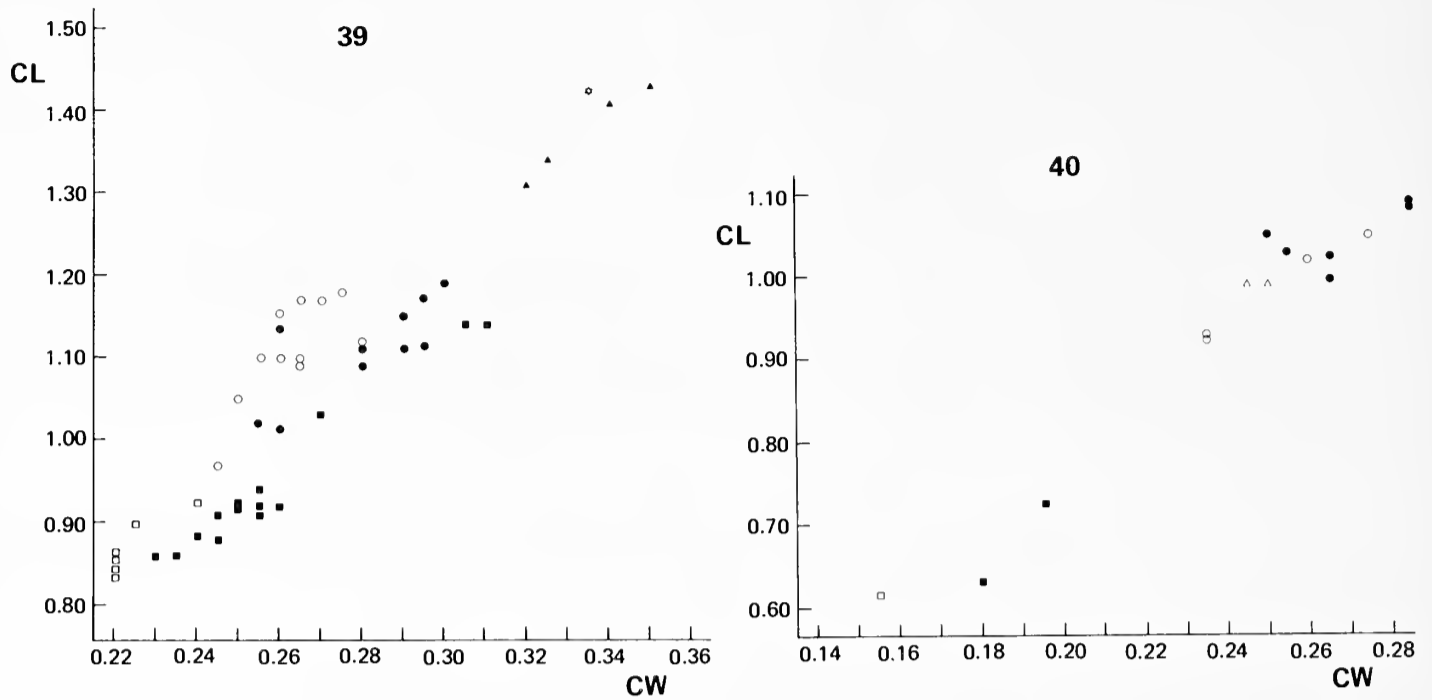
Figs. 39-40.—Graphs of chela (with pedicel) length (CL) versus width (CW), in mm; open symbols, males; closed symbols, females: 39, *Garyops depressus* Banks (circles), *G. sini* (Chamberlin) (squares), *G. centralis* Beier (triangles), *G.* (?) *ferrisi* (Chamberlin) (star); 40, *Idiogaryops paludis* (Chamberlin) (squares), *I. pumilus* (Hoff) (circles), *I.* sp. (triangles).

Paludis group

Diagnosis.—As for genus, except that the moveable chelal finger possesses two trichobothria, *b* and *t*.

Subordinate taxa.—*Idiogaryops paludis* (Chamberlin).

Idiogaryops paludis (Chamberlin)
Figs. 31, 37, 40-45; Map 2

Sternophorus paludis Chamberlin 1932a:142-143; Beier 1932:17-18; Hoff and Bolsterli 1956:164-165; Hoff 1958:19.

Idiogaryops paludis (Chamberlin): Hoff 1963:11-13, Figs. 7-9; Weygoldt 1969:27, Fig. 105; Rowland and Reddell 1976:19; Brach 1979:34-38.

Types.—Holotype male, no exact locality, Alachua County, Florida, U.S.A., 30 March 1925 (T. H. Hubbell), depository unknown, JC-725.01001 (slide?), not examined. Paratype female, Billy's Island, Okefinokee Swamp, Georgia, U.S.A., date? (C. R. Crosby), depository unknown, JC-43.02001 (slide?), not examined.

Distribution.—Arkansas, Florida, Georgia, Illinois, Mississippi, North Carolina, Texas, U.S.A. (Map 2).

Diagnosis.—Male genitalia with long dorsal apodemes. Small species: chela (without pedicel) [from Hoff and Bolsterli (1956) and Hoff (1963)] 0.61 to 0.67 (male), 0.61 to 0.715 mm (female) in length.

Description.—Supplementary to Chamberlin (1932a), Hoff and Bolsterli (1956) and Hoff (1963). Carapace (Fig. 44) only slightly constricted anteriorly. Male genitalia (Fig. 31) with long, tapering dorsal apodemes.

Habitat.—Hoff and Bolsterli (1956), Hoff (1963), Weygoldt (1969) and Brach (1979) have recorded this species from a variety of cortical habitats *(Pinus elliotti, Ilex cassine, Quercus virginianus, Platanus occidentalis* and *Carya alba).*

Remarks.—Previous authors have adequately described this species and little needs to be added here except for details of the male genitalia which were omitted in previous papers. Hoff (1963) recorded the occasional presence of a small, third median cribriform plate in some females.

Contrary to Chamberlin (1932a), the type specimens are not deposited at Cornell University (Dr. L. L. Pechuman, pers. comm.).

Specimens examined.—U.S.A.: FLORIDA; *Highlands Co.,* Archbold Biological Station, 14 April 1956 (C. C. Hoff), 1 female (AMNH, S-2826.2) (slide). Same data as above except 22 April 1956, 1 male (AMNH, S-2887.?) (slide). Same data as above except 1 May 1956, 1 female (AMNH, S-2951.3) (slide).

Pumilus group

Diagnosis.—As for genus, except that the moveable chelal finger possesses three trichobothria, *b, sb* and *t.*

Subordinate taxa.—*Idiogaryops pumilus* (Hoff).

Idiogaryops pumilus (Hoff), new combination
Figs. 32, 38, 40, 46-50; Map 2

Garyops depressa Banks 1909:305-306 (in part); Hounsome 1980:85 (misidentification).
Garyops pumila Hoff 1963:7-10, Figs. 5-6 (in part).

Types.—Holotype male, Parker Islands, near Lake Placid, Highlands County, Florida, U.S.A., under bark of live oak *[Quercus virginianus]*, 22 April 1956 (C. C. Hoff), AMNH, S-2886.8 (slide). Paratype female, Mahogany Hammock, Everglades National Park, Florida, U.S.A., [under bark of *Metopium toxiferum*], 8 February 1958 (F. C. Craighead), AMNH, S-3782.3 (slide). Paratype female, Punta Gorda, Charlotte County, Florida, U.S.A., date? [A. T. Slosson], MCZ, S-3791.3 (slide) (syntype of *G. depressus).* (The type series also consisted of other specimens which were not examined.)

Distribution.—Florida, U.S.A.; Little Cayman Island (Map 2).

Diagnosis.—Male genitalia with long, tapering dorsal apodemes. Chela (without pedicel) [from Hoff (1963)] 0.865 to 0.95 (male), 0.95 to 1.07 mm (female) in length.

Description.—Supplementary to Hoff (1963). Carapace (Fig. 46) 1.31 (male), 1.32 to 1.34 (female) times longer than broad, with 31 (male), 21? to 32 (female) setae. One female specimen (S-3782.3) has *et* missing from one chela (Fig. 49). Male genitalia (Fig. 32) with long, tapering dorsal apodemes.

Habitat.—Hoff (1963) briefly discussed the habitat preferences of this species and stated that it had been collected from the bark of oak *(Quercus virginianus)* and poison-wood *(Metopium toxiferum)* and from moss and rotted wood at the base of cabbage palmetto *(Sabal palmetto).* This is in contrast to the sympatric species *G. depressus,* which in Florida is only known from bark of slash pine *(Pinus elliotti). Idiogaryops pumilus* was not recorded in Brach's (1979) rigorous search for pseudoscorpions under slash pine bark, and highlights this interesting case of habitat partitioning. The specimens from Little Cayman were apparently taken from "marl facies with tall scrub" (Hounsome 1980).

Remarks.—Hoff described this Floridian species from four males and five females which included one of Banks' syntypes of *G. depressus.* His description is quite thorough and all that needs to be added here are details of the male genitalia and carapaceal ratios.
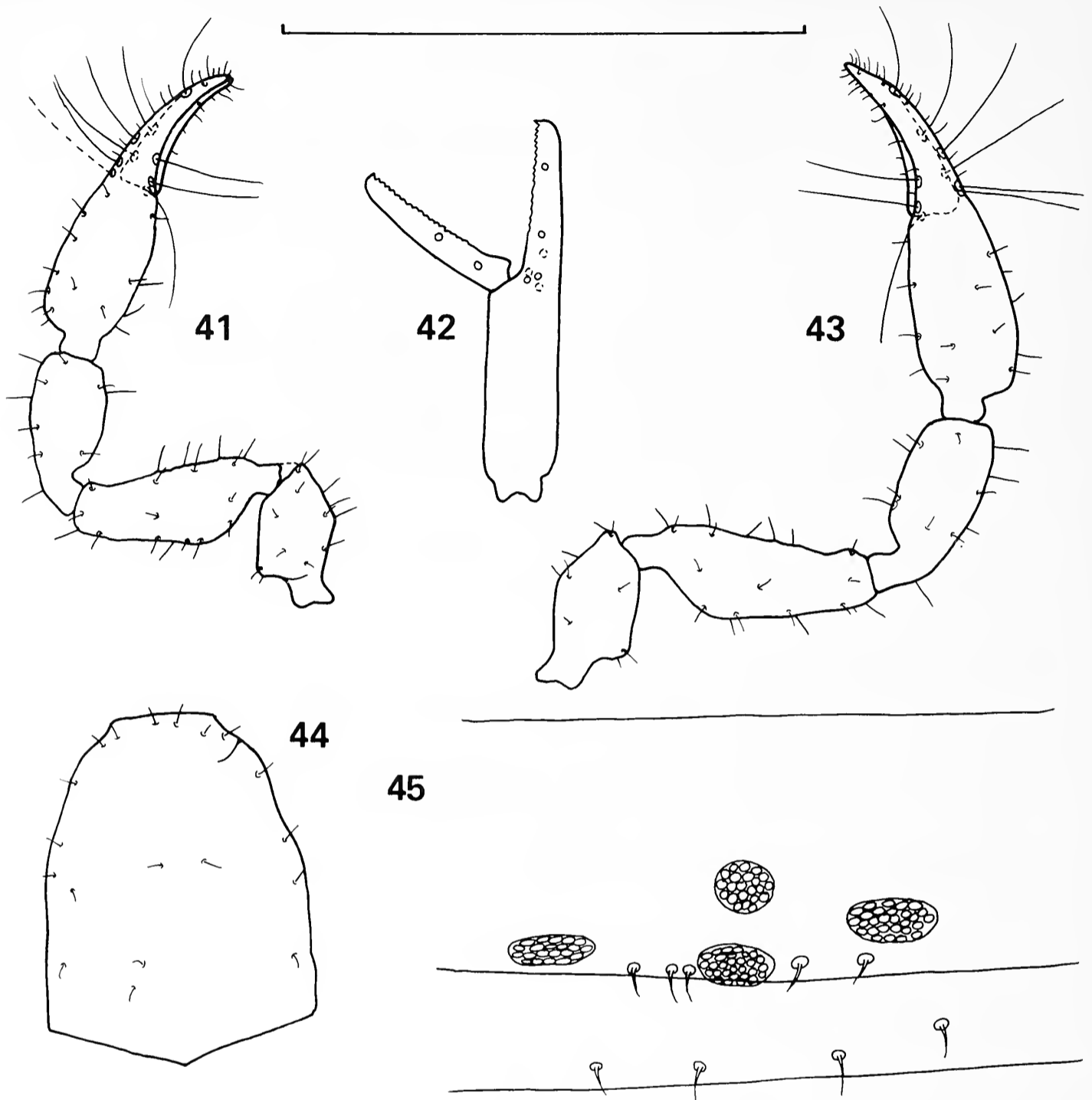
Figs. 41-45.—*Idiogaryops paludis* (Chamberlin): 41, dorsal aspect of left pedipalp, male, S-2887.?; 42, lateral aspect of left chela, female, S-2826.2; 43, dorsal aspect of right pedipalp, female, S-2826.2; 44, dorsal aspect of carapace, female, S-2826.2; 45, female genitalia and associated sternites, S-2828.2. Scale line = 1.00 mm (Figs. 41-44), 0.25 mm (Fig. 45).

As discussed below under *Idiogaryops* sp., one of the male paratypes of *G. pumilus* is not conspecific with the holotype of this species.

Other specimens examined.—U.S.A.: FLORIDA; Punta Gorda, date? [A. T. Slosson], 1 male, 1 female (MCZ) (spirit) (syntypes of *G. depressus*). LITTLE CAYMAN ISLAND: 3 August 1975 (M. V. Hounsome), 1 male, 1 female (NHMW) (spirit).

Idiogaryops sp.
Figs. 33, 40

Garyops pumila Hoff 1963:5-6 (in part).

Diagnosis.—Male genitalia with reduced dorsal apodemes.

Remarks.—Even though this specimen possesses pedipalpal morphometrics that are indistinguishable from *I. pumilus* (Fig. 40), the form of the male genitalia (Fig. 33) is
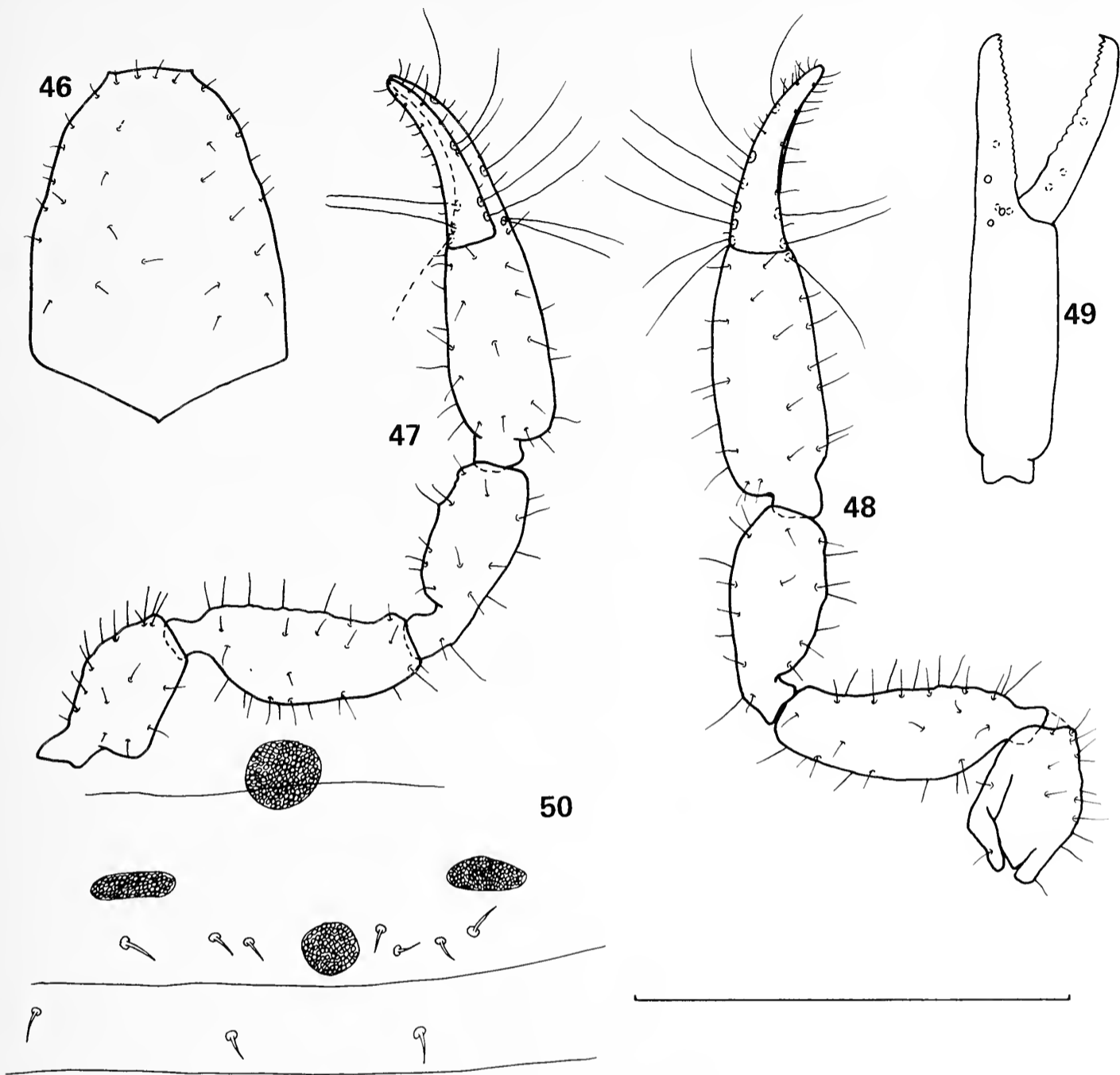
Figs. 46-50.–*Idiogaryops pumilus* (Hoff): 46, dorsal aspect of carapace, male from Little Cayman Island; 47, ventral aspect of left pedipalp, male from Little Cayman Island; 48, ventral aspect of right pedipalp, female from Little Cayman Island; 49, lateral aspect of right chela, female paratype, S-3782.3 (note absence of trichobothrium *et*); 50, female genitalia and associated sternites, from Little Cayman Island. Scale line = 1.00 mm (Figs. 46-49), 0.25 mm (Fig. 50).

substantially different from that species, and it undoubtedly represents a new species. I have not formally described it because I believe that more specimens, including females, should be examined. Indeed, it is possible that one or more of the female paratypes recorded by Hoff (1963) as *G. pumila* may be the female of this species.

Specimens examined.–U.S.A.: FLORIDA; *Highlands Co.,* Parker Islands, near Lake Placid, under bark of live oak *[Quercus virginianus]*, 22 April 1956 (C. C. Hoff), 1 male (AMNH, S-2886.2) (slide) (paratype of *G. pumila*).

Genus *Afrosternophorus* Beier, new status

Sternophorus Chamberlin: Beier 1932:16 (in part); Murthy and Ananthakrishnan 1977:118 (in part).
Sternophorus (Afrosternophorus) Beier 1967:81-82. Type species by original designation and monotypy *Sternophorus (Afrosternophorus) aethiopicus* Beier 1967.
Sternophorellus Beier 1971:371-372. Type species by original designation and monotypy *Sternophorellus araucariae* Beier 1971. NEW SYNONYMY.

Indogaryops Sivaraman 1981:322. Type species by original designation and monotypy *Indogaryops amrithiensis* Sivaraman 1981. NEW SYNONYMY.

Distribution.—New South Wales, Northern Territory, Queensland, Victoria, Australia; Ethiopia; India; Kampuchea; Laos; Papua New Guinea; Sri Lanka; Vietnam (Maps 3 to 6).

Diagnosis.—Females with one unspurred, median cribriform plate. Fixed chelal finger with seven trichobothria, moveable chelal finger with two or three trichobothria.

Subordinate taxa.—*Afrosternophorus aethiopicus* (Beier), *A. anabates,* new species, *A. araucariae* (Beier), *A. cavernae* (Beier), *A. ceylonicus* (Beier), *A. chamberlini* (Redikorzev), *A. cylindrimanus* (Beier), *A. dawydoffi* (Beier), *A. fallax,* new species, *A. grayi* (Beier), *A. hirsti* (Chamberlin), *A. nanus,* new species, *A. papuanus* (Beier), *A. xalyx,* new species.
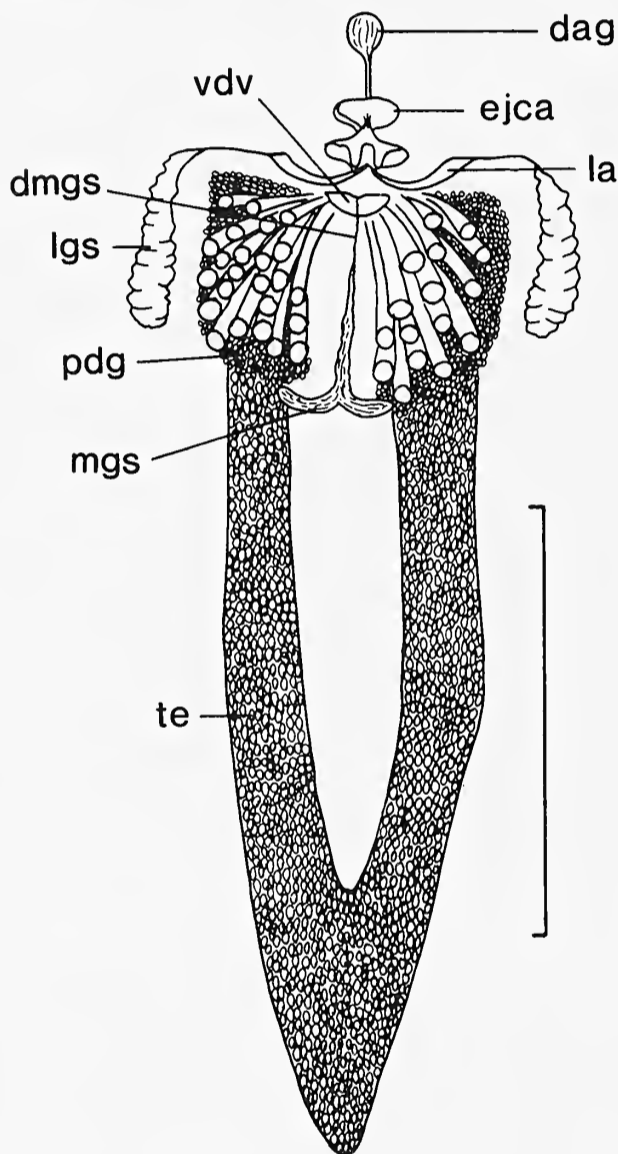
Fig. 51.—Ventral aspect of male genitalia of *Afrosternophorus hirsti* (Chamberlin), MH302.41. Scale line = 0.30 mm.

Remarks.—Beier (1967) originally described *Afrosternophorus* as a subgenus of the genus *Sternophorus;* the latter has been shown above to be a junior synonym of *Garyops.* Therefore, it is necessary to reassess the status of *Afrosternophorus.* Since females are needed to unequivocally place species in genera, it is unfortunate that *S. aethiopicus* (the type species of *Afrosternophorus*) is currently represented in collections by a single male. Nevertheless, I have raised *Afrosternophorus* to full generic status to accommodate those sternophorids in which females possess genitalia with one unspurred, median cribriform plate. If in the future it can be shown that *A. aethiopicus* is not congeneric with the remaining species I have included in the genus, *Sternophorellus* is the next available name.

Sternophorellus was erected by Beier (1971) for *S.araucariae* Beier from Papua New Guinea. It differed from other genera (except *Idiogaryops*) by possessing only two

trichobothria on the moveable chelal finger. This is no longer considered to be a valid character for separating genera, and we are left with the female genitalia to delimit the higher taxa. Unfortunately, females of *S. araucariae* have not been available for study, but females of the new species *A. fallax* from Vietnam and *A. xalyx* from Australia, which also have only two such trichobothria, possess genitalia with only one median cribriform plate. Therefore, *Sternophorellus* is synonymized with *Afrosternophorus*.
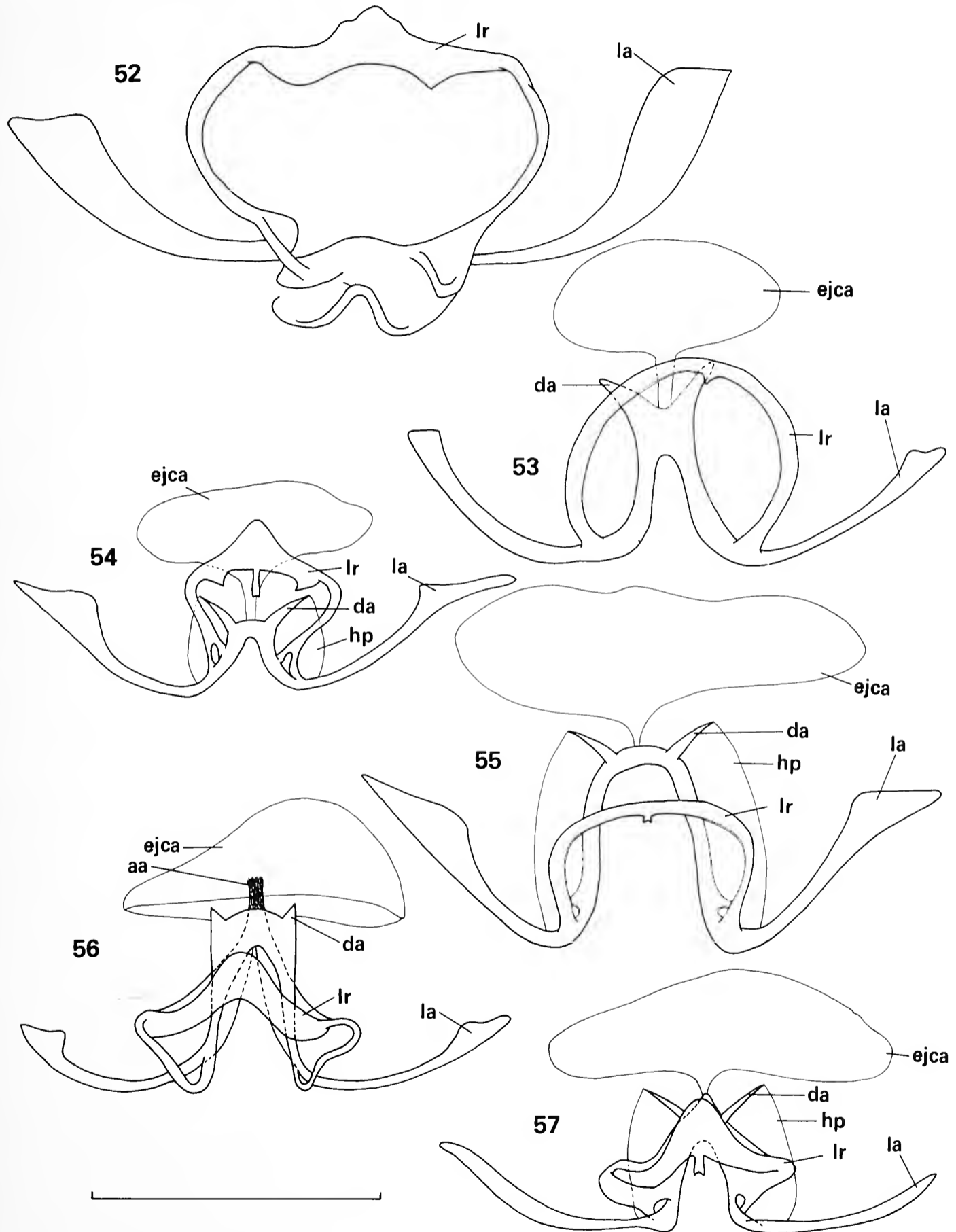
Figs. 52-57.—Anterior portion of male genitalia, ventral aspect: 52, *Afrosternophorus aethiopicus* (Beier), holotype (*ejca* not shown); 53, *A. ceylonicus* (Beier), paralectotype from Per Aru, Sri Lanka; 54, *A. chamberlini* (Redikorzev); 55, *A. dawydoffi* (Beier), paralectotype, MH430.01; 56, *A. hirsti* (Chamberlin), MH302.21; 57, *A. nanus,* new species, holotype. Scale line = 0.10 mm.
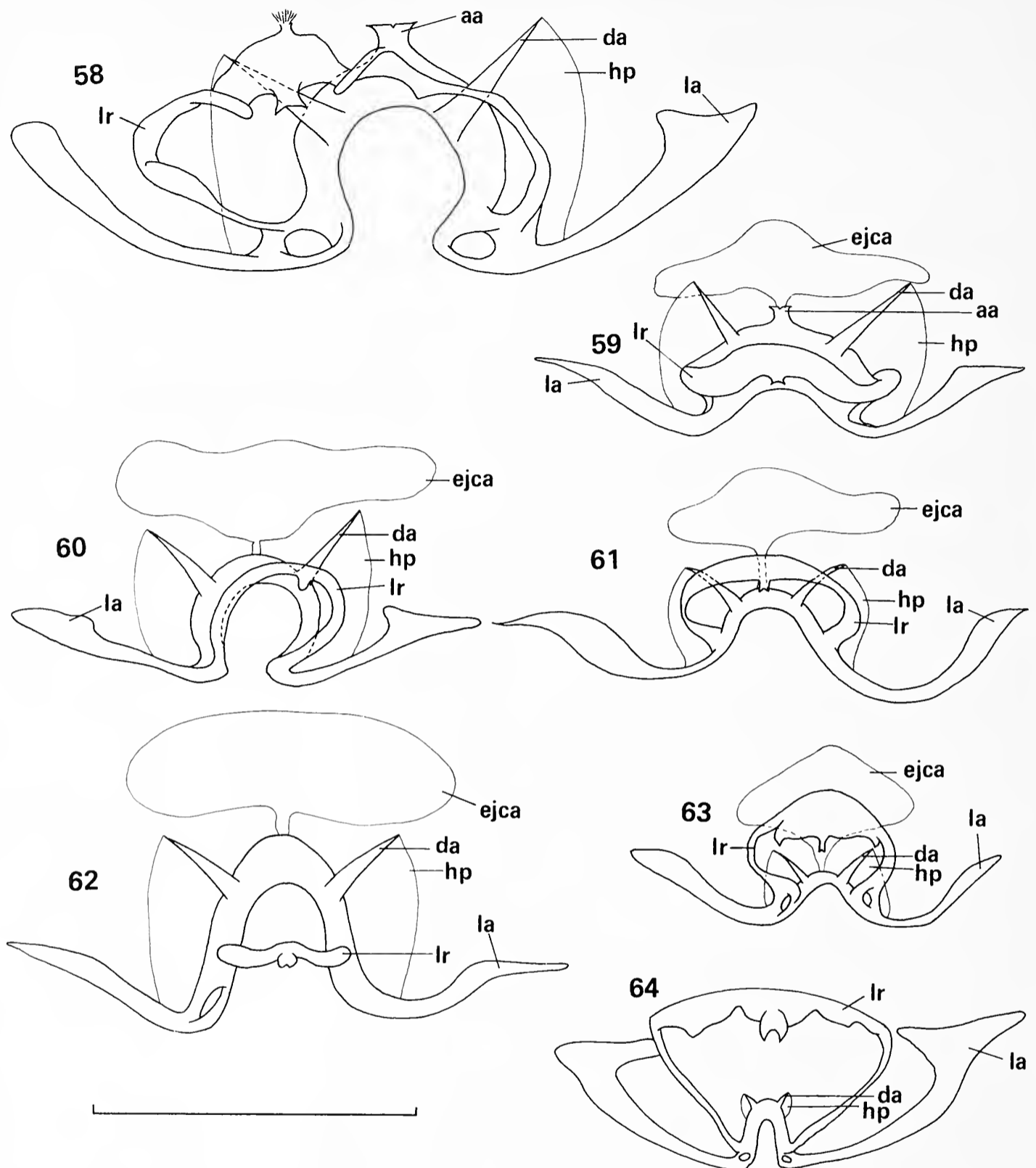
Figs. 58-64.—Anterior portion of male genitalia, ventral aspect: 58, *Afrosternophorus anabates*, new species, paratype, MH044.01 (*ejca* not shown); 59, *A. papuanus* (Beier), lectotype; 60, *A. grayi* (Beier), lectotype (slightly distorted); 61, *A. araucariae* (Beier), holotype; 62, *A. cavernae* (Beier), paratype; 63, *A. fallax*, new species, holotype; 64, *A. xalyx*, new species, holotype (*ejca* not shown). Scale line = 0.10 mm.

Indogaryops was erected by Sivaraman (1981) to include the Indian species *I. amrithiensis*. It was segregated from other genera by the presence of both a cucullus and an anterior constriction of the carapace. As discussed above, all sternophorid genera possess a cucullus, and the degree of constriction in the carapace may vary intraspecifically (see *A. dawydoffi*, Figs. 95-97); therefore, both characters are invalid at the generic level. More importantly, females of *I. amrithiensis* possess one median cribriform plate, and therefore *Indogaryops* falls into synonymy with *Afrosternophorus*. Furthermore, *I. amrithiensis* is a junior synonym of *A. ceylonicus*.
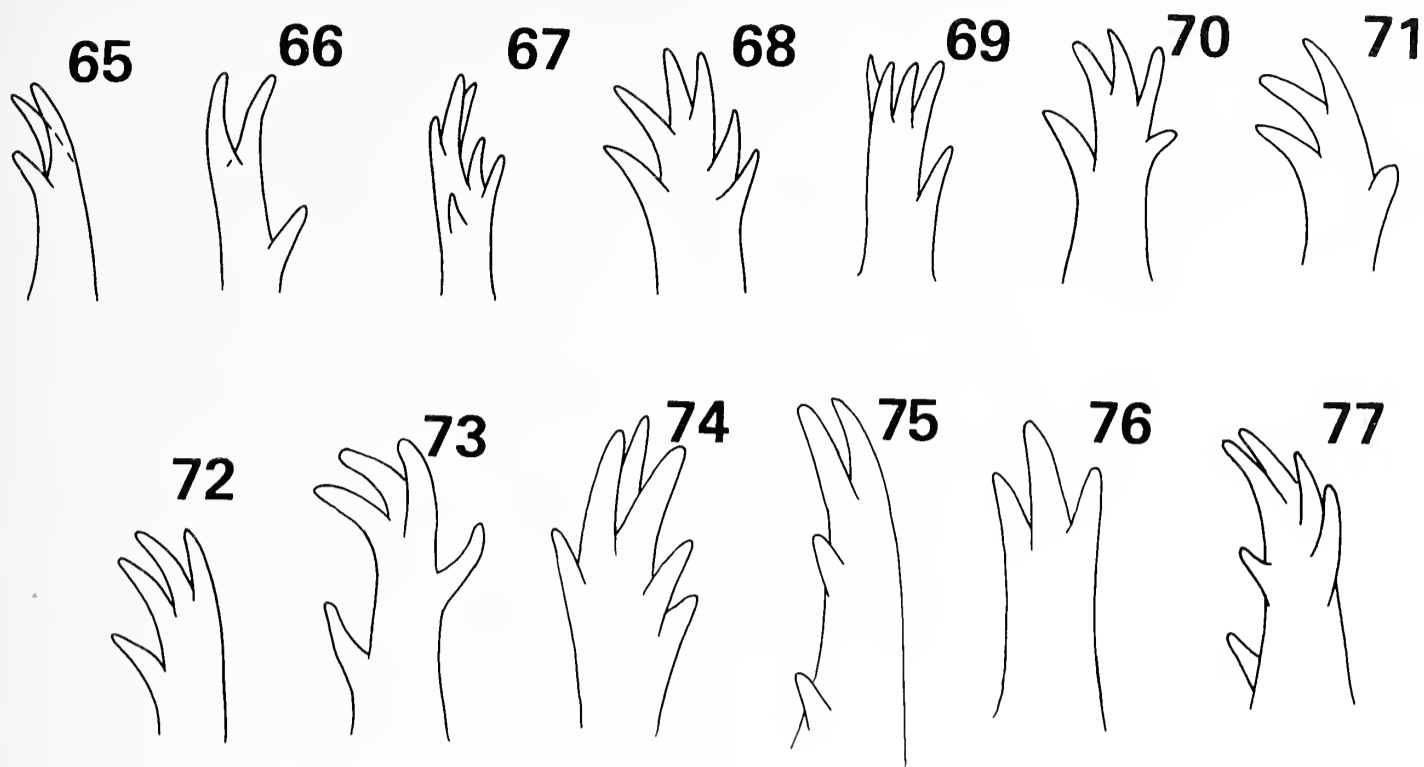
Figs. 65-77.—Female galeae: 65-66, *Afrosternophorus ceylonicus* (Beier), paralectotype from Chemiyanpattu, Sri Lanka; 67, *A. chamberlini* (Redikorzev); 68, *A. dawydoffi* (Beier), paralectotype from Roessei Chrum, Kampuchea; 69, *A. cylindrimanus* (Beier), paralectotype; 70, *A. hirsti* (Chamberlin), MH302.48; 71, *A. hirsti*, MH302.50; 72, *A. nanus,* new species, paratype, MH230.09; 73, *A. anabates,* new species, paratype, MH416.10; 74, *A. papuanus* (Beier), paralectotype; 75, *A. grayi* (Beier), paralectotype from Bulolo, Papua New Guinea; 76, *A. fallax,* new species, paratype; 77, *A. xalyx,* new species, paratype, K160. Not to same scale.

KEY TO SPECIES OF *AFROSTERNOPHORUS*

1. Moveable chelal finger with three trichobothria, *b, sb* and *t* . . . .
    . . . .*aethiopicus* group. . .2
    Moveable chelal finger with two trichobothria, *b* and *t* . . .   *araucariae* group. . . 11

2. Male genitalia with reduced dorsal apodemes 3
    Male genitalia with long, tapering dorsal apodemes. 5

3. Male genitalia with brush-like anterior apodeme; dorsal apodemes parallel sided; Australia . . . . *hirsti* (Chamberlin)
    Male genitalia without brush-like anterior apodeme; dorsal apodemes, if visible, not parallel sided 4

4. Chelal fingers long and strongly curved; male genitalia with short, but prominent, dorsal apodemes, slightly curved; female galea with two distal and one subdistal to subbasal rami; India, Sri Lanka. . . . . *ceylonicus* (Beier)
    Chelal fingers not especially long or strongly curved; male genitalia with much reduced dorsal apodemes, not visible; female galea unknown; Ethiopia . . . .
    . . . . *aethiopicus* (Beier)

5. Male genitalia with anterior apodeme distally broad; female galea with three distal, one subdistal and two (sometimes one) subbasal rami. 6
    Male genitalia with anterior apodeme not distally broad; female galea not as above 7

6. Chela (with pedicel) 0.83 to 0.895 (male), 0.835 to 1.03 mm (female) in length; Australia . . . . *anabates*, new species
    Chela (with pedicel) 0.61 to 0.69 (male), 0.73 to 0.74 mm (female) in length; Papua New Guinea. . . . . *papuanus* (Beier)

7. Lateral rod of male genitalia with long mid-piece; female galea with two distal, one subdistal and three subbasal rami; Vietnam, Laos (?) . . . *chamberlini* (Redikorzev)
    Lateral rod of male genitalia without, or with short, mid-piece; female galea never with three subbasal rami. 8

8. Chela (with pedicel) less than 0.74 mm in length; female galea with three distal to subdistal rami. 9
    Chela (with pedicel) greater than 0.90 mm in length; female galea with at least four distal to subdistal rami. 10

9. Chela (with pedicel) 0.645 to 0.70 (male), 0.68 to 0.74 mm (female) in length; Papua New Guinea. . . . . *grayi* (Beier)
    Chela (with pedicel) 0.55 to 0.59 (male), 0.56 to 0.61 mm (female) in length; Australia. . . . . *nanus*, new species

10. Chela (with pedicel) 1.07 to 1.35 (male), 1.11 to 1.38 mm (female) in length; female galea with six (sometimes five) distal to subdistal rami; Kampuchea, Vietnam . . . . *dawydoffi* (Beier)
    Chela (with pedicel) 0.935 to 0.95 (male), 1.02 mm (female) in length; female galea with four distal and one subbasal rami; Laos. . . . . *cylindrimanus* (Beier)

11. Male genitalia with reduced dorsal apodemes; female galea with two distal and four subdistal to subbasal rami; Australia . . . . *xalyx*, new species
    Male genitalia with long dorsal apodemes; female galea (when known) not as above 12

12. Chela (with pedicel) 0.805 to 0.82 mm (male) in length, 4.47 to 4.56 (male) times longer than broad; Papua New Guinea. . . . . *araucariae* (Beier)
    Chela (with pedicel) less than 0.70 mm in length, less than 4.00 times longer than broad 13

13. Lateral rod of male genitalia with short mid-piece; Papua New Guinea. . . . . *cavernae* (Beier)
    Lateral rod of male genitalia with long mid-piece; Vietnam . . . *fallax*, new species

Aethiopicus group

Diagnosis.—As for genus, except that the moveable chelal finger possesses three trichobothria, *b, sb* and *t*.

Subordinate taxa.—*Afrosternophorus aethiopicus* (Beier), *A. anabates*, new species, *A. ceylonicus* (Beier), *A. chamberlini* (Redikorzev), *A. cylindrimanus* (Beier), *A. dawydoffi* (Beier), *A. grayi* (Beier), *A. hirsti* (Chamberlin), *A. nanus*, new species, *A. papuanus* (Beier).

Map 3.—North Africa showing known distribution of *Afrosternophorus aethiopicus* (Beier).

Afrosternophorus aethiopicus (Beier), new combination
Figs. 52, 78-79; Map 3

Sternophorus (Afrosternophorus) aethiopicus Beier 1967:81-82, Fig. 6.

Type.—Holotype male, Alomata, Ethiopia (5000 ft) [= 1525 m], 16 January 1960 (E. S. Ross), CAS, Type No. 9386 (slide).

Distribution.—Ethiopia (Map 3).

Diagnosis.—Male genitalia with greatly reduced dorsal apodemes; lateral rod lying anteriorly to the rest of the genital armature. Chela (with pedicel) 0.895 mm (male) in length.

Description.—Male only. Pedipalpal trochanter large and inflated, 1.76, femur 2.68 to 2.76, tibia 1.90, chela (with pedicel) 3.52, chela (without pedicel) 3.49 times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Fig. 78). Serrula exterior of chelicera with 12 lamellae. Galea of male simple. Carapace anteriorly constricted (Fig. 79), with at least 12 setae; 1.37 times longer than broad. Male genitalia (Fig. 52) with greatly reduced dorsal apodemes; lateral rod lying anteriorly to the rest of the genital armature. Tergal chaetotaxy: 6:7:5:5:5:6:6:6:6:T1T4T1T:?:2. Sternal chaetotaxy: 0:6:(0)6[0?](0):(1)6(1):6:6:6:8?:7:T1T4T1T:?:2. Coxal chaetotaxy: 3:5:2-5:4.

Dimensions (mm): Body length 2.4; pedipalps: trochanter 0.37-0.38/0.21, femur 0.58 -0.59/0.21-0.22, tibia 0.47/0.205, chela (with pedicel) 0.895/0.245, chela (without pedicel) 0.855, moveable finger length 0.43; chelicera 0.17/0.09, moveable finger length 0.12; carapace 0.82/0.60; leg I: coxa 0.33/0.27, trochanter 0.12-0.13/0.10, femur I 0.12/0.12, femur II 0.17/0.12, tibia 0.21/0.075, tarsus 0.12-0.13/0.05; leg IV: coxa width 0.24-0.26, trochanter 0.15-0.17/0.13-0.15, femur I 0.22/0.20, femur II 0.26/ 0.20-0.21, tibia 0.35-0.36/0.12-0.13, tarsus 0.19/0.08-0.085.
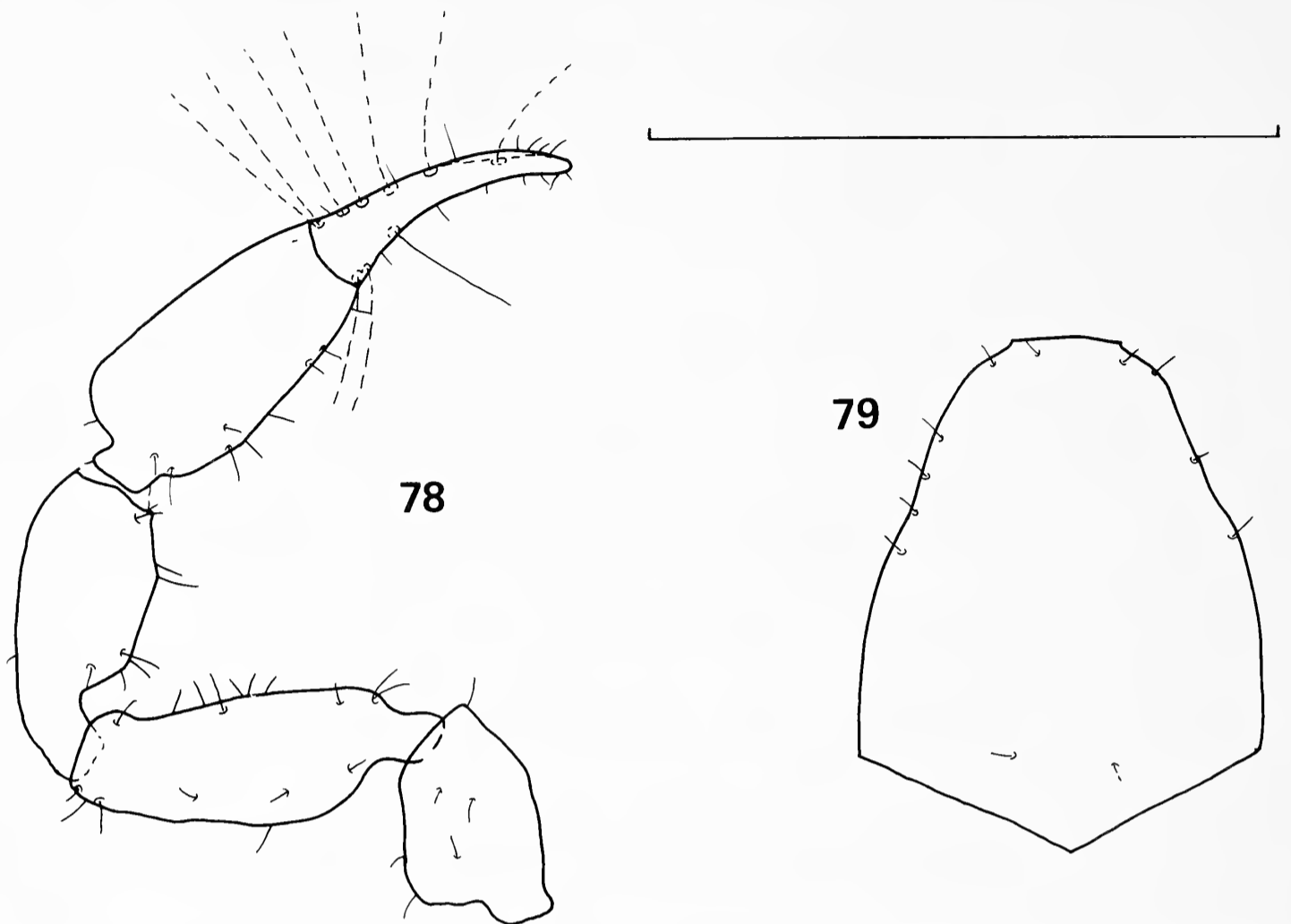
Figs. 78-79.—*Afrosternophorus aethiopicus* (Beier), male holotype: 78, ventral aspect of right pedipalp; 79, dorsal aspect of carapace. Scale line = 1.00 mm.

Habitat.—No habitat data accompanied the specimen.

Remarks.—The single available specimen is in poor condition and the sclerotized portions of the genitalia are ill-defined. The left pedipalpal tibia and chela were missing from the specimen.

Afrosternophorus ceylonicus (Beier), new combination
Figs. 53, 65-66, 80-85, 90; Map 4

Sternophorus ceylonicus Beier 1973b:47, Fig. 11.
Sternophorus indicus Murthy and Ananthakrishnan 1977:119-121, Fig. 39. NEW SYNONYMY.
Sternophorus (Sternophorus) transiens Murthy and Ananthakrishnan 1977:121-123, Fig. 40. NEW SYNONYMY.
Sternophorus (Sternophorus) montanus Sivaraman 1981:315-317, Fig. 1. NEW SYNONYMY.
Sternophorus (Afrosternophorus) femoratus Sivaraman 1981:317-319, Fig. 2. NEW SYNONYMY.
Sternophorus (Afrosternophorus) intermedius Sivaraman 1981:319-321, Fig. 3. NEW SYNONYMY.
Indogaryops amrithiensis Sivaraman 1981:322-324, Fig. 4. NEW SYNONYMY.

Types.—*Sternophorus ceylonicus:* Lectotype male (present designation), paralectotype female, Chemiyanpattu, 18 mi. [= 29 km] SE of Point Pedro, North Province, Sri Lanka, under bark of tree-like bush, 13 February 1962 (Brink, Anderson, Cederholm), LU, Type No. 539 (spirit). Paralectotype male, same data as above, NHMW (spirit). Two paralectotype males, paralectotype female, paralectotype tritonymph, Per Aru, 9 mi. [= 14.5 km] E of Mankulan, North Province, Sri Lanka, under log, 14 February 1962 (Brink, Anderson, Cederholm), LU, Type No. 539 (slides and spirit). Two males, same data as above,
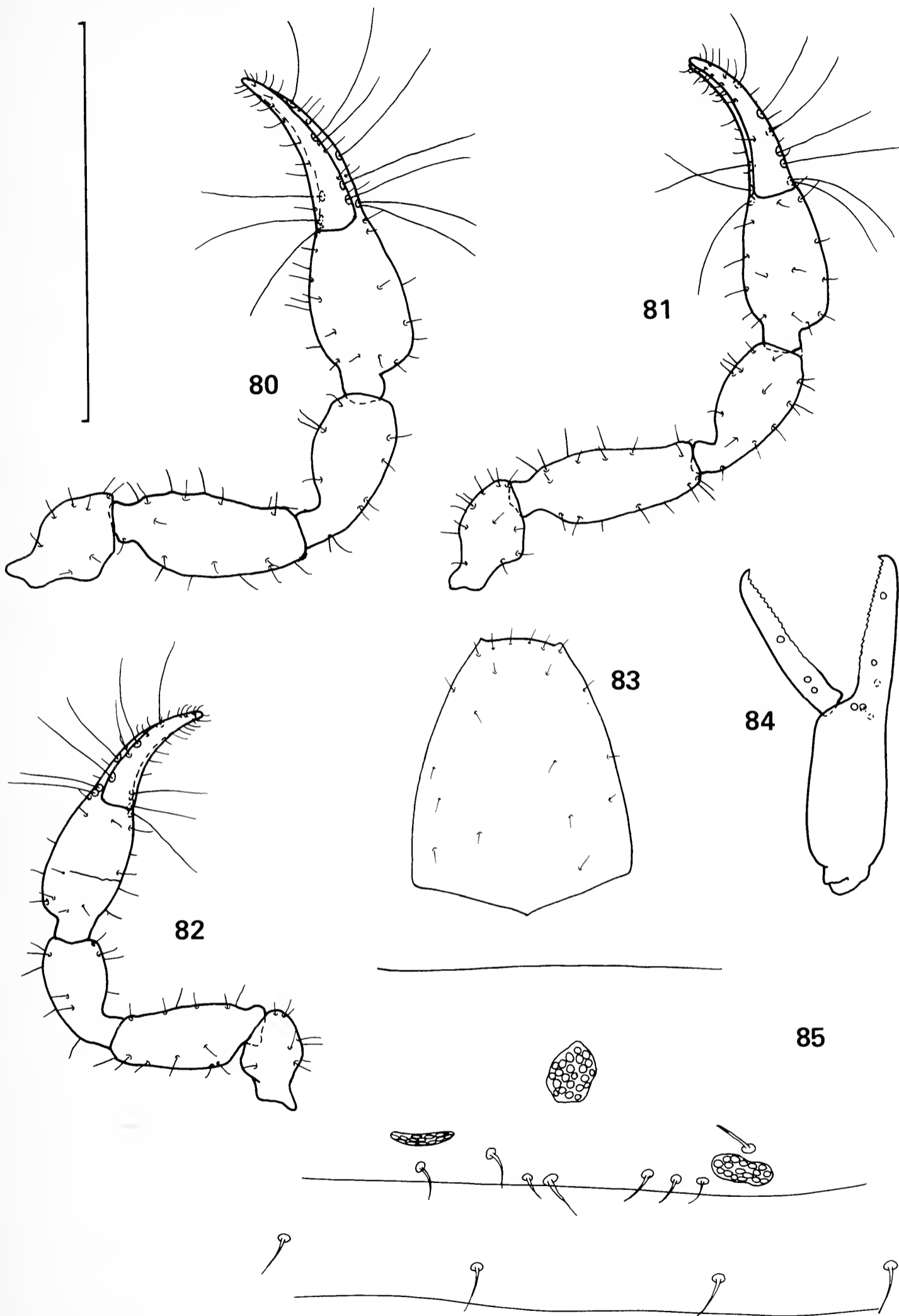
Figs. 80-85.—*Afrosternophorus ceylonicus* (Beier): 80, ventral aspect of left pedipalp, female paralectotype from Chemiyanpattu, Sri Lanka; 81, same, male lectotype; 82, ventral aspect of right pedipalp, tritonymph paralectotype from Per Aru, Sri Lanka; 83, dorsal aspect of carapace, male paralectotype from Per Aru; 84, lateral aspect of left chela, female paralectotype from Per Aru; 85, female genitalia and associated sternites, paralectotype from Per Aru. Scale line = 1.00 mm (Figs. 80-84), 0.25 mm (Fig. 85).

NHMW (spirit). Two paralectotype males, two paralectotype females, 5 mi. [= 8 km] NNE of Puttalam, North-West Province, Sri Lanka, 1 February 1962 (Brink, Anderson, Cederholm), NHMW (spirit). Five paralectotype males, five paralectotype females, same data as above, LU, lost (see Remarks).

Sternophorus indicus: Three paratype males, Tirupathi, Andhra Pradesh, India, under bark, 14 August 1960 (V. A. Murthy), VAM (slides).

Sternophorus transiens: Paratype male, paratype female, Shimoga, Karnataka, India, under bark, 4 January 1963 (V. A. Murthy), VAM (slides).

Sternophorus montanus: Holotype male, paratype female, Alakarkoil Hill forest, Madurai, Tamil Nadu, India, under bark, 15 July 1977 (S. Sivaraman), MHNG (slides).

Sternophorus femoratus: Holotype female, paratype male, Amrithi forest, North Arcot, Tamil Nadu, India, under bark, 2 October 1977 (S. Sivaraman), MHNG (slides).

Sternophorus intermedius: Holotype female, paratype male, Alakarkoil Hill forest, Madurai, Tamil Nadu, India, under bark, 15 July 1977 (S. Sivaraman), MHNG (slides).

Indogaryops amrithiensis: Holotype female, Amrithi forest, North Arcot, Tamil Nadu, India, under bark, 2 October 1977 (S. Sivaraman), MHNG (slide).

Distribution.—India, Sri Lanka (Map 4).

Diagnosis.—Male genitalia with short, but prominent, slightly curved dorsal apodemes; lateral rod lying anteriorly to the rest of the genital armature. Female galea with two distal and one subdistal to subbasal rami. Chelal fingers long and strongly curved. Chela (with pedicel) 0.75 to 0.835 (male), 0.80 to 0.94 mm (female) in length.

Description.—ADULTS: Pedipalpal trochanter 1.63 to 1.79 (male), 1.64 to 1.84 (female), femur 2.47 to 2.86 (male), 2.48 to 2.81 (female), tibia 2.00 to 2.29 (male), 1.95 to 2.29 (female), chela (with pedicel) 3.39 to 3.76 (male), 3.35 to 3.72 (female), chela (without pedicel) 3.20 to 3.56 (male), 3.20 to 3.50 (female) times longer than broad. Chelal fingers long and strongly curved (Figs. 80-81). Trichobothria as for *aethiopicus* group, in usual position (Figs. 80-81, 84). Serrula exterior of chelicera with 10 to 12 (male), 11 to 13 (female) lamellae. Galea of male simple, of female with two distal and one subdistal to subbasal rami (Figs. 65-66). Carapace usually unconstricted (Fig. 83), but sometimes a slight constriction is present, with 20 to 30 (male), 22 to 28 (female) setae; 1.26 to 1.46 (male), 1.21 to 1.33 (female) times longer than broad. Male genitalia (Fig. 53) with short, but prominent, slightly curved dorsal apodemes; lateral rod lying anteriorly to the rest of the genital armature. Female genitalia as for genus (Fig. 85). Tergal chaetotaxy: male, 5-6:4-6:3-4:6-7:5-7:5-7:6-7:5-7:4-8:T1T3-5T1T:?:2; female, 5-7:4-6: 3-5:5-7:4-7:6-8:5-7:6-8:6-8:T1T3-4T1T:?:2. Sternal chaetotaxy: male, 0:4-8:(0)3-4[4-6] (0):(1)4-5(1):5-8:6-7:6:6-7:6:T1T3-4T1T:?:2; female, 0:7-8:(0)4(0):(1)4-6(1):5-8:5-8: 6-7:6-7:4-8:T1T4T1T:?:2. Coxal chaetotaxy: male, 3-5:3-6:3-5:3-5; female, 3-5:3-5:2-5: 3-6.

Dimensions (mm): Body length 1.7-2.1 (2.1-2.9); pedipalps: trochanter 0.28-0.32/ 0.16-0.195 (0.295-0.36/0.17-0.20), femur 0.465-0.535/0.175-0.205 (0.495-0.605/0.18-0.225), tibia 0.375-0.44/0.175-0.205 (0.40-0.51/0.185-0.225), chela (with pedicel) 0.75-0.835/0.205-0.24 (0.80-0.94/0.22-0.27), chela (without pedicel) 0.72-0.80 (0.755-0.92), moveable finger length 0.37-0.43 (0.41-0.48); chelicera 0.155-0.175/0.09-0.095 (0.18-0.185/0.10-0.115), moveable finger length 0.11-0.13 (0.12-0.14); carapace 0.68-0.76/0.51-0.595 (0.74-0.89/0.56-0.68); leg I: coxa 0.19-0.23/0.235-0.255/0.26-0.30), trochanter 0.095-0.135/0.09-0.10 (0.12-0.15/0.095-0.11), femur I 0.095-0.115/0.10-0.12 (0.12-0.14/0.11-0.135), femur II 0.15-0.18/0.10-0.12 (0.17-0.20/0.11-0.135), tibia 0.17-0.21/0.065-0.08 (0.20-0.22/0.075-0.085), tarsus 0.105-0.13/0.05-0.055 (0.13-0.14/

0.05-0.055); leg IV: coxa width 0.21-0.26 (0.275-0.305), trochanter 0.14-0.175/0.105-0.12 (0.165-0.195/0.12-0.13), femur I 0.17-0.195/0.14-0.185 (0.215-0.24/0.175-0.18), femur II 0.22-0.26/0.14-0.19 (0.26-0.28/0.18-0.185), tibia 0.27-0.33/0.10-0.115 (0.32/0.105), tarsus 0.17-0.185/0.06-0.075 (0.18/0.07).

TRITONYMPHS: Pedipalpal trochanter 1.66 to 1.68, femur 2.44 to 2.52, tibia 2.00 to 2.03, chela (with pedicel) 3.47 to 3.63, chela (without pedicel) 3.32 to 3.39 times longer than broad. Fixed finger with seven trichobothria, moveable finger with two trichobothria (Fig. 82); *it*, *sb* and *st* absent. Serrula exterior of chelicera with 10 lamellae. Galea as for female. Carapace unconstricted, with 20 setae; 1.25 times longer than broad. Tergal chaetotaxy: 4:4:6:6:6?:6:6:6:6:T1T3T1T:?:2. Sternal chaetotaxy: 0:2:(0)4(0): (1)4(1):6:6:6:6:6:T1T3T1T:?:2. Coxal chaetotaxy: 4:3-4:3:2.

Dimensions (mm): Body length 1.9; pedipalps: trochanter 0.235-0.24/0.14-0.145, femur 0.39/0.155-0.16, tibia 0.31-0.315/0.155, chela (with pedicel) 0.66-0.69/0.19, chela (without pedicel) 0.63-0.645, moveable finger length 0.32-0.34; carapace 0.69/0.55.

Habitat.—The Chemiyanpattu specimens were taken from under bark of a "tree-like bush" and the Per Aru specimens were taken from under logs in jungle. Murthy and Ananthakrishnan's and Sivaraman's material was all taken from under bark.

Remarks.—Unfortunately, one vial containing type material (5 males, 5 females, Puttalam, Sri Lanka) was lost in transit from Lund to Monash University.

Beier (1973b) did not designate a primary type, and merely published and labelled some Chemiyanpattu specimens as "Typen". A lectotype male has been selected from this vial.

Through the characteristic generosity of Prof. V. A. Murthy, I have been able to examine some type specimens of *S. indicus* and *S. transiens*, as well as many other specimens from southern India. The type material of *S. montanus*, *S. femoratus*, *S. intermedius* and *I. amrithiensis* was also available for study. All of this material possesses the characteristic chelal finger shape, female galea and, most importantly, male genitalia of *A. ceylonicus*, and therefore these species are hereby synonymized with *ceylonicus*. Murthy and Ananthakrishnan (1977) erroneously included the chelal trichobothria *it* and *st* in their description and diagram of *S. indicus*. My examination of three paratypes reveals that these trichobothria are absent, as in all sternophorids.

Other specimens examined.—INDIA: TAMIL NADU; Alakarkoil Hill forest, Madurai, under bark, 15 July 1977 (S. Sivaraman), 3 males, 1 female (VAM) (spirit). Amrithi forest, North Arcot, under bark, 2 October 1977 (S. Sivaraman), 1 male, 1 female (VAM) (spirit). Same data as above except, date? (V. A. Murthy), 3 males, 1 tritonymph (ANIC, MH472.01-04) (spirit). No locality data, 2 males, 2 females (VAM) (spirit).

Afrosternophorus chamberlini (Redikorzev), new combination
Figs. 54, 67, 86-90; Map 4

Sternophorus chamberlini Redikorzev 1938:89-91, Figs. 17-18; Beier 1951:71-72, Fig. 16 (in part).

Types.—Lectotype female (present designation), Dalat [= Dà Lat, see Table 1], Vietnam, January 1931 (C. Dawydoff), MNHN (spirit). Paralectotype female, same data as lectotype except 3 February 1931, MNHN (spirit). One specimen, Abre-Broyé [= Ap̂ Trạm Hahn], Plateau du Lang-Biang [= Cao Nguyên Lâm Viên], Vietnam, 1,500 m, 20 January 1931 (C. Dawydoff), depository unknown, not examined.

Distribution.—Vietnam, Laos? (Map 4).
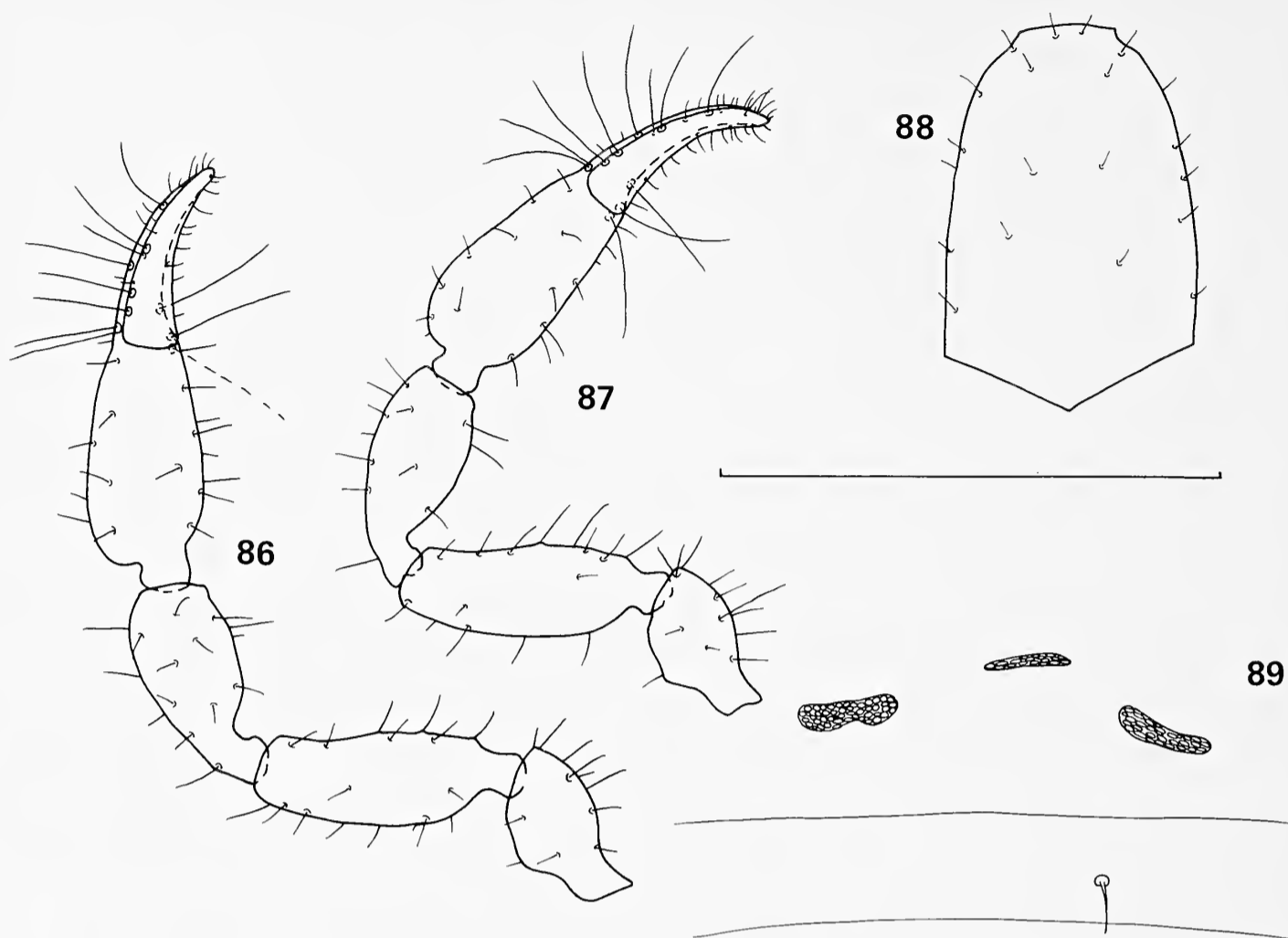
Figs. 86-89.—*Afrosternophorus chamberlini* (Redikorzev): 86, ventral aspect of right pedipalp, female; 87, same, male; 88, dorsal aspect of carapace, male; 89, female genitalia and associated sternites. Scale line = 1.00 mm (Figs. 86-88), 0.25 mm (Fig. 89).

Diagnosis.—Male genitalia with long, acute dorsal apodemes; mid-piece of lateral rod elongate. Female galea with two distal, one subdistal and three subbasal rami. Chela (with pedicel) 0.74 to 0.81 (male), 0.74 to 0.90 mm (female) in length.

Description.—Pedipalpal trochanter 1.79 to 1.87 (male), 1.75 to 2.00 (female), femur 3.00 to 3.16 (male), 2.73 to 3.17 (female), tibia 2.18 to 2.39 (male), 2.13 to 2.35 (female), chela (with pedicel) 3.68 to 3.95 (male), 3.47 to 4.20 (female), chela (without pedicel) 3.55 to 3.74 (male), 3.30 to 3.98 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 86-87). Serrula exterior of chelicera with 10 to 11 (male), 11 to 12 (female) lamellae. Galea of male simple, of female with two distal, one subdistal and three subbasal rami (Fig. 67). Carapace (Fig. 88) unconstricted, with 23 (male), 22 to 28 (female) setae; 1.50 to 1.51 (male), 1.44 to 1.56 (male) times longer than broad. Male genitalia with long, acute dorsal apodemes; mid-piece of lateral rod elongate (Fig. 54). Female genitalia as for genus (Fig. 89). Tergal chaetotaxy: male, 6:5:2:6:6:6:7:6:7:T1T4T1T:?:2; female, 6:4-6:2-4:6:6-8?:6-7:5-8:5-8:6-8:T1T4 T1T:?:2. Sternal chaetotaxy: male, 0:5:(0)5[8](0):(1)6(1):8:8:6:7:6:T1T4T1T:?:2; female, 0:6-9:(0)5-6(0):(1)6(1):5?-9:4-9:7-8:6:6-7:T1T4T1T:?:2. Coxal chaetotaxy: male, 4-5:3-5:5:4; female, 3-6:4-6:3-6:3-5.

Dimensions (mm): Body length 1.6-1.8 (2.0-2.7); pedipalps: trochanter 0.285-0.305/ 0.155-0.17 (0.28-0.36/0.16-0.19), femur 0.48-0.53/0.155-0.175 (0.45-0.59/0.165-0.205), tibia 0.37-0.44/0.165-0.185 (0.37-0.49/0.165-0.215), chela (with pedicel) 0.74-0.81/ 0.195-0.22 (0.74-0.90/0.20-0.25), chela (without pedicel) 0.705-0.78 (0.705-0.865), moveable finger length 0.345-0.38 (0.36-0.40); chelicera 0.13-0.16/0.08-0.09 (0.15-0.17/ 0.08-0.10), moveable finger length 0.105-0.115 (0.105-0.12); carapace 0.665-0.69/

0.44-0.46 (0.64-0.86/0.49-0.555); leg I: coxa 0.185-0.19/0.20-0.21 (0.195-0.22/
0.21-0.25), trochanter 0.105-0.11/0.07 (0.11-0.12/0.075-0.08), femur I 0.10/0.105-0.11
(0.105-0.12/0.095-0.11), femur II 0.14/0.10-0.11 (0.15-0.16/0.095-0.105), tibia 0.16-
0.165/0.065 (0.18/0.07), tarsus 0.10-0.11/0.045 (0.11-0.12/0.045); leg IV: coxa width
0.18-0.21 (0.21-0.24), trochanter 0.12-0.155/0.09-0.10 (0.15-0.165/0.10-0.11), femur I
0.175-0.20/0.15-0.18 (0.205/0.165), femur II 0.205-0.255/0.14-0.18 (0.22/0.165), tibia
0.275-0.32/0.09-0.10 (0.275-0.32/0.09-0.10), tarsus 0.165-0.17/0.065 (0.16-0.17/0.06-
0.07).

Habitat.—No habitat data accompanied the specimens.

Remarks.—Redikorzev did not designate a holotype and thus a lectotype has been
selected. Beier's (1951) material was composed of two species: *chamberlini* and *fallax*,
new species. *Afrosternophorus fallax* is substantially different from *A. chamberlini* and
can be separated by several characters, particularly the presence of only two trichobothria
on the moveable chelal finger. Beier's (1951) description of *chamberlini* was a composite
of these two species. His male pedipalp measurements were of *fallax*, and his female
measurements were of *chamberlini*.

Beier (1951) erroneously included the chelal trichobothrium *it* in his diagram of this
species. He also recorded one female from Plateau des Bolovens, Laos. This specimen
needs to be re-examined to determine its true status. A deutonymph of *Stenatemnus
annamensis* Beier (?) was present in one vial.

The NHMW material is in poor condition, and few specimens could be fully scored for
setation or leg measurements.

Specimens examined.—VIETNAM: Plateau von Langbian [= Cao Nguyên Lâm Viên], 1938-1939
(C. Dawydoff), 3 males, 9 females (NHMW) (spirit).

Afrosternophorus dawydoffi (Beier), new combination
Figs. 55, 68, 90-97; Map 4

Sternophorus dawydoffi Beier 1951:70-71, Fig. 15.
Sternophorus cylindrimanus Beier 1951:73-74, Fig. 17 (in part).

Types.—*Sternophorus dawydoffi:* Lectotype male (present designation), four paralec-
totype males, two paralectotype females, Rusei Chrum [= Roessei Chrum, see Table 1],
Kampuchea, March 1939 (C. Dawydoff), NHMW (spirit). Paralectotypes: one male, one
female, same data as above, ANIC, MH430.01-02 (slides). One male, two females, same
locality as above, April 1939 (C. Dawydoff), NHMW (spirit). One male, three females,
Beng Mealea [= Phumĭ Boĕng Méalea], Kampuchea, April 1939 (C. Dawydoff), NHMW
(spirit). Two females, Phailin [= Pailĭn], Kampuchea, March 1939 (C. Dawydoff), NHMW
(spirit). Two males, three females, Prah Khan [= Prasat Preăh Khăn], Kampuchea, April
1939 (C. Dawydoff), NHMW (spirit). Five males, two females, Réam [= Phsar Ream],
Kampuchea, April 1939 (C. Dawydoff), NHMW (spirit). Two males, one female, Sré
Umbell [= Srê Âmbĕl], Kampuchea, March 1939 (C. Dawydoff), NHMW (spirit). One
male, three females, Insel Phu-Quoc [= Đảo Phú Quốc], Vietnam, March 1939 (C. Dawy-
doff), NHMW (spirit).

Sternophorus cylindrimanus: Paralectotype female, Krongpha [= Thôn Sông Pha],
Vietnam, 30 April 1939 (C. Dawydoff), NHMW (spirit).

Distribution.—Kampuchea, Vietnam (Map 4).

Diagnosis.—Male genitalia with long, acute dorsal apodemes. Female galea with six
(sometimes five) distal to subdistal rami. Large species: chela (with pedicel) 1.07 to 1.35
(male), 1.11 to 1.38 mm (female) in length.
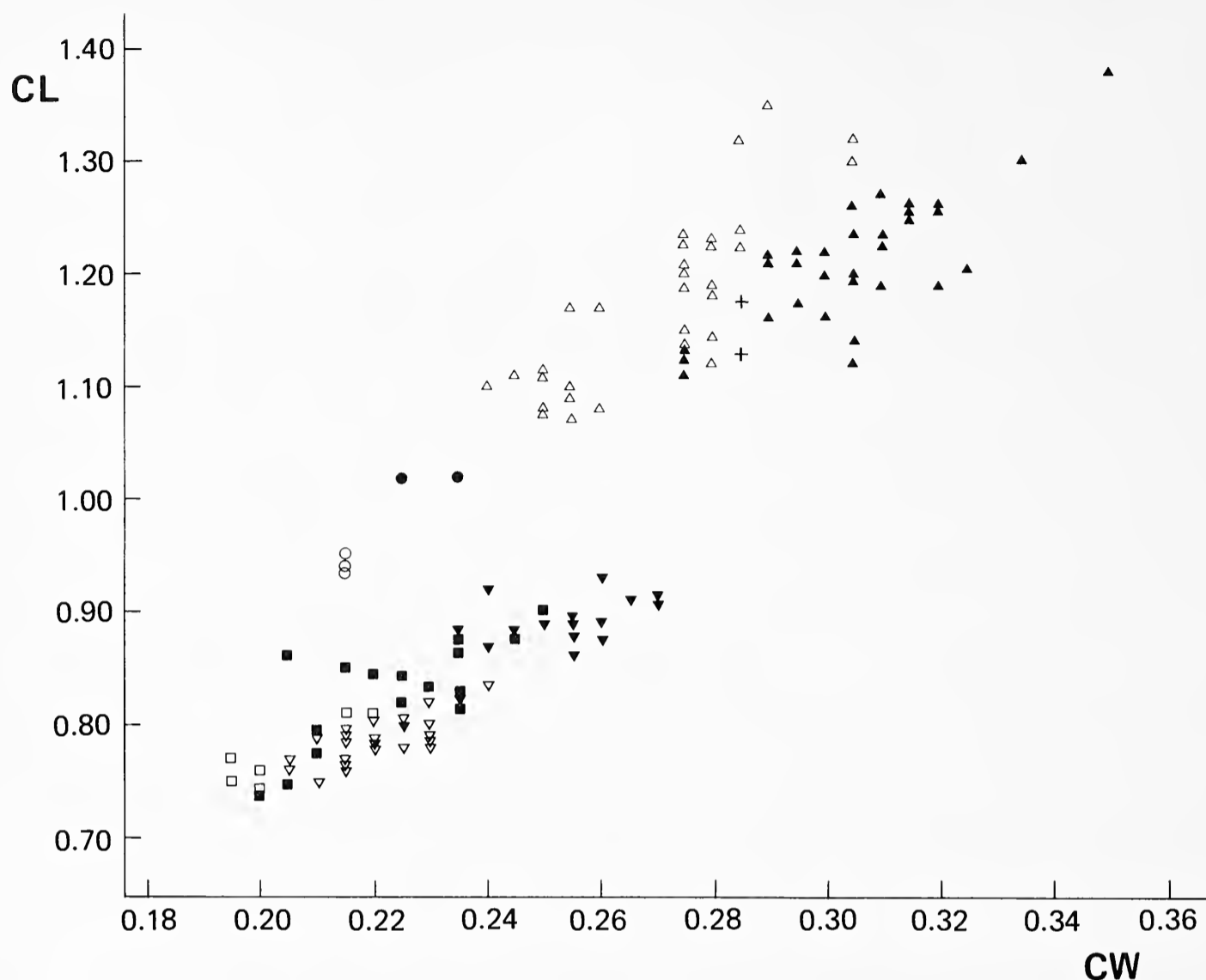
Figs. 90.—Graph of chela (with pedicel) length (CL) versus width (CW), in mm; open symbols, males; closed symbols, females: *Afrosternophorus ceylonicus* (Beier) (inverted triangles), *A. chamberlini* (Redikorzev) (squares), *A. dawydoffi* (Beier) (upright triangles), *A. dawydoffi*, paralectotype female of *A. cylindrimanus* (Beier) (crosses), *A. cylindrimanus* (circles).

Description.—Pedipalpal trochanter relatively inflated, 1.88 to 2.27 (male), 1.81 to 2.02 (female), femur elongate, 3.18 to 3.72 (male), 2.96 to 3.30 (female), tibia 2.60 to 2.88 (male), 2.35 to 2.63 (female), chela (with pedicel) 4.00 to 4.46 (male), 3.67 to 4.13 (female), chela (without pedicel) 3.84 to 4.40 (male), 3.44 to 3.97 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 91-93). Serrula exterior of chelicera with 12 to 15 (male), 11 to 15 (female) lamellae. Galea of male simple, of female with six (occasionally five) distal to subdistal rami (Fig. 68). Carapace usually unconstricted (Fig. 95), but sometimes a slight (Fig. 96) or a conspicuous constriction is present (Fig. 97), with 24 to 32 (male), 24 to 31 (female) setae; 1.24 to 1.52 (male), 1.30 to 1.55 (female) times longer than broad. Male genitalia with long, acute dorsal apodemes (Fig. 55). Female genitalia as for genus (Fig. 94). Tergal chaetotaxy: male, 4-6:4-6:3-4:4-6:5-6:5-7:6:6-7:6:T1T4-5T1T:?:2; female, 4-6:5-6:2-4:4-7:6: 5-6:4-7:5-7:5-6:T1T4T1T:?:2. Sternal chaetotaxy: male, 0:2-6:(0)4-6[7-8](0):(1)4-6(1): 4-9:6-8:5-6:5-8:5-7:T1T4T1T:?:2; female, 0:5-9:(0)4-5(0):(1)4-6(1):6:5-6:6:6-7:5-7: T1T4T1T:?:2. Coxal chaetotaxy: male, 3-6:3-6:3-7:3-5; female, 3-6:3-6:3-6:3-5.

Dimensions (mm): Body length 2.0-3.3 (2.4-3.3); pedipalps: trochanter 0.43-0.545/ 0.215-0.265 (0.44-0.555/0.23-0.29), femur 0.72-0.93/0.21-0.27 (0.74-0.95/0.23-0.295), tibia 0.60-0.77/0.22-0.275 (0.595-0.76/0.24-0.305), chela (with pedicel) 1.07-1.35/ 0.24-0.305 (1.11-1.38/0.275-0.35), chela (without pedicel) 1.02-1.275 (1.05-1.32), moveable finger length 0.47-0.61 (0.53-0.66); chelicera 0.20-0.23/0.11-0.13 (0.21-0.28/

0.12-0.14), moveable finger length 0.14-0.16 (0.15-0.175); carapace 0.90-1.13/0.645-0.795 (0.96-1.215/0.71-0.83); leg I: coxa 0.25-0.31/0.29-0.36 (0.275-0.35/0.32-0.41), trochanter 0.145-0.185/0.105-0.125 (0.15-0.20/0.11-0.14), femur I 0.13-0.165/0.14-0.175 (0.15-0.19/0.15-0.19), femur II 0.24-0.30/0.14-0.18 (0.25-0.315/0.15-0.19), tibia 0.25-0.29/0.085-0.115 (0.26-0.32/0.095-0.115), tarsus 0.12-0.175/0.06-0.07 (0.15-0.195/0.06-0.075); leg IV: coxa width 0.27-0.33 (0.29-0.37), trochanter 0.20-0.25/0.14-0.16 (0.21-0.275/0.14-0.175), femur I 0.255-0.305/0.22-0.285 (0.27-0.345/0.25-0.325), femur II 0.39-0.51/0.225-0.285 (0.40-0.50/0.25-0.33), tibia 0.405-0.51/0.13-0.165 (0.45-0.56/0.14-0.18), tarsus 0.205-0.255/0.08-0.10 (0.23-0.27/0.075-0.105).

Habitat.—No habitat data accompanied the specimens.
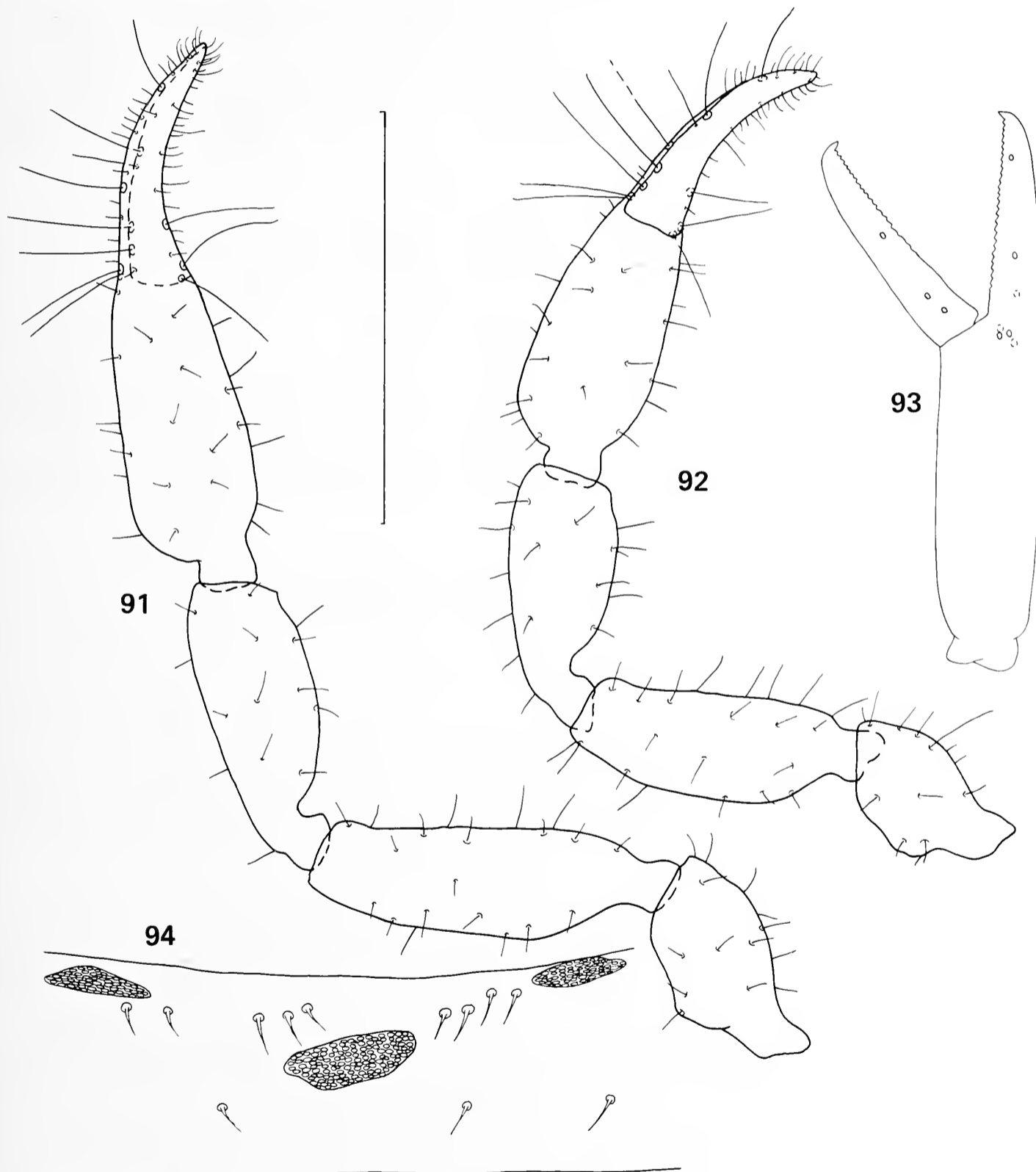
Figs. 91-94.—*Afrosternophorus dawydoffi* (Beier): 91, dorsal aspect of left pedipalp, male lectotype; 92, ventral aspect of right pedipalp, female paralectotype from Roessei Chrum, Kampuchea; 93, lateral aspect of left chela, male paralectotype, MH430.01; 94, female genitalia and associated sternites, paralectotype from Roessei Chrum. Scale line = 1.00 mm (Figs. 91-93), 0.25 mm (Fig. 94).
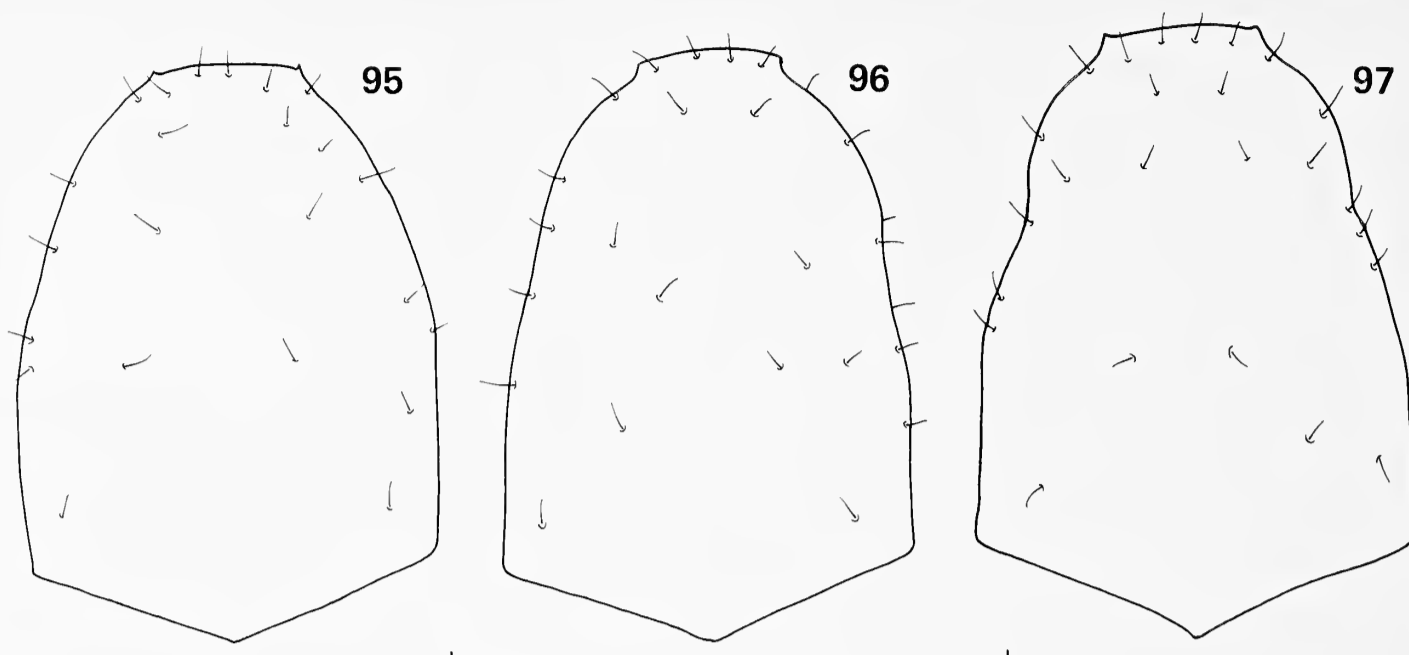
Figs. 95-97.—*Afrosternophorus dawydoffi* (Beier), dorsal aspect of carapace, specimens from Roessei Chrum, Kampuchea: 95, female paralectotype; 96, male lectotype; 97, female paralectotype. Scale line = 1.00 mm.

Remarks.—The anterior constriction of the carapace of this species is quite variable (Figs. 95-97; all specimens from Roessei Chrum) and clearly shows that this character cannot be used at the generic level.

The female paralectotype of *S. cylindrimanus* referred to above is discussed under that species.

Beier (1951) erroneously included the chelal trichobothrium *it* in his diagram of this species, as well as mis-sexing many specimens.

Beier did not designate a primary type in the original description, and merely published and labelled one vial as "Typen". A lectotype male has been selected from this vial.

The alternative spelling of the localities given above is discussed in the Materials and Methods and Table 1.

Afrosternophorus cylindrimanus (Beier), new combination
Figs. 69, 90, 98-100; Map 4

Sternophorus cylindrimanus Beier 1951:73-74, Fig. 17 (in part).

Types.—Lectotype male (present designation), paralectotype male, paralectotype female, Paclay [= Pak-Lay, see Table 1], Laos, January 1938 (C. Dawydoff), NHMW (spirit).

Distribution.—Laos (Map 4).

Diagnosis.—Male genitalia with long, acute dorsal apodemes. Female galea with four distal and one subbasal rami. Chela (with pedicel) 0.935 to 0.95 (male), 1.02 mm (female) in length.

Description.—Pedipalpal trochanter 1.95 to 2.00 (male), 2.00 to 2.05 (female), femur 3.31 to 3.37 (male), 3.42 to 3.50 (female), tibia 2.48 to 2.60 (male), 2.48 (female), chela (with pedicel) 4.37 to 4.42 (male), 4.34 to 4.53 (female), chela (without pedicel) 4.19 to 4.26 (male), 4.15 to 4.31 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 98-99). Serrula exterior of chelicera with 9 to 10 (male), 12 (female), lamellae. Galea of male simple, of female with four distal and one subbasal rami (Fig. 69). Carapace (Fig. 100), with 23 to 24 (male), ? (female) setae; 1.34
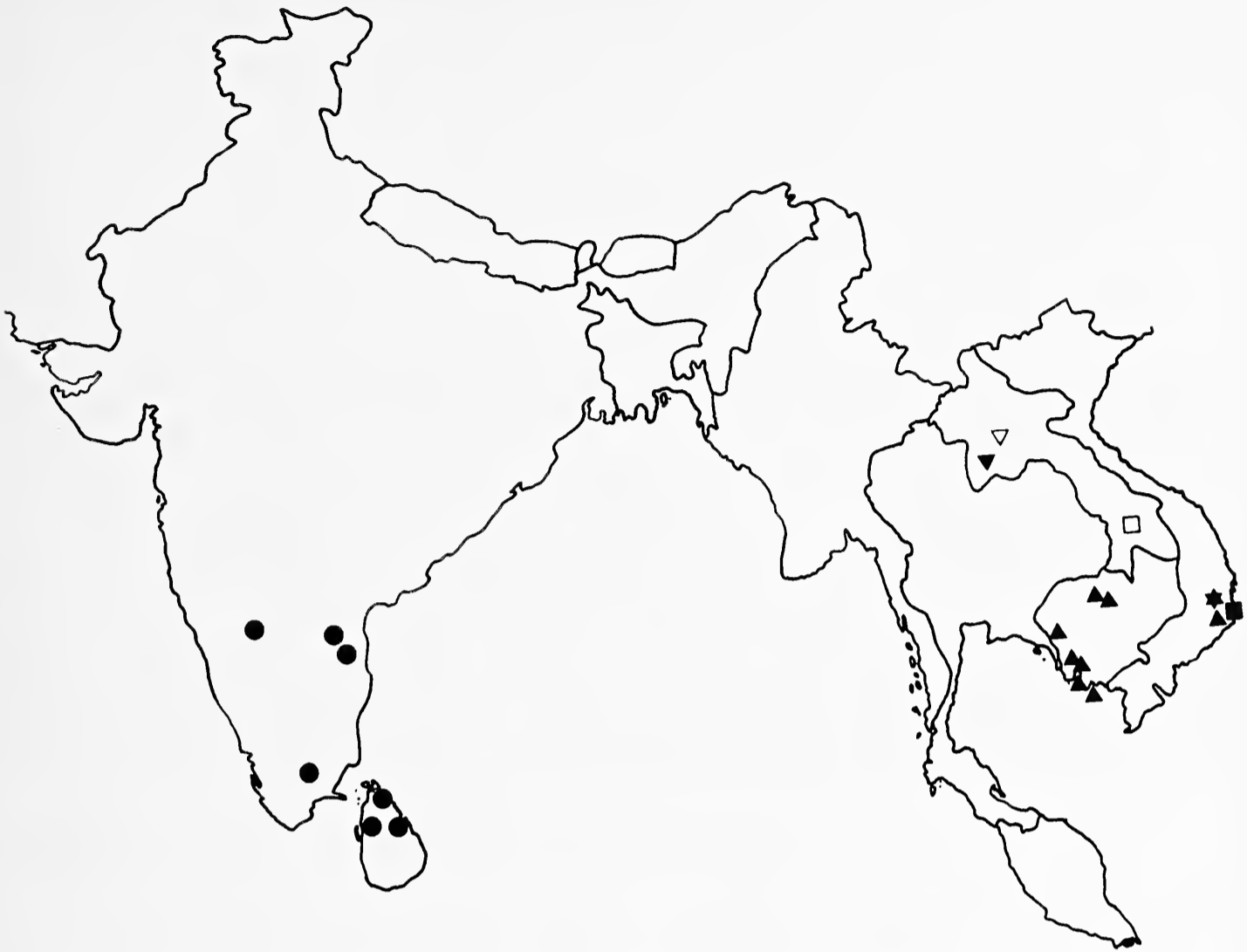
Map 4.—South-east Asia showing known distribution of *Afrosternophorus ceylonicus* (Beier) (circles), *A. chamberlini* (Redikorzev) (squares), *A. dawydoffi* (Beier) (upright triangles), *A. cylindrimanus* (Beier) (inverted triangles) and *A. fallax*, new species (star). Open symbols represent literature records only.

to 1.47 (male), 1.41 (female) times longer than broad. Male genitalia very obscure, dorsal apodemes long and acute. Female genitalia as for genus. Tergal chaetotaxy: male, 5-6:5-6: 3-4:6:5-6:5-6:5-6:6:4-5:T1T?T1T:?:2; female, ?:?:?:?:?:6:6:6:6:T1T4T1T:?:2. Sternal chaetotaxy: male, ?; female, 0:?:(0)?(0):(?)4(1):6:5:?:?:6:T1T4T1T:?:2. Coxal chaetotaxy: male, 4:3:3-4:2; female, ?.

Dimensions (mm): Body length 2.1-2.2 (2.5); pedipalps: trochanter 0.37-0.39/0.19-0.195 (0.41-0.42/0.205), femur 0.59-0.605/0.175-0.18 (0.615-0.63/0.18), tibia 0.515-0.52/0.20-0.21 (0.52/0.21), chela (with pedicel) 0.935-0.95/0.215 (1.02/0.225-0.235), chela (without pedicel) 0.88-0.915 (0.97-0.975); chelicera 0.16/0.08-0.095 (?/?), moveable finger length 0.10-0.12 (?); carapace 0.75-0.765/0.52-0.56 (0.86/0.61); legs: ?.

Habitat.—No habitat data accompanied the specimens.

Remarks.—This species is very similar to *A. dawydoffi*, from which it can be separated only by its smaller size (Fig. 90) and the form of the female galea (Fig. 69). The latter character appears to be slightly variable, and may prove to be of little significance for these two species. Only further collecting will determine whether *A. cylindrimanus* is merely a smaller form of *A. dawydoffi*, and hence synonymous with it.

Beier (1951) described this species from two other specimens: a female from Louang-phrabang, Laos, and a female from Thôn Sông Pha, Vietnam. The former specimen was not available for study, and should be re-examined to determine its true status. It is geographically intermediate between the known distributions of *A. cylindrimanus* and *A. dawydoffi*, and may resolve the probable synonymy of these two species.
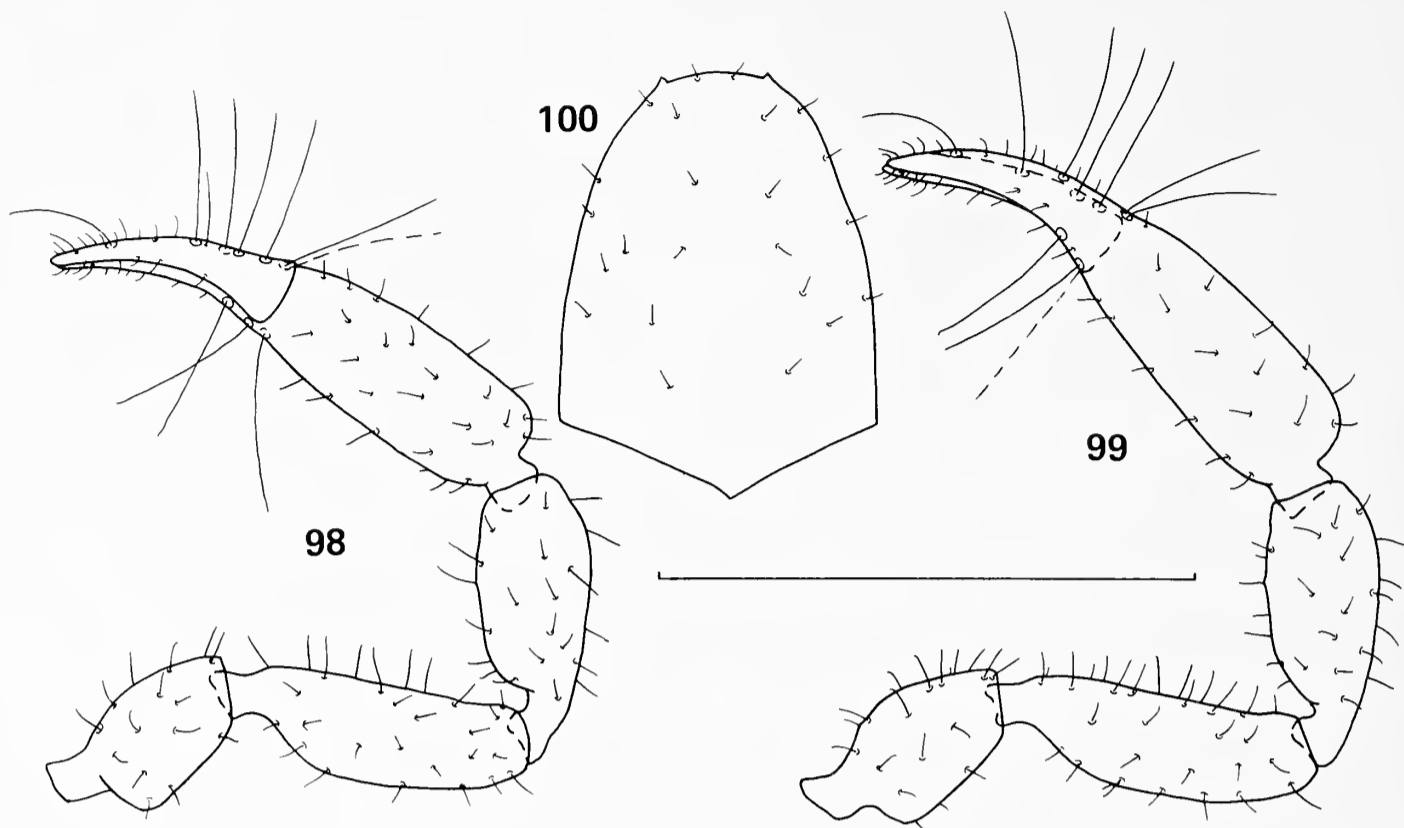
Figs. 98-100.—*Afrosternophorus cylindrimanus* (Beier): 98, ventral aspect of left pedipalp, male lectotype; 99, dorsal aspect of right pedipalp, female paralectotype; 100, dorsal aspect of carapace, male lectotype. Scale line = 1.00 mm.

Beier identified the Thôn Sông Pha specimen as *cylindrimanus* because it possessed a broad pseudosternum, which was his criterion for separating *dawydoffi* and *cylindrimanus*. My observations indicate that the relative sizes of the pseudosternum are variable and must be viewed with caution. The following values were obtained for the width of the pseudosternum over the width of the second coxa [the ratio used by Beier (1951)]: 3.00 to 6.00 for 11 specimens of *A. dawydoffi;* 1.65 to 2.12 for the two Pak-Lay males of *A. cylindrimanus* (the female was damaged and unmeasurable); and 2.08 for the Thôn Sông Pha female. Nevertheless, on the basis of pedipalpal morphometrics (Fig. 90) and distribution (Map 4), it is believed that the latter specimen is better placed in *A. dawydoffi*.

The Pak-Lay specimens are in poor condition, and many characters could not be properly scored or drawn (e.g. genitalia).

Beier (1951) erroneously included the chelal trichobothrium *it* in his diagram of this species.

Beier (1951) did not designate a primary type in his original description, and merely published and labelled one vial as "Typen". A lectotype male has been selected from this vial.

The alternative spelling of the type locality is discussed in the Materials and Methods and Table 1.

Afrosternophorus hirsti (Chamberlin), new combination
Figs. 1-7, 51, 56, 70-71, 101-108, 129; Map 5

Sternophorus hirsti Chamberlin 1932a:143; Beier 1932:18; Harvey 1981b:244.
"Sternophorus" hirsti Chamberlin: Harvey 1982:192, Fig. 1.

Type.—Holotype male, Barringun, New South Wales, Australia, 1927 (F. S. Hirst), JCC, JC-480.01001 (slide).

Distribution.—New South Wales, Queensland, Australia (Map 5).

Diagnosis.—Male genitalia with brush-like anterior apodeme; dorsal apodemes parallel sided, much reduced. Female galea with three distal, one subdistal and one subbasal rami, the subdistal ramus occasionally absent. Chela (with pedicel) 0.715 to 0.815 (male), 0.66 to 0.91 mm (female) in length.

Description.—ADULTS: Pedipalpal trochanter 1.64 to 1.90 (male), 1.60 to 1.94 (female), femur 2.42 to 2.89 (male), 2.33 to 2.89 (female), tibia 2.05 to 2.44 (male), 1.96 to 2.35 (female), chela (with pedicel) 3.25 to 3.77 (male) 3.08 to 3.71 (female),
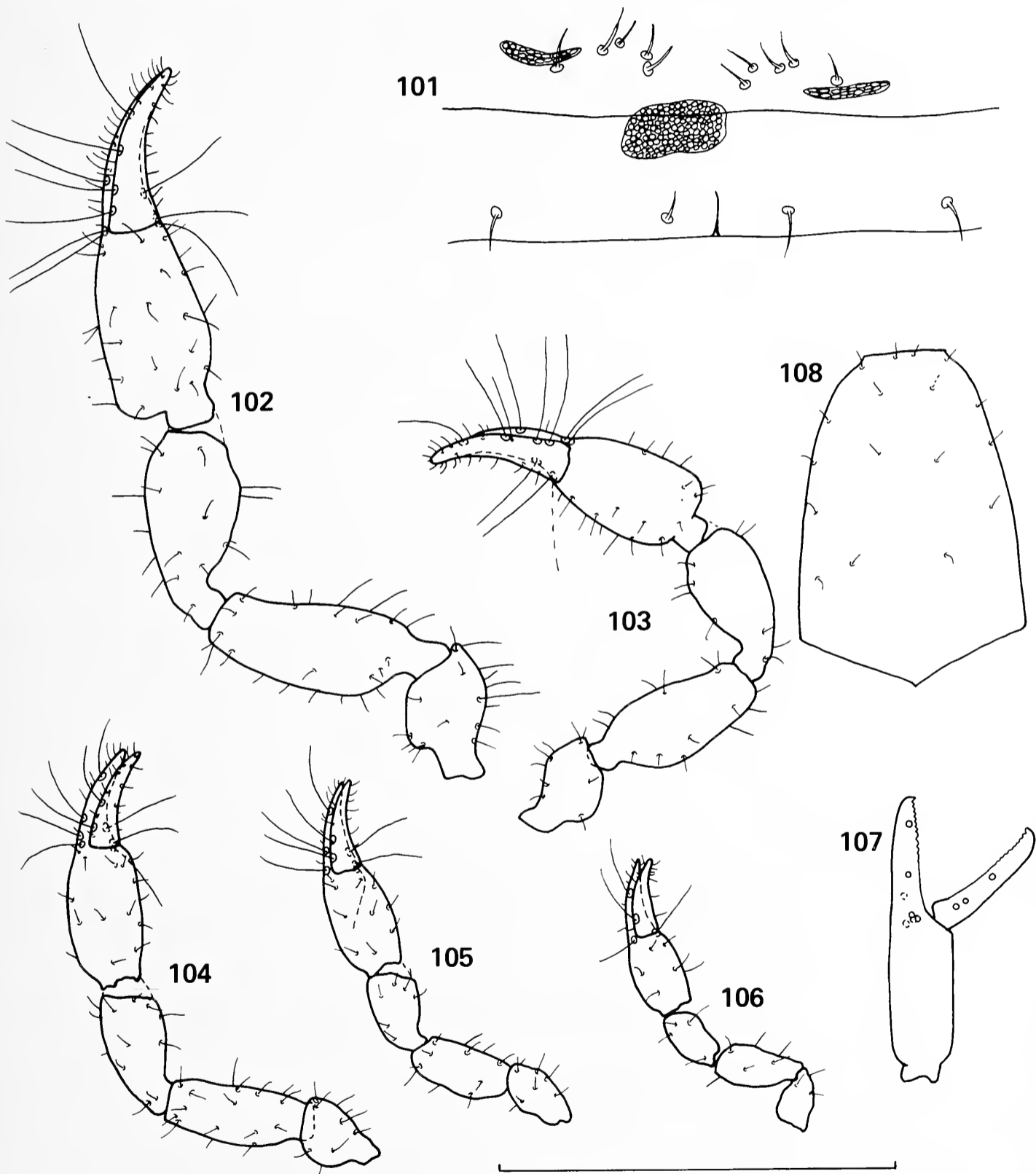
Figs. 101-108.—*Afrosternophorus hirsti* (Chamberlin): 101, female genitalia and associated sternites, MH302.24; 102, ventral aspect of right pedipalp, female, MH237.02; 103, ventral aspect of left pedipalp, male holotype; 104, ventral aspect of right pedipalp, tritonymph, MH237.05; 105, same, deutonymph, MH302.57; 106, same protonymph, MH237.07; 107, lateral aspect of right chela, male holotype; 108, dorsal aspect of carapace, female, MH210.03. Scale line = 1.00 mm (Figs. 102-108), 0.25 (Fig. 101).

chela (without pedicel) 3.11 to 3.58 (male), 2.94 to 3.55 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 1, 102-103, 107). One male (MH302.15) has *sb* missing from one chela. Serrula exterior of chelicera with 11 to 12 (male), 10 to 12 (female) lamellae. Galea of male simple, of female with three distal, one subdistal and one subbasal rami, the subdistal ramus occasionally absent (Figs. 70-71). Carapace (Figs. 2, 108) usually unconstricted, but sometimes a slight constriction is apparent, with 20 to 24 (male), 20 to 27 (female) setae; 1.43 to 1.67 (male), 1.32 to 1.55 (female) times longer than broad. Male genitalia (Figs. 51, 56) with distinctive brush-like anterior apodeme, dorsal apodemes parallel sided, much reduced; foramen relatively large. Female genitalia as for genus (Fig. 101). Tergal chaetotaxy: male, 4-7: 3-6:4-6:4-7:5-7:5-7:6-7:5-7:5-6:T1T22-5T1T:?:2; female, 4-7:4-6:3-6:5-8:5-8:6-7:5-7: 6-7:6-7:T1T2-4T1T:?:2. Sternal chaetotaxy: male, 0:3-8:(0)4-5[5-8](0):(1)3-6(1):5-8: 5-7:5-7:4-7:5-6:T1T3-4T1T:?:2; female, 0:7-11:(0)3-5(0):(1)4-6(1):5-9:5-8:5-7:3-8:5-8: T1T3-4T1T:?:2. Coxal chaetotaxy: male, 4-5:5:2-4:4-5; female, 4-6:4-6:3-5:3-5.

Dimensions (mm): Body length 2.0-2.3 (1.8-2.9); pedipalps: trochanter 0.275-0.33/ 0.155-0.18 (0.255-0.36/0.15-0.225), femur 0.46-0.545/0.165-0.21 (0.41-0.60/0.16-0.24), tibia 0.39-0.475/0.175-0.22 (0.36-0.51/0.16-0.26), chela (with pedicel) 0.715-0.815/ 0.20-0.24 (0.66-0.91/0.19-0.28), chela (without pedicel) 0.68-0.775 (0.63-0.87), moveable finger length 0.33-0.38 (0.315-0.42); chelicera 0.15-0.16/0.08-0.095 (0.135-0.19/ 0.08-0.11), moveable finger length 0.10-0.11 (0.095-0.13); carapace 0.67-0.80/0.45-0.52 (0.65-0.87/0.47-0.65); leg I: coxa 0.19-0.20/0.22-0.23 (0.185-0.25/0.20-0.29), trochanter 0.09-0.11/0.08-0.09 (0.08-0.13/0.07-0.11), femur I 0.10-0.11/0.095-0.105 (0.085-0.13/ 0.09-0.13), femur II 0.145-0.16/0.10-0.105 (0.13-0.19/0.09-0.13), tibia 0.17-0.19/ 0.065-0.07 (0.15-0.22/0.06-0.08), tarsus 0.07-0.095/0.045-0.05 (0.095-0.13/0.045- 0.055); leg IV: coxa width 0.18-0.24 (0.19-0.27), trochanter 0.125-0.14/0.10-0.11 (0.125-0.17/0.09-0.125), femur I 0.15-0.19/0.165-0.175 (0.15-0.22/0.145-0.225), femur II 0.22-0.26/0.16-0.175 (0.21-0.32/0.145-0.225), tibia 0.275-0.31/0.09-0.105 (0.255 -0.37/0.085-0.12), tarsus 0.16/0.06-0.07 (0.14-0.19/0.055-0.075).

TRITONYMPHS: Pedipalpal trochanter 1.33 to 1.83, femur 2.32 to 2.72, tibia 1.94 to 2.30, chela (with pedicel) 3.10 to 3.84, chela (without pedicel) 3.00 to 3.65 times longer than broad. Fixed finger with seven trichobothria, moveable finger with two trichobothria (Fig. 104); *it, sb* and *st* absent. Serrula exterior of chelicera with 10 to 11 lamellae. Galea as for female. Carapace with 21 to 23 setae; 1.41 to 1.55 times longer than broad. Tergal chaetotaxy: 4-6:4-5:4:5-6:5-6:6:6:6:6:T1T2T1T:?:2. Sternal chaetotaxy: 0:2: (0)4(0):(1)4(1):6:6:5-6:5-6:6:T1T2T1T:?:2. Coxal chaetotaxy: 3-5:4-5:3:3.

Dimensions (mm): Body length 1.5-2.2; pedipalps: trochanter 0.22-0.265/0.125- 0.165, femur 0.34-0.36/0.135-0.165, tibia 0.305-0.36, chela (with pedicel) 0.59-0.72/ 0.155-0.195, chela (without pedicel) 0.56-0.685, moveable finger length 0.275-0.33; carapace 0.61-0.71/0.39-0.48.

DEUTONYMPH: Pedipalpal trochanter 1.40 to 1.71, femur 2.08 to 2.25, tibia 1.85 to 1.92, chela (with pedicel) 3.13, chela (without pedicel) 3.10 times longer than broad. Fixed finger with six trichobothria, moveable finger with two trichobothria (Fig. 105); *it, esb, sb* and *st* absent. Serrula exterior of chelicera with 9 lamellae. Galea as for female. Carapace with 16 setae; 1.43 times longer than broad. Tergal chaetotaxy: 4:4:4:5:4:4:4: 4:4:T1T2T1T:?:2. Sternal chaetotaxy: 0:0:(0)4(0):(1)4(1):4:4:4:4:4:T1T4T1T:?:2. Coxal chaetotaxy: 3:3:2:2.

Dimensions (mm): Body length 1.5; pedipalps: trochanter 0.175-0.18/0.105-0.125, femur 0.27/0.12-0.13, tibia 0.24/0.125-0.13, chela (with pedicel) 0.485/0.155, chela (without pedicel) 0.48, moveable finger length 0.24; carapace 0.50/0.35.

PROTONYMPH: Although the single available protonymph is in poor condition, the following observations could be made. Pedipalpal trochanter 1.63, femur 2.67, tibia 1.94, chela (with pedicel) 3.50, chela (without pedicel) 3.45 times longer than broad. Fixed finger with three trichobothria, moveable finger with one trichobothrium (Fig. 106); *eb, et, ib* and *t* present. Serrula exterior of chelicera with 9 lamellae; seta *gs* absent. Carapace with 10 setae; 1.23 times longer than broad.

Dimensions (mm): Pedipalps: trochanter 0.13/0.08, femur 0.20/0.075, tibia 0.165/0.085, chela (with pedicel) 0.385/0.11, chela (without pedicel) 0.38, moveable finger length 0.20; carapace 0.38/0.31.

Habitat.—This species has been taken from under bark of *Eucalyptus* spp., *Melaleuca* sp. and *Gyrocarpus americanus.*

Remarks.—*Afrosternophorus hirsti* is a widely distributed species which is easily recognized by the form of the male genitalia.

I (Harvey 1982) recorded the presence of a nematode (Mermithidae) from a female (MH302.51) which was collected near Tenterfield, N.S.W.

Other specimens examined.—AUSTRALIA: NEW SOUTH WALES; 32 km SW of Forbes, under bark of *Eucalyptus* sp., 6 May 1981 (M. S. Harvey and M. Kotzman), 1 male (AM, KS 8365, MH 295.01) (spirit). 3 km E of Tabulam 28°53′S 152°34′E, under bark of *E.* sp., 23 November 1983 (M. S. Harvey and D. C. F. Rentz), 3 males, 1 tritonymph (ANIC, MH536.01-04) (spirit). 53 km W of Tenterfield, under bark of *E.* sp., 13 May 1981 (M. S. Harvey and M. Kotzman), 13 males, 9 females, 2 tritonymphs, 1 deutonymph (MV, MH302.29-32, 35-45, 48-57) (slides and spirit). Same data as above, 5. males, 5 females (AM, KS 8366, MH302.01-10) (slides and spirit). Same data as above, 5 males, 5 females (QM, S994-1003, MH302.11-20) (slides and spirit). Same data as above, 2 males, 2 females (ANIC, MH302.21-24) (slides). Same data as above, 2 males, 2 females (VAM, MH302.33-34, 46-47) (spirit). Same data as above, 2 males, 2 females (MHNG, MH302.25-28) (spirit). 13 km SW of Texas, under bark of *E.* sp., 1 June 1980 (C. Silveira), 1 female (AM, KS 8364, MH218.01) (slide). 16 km S of Texas, 29°00′S 151°09′E, under bark of *E.* sp., 24 November 1983 (D. C. F. Rentz and M. S. Harvey), 19 males, 17 females, 1 tritonymph (ANIC, MH538.05-41) (spirit). 19 km SSW of Texas, 29°00′S 151°05′E, under bark of *E.* sp., 24 November 1983 (D. C. F. Rentz and M. S. Harvey), 2 females, 1 tritonymph (ANIC, MH539.01-03) (spirit). 20 km SW of Texas, under bark of *E.* sp., 18 May 1980 (C. Silveira), 2 females (MV, MH210.03-04) (slides): QUEENSLAND; 6 km E of Chillagoe, under bark of *Melaleuca* sp., 10 December 1980 (M. Kotzman), 1 female, 1 tritonymph (MV, MH 268.01-02) (slides). Chillagoe, under bark of *E.* sp., 13 December 1980 (M. Kotzman), 3 females (QM, S988-990, MH270.01-03) (slides). 3 km W of Chillagoe, under bark of *E.* sp., 14 December 1980 (M. Kotzman), 1 female (QM, S991, MH271.01) (slide). 3 km S of Chillagoe, under bark of *E.* sp., 17 December 1980 (M. Kotzman), 1 male (QM, S992, MH272.01) (slide). 10 km NNE of Condamine, under bark of *E.* sp., 28 August 1980 (M. S. Harvey), 1 male, 2 females, 3 tritonymphs, 1 protonymph (QM, S980-986, MH273.01-07) (slides). Davies Creek National Park, 39 km E of Mareeba, under bark of *E.* sp., 23 August 1981 (N. and S. Wentworth), 1 female (QM, S1004, MH345.01) (spirit). Dome Rock, near Chillagoe, under bark of *Gyrocarpus americanus,* 31 December 1982 (M. Kotzman), 5 males, 8 females (ANIC, MH474.06-18) (spirit and points). 14 km N of Mt. Isa, under bark of *E.* sp., 22 August 1980 (M. S. Harvey), 1 female (QM, S979, MH234.06) (slide). 2 km S of Rookwood Homestead, near Chillagoe, under bark of *M.* sp., 12 December 1980 (M. Kotzman), 1 female (QM, S987, MH269.02) (slide). 68 km WSW of Warwick, under bark of *E.* sp., 7 May 1981 (M. S. Harvey and M. Kotzman), 1 female (QM, S993, MH296.01) (spirit).

Afrosternophorus nanus, new species
Figs. 57, 72, 109-113, 129; Map 5

Types.—Holotype male, three paratypes males, paratype female, paratype female?, two paratype tritonymphs, Rum Jungle, Northern Territory, Australia, under bark of *Eucalyptus* sp., 13 August 1980 (M. S. Harvey), NTM, A1-A8, MH230.01-04, 09-12 (slides).

Two paratypes males, same data as above, MV, K054-K055, MH230.07-08 (slides). Two paratype males, same data as above, ANIC, MH230.05-06 (slides).

Etymology.—The specific epithet refers to the small size of this species (*nanus* L. a dwarf).

Distribution.—Northern Territory, Australia (Map 5).

Diagnosis.—Male genitalia with long, tapering dorsal apodemes. Female galea with three distal and one subbasal rami. Small species: chela (with pedicel) 0.55 to 0.59 (male), 0.56 to 0.61 mm (female) in length.

Description.—ADULTS: Pedipalpal trochanter 1.57 to 1.91 (male), 1.75 to 1.84 (female), femur stout 2.35 to 2.57 (male), 2.40 to 2.62 (female), tibia 1.97 to 2.21 (male), 1.94 to 2.07 (female), chela (with pedicel) 2.95 to 3.47 (male), 3.03 to 3.22 (female), chela (without pedicel) 2.82 to 3.32 (male), 2.89 to 3.05 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 109-110). Serrula exterior of chelicera with 11 (male, female) lamellae. Galea of male simple, of female with three distal and one subbasal rami (Fig. 72). Carapace (Fig. 112) unconstricted, with 20 to 24 (male), 21 (female) setae; 1.33 to 1.56 (male), 1.36 to 1.81 (female) times longer than broad. Male genitalia (Fig. 57) with long, tapering dorsal apodemes which are often difficult to observe. Female genitalia as for genus (Fig. 113).

Map. 5.—Australia showing known distribution of *Afrosternophorus hirsti* (Chamberlin) (circles), *A. nanus,* new species (squares), *A. anabates,* new species (triangles) and *A. xalyx,* new species (star).

Tergal chaetotaxy: male, 4-6:3-6:3-6:4:4-5:3-5:4-6:4-7:4-7:T1T2-4T1T:?:2; female, 5:5:4:4:?:?:?:?:?:?:?:2. Sternal chaetotaxy: male, 0:6-7:(0)4[6-8](0):(1)4-5(1):4-5:4-6: 4-6:4-6:4-7:T1T2-4T1T:?:2; female, 0:7:(0)4(0):(1)4(1):?:?:?:?:?:?:?:2. Coxal chaeto-taxy: male, 3-6:4-6:3-5:4; female, 4-5:4-5:4-5:4.

Dimensions (mm): Body length 1.6-1.7 (?); pedipalps: trochanter 0.21-0.23/0.11-0.14 (0.21-0.23/0.12-0.125), femur 0.345-0.385/0.135-0.155 (0.36-0.38/0.145-0.155), tibia 0.295-0.33/0.14-0.16 (0.31-0.34/0.15-0.165), chela (with pedicel) 0.55-0.59/0.165-0.19 (0.56-0.61/0.18-0.19), chela (without pedicel) 0.515-0.565 (0.535-0.58), moveable finger length 0.26-0.285 (0.27-0.29); chelicera 0.12-0.13/0.065-0.085 (0.13-0.135/0.08), moveable finger length 0.07-0.09 (0.09); carapace 0.53-0.57/0.36-0.40 (0.56-0.61/0.31-0.45); leg I: coxa 0.15-0.18/0.17-0.18 (0.16/0.19), trochanter 0.075-0.08/0.065-0.07 (0.08-0.11/0.065-0.075), femur I 0.07-0.08/0.08-0.09 (0.085-0.10/0.075-0.10), femur II 0.11-0.12/0.08-0.09 (0.105-0.13/0.075-0.10), tibia 0.135-0.15/0.055-0.065 (0.14-0.15/ 0.06-0.105), tarsus 0.07-0.09/0.035-0.045; leg IV: coxa width 0.17-0.19 (?), trochanter 0.105-0.11/0.075-0.085 (0.11-0.13/0.085-0.095), femur I 0.13-0.14/0.125-0.145 (0.145-0.15/0.14-0.16), femur II 0.16-0.19/0.13-0.145 (0.18-0.20/0.145-0.16), tibia 0.215-0.23/ 0.075-0.085 (0.22-0.245/0.085-0.10), tarsus 0.12-0.125/0.05 (0.115-0.15/0.055-0.075).

TRITONYMPHS: Pedipalpal trochanter 1.60 to 1.70, femur 2.29 to 2.64, tibia 2.00 to 2.19, chela (with pedicel) 3.15 to 4.07, chela (without pedicel) 3.05 to 3.93 times longer than broad. Fixed finger with seven trichobothria, moveable finger with two trichobo-thria (Fig. 111); *it, sb* and *st* absent. Serrula exterior of chelicera with 10 to 11 lamellae. Galea as for female. Carapace unconstricted, with 18 to 22 setae; 1.38 times longer than broad. Tergal chaetotaxy: 4-5:4:3-4:3-6:5:6:5:5:6:T1T2T1T:?:2. Sternal chaetotaxy: 0:2:(0)4(0):(1)3(1):6:6:6:6:6:T1T2T1T:?:2. Coxal chaetotaxy: 3-4:4:2-4:3-4.

Dimensions (mm): Body length 1.5; pedipalps: trochanter 0.16-0.24/0.10-0.15, femur 0.28-0.39/0.11-0.17, tibia 0.23-0.36/0.115-0.175, chela (with pedicel) 0.59-0.65/0.145-0.205, chela (without pedicel) 0.57-0.625, moveable finger length 0.235-0.31; carapace 0.62/0.45.
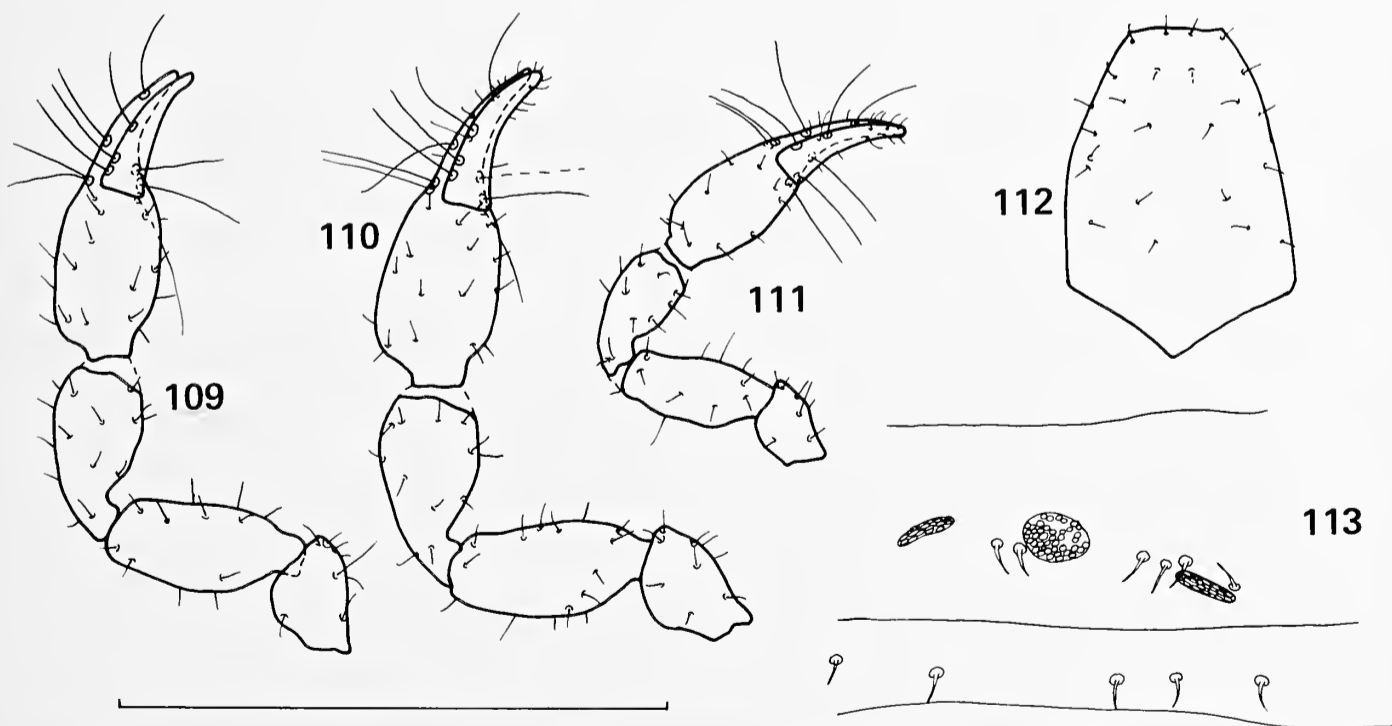
Figs. 109-113.—*Afrosternophorus nanus*, new species: 109, ventral aspect of right pedipalp, male holotype: 110, same, female paratype, MH230.09; 111, same, tritonymph paratype, MH230.12; 112, dorsal aspect of carapace, male holotype; 113, female genitalia and associated sternites, paratype, MH230.09. Scale line = 1.00 (Figs. 109-112), 0.25 mm (Fig. 113).

Habitat.—The types were collected together under the bark of a single tree (*Eucalyptus* sp.). The Roper Bar tritonymph was collected from under the bark of a tree.

Remarks.—This species is easily distinguished from all other species of the genus by its small size and the form of the male genitalia. It appears to be most similar to *A. grayi*, but the two are separable on size (Fig. 129). The "paratype female?" referred to above is in poor condition and its gender is difficult to ascertain. It possesses an adult trichobothrial pattern, but due to the contorted and shrivelled state of the abdomen, the presence of cribriform plates cannot be confirmed. The tritonymph from Roper Bar has not been designated as a type specimen because it is slightly larger than tritonymphs of the type series. Nevertheless, it is believed to be a member of this species, but adult material is needed to confirm this record.

Other specimens examined.—AUSTRALIA: NORTHERN TERRITORY; 13.5 km SE of Roper Bar, under bark of tree, 17 July 1980 (C. Silveira), 1 tritonymph (NTM, MH222.04) (slide).

Afrosternophorus anabates, new species
Figs. 8, 58, 73, 114-120, 129; Map 5

Types.—Holotype male, one paratype male, three paratype females, one paratype tritonymph, 15 km WNW of Yaapeet, Lake Albacutya Park, Victoria, Australia, under bark of *Eucalyptus camaldulensis*, 2 July 1982 (M. S. Harvey and B. E. Roberts), MV, K125-K129, K145, MH416.05-06, 11-14 (slides and spirit). Two paratype males, two paratype females, same data as above, ANIC, MH416.07-10 (slides). Paratype male, paratype female, paratype protonymph, same data as above except 3 July 1982, MV, K130-132, MH419.03-05 (slides). Paratype male, paratype tritonymph, Mt. Killawarra, 17 km NW of Wangaratta, Victoria, Australia, ex *Delena cancerides* Walckenaer (Sparassidae: Araneae), 7 November 1978 (M. S. Harvey), MV K053-053a, MH044.01-02 (slides). Two paratype females, Reedy Lake, near Nagambie, Victoria, Australia, ex *D. cancerides* or *Isopoda* sp. (Sparassidae), 23 November 1979 (H. E. Parnaby), MV, K050-051, MH151.01-02 (slides). Paratype female, 6.5 km SSW of Stuart Mill, Victoria, Australia, ex *D. cancerides*, 3 December 1977 (M. S. Harvey), MV, K052, MH004.01 (slide).

Etymology.—The specific epithet refers to the phoretic habit exhibited by some of the specimens (*anabates* Gr. rider, passenger).

Distribution.—Victoria, Australia (Map 5).

Diagnosis.—Male genitalia with anterior apodeme distally broad; lateral apodemes elongate, tapering. Female galea with three distal, one subdistal and two (sometimes one) basal to subbasal rami. Chela (with pedicel) 0.83 to 0.895 (male), 0.835 to 1.03 mm (female) in length. Sometimes phoretic on huntsman spiders.

Description.—ADULTS: Pedipalpal trochanter 1.71 to 1.89 (male), 1.51 to 1.90 (female), femur elongate, 2.77 to 3.08 (male), 2.43 to 3.13 (female), tibia 2.31 to 2.59 (male), 2.04 to 2.52 (female), chela (with pedicel) 3.56 to 4.15 (male), 3.38 to 4.00 (female), chela (without pedicel) 3.38 to 3.90 (male), 3.27 to 3.79 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 114-116). Serrula exterior of chelicera with 11 to 13 (male), 11 to 12 (female) lamellae. Galea of male simple, of female with three distal, one subdistal and two (sometimes one) basal to subbasal rami (Fig. 73). Carapace usually unconstricted (Fig. 119), but occasionally a slight constriction is apparent; with 16 to 23 (male), 18 to 27 (female) setae; 1.46 to 1.59 (male), 1.38 to 1.55 (female) times longer than broad. Male genitalia (Fig. 58) with anterior apodeme distally broad, lateral apodemes long and tapering. Female genitalia as

for genus (Fig. 120). Tergal chaetotaxy: male, 6:5-7:4:5-8:6-7:6:6-7:6:6:T1T3-4T1T:?:
2; female, 5-7:5-6:3-4:4-6:4-7:4-7:6-7:5-7:6-7:T1T4-5T1T:?:2. Sternal chaetotaxy: male,
0:4-8:(0)4-5[6-8](0):(1)5-6(1):6-8:5-7:6-7:6-8:6:T1T3-4T1T:?:2; female, 0:6-8:(0)4-5
(0):(1)2-6(1):6-8:6-9:6-8:6-7:6-7:T1T4T1T:?:2. Coxal chaetotaxy: male, 3-5:4-6:4-5:
3-5; female, 3-6:3-7:3-5:3-5.

Dimensions (mm): Body length 2.2-2.5 (2.4-3.4); pedipalps: trochanter 0.325-0.375/
0.175-0.205 (0.335-0.40/0.175-0.245), femur 0.55-0.595/0.175-0.215 (0.52-0.695/0.19-
0.235), tibia 0.475-0.525/0.185-0.225 (0.465-0.60/0.195-0.27), chela (with pedicel)
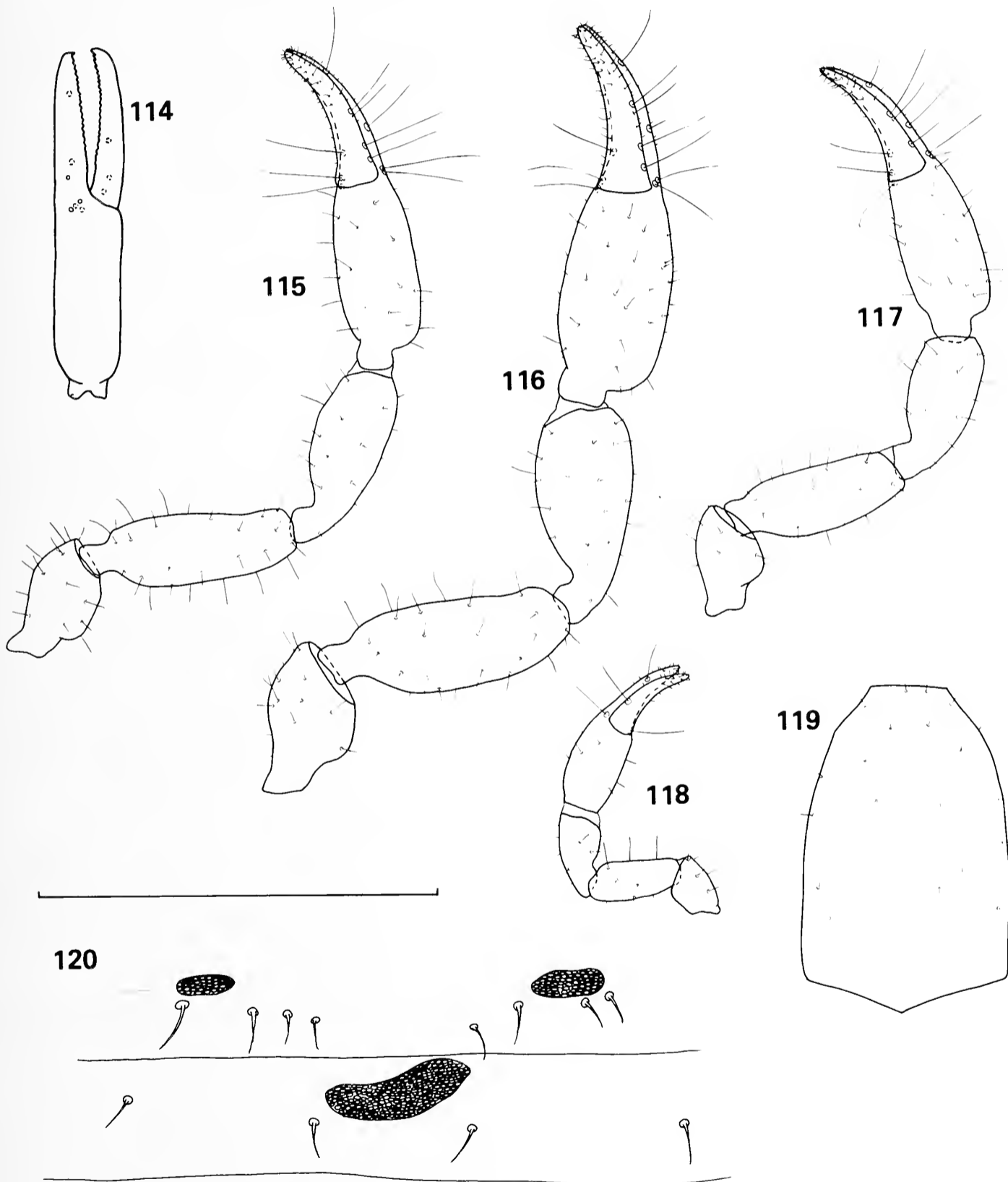
Figs. 114-120.—*Afrosternophorus anabates,* new species: 114, lateral aspect of left chela, male
paratype, MH044.01; 115, ventral aspect of left pedipalp, male holotype; 116, same, female paratype,
MH416.09; 117, same, tritonymph paratype, MH416.14; 118, ventral aspect of right pedipalp, proto-
nymph paratype, MH419.05; 119, dorsal aspect of carapace, male holotype; 120, female genitalia
and associated sternites, paratype, MH416.09. Scale line = 1.00 mm (Figs. 114-119), 0.25 mm (Fig.
120).

0.83-0.895/0.205-0.25 (0.835-1.03/0.21-0.28), chela (without pedicel) 0.795-0.855 (0.795-0.98), moveable finger length 0.39-0.425 (0.40-0.475); chelicera 0.16-0.185/ 0.095-0.10 (0.165-0.20/0.10-0.11), moveable finger length 0.11-0.125 (0.12-0.14); carapace 0.82-0.89/0.52-0.59 (0.83-1.005/0.555-0.695); leg I: coxa 0.21-0.24/0.24-0.265 (0.23-0.29/0.26-0.30), trochanter 0.12-0.13/0.08-0.10 (0.12-0.15/0.095-0.12), femur I 0.11-0.13/0.11-0.13- (0.12-0.145/0.115-0.15), femur II 0.175-0.195/0.115-0.135 (0.18-0.22/0.12-0.155), tibia 0.20-0.225/0.07-0.085 (0.21-0.255/0.075-0.09), tarsus 0.11-0.13 /0.05-0.055 (0.12-0.13/0.05-0.06); leg IV: coxa width 0.22-0.24 (0.26-0.29), trochanter 0.155-0.16/0.105-0.12 (0.16-0.19/0.115-0.135), femur I 0.205-0.22/0.175-0.225 (0.215-0.27/0.20-0.26), femur II 0.285-0.33/0.185-0.235 (0.30-0.37/0.205-0.26), tibia 0.34-0.375/0.11-0.135 (0.35-0.43/0.115-0.14), tarsus 0.16-0.19/0.07-0.085 (0.18-0.21/0.07-0.09).

TRITONYMPHS: Pedipalpal trochanter 1.51 to 1.81, femur 2.38 to 2.73, tibia 2.08 to 2.29, chela (with pedicel) 3.44 to 3.85, chela (without pedicel) 3.30 to 3.69 times longer than broad. Fixed finger with seven trichobothria, moveable finger with two trichobothria (Fig. 117); it, sb and st absent. Serrula exterior of chelicera with 11 lamellae. Galea with three distal to subdistal and two subbasal rami. Carapace with 17 setae; 1.46 to 1.53 times longer than broad. Tergal chaetotaxy: 6-7:4-5:4:4-5:4-5:4-6:5-6:5-7:5-6:T1T2T1T: ?:2. Sternal chaetotaxy: 0:2:(0)4(0):(1)4-5(1):6:5-6:6-7:6:6:T1T2T1T:?:2. Coxal chaetotaxy: 3-4:3-4:3:3.

Dimensions (mm): Body length 2.3-2.5; pedipalps: trochanter 0.265-0.28/0.155-0.175, femur 0.44-0.46/0.165-0.185, tibia 0.375-0.39/0.17-0.18, chela (with pedicel) 0.735-0.75/0.195-0.215, chela (without pedicel) 0.705-0.725, moveable finger length 0.345-0.36; carapace 0.70-0.75/0.48-0.49.

PROTONYMPHS: Pedipalpal trochanter 1.68 to 1.78, femur 2.53 to 2.61, tibia 1.95 to 2.05, chela (with pedicel) 3.60 to 3.71, chela (without pedicel) 3.52 to 3.54 times longer than broad. Fixed finger with three trichobothria, moveable finger with one trichobothrium (Fig. 118); eb, et, ib and t present. Serrula exterior of chelicera with 9 to 10 lamallae. Seta gs absent. Galea with three distal to subdistal rami. Carapace with 14 setae; 1.26 times longer than broad. Tergal chaetotaxy: 4:2:0:4:4:4:4:4:4:TTTT:TTTT: 2. Sternal chaetotaxy: 0:0:(0)2(0):(1)2(1):4:4:4:4:4:TTTT:TT:2. Coxal chaetotaxy: 1:1:1:1.

Dimensions (mm): Body length 1.5; pedipalps: trochanter 0.16/0.09-0.095, femur 0.235-0.24/0.09-0.095, tibia 0.205/0.10-0.105, chela (with pedicel) 0.445-0.45/0.12-0.125, chela (without pedicel) 0.425-0.44, moveable finger length 0.22-0.23; carapace 0.48/0.38.

Habitat.—As discussed in detail below, some specimens were taken from spiders of the family Sparassidae (*Delena cancerides* and *Isopoda* sp.), whereas others were taken from under bark of *Eucalyptus camaldulensis*.

Remarks.—This species is easily distinguished from other members of the genus except *A. papuanus* by the shape of the male genitalia (distally broad anterior apodeme) and the form of the female galea. It differs from *A. papuanus* only in size; *papuanus* is smaller than *anabates*. It is thought that these two species are sister-species because they possess a synapomorphy in the form of the anterior apodeme.

Three of the five known collections of *A. anabates* have been taken from sparassid spiders. The Mt. Killawarra specimens were found clinging to leg setae of a male of *D. cancerides* which was found under bark of *Eucalyptus melliodora*. The Reedy Lake material was removed from a vial containing specimens of *D. cancerides* and *Isopoda* sp.

which were collected under bark of *Eucalyptus* sp. Since the sternophorids were not collected from the bark of the tree (H. E. Parnaby, pers. comm.), they were obviously phoretic on one or both of the spider species. The Stuart Mill specimen was taken from a leg seta of a male of *D. cancerides* which was found under bark of a log. Extensive collecting at Stuart Mill and Mt. Killawarra failed to disclose any further sternophorids, even though many corticolous species of the families Atemnidae, Chernetidae and Cheliferidae were found. Conversely, at Lake Albacutya, *A. anabates* was only found under bark of *E. camaldulensis* and was not found on any sparassids that also occurred in the area (*D. cancerides, Isopoda* spp.). It is of interest to note that the phoretic nature of this species may be seasonal. It has been collected from spiders in November and December, and it has been found under bark in July. Naturally, much more collecting is needed before any definite statements may be made. It would be very interesting to examine this aspect of the pseudoscorpion's biology in relation to the time of year that mating and egg production takes place. Unfortunately, no such data is available for *A. anabates,* or, for that matter, any other sternophorid species.

The only other pseudoscorpion species that is known to be phoretic on a spider is the chernetid *Lustrochernes grossus* (Banks) from southern U.S.A. (Hoff and Jennings 1974). The spider from which it was taken was also a sparassid (= Heteropodidae; Platnick and Levi 1973), *Olios fasciculatus* Simon. In contrast to *A. anabates, L. grossus* has been found in a variety of habitats, including the bark of trees and under the elytra of cerambycid beetles (Hoff and Jennings 1974, Benedict and Malcolm 1982). Dr. Jennings (pers. comm.) kindly informed me that no further records of *L. grossus* on *O. fasciculatus* have been detected.

Hoff and Jennings suggested that the aggressive nature of spiders accounted for the lack of phoretic pseudoscorpions. The two specimens of *L. grossus* that Hoff and Jennings examined were found clinging to "dorsal abdominal setae", where, they suggest, the spider could not reach, and hence, dislodge and eat the pseudoscorpions. *Afrosternophorus anabates* has been taken from leg setae, a position which would be easily accessible to cleaning. Mites also are not uncommon on sparassids, which suggests that they do not clean themselves as rigorously as Hoff and Jennings imply. Heavily infested specimens are often in poor physical condition, yet it cannot be ascertained whether the mites are responsible for this state, or whether they are attracted to, or reproduce vigorously on weak specimens.

Afrosternophorus papuanus (Beier), new combination
Figs. 59, 74, 121-124, 129; Map 6

Sternophorus papuanus Beier 1974:211-212, Fig. 5.

Types.—Lectotype male (present designation), paralectotype male, two paralectotype females, Americ, Madang District, Papua New Guinea, 1972 (B. Gray), NHMW (spirit).

Distribution.—Papua New Guinea (Map 6).

Diagnosis.—Male genitalia with anterior apodeme distally broad; lateral apodemes long and tapering. Female galea with three distal, one subdistal and two subbasal rami. Chela (with pedicel) 0.61 to 0.69 (male), 0.73 to 0.74 mm (female) in length.

Description.—Pedipalpal trochanter 1.82 to 1.89 (male), 1.83 to 1.87 (female), femur 3.00 to 3.19 (male), 2.87 to 2.93 (female), tibia 2.38 to 2.57 (male), 2.12 to 2.32 (female), chela (with pedicel) 3.97 to 4.18 (male), 3.65 to 3.79 (female), chela (without

pedicel) 3.73 to 4.20 (male), 3.45 to 3.56 (female) times longer than broad. Trichobothria as for *aethiopicus* group, in usual position (Figs. 121-122). Serrula exterior of chelicera with 11 (male), 12 (female) lamellae. Galea of male simple, of female with three distal, one subdistal and two subbasal rami (Fig. 74). Carapace (Fig. 123) unconstricted, with 24 (male, female) setae; 1.45 (male), 1.51 to 1.52 (female) times longer than broad. Male genitalia (Fig. 59) with distally broad anterior apodeme; lateral apodemes long and tapering. Female genitalia as for genus (Fig. 124). Tergal chaetotaxy: male, 6:5:2:4:5:6: 6:6:6:T1T4T1T:?:2; female, 6:6:2:4:5-6:5-6:5-6:6:6:T1T3-4T1T:?:2. Sternal chaetotaxy: male, 0:6:(0)4[6](0):(1)5(1):?:?:?:6:6:T1T4T1T:?:2; female, 0:8-9:(0)4(0): (1)4(1):6-7:6:6:6:6-7:T1T4T1T:?:2. Coxal chaetotaxy: male, 3:2-4:3:3; female, 2-4:2-4: 3:3-4.

Dimensions (mm): Body length 1.7-2.0 (2.3-2.5); pedipalps: trochanter 0.255-0.265/ 0.14 (0.275-0.285/0.15-0.155), femur 0.405-0.42/0.135 (0.425-0.445/0.145-0.155), tibia 0.345-0.36/0.14-0.145 (0.35-0.36/0.155-0.165), chela (with pedicel) 0.655-0.69/0.165-0.17 (0.73-0.74/0.195-0.20), chela (without pedicel) 0.61-0.645 (0.69-0.695), moveable finger length 0.30-0.335 (0.375-0.385); chelicera 0.125-0.13/0.08-0.085 (0.13-0.135/ 0.08-0.09), moveable finger length 0.085-0.095 (0.10-0.105); carapace 0.64/0.44 (0.68-0.70/0.45-0.46); leg I: coxa ?/? (0.195-0.20/0.225-0.23), trochanter 0.095/0.07 (0.10/ 0.075), femur I 0.10/0.09 (0.095/0.085-0.095), femur II 0.10/0.09 (0.15-0.155/0.085-0.095), tibia 0.16/0.055 (0.16/0.06), tarsus 0.10/0.035 (0.11/0.045); leg IV: coxa width 0.17 (0.23), trochanter 0.135/0.085 (0.14/0.095), femur I 0.18/0.125 (0.18/0.145), femur II 0.21/0.13 (0.23/0.15), tibia 0.23/0.085 (0.255/0.09), tarsus 0.12/0.06 (0.12/ 0.055).
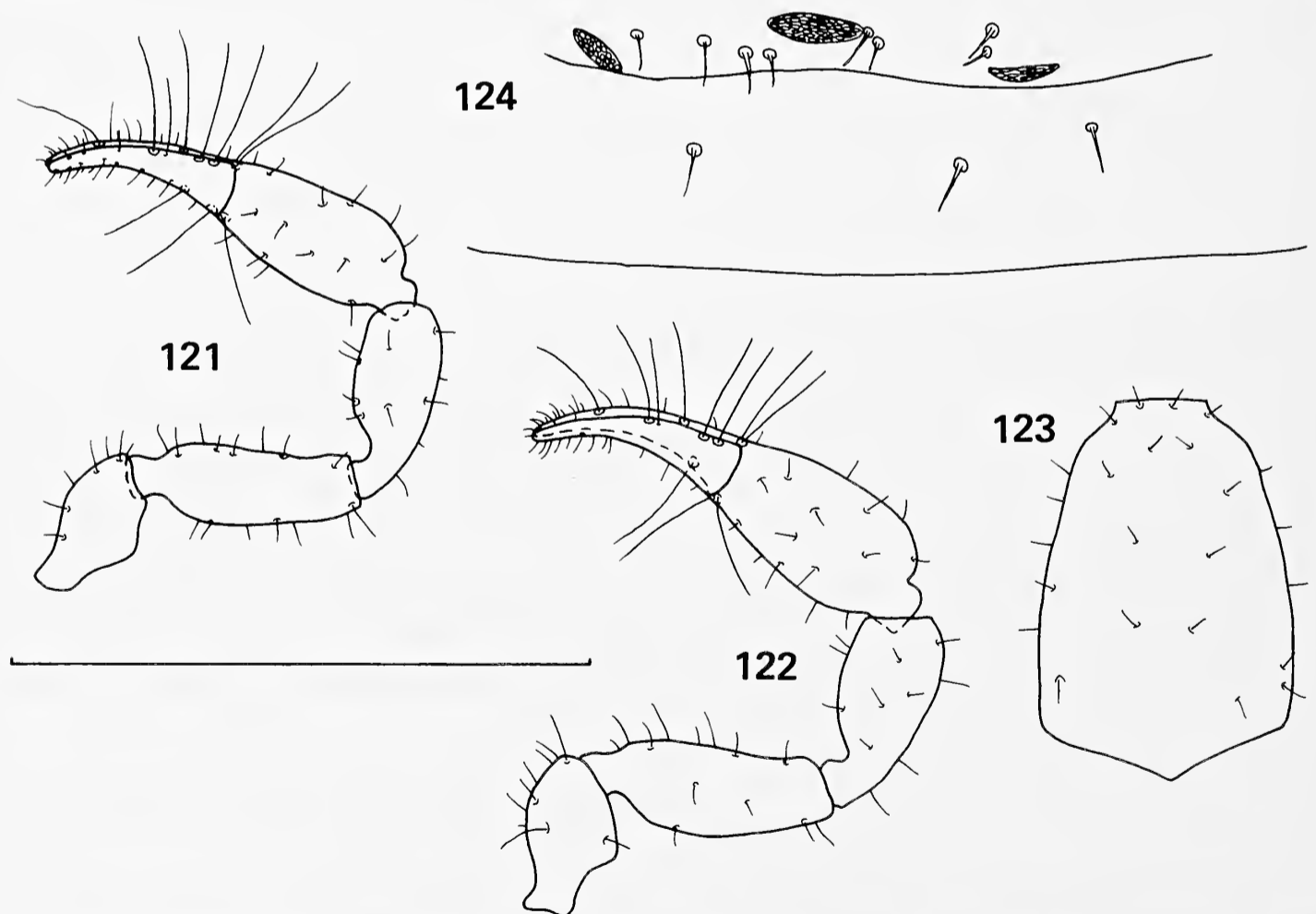
Figs. 121-124.—*Afrosternophorus papuanus* (Beier): 121, ventral aspect of left pedipalp, male lectotype; 122, same, female paralectotype; 123, dorsal aspect of carapace, male lectotype; 124, female genitalia and associated sternites, paralectotype. Scale line = 1.00 mm (Figs. 121-123), 0.25 mm (Fig. 124).

Map 6.—Papua New Guinea and Irian Jaya showing known distribution of *Afrosternophorus papuanus* (Beier) (circle) (district record only), *A. grayi* (Beier) (squares), *A. araucariae* (Beier) (triangle) and *A. cavernae* (Beier) (star). Open symbol represents literature record only.

Habitat.—No habitat data accompanied the specimens.

Remarks.—*Afrosternophorus papuanus* is easily separated from its congeners, except *A. anabates,* by the form of the male genitalia (distally broad anterior apodeme) and the female galea. It can be distinguished from *A. anabates* only by its smaller size (Fig. 129). These two species are thought to be sister-species because both possess the distally broad anterior apodeme, which is a synapomorphy.

The locality of "Americ" cannot be traced, and the map shows the district (Madang) record only.

Beier (1974) recorded the type material as "Type und Paratypen: 2 ♂, 2 ♀", yet failed to distinguish a holotype in the collection. Therefore, a male lectotype has been herein selected.

Afrosternophorus grayi (Beier), new status, new combination
Figs. 60, 75, 125-129; Map 6

Sternophorus hirsti grayi Beier 1971:370-371, Fig. 2.

Types.—Lectotype male (present designation), six paralectotype males, five paralectotype females, Bulolo, Morobe District, Papua New Guinea, 18 August 1970 (B. Gray), NHMW (spirit). Two paralectotype females, Bunu, Lake Kutubu, Southern Highlands District, Papua New Guinea, 22 November 1969 (B. Gray), NHMW (spirit).

Distribution.—Papua New Guinea (Map 6).

Diagnosis.—Male genitalia with long, acute dorsal apodemes. Female galea with two distal, one subdistal and one subbasal rami. Chela (with pedicel) 0.645 to 0.70 (male), 0.68 to 0.74 mm (female) in length.

Description.—Pedipalpal trochanter 1.68 to 1.86 (male), 1.66 to 1.86 (female), femur stout, 2.30 to 2.65 (male), 2.21 to 2.58 (female), tibia 2.03 to 2.29 (male), 1.92 to 2.23 (female), chela (with pedicel) 3.42 to 3.94 (male), 2.96 to 3.94 (female), chela (without pedicel) 3.21 to 3.51 (male), 2.70 to 3.75 (female) times longer than broad. Trichobo-

thria as for *aethiopicus* group, in usual position (Figs. 125-126). Serrula exterior of chelicera with 12 (male), 11 to 13 (female) lamellae. Galea of male simple, of female with two distal, one subdistal and one subbasal rami (Fig. 75). Carapace (Fig. 127) uncon-stricted, with 21 to 23 (male), 19 to 24 (female) setae; 1.40 to 1.51 (male), 1.09 to 1.39 (female) times longer than broad. Male genitalia (Fig. 60) obscure, slightly distorted; dorsal apodemes long and tapering. Female genitalia as for genus (Fig. 128). Tergal chaetotaxy: male, 6:5-6:2-3:4-5:4-5:5:5-6:5-6:6:T1T2?-4T1T:?:2; female, 5-6:5-7:1-4: 4-6:3?-6:4-6:5-6:5-6:5-6:T1T2?-3T1T:?:2. Sternal chaetotaxy: male, 0:3-6:(0)4-6[5-6] (0):(1)4(1):4-6:5-6:3?-6:5-6:5-6:T1T2-4T1T:?:2; female, 0:6-10:(0)4-6(0):(1)4-5(1):6: 5-6:4-6:5-6:5-6:T1T2-4T1T:?:2. Coxal chaetotaxy: male, 3-6:3-5:3-5:3-5; female, 3-5:3-5:3-4:4-5.

Dimensions (mm): Body length 1.4-2.1 (1.8-2.7); pedipalps: trochanter 0.235-0.27/ 0.135-0.155 (0.24-0.295/0.14-0.165), femur 0.385-0.445/0.155-0.185 (0.39-0.465/ 0.165-0.195), tibia 0.32-0.37/0.14-0.175 (0.33-0.39/0.155-0.195), chela (with pedicel) 0.645-0.70/0.17-0.195 (0.68-0.74/0.18-0.23), chela (without pedicel) 0.61-0.66 (0.62-0.70), moveable finger length 0.315-0.36 (0.325-0.38); chelicera 0.145-0.16/0.08-0.085 (0.14-0.165/0.08-0.10), moveable finger length 0.10-0.11 (0.09-0.115); carapace 0.65-0.68/0.43-0.47 (0.645-0.72/0.49-0.59); leg I: coxa 0.18-0.19/0.20-0.21 (0.185-0.21/ 0.205-0.25), trochanter 0.095-0.11/0.07-0.085 (0.10-0.115/0.075-0.08), femur I 0.095-
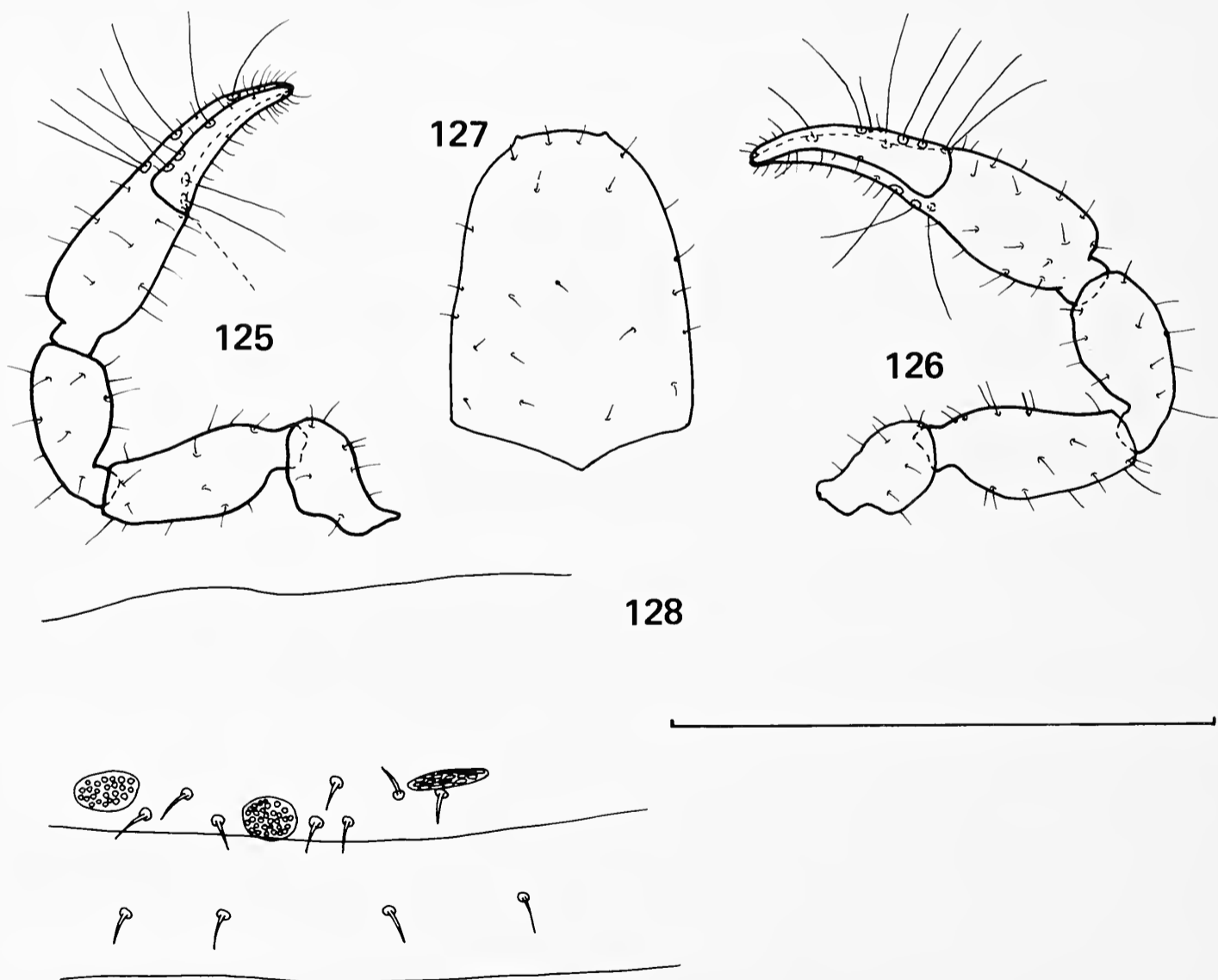
Figs. 125-128.—*Afrosternophorus grayi* (Beier): 125, ventral aspect of right pedipalp, male lecto-type; 126, ventral aspect of left pedipalp, female paralectotype from Bulolo, Papua New Guinea; 127, dorsal aspect of carapace, male lectotype; 128, female genitalia and associated sternites, paralectotype from Bulolo. Scale line = 1.00 mm (Figs. 125-127), 0.25 mm (Fig. 128).

0.11/0.085-0.11 (0.10-0.115/0.095-0.105), femur II 0.14-0.155/0.085-0.11 (0.14-0.16/
0.095-0.105), tibia 0.16-0.165/0.07-0.075 (0.145-0.185/0.065-0.075), tarsus 0.09-0.10/
0.045 (0.09-0.125/0.045-0.055); leg IV: coxa width 0.18-0.23 (0.215-0.22), trochanter
0.125-0.15/0.09-0.10 (0.14-0.155/0.09-0.115), femur I 0.165-0.175/0.155-0.18 (0.16-
0.185/0.14-0.175), femur II 0.215-0.23/0.165-0.18 (0.215-0.25/0.14-0.18), tibia 0.255-
0.27/0.095-0.105 (0.265-0.29/0.09-0.115), tarsus 0.135-0.14/0.065-0.07 (0.11-0.155/
0.055-0.07).

Habitat.—This species has been taken from under bark of *Araucaria cunninghamii* and
A. hunsteinii (Beier 1971), a fact which is not stated on the locality labels.

Remarks.—This species was originally described from many specimens, most of which
were apparently returned to Dr. B. Gray, Entomology Section, Department of Forests,
Bulolo, Papua New Guinea; despite repeated requests to this institution concerning the
remaining material, it has not been available for study.

Beier labelled the Bunu specimens "Typen" and failed to designate a holotype. Fur-
thermore, he stated in the original description that one male and one female were present
in the vial. Both specimens are in fact females, and since it appears advantageous that the
primary type be a male, a male lectotype has been selected from the Bulolo vial.

Beier also labelled the Bunu specimens as "*Sternophorus grayi* n. sp.", and the Bulolo
specimens as "*Sternophorus hirsti grayi* n. sp.", even though he published the description
under the latter combination.

As can be seen from the description, *A. grayi* is substantially different from *A. hirsti*,
and Beier's decision to relegate it to subspecific rank cannot be justified. *Afrosterno-
phorus grayi* appears to be most closely related to the Australian species *A. nanus*, from
which it can be distinguished only by its larger size.

Araucariae group

Diagnosis.—As for genus, except that the moveable chelal finger possesses two tricho-
bothria, *b* and *t*.

Subordinate taxa.—*Afrosternophorus araucariae* (Beier), *A. cavernae* (Beier), *A. fallax*,
new species, *A. xalyx*, new species.

Afrosternophorus araucariae (Beier), new combination
Figs. 61, 130-132; Map 6

Sternophorellus araucariae Beier 1971:372-373, Fig. 3.

Types.—Holotype male, two chelae of paratype adult, Mt. Dayman, Milne Bay District,
Papua New Guinea, under bark of *Araucaria cunninghamii*, 20 July 1969 (B. Gray),
NHMW (spirit). The type series also contained two male and a female paratype which
were not available for study.

Distribution.—Papua New Guinea (Map 6).

Diagnosis.—Male genitalia with long, acute, slightly curved dorsal apodemes. Chela
(with pedicel) 4.47 to 4.56 (male) times longer than broad.

Description.—Male only. Pedipalpal trochanter 1.88, femur elongate, 3.34 to 3.55,
tibia 2.58 to 2.84, chela (with pedicel) slender, 4.47 to 4.56, chela (without pedicel) 4.19
to 4.28 times longer than broad. Trichobothria as for *araucariae* group, in usual position
(Fig. 131). Serrula exterior of chelicera with 10 lamellae. Galea of male simple. Carapace
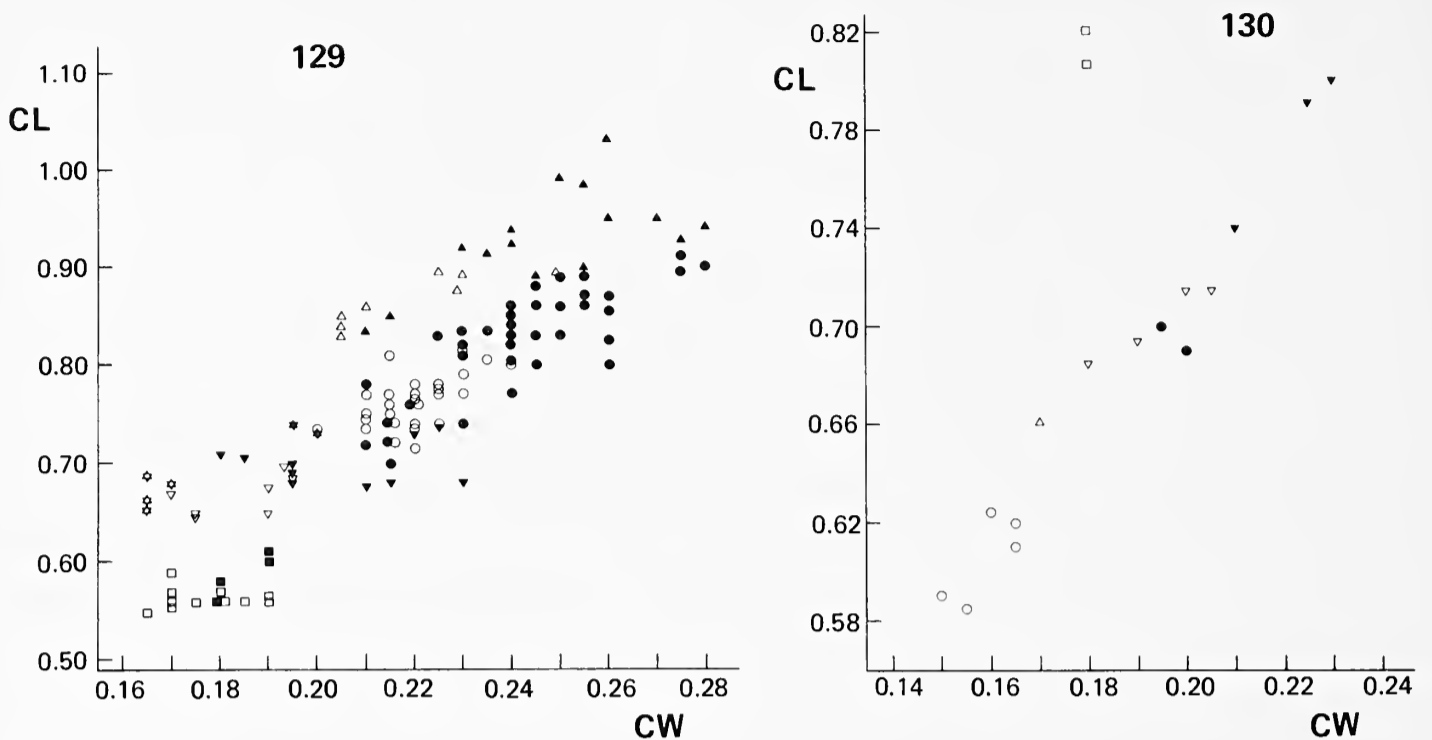
Figs. 129-130.—Graphs of chela (with pedicel) length (CL) versus width (CW), in mm; open symbols, males; closed symbols, females: 129, *Afrosternophorus hirsti* (Chamberlin) (circles), *A. nanus,* new species (squares), *A. anabates,* new species (upright triangles), *A. papuanus* (Beier) (stars), *A. grayi* (Beier) (inverted triangles); 130, *A. araucariae* (Beier) (squares), *A. cavernae* (Beier) (triangle), *A. fallax,* new species (circles), *A. xalyx,* new species (inverted triangles).

slightly constricted (Fig. 132), with 23 setae; 1.41 times longer than broad. Male genitalia with long, acute, slightly curved dorsal apodemes; mid-piece of lateral rod small (Fig. 61). Tergal chaetotaxy: 6:5:4:5:6:6:6:6:6:T1T3T1T:?:2. Sternal chaetotaxy: 0:5: (0)4[6](0):(1)4(1):7:6:7:7:7:T1T3T1T:?:2. Coxal chaetotaxy: 4-5:3:3-5:4-5.

Dimensions (mm): Body length 2.2; pedipalps: trochanter 0.30/0.16, femur 0.535-0.55/0.155-0.16, tibia 0.425-0.44/0.155-0.165, chela (with pedicel) 0.805-0.82/0.18, chela (without pedicel) 0.755-0.77, moveable finger length 0.375-0.39; chelicera 0.16/0.095, moveable finger length 0.11-0.115; carapace 0.705/0.50; leg I: coxa 0.20/0.18, trochanter 0.12/0.085, femur I 0.105/0.105, femur II 0.175/0.105, tibia 0.185/0.07, tarsus ?/0.05; leg IV: coxa width 0.19, trochanter 0.16/0.095, femur I 0.175/0.145, femur II 0.26/0.145, tibia 0.30/0.09, tarsus 0.14/0.06.

Habitat.—The type specimens were taken from under bark of *Araucaria cunninghamii* (Beier 1971).

Remarks.—Beier originally described this species from three males and one female. The holotype male is deposited in NHMW, but the remaining specimens were probably returned to Dr. B. Gray of the Entomology Section, Department of Forests, Bulolo, Papua New Guinea. Repeated requests to this institution concerning the material have failed to elicit a response, and as a result, the female of *araucariae* remains unstudied. This is unfortunate since the form of the female genitalia is crucial in correctly assigning species to genus. Nevertheless, females of the closely related species *A. fallax* and *A. xalyx* possess the typical *Afrosternophorus* genitalia.

Two badly crushed, isolated chelae were present in the vial containing the holotype. They most probably belong to one of the aforementioned paratypes.

This species is easily distinguished from other species of the species group on the basis of its elongate pedipalps (Fig. 130).
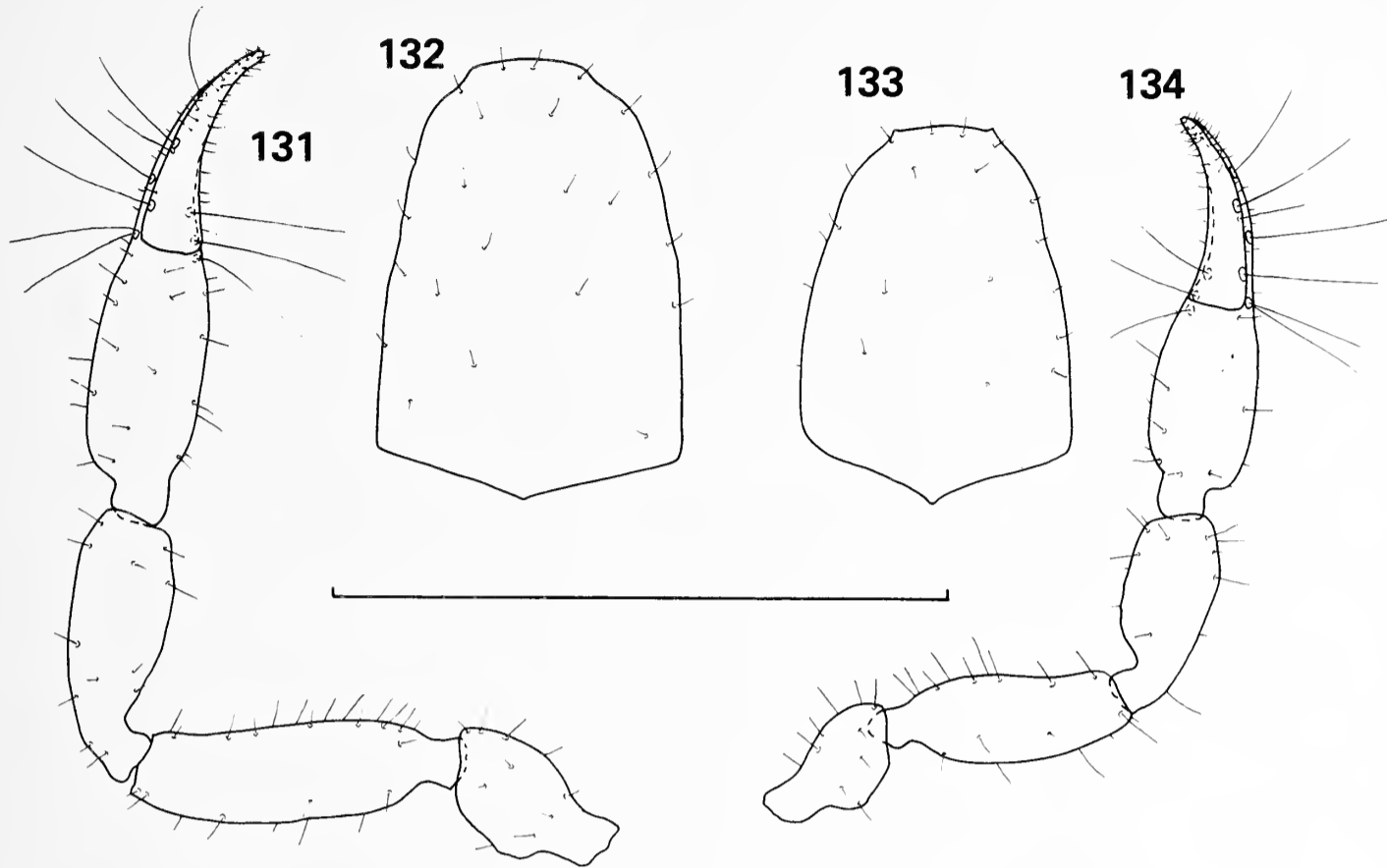
Figs. 131-132.—*Afrosternophorus araucariae* (Beier), male holotype: 131, ventral aspect of right pedipalp; 132, dorsal aspect of carapace. Figs. 133-134.—*Afrosternophorus cavernae* (Beier), male paratype: 133, dorsal aspect of carapace; 134, ventral aspect of left pedipalp. Scale line = 1.00 mm.

Afrosternophorus cavernae (Beier), new combination
Figs. 62, 130, 133-134; Map 6

Sternophorellus cavernae Beier 1982:44-45, Fig. 1.

Types.—Holotype male, Selminum tem Cave [near Tifalmin], West Sepic District, Papua New Guinea, 1 November 1975 (P. Chapman), National Natural History Museum, Sofia (spirit), not examined. Paratype male, same data as above except 1 October 1975 (P. Beron), NHMW (spirit).

Distribution.—Papua New Guinea (Map 6).

Diagnosis.—Male genitalia with long, acute dorsal apodemes; mid-piece of lateral rod not elongate. Chela (with pedicel) 0.66 mm (male) in length.

Description.—Male only. Pedipalpal trochanter 1.92 to 2.00, femur 2.93 to 2.97, tibia 2.20 to 2.27, chela (with pedicel) 3.88, chela (without pedicel) 3.62 to 3.65 times longer than broad. Trichobothria as for *araucariae* group, in usual position (Fig. 134). Serrula exterior of chelicera with 12 lamellae. Galea of male simple. Carapace unconstricted (Fig. 133), with 20 setae; 1.39 times longer than broad. Male genitalia with long, acute dorsal apodemes; mid-piece of lateral rod small (Fig. 62). Tergal chaetotaxy: 7:6:6:6:6:7:6:7:8: T1 T4T1 T:?:2. Sternal chaetotaxy: ? Coxal chaetotaxy:?

Dimensions (mm): Body length 1.7; pedipalps: trochanter 0.25-0.26/0.13, femur 0.425-0.43/0.145, tibia 0.33-0.34/0.15, chela (with pedicel) 0.66/0.17, chela (without pedicel) 0.615-0.62, moveable finger length 0.32-0.325; chelicera 0.135-0.14/0.08, moveable finger length 0.10; carapace 0.61/0.44; legs: ?.

Habitat.—The type specimens were taken from a cave, but it is not known whether or not this is simply fortuitous.

Remarks.—*Afrosternophorus cavernae* is very similar to *A. fallax* and the two species can be distinguished only on details of the male genitalia. Additional material of both species may yield subtle differences in pedipalpal morphometrics, but the paucity of specimens precludes such a study at the present time. Both of these species differ from *A. araucariae* by their stout pedipalps (Fig. 130), and from *A. xalyx* in possessing long dorsal apodemes.

Unfortunately, females of *A. cavernae* have not been available for study, but it is presumed that they will possess the genitalia typical of the remaining species of the genus. Females of the closely related species *A. fallax* and *A. xalyx* possess such genitalia.

The occurrence of this species in a cave is very surprising because all other sternophorid species (with known locality data) are corticolous. It does not display any troglobitic adaptations such as attenuate appendages or unusually pale colouration and this cavernicolous record may be simply fortuitous. Selminum tem Cave is 20 km long (Moore 1978) and the locality data given by Beier (1982) or the data on the label of the paratype that I examined did not state from where in the cave system the specimens were taken. Further collections and more detailed observations on its biology are needed to support the alleged cavernicolous nature of the species.

Beier (1982) stated that Selminum tem Cave was situated in the Western District of Papua New Guinea. Although I cannot locate this cave on any maps or gazetteers at my disposal, Moore (1978) indicated that it is situated near the township of Tifalmin, which, in fact, is in the West Sepic District.

Afrosternophorus fallax, new species
Figs. 63, 76, 130, 135-138; Map 4

Sternophorus chamberlini Redikorzev: Beier 1951:71-72 (in part).

Types.—Holotype male, paratype male, paratype female, Plateau von Langbian [= Cao Nguyên Lâm Viên, see Table 1], Vietnam, 1938-1939 (C. Dawydoff), NHMW (spirit). Paratype male, same data as above, ANIC, MH431.01 (slide).

Etymology.—The specific epithet refers to this species being confused with *chamberlini* by Beier (*fallax* L. deceitful, false).

Distribution.—Vietnam (Map 4).

Diagnosis.—Male genitalia with long, acute dorsal apodemes; mid-piece of lateral rod elongate. Female galea with three distal to subdistal rami. Chela (with pedicel) 3.70 to 3.91 (male), 3.45 to 3.59 (female) times longer than broad.

Description.—Pedipalpal trochanter 1.68 to 1.88 (male), 1.86 to 1.89 (female), femur 2.88 to 3.08 (male), 2.83 to 2.90 (female), tibia 2.14 to 2.38 (male), 2.16 to 2.25 (female), chela (with pedicel) 3.70 to 3.91 (male), 3.45 to 3.59 (female), chela (without pedicel) 3.45 to 3.73 (male), 3.33 to 3.38 (female) times longer than broad. Trichobothria as for *araucariae* group, in usual position (Figs. 135-136). Serrula exterior of chelicera with 12 to 13 (male), 12 (female) lamellae. Galea of male simple, of female with three distal to subdistal rami (Fig. 76). Carapace unconstricted (Fig. 137), with 22 (male), 20 (female) setae; 1.33 to 1.41 (male), 1.45 (female) times longer than broad. Male with long, acute dorsal apodemes; mid-piece of lateral rod elongate (Fig. 63). Female genitalia as for genus (Fig. 138). Tergal chaetotaxy: male, 6:4-6:2:6:5-6:6:6:5-6:6:T1T3 T1T:?:2; female, 6:5:2:6:6:6:6:6:6:T1T4T1T:?:2. Sternal chaetotaxy: male, 0:4:(0)4[5-6](0):(1)4(1):6:6:6:6:6:T1T2-3T1T:?:2; female, 0:5:(0)4(0):(1)4(1):6:6:6:6:6:T1T3 T1T:?:2. Coxal chaetotaxy: male, 4-5:3-5:2-4:3-5; female, 5:4-5:3:3.

Dimensions (mm): Body length 1.5-1.7 (1.9); pedipalps: trochanter 0.21-0.235/0.12-0.125 (0.26-0.265/0.14), femur 0.375-0.385/0.125-0.13 (0.425/0.15), tibia 0.30-0.31/0.13-0.14 (0.345-0.36/0.16), chela (with pedicel) 0.585-0.625/0.15-0.165 (0.69-0.70/0.195-0.20), chela (without pedicel) 0.55-0.595 (0.66-0.665), moveable finger length 0.28-0.30 (0.32); chelicera 0.125-0.13/0.07-0.075 (0.145/0.08), moveable finger length 0.095-0.10 (0.105); carapace 0.56-0.58/0.41-0.42 (0.665/0.46); leg I: coxa 0.155/0.165 (0.18/0.195-0.20), trochanter 0.08-0.085/0.065 (0.095-0.10/0.07), femur I 0.09/0.075 (0.085/0.085), femur II 0.12/0.08 (0.135-0.14/0.085), tibia 0.13/0.055 (0.14/0.06), tarsus ?/? (?/?); leg IV: coxa width 0.16-0.19 (0.195-0.21), trochanter 0.11-0.12/0.075-0.085 (0.14/0.085-0.09), femur I 0.14-0.165/0.11-0.115 (0.175-0.18/0.125-0.13), femur II 0.17-0.18/0.115-0.12 (0.21-0.215/0.13-0.135), tibia 0.19-0.20/0.07-0.075 (0.22-0.24/0.08-0.085), tarsus 0.105-0.13/0.045-0.05 (0.13/0.06).

Habitat.—No habitat data accompanied the specimens.

Remarks.—As discussed under *Afrosternophorus chamberlini*, Beier's (1951) description of that species was a composite of *chamberlini* and *fallax*. His male pedipalp measurements were of the latter, and his female measurements were of the former.

This species is very similar to the Papua New Guinean species *A. cavernae*. It may be distinguished from this species by the presence of a long mid-piece on the lateral rod of the male genitalia.

Afrosternophorus xalyx, new species
Figs. 64, 77, 130, 139-143; Map 5

Types.—Holotype male, two paratype males, four paratype females, Townsville, Queensland, Australia, under bark of eucalypt tree, date? (collector?), MV, K154-K160 (slides and spirit).

Etymology.—The specific epithet is an arbitrary combination of letters.
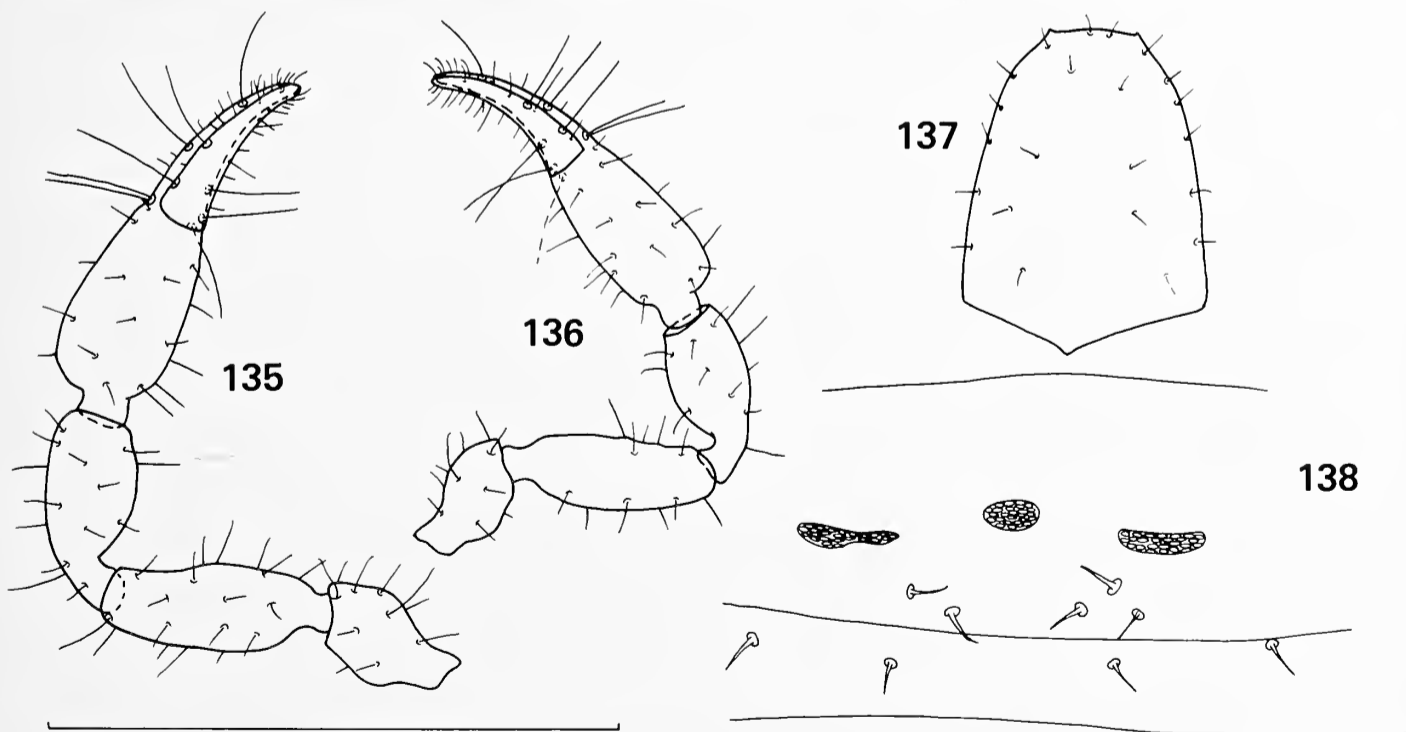
Figs. 135-138.—*Afrosternophorus fallax*, new species: 135, ventral aspect of right pedipalp, female paratype; 136, ventral aspect of left pedipalp, male holotype; 137, dorsal aspect of carapace, male holotype; 138, female genitalia and associated sternites, paratype. Scale line = 1.00 mm (Figs. 135-137), 0.25 mm (Fig. 138).

Diagnosis.—Male genitalia with reduced dorsal apodemes; mid-piece of lateral rod with distinct posterior notch. Female galea with two distal and four subdistal to subbasal rami. Chela (with pedicel) 0.685 to 0.72 (male), 0.74 to 0.79 mm (female) in length, 3.49 to 3.81 (male), 3.43 to 3.52 (female) times longer than broad.

Description.—Pedipalpal trochanter 1.61 to 1.89 (male), 1.67 to 1.81 (female), femur 2.64 to 2.93 (male), 2.71 to 2.94 (female), tibia 2.03 to 2.25 (male), 2.08 to 2.24 (female), chela (with pedicel) 3.49 to 3.81 (male), 3.43 to 3.52 (female), chela (without pedicel) 3.32 to 3.58 (male), 3.26 to 3.38 (female) times longer than broad. Trichobothria as for *araucariae* group, in usual position (Figs. 139-141). Serrula exterior of chelicera with 12 to 13 (male), 12 (female) lamellae. Galea of male simple, of female with two distal and four subdistal to subbasal rami (Fig. 77). Carapace not constricted (Fig. 142) with 16 to 19 (male), 21 to 23 (female) setae; 1.30 to 1.37 (male), 1.20 to 1.34 (female) times longer than broad. Male genitalia with reduced dorsal apodemes; midpiece of lateral rod with a distinct posterior notch (Fig. 64). Female genitalia as for genus (Fig.
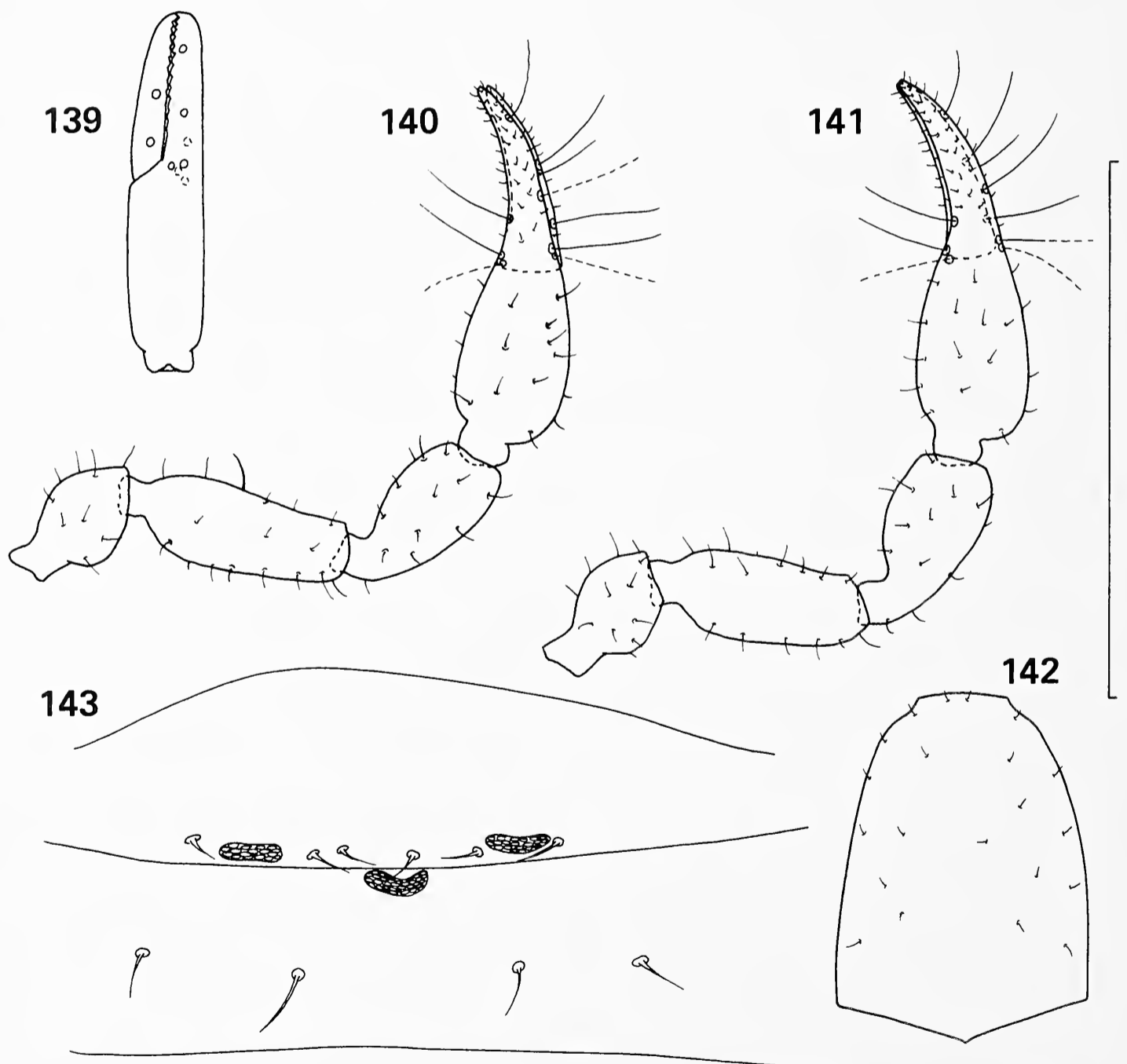
Figs. 139-143.—*Afrosternophorus xalyx*, new species: 139, lateral aspect of left chela, male paratype, K155; 140, dorsal aspect of right pedipalp, male holotype; 141, same, female paratype, K157; 142, dorsal aspect of carapace, female paratype, K157; 143, female genitalia and associated sternites, paratype, K157. Scale line = 1.00 mm (Figs. 139-142), 0.25 mm (Fig. 143).

143). Tergal chaetotaxy: male, 5-6:6-7:5-6:6-8:6-8:5-8:6-7:6-8:6:T1T4T1T:?:2; female, 6-7:6-8:4:6:6-7:6-7:6-7:6:6-8:T1T4-5T1T:?:2. Sternal chaetotaxy: male, 0:4-7:(0)4[10-12](0):(1)4-5(1):6:6:6-7:6-8:6:T1T3-4T1T:?:2; female, 0:8:(0)4(0):(1)4-6(1):6-8:6-8:5-6:5-6:5-7:T1T3-4T1T:?:2. Coxal chaetotaxy: male, 3-4:4-5:3-5:4; female, 3-4:4-6:4-6:3-4.

Dimensions (mm): Body length 1.6-1.8 (1.7-2.5); pedipalps: trochanter 0.25-0.265/0.135-0.155 (0.265-0.295/0.155-0.17), femur 0.42-0.455/0.145-0.165 (0.45-0.50/0.16-0.18), tibia 0.345-0.375/0.155-0.17 (0.375-0.405/0.17-0.19), chela (with pedicel) 0.685-0.72/0.18-0.205 (0.74-0.79/0.21-0.23), chela (without pedicel) 0.645-0.69 (0.70-0.76), moveable finger length 0.34-0.365 (0.375-0.405); chelicera 0.13-0.145/0.07-0.08 (0.155-0.16/0.085-0.10), moveable finger length 0.10 (0.11-0.12); carapace 0.635-0.67/0.48-0.49 (0.66-0.73/0.52-0.61); leg I: coxa 0.18-0.21/0.19-0.205 (0.20-0.21/0.23-0.25), trochanter 0.095-0.105/0.07 (0.125/0.09), femur I 0.09-0.095/0.115-0.12 (0.105/0.13-0.135), femur II 0.155-0.16/0.11-0.12 (0.18/0.08), tibia 0.175-0.18/0.05-0.075 (0.19/0.08), tarsus 0.13/0.05 (0.13-0.14/0.05-0.06); leg IV: coxa width 0.21-0.22 (0.235-0.24), trochanter 0.135-0.145/0.10 (0.155/0.11), femur I 0.155-0.165/0.175-0.18 (0.175-0.185/0.175-0.19), femur II 0.22-0.23/0.175-0.18 (0.23-0.255/0.18-0.205), tibia 0.29/0.09-0.10 (0.30-0.31/0.105-0.12), tarsus 0.165/0.06 (0.17-0.18/0.06-0.07).

Habitat.—The specimens were taken from "under bark of eucalypt tree".

Remarks.—Even though the type specimens are in poor condition, there can be no doubt that they represent a new and distinct species of the *araucariae* group.

Males of *A. xalyx* differ from the other three species of the *araucariae* group in possessing reduced dorsal apodemes, and females differ from *A. fallax* (the only other species of the group in which females are known) by possessing more galeal rami. In addition, *A. xalyx* is slightly larger (Fig. 130).

A second label with the specimens reads "presented by G. F. Hill 24/4/23".

EVOLUTION

A speculative phylogeny of the three sternophorid genera, and their species or groups, is presented in Fig. 144. Table 3 summarizes the characters utilized in the cladogram. The techniques advocated by Hennig (1965, 1966) for cladogram construction were used.

1. Female median cribriform plate(s). Even though data for many genera are lacking, most genera of all of the monosphyronid families (with the exception of the Pseudogarypidae, whose female genitalia are unknown) possess only one median cribriform plate. Exceptions that possess two plates include most Cheliferini (Chamberlin 1932b), the chernetids *Metagoniochernes milloti* Vachon (Vachon 1951) and *Lamprochernes* sp. (pers. obs.) and the two sternophorid genera *Garyops* and *Idiogaryops*. *Neocheiridium africanum* Mahnert and *N. pusillum* Mahnert (Cheiridiidae) possess three such plates (Mahnert 1982a), as do some females of *Idiogaryops paludis* (Hoff 1963). Chamberlin (1952) stated that two plates represent the primitive condition, and that several independent fusions have occurred to form one plate. If this is so, then fusion has occurred in all of the monosphyronid families; the alternative hypothesis is preferred here because this involves a minimum of only four changes within the suborder (one each in the Sternophoridae and Cheiridiidae, and one or more in the Cheliferidae and Chernetidae).

Thus, the character state displayed by the genus *Afrosternophorus* is thought to be plesiomorphic, and the character state displayed by *Garyops* and *Idiogaryops* is assumed to be apomorphic.

Table 3.—Characters used in the construction of the cladogram of the Sternophoridae (Fig. 144).

Character	Plesiomorphic state	Apomorphic state
1. Female median cribriform plate(s)	1	2
2. Female median cribriform plate(s)	without spurs	with spurs
3. Trichobothria of moveable chelal finger	3	2
4. Trichobothria of moveable chelal finger	3	2
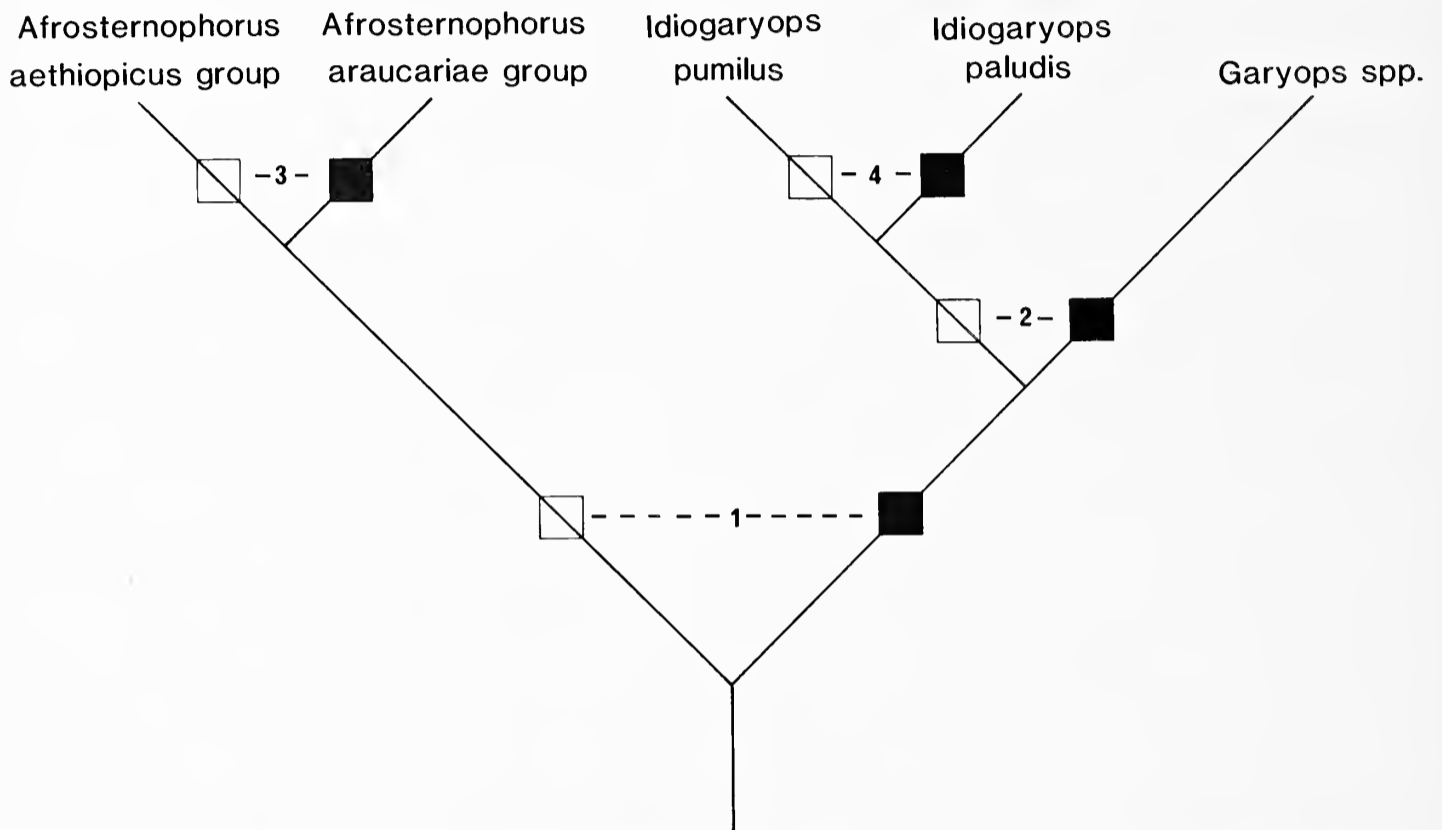
Fig. 144.—Cladogram of the Sternophoridae: open squares, plesiomorphic character states; closed squares, apomorphic character states.

2. Female median cribriform plates(s). Lateral spurs on the median cribriform plates are unique within the Pseudoscorpionida, and undoubtedly represent an autapomorphy for *Garyops*.

3. and 4. Trichobothria of moveable chelal finger. Because most pseudoscorpions possess 8/4 (i.e., eight trichobothria on the fixed chelal finger and four trichobothria on the moveable chelal finger), it is assumed that this is the most plesiomorphic condition within the order. If a lower number is considered to be the primitive state, then one must postulate a series of independent additions to the trichobothriotaxies of all of the pseudoscorpion families. If 8/4 is the primitive condition, then one need only assumed that reductions have occurred independently in a few families, such as the Garypidae, Olpiidae, Neobisiidae, Sternophoridae, Cheiridiidae and Chernetidae. The highest number in the Sternophoridae is 7/3 and this is regarded as the plesiomorphic condition for the family. Deviations from this pattern are known in five species of two genera *(A. araucariae, A. cavernae, A. fallax, A. xalyx* and *I. paludis)* where each species lacks the trichobothrium *sb* of the moveable chelal finger. This is considered to be apomorphic. Since it has occurred in two separate genera, it obviously represents an interesting case of parallelism.

This loss of a trichobothrium appears to be neotenic, since the tritonymphs of the 7/3 species possess 7/2 trichobothria and once again *sb* is absent. Thus, it is not so much a case of "losing" a trichobothrium, but of having a trichobothrium fail to appear in the post-embryonic development of a species. Developmental data on these species with reduced trichobothriotaxies are completely lacking.

The analysis of phylogenetic trends within the genera *Garyops* and *Afrosternophorus*, especially the large *A. aethiopicus* group, is an extremely difficult task which has not been attempted. This is mainly due to a series of apomorphic character states whose sequence in time are virtually impossible to interpret. They are only briefly summarized here: *G. centralis* (increased number of female galeal rami), *A. aethiopicus* (reduction of dorsal apodeme), *A. ceylonicus* (reduction of dorsal apodeme; decreased number of galeal rami), *A. chamberlini* (midpiece of lateral rod elongate; increased number of female galeal rami), *A. hirsti* (reduction of dorsal apodeme; anterior apodeme brush-like), *A. anabates* (anterior apodeme distally broad; often phoretic on sparassid spiders), *A. papuanus* (anterior apodeme distally broad), *A. fallax* (midpiece of lateral rod elongate) and *A. xalyx* (dorsal apodemes reduced). *Afrosternophorus anabates* and *A. papuanus* are synapomorphic sister-species that are united by the presence of a distally broad anterior apodeme.

Since *Afrosternophorus* and *Idiogaryops* are not based upon apomorphic character states, and are defined by plesiomorphies, the possibility exists that they are paraphyletic. Nevertheless, at the expense of a strict cladistic classification where such groups would not be recognized, I have retained the three generic names because they are useful labels denoting distinct differences in the female genitalia.

BIOGEOGRAPHY

The Sternophoridae is currently distributed in most parts of the world (Maps 1-6), but it appears to conform quite readily to a "trans-antarctic" pattern, and may have had its origins in Gondwanaland. Nevertheless, anomalies occur which need clarification before definite statements may be made. These include:

(1) The absence of Neotropical records: If it is assumed that sternophorids originated in Gondwanaland, then there are two hypotheses that may be presented to explain their absence from South America: (a) they are extinct, or (b) they have yet to be collected. I consider that the latter is the most plausible hypothesis since sternophorids are small, pale, corticolous pseudoscorpions that, unless specifically searched for, are difficult to find.

(2) Presence in Laurasia (North America): Many "Gondwanaland" organisms invaded North America from South America when those two continents joined during the Cretaceous (Dietz and Holden 1970). Thus, it is not particularly surprising to find that at least one pseudoscorpion group has undertaken a similar journey. Others apparently include the Pseudogarypidae, Garypidae, Tridenchthoniidae and Atemnidae.

(3) Presence in Indo-China: This apparent anomaly may be explained by two models. The first assumes that migration occurred from India after that subcontinent became attached to Asia during the Cretaceous (Dietz and Holden 1970), and the second has its foundations in recent studies which have shown that various portions of south-east Asia may have been an integral part of Gondwanaland (Burton 1970, Ridd 1971, Crawford 1974, Stauffer 1974, Cooper 1980 and others), possibly lying between India and Australia (Ridd 1971).

The presence of *Idiogaryops pumilus* on Little Cayman Island in the Caribbean is also quite interesting. Perfit and Heezen (1978) hypothesized that during the Miocene, localized uplift elevated the Cayman Islands (among others) above sea level. This suggests that *I. pumilus* arrived on Little Cayman Island by phoresy or rafting subsequent to the island's appearance.

It is of interest to note that two sister-species united by a single synapomorphy, *Afrosternophorus anabates* and *A. papuanus,* are geographically isolated, the former in south-eastern Australia (Map 5) and the latter in Papua New Guinea (Map 6). New Guinea (which includes Papua New Guinea and Irian Jaya) is now firmly considered to be an integral part of the Australian continent (Nix 1982), and the two countries are thought to have separated during the Eocene or Pliocene (Doutch 1972).

It is of interest to note the congruence between the generic classification proposed in this study and the biogeography of each of the genera. *Garyops* and *Idiogaryops* are found only in the New World and are more closely related to each other than to *Afrosternophorus.*

ACKNOWLEDGMENTS

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TWO-YEAR LIFE CYCLE AND LOW PALPAL CHARACTER VARIANCE IN A GREAT SMOKY MOUNTAIN POPULATION OF THE LAMP-SHADE SPIDER (ARANEAE, HYPOCHILIDAE, *HYPOCHILUS*)

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ABSTRACT

Size-frequency histograms and other data generated from four samples (totaling 926 specimens) collected during a complete year show that a *Hypochilus* population in the Great Smoky Mountains has a two-year life cycle with the following schedule: spiderlings emerge from egg sacs and construct their first webs in late May; 15 to 18 months later, during their second autumn, these spiders mature, mate, and lay eggs. The growth rate and adult body size variances of this population are very large. The coefficients of variation of three palpal dimensions in a sample of 38 males are significantly smaller than those of tibia I length or carapace length. Such relative constancy of palpal characters within a population may be common in spiders and may result from stabilizing selection in one or both of the following forms: selection for the mechanical compatibility necessary for effective sperm placement during copulation, and sexual selection by female choice.

INTRODUCTION

In his study of several populations of the lamp-shade spider, *Hypochilus,* Fergusson (1972) concluded, chiefly from the frequency distribution of tibia I lengths of 164 individuals collected in late October, that this species has a two-year life cycle. The current study was undertaken primarily to rigorously test this life-cycle hypothesis and, secondarily, to determine whether the coefficients of variation (standard deviation x 100/ mean) of palpal dimensions are less than the large coefficients of variation of male body dimensions in this population. Even though the relative constancy of genital characters is often noted in taxonomic revisions (for example Reiskind 1969, Levi 1981) and may be one of the reasons taxonomists rely so heavily on genital characters to diagnose species of spiders and many other animals (Mayr 1969), I am not aware of any rigorous statistical attempt to confirm its occurrence in any species of spider. It is important to note that Hoffman (1982, pers. comm.) recently concluded that the southern Blue Ridge Province populations of *Hypochilus* which Fergusson (1972) and I have studied represent a new species (as yet undescribed) that is distinct from the Appalachian Plateau populations of *Hypochilus thorelli.*

METHODS

Life History.—Four collections of individuals from a single, dense *Hypochilus* population living on rock outcrops along Little River Road on the Tennessee side of the Great Smoky Mountain National Park were made between 1.5 miles upriver and 1.5 miles downriver from The Sinks on the following days (sample size in parentheses): 1 October 1982 (207), 8 May 1983 (134), 1 June 1983 (287), and 30 September 1983 (298). For each collection an attempt was made to carefully examine entire areas of rock outcrop surface (different for each collection) and collect every *Hypochilus* individual within reach. However, during the October 1 collection a number of adult males and females that were spotted were not collected, and during the June 1 collection it was possible that not all reachable spiderlings were collected since these are very small and difficult to see.

All specimens were preserved in 70% ethanol. The length of the first tibia of each specimen was measured by me with a Wild M5 stereomicroscope fitted with 20x eyepiece lenses with a 100-unit eyepiece reticle scale. Tibia I length was selected as an indicator of body size because measuring carapace or sternum dimensions would have required the removal of all legs. Tibia I length is defined as the straight line distance between the proximal and distal ends of the article in lateral view with the article on the horizontal plane. In order to avoid using a value for a regenerating leg, both the left and right tibia I were measured and the value for the left recorded unless it was more than three scale units shorter than the right tibia. Measurements were recorded to the nearest half unit and repeated measurements of two specimens indicated that measurements were precise to within 0.04 mm for the smallest specimens and 0.23 mm for the largest ones. If a specimen belonged in any of the following categories, such was noted: adult female (any female with developing or fully developed eggs and a markedly hirsute area just anterior to the genital groove); adult male; penultimate male (identified by swollen pedipalp tarsi); about to molt (any individual with dark setae of new exoskeleton visible under old exoskeleton).

Palpal Character Variance.—Measurements were recorded for two non-genital characters that are frequently used as indicators of body size and three palpal characters on each of the 38 adult *Hypochilus* males collected on September 30. Extreme care was taken to minimize measurement imprecision, an especially important goal when generating coefficients of variation (Rohlf, Gilmartin, and Hart 1983). Structures were selected which can be consistently positioned, and whose linear dimension has well-defined end points. The two non-genital characters are defined as follows: ITL = tibia I length as defined above; CL = distance along median longitudinal line connecting anterior edge of carapace to median indented posterior edge of carapace with all legs removed and carapace horizontal. The three palpal characters were measured on the left pedipalp after it was removed from the body and are defined as follows: PTC = width of palpal tarsus "clasper" in retrolateral view (Fig. 1); PL = length of palpus in retrolateral view (Fig. 1); CdL = length of palpal conductor in prolateral view (Fig. 2). The measurements were performed by me with the optical equipment described above. ITL was measured to the nearest end point of a scale-unit 0.077 mm long, CL to the nearest 0.037 mm scale-unit end point, and the palpal characters to the nearest 0.009 mm scale-unit end point. In order to determine the imprecision involved in making these measurements, one specimen was remeasured ten times
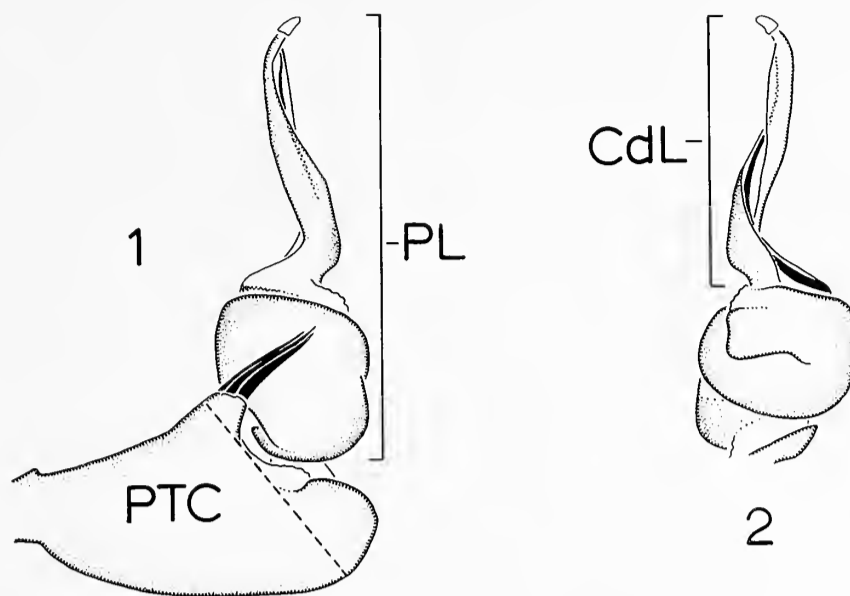
Fig. 1-2.—Left palpal tarsus and palpus of *Hypochilus* male showing three palpal measurements as defined in text: 1, retrolateral view; 2, prolateral view.

over the period of a week (after each set of five measurements was recorded the examining dish was swirled so that each part would have to be repositioned during the next set of measurements), and the coefficient of variation was calculated for each of the five measurement characters for that sample of ten remeasurements.

RESULTS

Life History.—Frequency distribution histograms of tibia I length for each of the four collections are presented in Fig. 3, and statistical values for the age, sex, and molting classes represented in these histograms are presented in Table 1. The May 8 collection histogram indicates that there is only a single age class—all juveniles—present at that time. Although the size range is large, the distribution is monomodal and is not skewed markedly to the right, indicating that it does not comprise two or more age classes. The relatively small size of individuals about to molt also supports this conclusion because, in a homogeneous and relatively young age class with non-synchronous molting, small individuals should be further in time than large individuals from their last molt, and thus more likely to molt than large individuals. The June 1 collection reveals two age classes, a class of spiderlings recently emerged from egg sacs and a class of older juveniles. The latter class, despite its large size range, exhibits those characteristics (non-skewed shape and restriction of molting to smaller individuals) which indicate that it is one age class.

The age class patterns of the histograms for both fall collections are similar to each other. In each there is a single juvenile class with large size variance but with the non-skewed size distribution and molting activity pattern which indicate age homogeneity. In addition, each collection contains an adult age class with an extremely large size variance but with only a slight size overlap with the juvenile class. That this adult class is made up of same aged individuals in their second autumn is indicated by the absence of adults during the spring and early summer

and by the simultaneous presence of a single juvenile age class. In both fall collections some penultimate males, half of which are beginning to molt, are present. The distinct difference between the frequency distributions of adult females and adult males is due to the allometric growth of legs in the final male molt.

The large body size variance of the juvenile classes as compared to the spiderling class (Table 1) shows that there is a large variance in growth rate, with some individuals growing five to six times (linear dimensions) faster than their slowest growing contemporaries during the first full year of growth following spiderling emergence. This early growth rate variance helps create the large variance in body size of adult female and adult male subsamples of the population. This large growth rate variance and the slight overlap between the
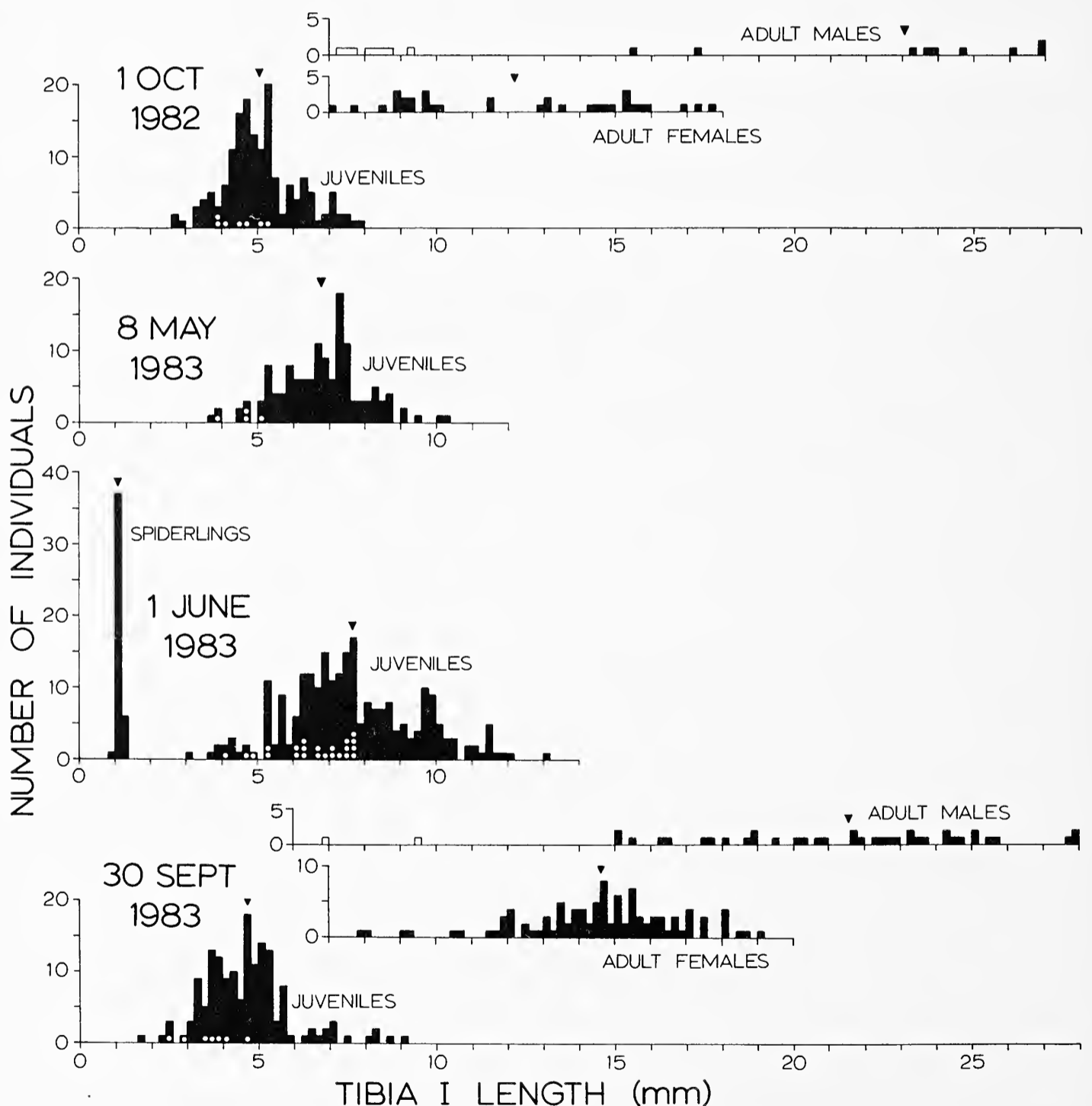
Fig. 3.—Frequency distributions of tibia I lengths for four collections from a *Hypochilus* population. Adults of each sex grouped on separate scale lines. Each square represents one specimen. White squares represent penultimate males. White circles represent individuals ready to molt. Triangles mark means of each age/sex class sample.

Table 1.—Statistical values for tibia I length (in mm) for the age/sex/molting classes of the *Hypochilus* population samples represented in Fig. 1.

Class	Date	N	Range	Mean	Variance	Coefficient of Variation
Spiderlings	1 June '83	44	0.92-1.30	1.13	0.004	5.60
Juveniles (Year 1)	1 Oct. '82	156	2.72-7.85	5.09	1.07	20.32
About to Molt	1 Oct. '82	7	3.85-5.39	4.48	0.31	12.43
Juveniles (Year 1)	30 Sept. '83	155	1.72-9.09	4.68	1.48	26.00
About to Molt	30 Sept. '83	7	2.59-4.70	3.61	0.44	18.37
Juveniles (Year 2)	8 May '83	134	3.70-10.32	6.80	1.49	17.95
About to Molt	8 May '83	4	3.81-5.01	4.57	0.20	9.79
Juveniles (Year 2)	1 June '83	243	3.18-13.09	7.66	3.23	23.46
About to Molt	1 June '83	23	4.16-7.70	6.53	1.03	15.54
Adult Females	1 Oct. '82	34	7.16-17.79	12.20	9.74	25.58
Adult Females	30 Sept. '83	103	7.85-19.02	14.63	4.92	15.16
Adult Males	1 Oct. '82	9	15.40-26.80	23.09	14.66	16.58
Adult Males	30 Sept. '83	38	15.02-27.87	21.56	12.49	16.39

juvenile and adult classes in tibia I length in the fall raise the possibility, albeit very remote, that a very fast growing individual might occasionally mature in its first fall and that a very slow growing individual might, on occasion, fail to mature until its third fall.

Each of the ten egg sacs collected on October 1 and September 30 contained eggs, many of which contained embryos with appendage buds readily visible. Of the eight egg sacs collected on May 8, five were preserved and contained faintly pigmented spiderlings, whereas the remaining three were kept in the laboratory until spiderlings emerged on 13, 22, and 24 May. These spiderlings had longer legs, more hair, and more pigment than those preserved on May 8, and had the same tibia I lengths as those collected in their webs on 1 June. They spun silk in the glass vial within which they emerged and, when disturbed, bounced on this webbing. Each of the 12 egg sacs collected on June 1 had been vacated. Apparently the great majority of spiderlings in this population had emerged from their egg sacs between May 8 and June 1. In spite of diligent searching on June 1, fewer of these spiderlings were found than expected. These newly emerged spiderlings were found (in their webs) only on the more sheltered outcrop surfaces where the light intensity was lowest (and probably the humidity was highest). On the more exposed outcrop surfaces these spiders and their webs were absent or only the bases of their abandoned webs were present, even though older spiders were common. Perhaps these spiderlings tend to hide in crevices during dry periods and build capture webs only at night and/or during humid days.

In summary, the size/age frequency distribution, egg sac, and spiderling data show that this *Hypochilus* population has a two-year life cycle with the following schedule: eggs are deposited in the fall, spiderlings emerged from egg sacs and construct their first webs during the second half of May, these spiderlings then eventually mature, mate, and lay eggs 15 to 18 months later in their second fall, and adults seldom, if ever, survive to reproduce for more than one breeding season.

Palpal Character Variance.—For the sample of 38 males the coefficient of variation of each palpal character (PTC, PL, CdL; Table 2) is significantly less (using Lewontin's (1966) method, P < 0.01) than the coefficient of variation of either non-genital character (ITL, CL). Since the measurement imprecision indices (Table 2) indicate that the three palpal characters are more difficult to measure accurately than are the non-genital characters, factoring out the effect of measurement imprecision on the coefficient of variation of the sample should not reduce (indeed, it would increase) the significance of these differences. It is important to point out that the difference between the coefficients of variation of ITL and CL is largely due to the allometric increase of leg length during the final molt.

DISCUSSION

Life History.—These results strengthen Fergusson's (1972) hypothesis that *Hypochilus* populations in the southern Blue Ridge Province have a two-year life cycle, with adult females rarely, if ever, surviving to a second year of reproduction. Although spiders generally exhibit large intrapopulation size variation as adults (Jocqué 1981), the very large variation in growth rate and, consequently, adult body size observed in this *Hypochilus* population and in some araneid populations (Crome and Crome 1961, Vollrath 1980, Levi 1981) appears to surpass that of most other spiders investigated (for example Dondale 1961, Reiskind 1969, Vogel 1970, Brady 1979, Jocqué 1981). It seems reasonable to postulate that the most probable primary cause of this especially large growth rate variance in *Hypochilus* and some other spiders is a large variance in prey capture success. Whether this prey capture variance results mainly from a patchy prey distribution and an inability to move webs quickly to more profitable sites, or from other factors, remains to be investigated. Riechert and Cady (1983) present evidence suggesting that the spiders *Achaearanea tepidariorum* and *Coelotes montanus,* both common inhabitants of the rock outcrops where *Hypochilus* lives, may have an important impact on *Hypochilus* foraging success by serving as a source of food *(A. tepidariorum)* or by competing for space (*C.*

Table 2.—Statistics for five measurement (mm) characters for a population sample of 38 adult male *Hypochilus.* Measurement imprecision index is the coefficient of variation of a sample of ten remeasurements of a single specimen. Characters are defined in text. The coefficient of variation for each a palpal character is significantly less (P<0.01) than that of either non-genital character.

Character	Range	Mean	Variance	Coefficient of Variation	Measurement Imprecision Index
Non-Genital					
ITL	15.02-27.87	21.56	12.49	16.40	0.348
CL	2.73-4.54	3.69	0.23	12.85	0.293
Palpal					
PTC	0.52-0.70	0.61	0.002	8.15	1.149
PL	1.07-1.37	1.25	0.006	6.39	0.362
CdL	0.65-0.82	0.75	0.002	6.37	1.005

montanus). It is therefore possible that a patchy distribution of these species over the outcrop surfaces inhabited by *Hypochilus* might help create a large variance in *Hypochilus* foraging success.

Palpal Character Variance.—The widespread reliance of spider systematists upon genital characters to diagnose species is presumably due primarily to the tendency of these characters to evolve more rapidly and divergently than other characters. However, the analysis of variance in this sample of *Hypochilus* males suggests that the usefulness of genital characters for diagnosing species may also be due to a tendency for genitalia to vary less than other characters within populations and groups of freely interbreeding populations. Such genital character constancy is frequently implied or demonstrated indirectly in taxonomic papers (for example McCrone 1963, Reiskind 1969). Vollrath's (1980) data for a sample of 38 *Nephila clavipes* males indicate relatively low variance in palpal conductor length. With a sample of only two *Tetragnatha elongata* males, Levi (1981) has illustrated the same phenomenon of relative palpal character constancy. Whether this phenomenon is widespread in spiders awaits analyses of variance in other taxa, but it seems heuristic to suggest two possible causes for such a phenomenon.

If, as seems likely, there is some optimal range of palpus size and shape required for quick and accurate insertion into the copulatory bursae and spermathecae of the females of this *Hypochilus* population in order to achieve effective semen transfer, there should then be selection for a developmental mechanism that insures that a male's palpus will approach that optimum form independent of his body size. In other words, although there is no evidence to suggest that the species-specific shape of *Hypochilus* genitalia (Gertsch 1958, 1964, Hoffman 1963) is a mechanical (lock and key) reproductive isolating mechanism (indeed the unsclerotized nature of the female genital region, bursa, and spermathecae [Coyle et al. 1983] argue against such a function), selection could be acting to maintain some degree of mechanical compatibility in these copulatory structures.

Sexual selection by female choice acting late in courtship or during copulation may be another cause for relatively low intrapopulation variance in palpal characters. As suggested by Eberhard (in press), the tactile information produced by the male palpus during copulation may affect the behavior and/or physiology of the female in a way that affects the male's success in fertilizing her eggs. That is, the female may be selecting mates partly on the basis of her tactile perception of palpus form. Once a preference is established by a proportion of the population's females, there may be strong stabilizing selection for that palpus size and shape and, consequently, a developmental mechanism that regulates palpus size independent of body size. Although West-Eberhard (1983) has justifiably emphasized the probable importance of sexual selection in causing rapid evolution that may accelerate speciation, it is also important to recognize that under some circumstances sexual selection may instead have a stabilizing effect.

ACKNOWLEDGMENTS

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EGG FEEDING BY *TEGENARIA* SPIDERLINGS
(ARANEAE, AGELENIDAE)[1]

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ABSTRACT

Egg feeding activity has been observed within the egg sac in spiderlings of two species of *Tegenaria* Latreille (Agelenidae), in which this phenomenon had not been previously reported. The two species differ in their proportion of egg consumption; their ecological characteristics and life cycle are probable factors that account for the proportional difference in egg feeding.

INTRODUCTION

In spiders, eclosion leads to a stage in which spiders are still incompletely developed. They have little motility and cannot weave or capture prey. In order to complete their development they must remain within the egg sac during a certain length of time which varies according to the species and the conditions of development. This stage, named incomplete (Holm 1940), larval (Vachon 1957), deutovum (Gertsch 1949) or quiescent (Valerio 1974), consists of one or more phases, separated by the shedding of the vitelline membranes. At the end of this stage the first true molt takes place and the larva transforms into a nymph, which is defined as being complete, active and with functioning venom and silk glands (Vachon 1957, Foelix 1979). This nymph remains inside the egg sac for some time before emerging to begin its solitary life. Some authors (Burch 1979, Turnbull 1973) assume that when the nymphs emerge from the egg sac they still have vitelline reserves from which they feed until dispersion occurs. Nevertheless it is known that in several species, the spiderlings (larvae or nymphs) feed on inviable eggs before emergence, as in the families Loxoscelidae (Galiano

1967), Clubionidae (Lecaillon 1904, Mansour et al. 1980, Peck and Whitcomb 1970), Gnaphosidae (Holm 1940), Thomisidae (Schick 1972) and Theridiidae (Juberthie 1964, Kaston 1970, Valerio 1974).

I have detected egg feeding by first nymphs in two species of *Tegenaria* Latreille (Agelenidae), with a remarkable difference in the proportion in which the phenomenon occurs in each species. I believe the difference might probably be determined as much by ecological dissimilarities in the habitat of each of these species as by their life cycles.

MATERIALS AND METHODS

The first observations were made on *Tegenaria* sp. during a study on the predatory behavior of this species (Ibarra 1983, in press). Adults were collected in a tropical forest (Chiapas, Mexico) and were kept and mated in the laboratory. The females wove their egg sacs, from which the spiderlings later emerged, within the cages. A record was kept of the number of spiderlings that emerged from each egg sac and later they were separated individually to start the predatory behavior study.

Later, adult *T. saeva* Blackwall were collected in buildings in the suburbs of Paris (France). These spiders were mated in the laboratory and four egg sacs were removed from the cages a short time after they were woven. Each of these was cut approximately one centimeter in length along its external silk layer, in order to open it enough to display the eggs in its interior. Each egg sac was placed in a plastic box with the observation window facing upwards. Two pieces of sponge at either side supported a slide which covered the observation window in order to protect the eggs from air currents and possible intruders, without obstructing their observation. The egg sacs were observed once a day, until eclosion took place. From that moment on, three observations were made daily, each consisting of five minutes. One of the egg sacs was exposed to programmed photographic equipment and photographs were taken every two hours.

RESULTS

In 350 spiderlings of *Tegenaria* sp. that emerged from six egg sacs, no evident difference in size was observed, except for 15 individuals which had a considerably larger opisthosoma than the rest, all these 15 emerged from the same egg sac (this being the last produced by one of the reproductive females). These spiderlings had an accelerated rate of development and underwent the second molt between four and seven days after they emerged, whereas the rest took from 21 to 45 days to do so.

In the four egg sacs of *T. saeva* 162 spiderlings hatched from the eggs, but four died before the emergence from the egg sac. I have observed egg feeding by 14 individuals, and a progressive enlarging of the opisthosoma in many others (Figures 1 and 2). At emergence all of the 158 survivors had an expanded opisthosoma, and there was no evident difference in size between them. The observations on the behavior of these spiderlings inside the egg sac are
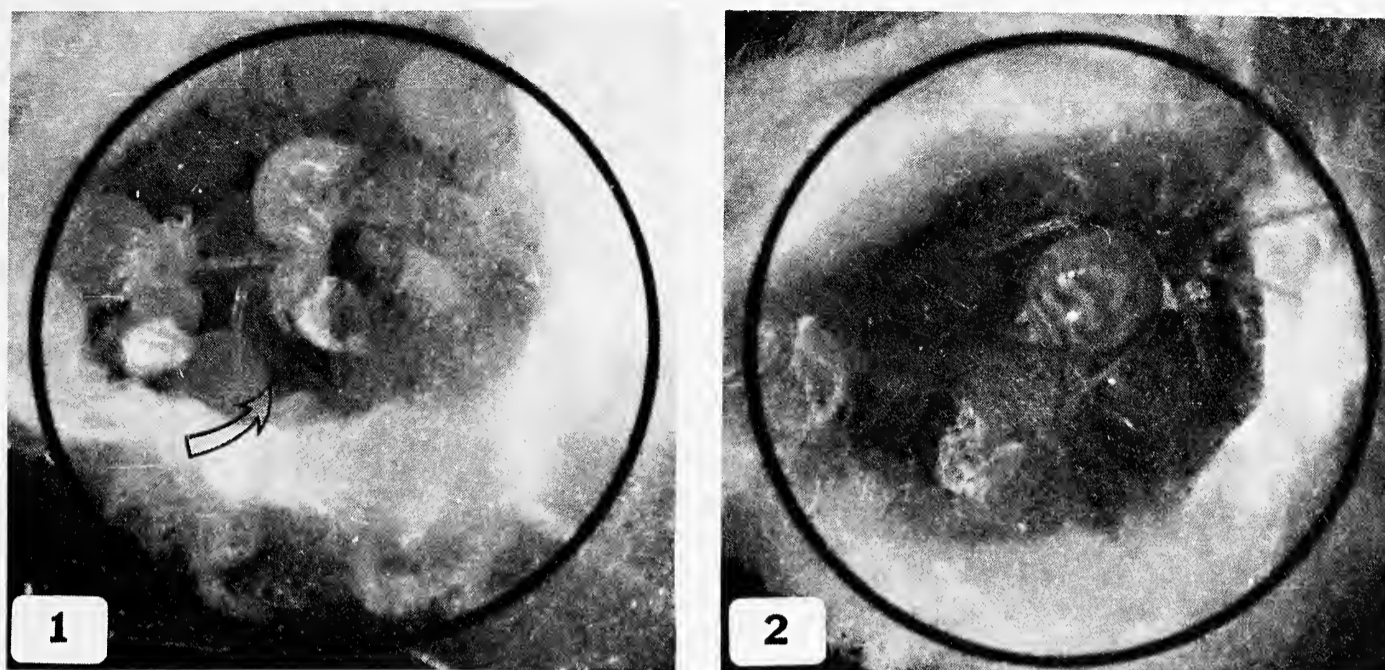
Figs. 1-2.—First nymphs of *Tegenaria saeva* inside the egg sac: 1, two days after molting, a nymph is feeding on an egg (arrow); 2, four days after molting, note the more bulky opisthosomae because of egg feeding. The circle is 5 mm in diameter.

summarized as follows: A) There is a close synchronization between individuals for the eclosion, and later for the first molt. B) The motility of the larvae is highly reduced in comparison to that of the nymphs. C) The nymphs can feed repeatedly on eggs from the day after they undergo the first molt. D) An egg is not consumed all at once, but progressively. In the majority of these cases, the egg is consumed completely; only the chorion, which looks like a deflated ball, is left. The increase in the volume of the opisthosoma is then clearly noticeable (Figures 1 and 2). E) No aggressive act of behavior was observed, either among the nymphs or the larvae. F) In the majority of these cases (153) the nymphs molted the second time without any additional food.

DISCUSSION

The enlarged opisthosomae of 15 individuals of *Tegenaria* sp. made me suspect a case of egg feeding. Forster (1977) observed that in salticid spiderlings, any reinforcement in feeding results in the reduction in length of the first nymphal instar. So the accelerated rate of development of the same 15 individuals of *Tegenaria* sp. is a further evidence to assume that they fed on eggs. Therefore in this species the proportion of egg feeding detected is 4.2% of the total number of eclosed spiderlings. The egg feeding directly observed in several individuals of *T. saeva,* the similarity in size in all the survivors at emergence, and the fact that a great number of survivors molted the second time without having any additional food, permit me to state that all of them fed on eggs. So in this species, the proportion of egg feeding is 97.6% for all the eclosed spiderlings; this value differs greatly from that found in *Tegenaria* sp.

I can tell that the cases reported here are of spiderlings that fed on inviable eggs and not on other spiderlings because: A) the nymphs tolerated one another while they were feeding on the eggs, I saw no instance of aggression between them, and the small number of spiderlings that died before the emergence is proof that this should be rare; B) the *Tegenaria* spiderlings become capable of feeding at the first nymphal stage, the larvae being too immobile to do it; C) The reduced

motility of the larvae make them probably subjects of cannibalism by the nymphs, but the synchronized development prevents this, and allows only the inviable eggs (when these are present in the egg sac) as food for the nymphs.

Thus the difference in the percentages of egg feeding between the two species is due in all probability to the proportion of inviable eggs which the female deposits in the egg sac. So in *Tegenaria* sp. practically all of the eggs were viable, except those in one sac, whereas in each sac of *T. saeva* there was a proportion of inviable eggs sufficiently large enough for the nymphs to feed on before they emerged from the sac. In various species of spiders, it has been observed that the proportion of viable eggs drops in the last egg sacs of each female (Christenson, Wenzl and Legum 1979, Horner and Starks 1972, Jackson 1978). This might be the explanation for the single case of egg feeding detected in *Tegenaria* sp. It might further indicate that the presence of eggs (whether they be viable or not) is capable of evoking the egg feeding behavior in these nymphs.

Valerio (1974) demonstrated that egg feeding helps to prolong the survival of the first nymphs. Thus, egg sacs with a higher proportion of inviable eggs have a higher probability of egg feeding; though their rate of eclosion is diminished; the possibilities of survival for the emerged spiderlings are increased.

There seem to be two ways for optimizing the reproduction as a function of the number of viable and inviable eggs in each sac. In one case, the vitellum produced by the female is used to produce the largest number possible of spiderlings (as in *Tegenaria* sp.). On the other hand the vitellum is used to produce stronger individuals, but in smaller numbers (as in *T. saeva*). What determines the predominating way in each species? I believe the answer lies on the particular life cycle and the characteristics of the habitat of each species.

In *Tegenaria* sp. the females make their egg sacs from November to March, whereas *T. saeva* does so from September to December. In the habitat of the first species potential prey are abundant during the whole year, but for the second species potential prey become scarce in the autumn, precisely when the spiderlings emerge. The females of *T. saeva* must then spend part of their reproductive potential in inviable eggs so that a small number of nymphs develop enough to survive the winter season, when the potential prey have practically disappeared and the weather is unsuitable for active life. Because the *Tegenaria* sp. nymphs do not have to face the scarcity of prey (neither at the moment of emergence nor later), it is more profitable for the females of this species to produce the highest number of nymphs possible. Thus each species optimizes the use of its own resources (vitellum produced) in function of its possibilities to exploit the resources of its habitat (potential prey).

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BALLOONING METHODOLOGY: EQUATIONS FOR ESTIMATING MASSES OF STICKY-TRAPPED SPIDERS

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ABSTRACT

Most empirical studies of spider ballooning use sticky traps to sample the aeronaut fauna. Once the animals are removed from the adhesive and passed through solvents into preservative, biologically meaningful masses cannot be determined directly. We use simple linear regressions to describe relationships between live masses of wild-caught animals and a volume estimate which treats the spider as a cylindrical solid with diameter equal to the mean of greatest carapace and abdomen width and height equal to total length. Of regressions for six families studied in detail, the slope for tetragnathids differs significantly from those for all but one of the other five. Pair-wise comparisons of slopes for the five non-tetragnathid families show no statistically significant differences. We therefore present two linear regression equations, one for tetragnathids and other similar-shaped spiders, and the other for "typical" (all other) spiders. Limited data from one species each of pisaurid and linyphiid are statistically indistinguishable from the "typical" regression but highly significantly different from the tetragnathid regression, lending added support to a dichotomy in shape between tetragnathids and other spiders. Simple linear regressions of mass on the volume estimate tend to explain more of the variation in mass than traditional power functions of mass on measurements of single body dimensions.

INTRODUCTION

Ballooning (aerial dispersal) in spiders is a dramatic and widespread phenomenon. Although a fair amount is known about the taxonomic composition, seasonal occurrence, and reproductive maturity of aeronauts, nothing has been published on their mass frequency distributions. The masses of ballooning spiders are of fundamental interest since one wonders how massive a flightless animal can be and still be passively carried by the wind. The masses of ballooners also have profound biogeographic implications, since, within a species, larger (more massive) animals will have higher reproductive value and hence higher colonizing potential (MacArthur and Wilson 1967). By the same token certain species may have very low colonizing potential because they are larger as adults and can only balloon at very early stages when reproductive value is low.

The most desirable way to sample the aeronaut fauna would be with continuously operating suction traps (Taylor 1974), which can be calibrated to give absolute estimates of aerial density. However they are expensive and require the availability of electricity. This has led most workers to use sticky traps of one form or another (Duffey 1956, van Wingerden and Vugts 1974, Yeargan 1975). Of course after a spider has been removed from the trap and placed in one or more solvents to remove the adhesive and preserve it, direct measurements of mass are meaningless. The present study was undertaken to develop methods to estimate the live masses of spiders collected from sticky traps.

Live spiders were collected from late may to late July in a variety of habitats in North Central Missouri, viz., the Tucker Preserve (native tall grass prairie), The University of Missouri Ashland Wildlife Area (mixed hardwood forest understory and woodland clearings), The University of Missouri, Columbia campus (ornamental shrubs), the U.S. Department of Agriculture, Biological Control of Insects Research Laboratory study plot (alfalfa), and the University of Missouri South Farms (soybeans). With the exception of Tucker Prairie, which is in Callaway County, all localities are in Boone County. Spiders were separated from vegetation by sweeping, beating or aspiration, dumped in a sleeve cage or on a drop cloth for sorting and placed in individual shell vials. The live spiders were transported in a styrofoam chest to the laboratory where they were weighted to the nearest 0.1 mg in a tared gelatin capsule on a Mettler AE 160 electronic balance. After weighing they were killed and preserved in 70% ethanol.

A few days later the following three measurements were made on each animal to the nearest 0.05 mm, using a wild M5 stereo microscope with ocular micrometer at 120 x magnification: total length, greatest width of cephalothorax, and greatest width of abdomen. An estimate of each spider's volume was obtained by treating it as a cylindrical solid having radius equal to half the mean of the two width measurements and height equal to total length, i.e.

$$\text{Volume} = (\text{Total length}) \, \pi \, [(\text{Width Abd} + \text{Width Ceph})/4]^2$$

Assuming further that the density of material is homogeneous throughout a spider's body and fixed regardless of absolute mass, we expected to find a linear relationship between the measured mass and estimated volume.

Because spiders are not perfectly cylindrical we expected families to show different mass-volume relationships. In particular we expected to find significant differences among the tetragnathids, which are most nearly cylindrical, the thomisids (in the broad sense, including philodromids) which tend to be flattened dorsoventrally, and most other families, whose members can be idealized as two more or less overlapping subspherical pieces. Only animals less than 20 mg in mass were studied because more massive animal were not expected to be common ballooners.

RESULTS AND DISCUSSION

The raw data for eight families are presented in Fig. 1. Sample sizes and least squares regression parameters are presented in Table 1. All are highly significant (p < 0.01). The data were subjected to Bartlett's Test for Homogeneity of
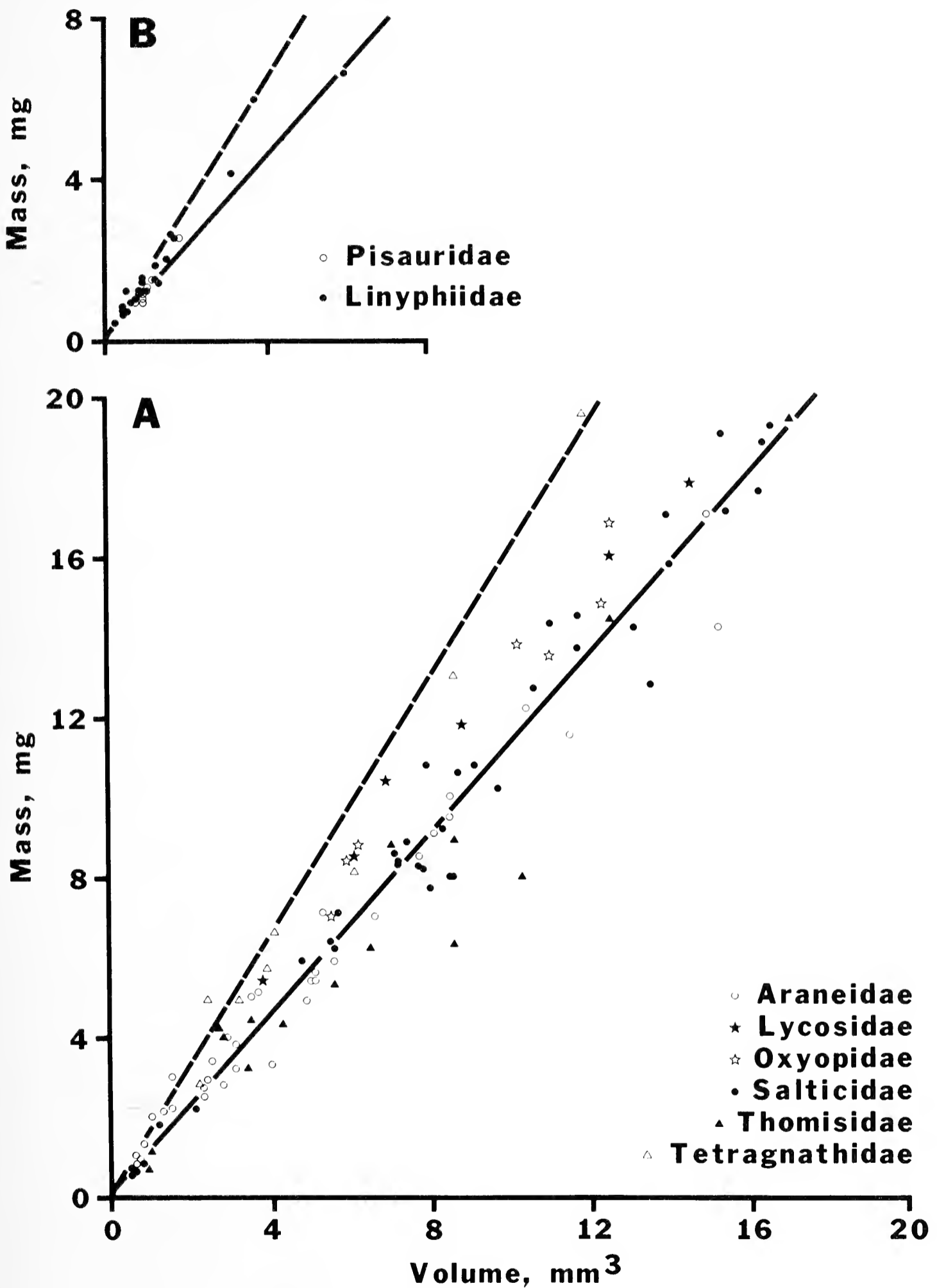
Fig. 1.—Raw data and regressions for mass-volume relationships: A, Tetragnathidae (dashed line) and combined data for the remaining five families (solid line); B, Raw data for the Lyniphiidae and Pisauridae (lines in Fig. 1A).

Table 1.—Individual regression parameters. V = linear regression of mass on volume, C = power curve of mass versus cephalothroax width, TL = power curve of mass versus total length, N = sample size, a = regression intercept, b = regression slope, R^2 = coefficient of determination.

Family	N	a_v	b_v	R^2_v	R^2_c	R^2_{TL}
Lycosidae	6	1.69	1.14	0.99	0.30	0.99
Salticide	37	−0.01	1.14	0.97	0.91	0.76
Araneidae	36	0.55	1.02	0.97	0.84	0.89
Oxyopidae	7	1.14	1.17	0.97	0.16	0.58
Tetragnathide	8	0.31	1.61	0.98	0.74	0.90
Thomisidae	15	−0.01	1.05	0.92	0.92	0.97
Pisauride	8	−0.33	1.57	0.97	0.75	0.82
Linyphiide	28	0.26	1.20	0.94	0.52	0.92

Variance (Sokal and Rohlf 1969) and found to be significantly heterogeneous (X^2_7 = 62.159, p < 0.001) prohibiting overall parametric analysis. Inspection of Fig. 1 suggests that this result was due to the smaller range of variation exhibited by the pisaurids (comprising eight *Pisaurina* spiderling) and the linyphiids (comprising only individuals of the single species *Frontinella pyramitela*). When only the remaining six families data are subjected to Bartlett's Test there is no evidence of significant heterogeneity of variances (X_5 = 3.848, p > 0.5), permitting an analysis of Covariance (Snedecor and Cochran 1967) to test the hypothesis of no differences among mass-volume regressions. This revealed highly significant differences among slopes ($F_{5, 97}$ = 3.339, p < 0.01). In order to determine where these differences lie, all possible pair-wise t-tests on slopes were performed. The method of Bonferroni (Morrison 1983) was used to derive the critical value for an overall error rate error less than 0.05. Results of these tests are presented in Table 2. As expected the tetragnathids differ significantly from most of the other families (the sole exception was the Oxyopidae, with 0.05 < p < 0.10). However the thomisids do not differ significantly from the other families, owing perhaps to their higher variance (See Fig. 1 and the R^2's in Table 1), i.e. to their failure to conform as well to the assumptions of the mass-volume model. Given these data, we suggest that workers wishing to estimate the masses of preserved spiders may do so by using the cylindrical approximation to volume as the independent variable for one of two regressions. If the animal is a tetragnathid, use:

Mass(in mg) = 1.61 (volume in mm³) + 0.31   (see Table 1 and Fig 1A)

(We predict that other patently cylindrical spiders, such as *Tibellus* and *Larinia* spp. which were not collected in this study, will also fit this model). The following

Table 2.—t values and levels of significance for pair-wise t-tests on slopes. Levels of significance are coded as n.s. (>0.1) and * (<0.05). See text for explanation.

	Salticidae	Araneidae	Oxyopidae	Tetragnathide	Thomisidae
Lycosidae	−0.034, n.s.	1.444, n.s.	0.292, n.s.	−3.760, *	0.544, n.s.
Salticidae	—	2.615, n.s.	−0.244, n.s.	4.363, *	1.213, n.s.
Araneidae	—	—	−1.542, n.s.	6.710, *	−0.428, n.s.
Oxyopidae	—	—	—	−3.014, n.s.	0.6541, n.s.
Tetragnathidae	—	—	—	—	3.450, *
Thomisidae	—	—	—	—	—

overall regression for all other families, which could be considered as having "typical" shape, was derived by combining the data from the non-tetragnathid families in Fig. 1A:

$$\text{Mass (in mg)} = 1.12 \text{ (volume in mm}^3) + 0.23$$

The utility of these equations, and particularly the assumption that all spiders besides tetragnathids and their look-alikes are essentially the same shape and homogeneous with respect to density, will be determined with time. As a partial test we offer the "goodness of fit" of the pisaurid and linyphiid data, which have lower variance than the other six families but show an obvious linear relationship between mass and volume (Fig. 1B), to the two regressions. Lines of least squares are fit such that half the points lie above and half lie below the line. If pisaurids and linyphiids are shaped like "typical" spiders, then the proportion of points lying above (and below) the "typical" regression line should not differ significantly from 0.5, whereas the proportions of points and below the tetragnathid line *should* differ significantly from 0.5. The numbers of points on each side of both lines for both regressions in each family are given in Table 3. The proportions of points above or below the "typical" regression line do not differ significantly form 0.5 using the Binomial Test (Siegel 1956) ($p > 0.29$ and $p > 0.34$, pisaurids and linyphiids, respectively) but are highly significantly different from 0.5 for the tetragnathid regression ($p < 0.008$ and $p < 0.0001$, respectively), supporting our contention that the linyphiids and pisaurids have a "typical" spider shape different from that of tetragnathids.

The most commonly used index of size for spiders has been cephalothorax width. It is a logical index of instar, since as a single sclerotized plate the carapace is not apt to change its dimensions very much during the instar (see Hagstrum 1971 and references cited therein). On the other hand it cannot be expected to be a good indicator of mass, which can vary widely within an instar due to nutritional and reproductive state. Breymeyer (1967) used simple linear regression and Sage (1982) used step-wise linear regression to derive a relationship between mass and total length. Rogers et al. (1977) found that a power function gave the best fit for the total length vs. mass relationship for spiders. In Table 1 we present the coefficients of determination for the simple linear regressions of mass on volume (V) and for the power curves of mass on cephalothorax width (C) and mass on total length (TL), for each family. The simple linear regression of mass on volume is clearly a better description of the relationship than either power curve in most cases. An alternative approach is to take the oven-dried weight of the spider after removal from the trap and apply a conversion factor (S. E. Riechert, pers. commun.). This is less time-consuming but not useful if one wishes to save the specimen for identification.

Table 3.—Numbers of pisaurid and linyphiid points lying above (+) and below (−) calculated overall and tetragnathid regression lines.

| | Overall Regression | | Tetragnathid Regression | |
	+	−	+	−
Pisauridae	2	6	0	8
Linyphiidae	16	12	1	27

As Table I shows, an estimate of volume will tend to be a more accurate predictor of mass than a single linear measurement. The method presented here is tedious but accurate. A logical extension of our technique would be to determine the frontal sectional area of the image of the spider by projecting the surface of a digitizing tablet into the microscope field with a drawing tube. This area estimate could then be rotated by an appropriate algorithm in a microcomputer to produce a spider-shaped, rather than a cylindrical, estimate of the volume.

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PREDATORY BEHAVIOR OF SPITTING SPIDERS (ARANEAE: SCYTODIDAE) AND THE EVOLUTION OF PREY WRAPPING[1]

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ABSTRACT

The predatory behavior of the spitting spider *Scytodes* sp. was studied in the laboratory, and an ethogram of the predatory behavior was developed. The principal components usually occur in the order: tapping, spitting, biting, wrapping, feeding. Spitting results in a pair of sticky, zig-zag, transverse bands which pin the prey to the substrate. At the capture site scytodids wrap the prey using the typical form seen in the "higher" spiders: the spider holds the prey in both third legs and alternates the use of right and left fourth legs in applying silk. Prey are eaten at the capture site.

A comparison of prey wrapping by spiders in primitive aerial-web building species with that used by typically "vagrant" species which forage on elevated substrates shows two very different forms of prey wrapping. We argue that prey wrapping at the capture site is an early adaptation of spider radiation into the aerial niche based on the presence of one form or the other in most taxa foraging above ground. Further, the extreme similarity of form of prey wrapping in "higher" spiders which build aerial webs is indicative of a stronger selective pressure for efficient prey handling than for actual prey capture behavior or web geometry.

INTRODUCTION

Spiders of the genus *Scytodes* (Latreille) have the curious behavior of ejecting a mucilagenous glue from the chelicerae at their prey during attack (Monterosso 1927, 1928, Kovoor and Zylberberg 1972) or at predators in self-defense (McAlister 1960, Gilbert and Rayor 1983). Although these spiders are considered primitive on the basis of web structure and several morphological characters (Lehtinen 1967), several aspects of their use of silk during predatory behavior are analogous with those of aerial-web building spider taxa with more advanced characteristics. We examined these behaviors in an undescribed species of *Scytodes* in order to make inferences about the evolutionary stages in the transition from ground-dwelling to aerial-web weaving.

The evolution of web-building spiders from primitive vagrant ancestors to species using silken aerial webs has been the focus of many studies (Kaston 1964,

1966, Robinson 1975). It is generally agreed that early aerial webs were derived from an accumulation of draglines around the spider's resting place or retreat. Selective pressures for more efficient prey capture favored the construction of more elaborate, structured, and sticky webs.

As spiders radiated into the aerial niche they faced different selective pressures on the mechanics of prey capture. Prey immobilized on an aerial web can fall to the ground and be lost if the spider loses contact with it. Most aerial spiders wrap their prey during predation. Wrapping serves, among other functions, to sequester the prey and frees a spider from the necessity of eating its prey immediately. A further evolution in the use of prey wrapping has moved this behavior from late to earlier in an attack sequence. In situations when struggling prey could injure a spider as it approaches to bite the prey or when its struggles could allow it to escape quickly, many spiders first wrap the prey in silk to immobilize it, then approach and bite (Robinson and Robinson 1976). This method of prey immobilization is obligatory in cribellate orb-weavers of the family Uloboridae in which the poison glands are absent (Marples 1962).

Because *Scytodes* possesses several primitive morphological characteristics, yet builds an aerial web, we consider that our observations on its predatory contribute insight into possible stages in the transition from living on the ground to aerial habits.

MATERIALS AND METHODS

Spiders of a currently undescribed species in the genus *Scytodes* were collected from under picnic shelter eaves and around stones at two Texas localities: Lake Corpus Christi, San Patricio Co., and Tyler State Park, Smith Co. Voucher specimens are deposited in the American Museum of Natural History and Museo de Zoologia, Universidad de Costa Rica. The spiders were transported to Lawrence, Kansas, and housed individually in clear plastic boxes, 11 x 11 x 3 cm high, each supplied with a cotton-stoppered vial of water. The temperature was 25°C and the light cycle was irregular, but approximately L:D, 14:10. Prey were principally vestigial-winged fruit flies, *Drosophila melanogaster* (Meig.). However, cockroach nymphs (Blattaria), lacewings (Neuroptera), and small moths (Lepidoptera) were occasionally presented as well. A second generation box design employed a cork-stoppered hole through which prey were delivered singly or in groups of three to ten individuals. Subsequent predatory behavior was directly observed with (usually) two observers reporting their observations into a tape recorder. The tapes were later transcribed and the data analyzed as detailed below. After the conclusion of the sequence, the pattern of spit was observed through a binocular microscope equipped with an ocular micrometer, then sketched.

From observations of more than 70 predation attempts on a variety of prey by 15 spiders (males, females, and late juvenile instars) we developed an ethogram of the components of predatory behavior. Complete predation sequences (N = 31, 8 individuals) were then described in terms of the defined behavioral components. Durations were not recorded. The principal behaviors were serially ordered for analysis and a particular component could not follow itself in

successive acts in a sequence. The components were then put into a first-order transition matrix and transition frequencies calculated. This procedure was performed for each capture sequence of each spider. Individual results were compared and no major differences were observed between the sexes or instars. Data from all sequences were summed into one transition matrix and displayed graphically as a flow diagram.

RESULTS

Twelve behaviors comprise the ethogram of predatory behavior for *Scytodes* sp.

Alert posture.—*Structures used:* Entire body. *Action:* Space-filling posture with spider "up" on its legs. Much extension at all joints. *Context:* When walking about or just after prey contacts web lines.

Retracted posture.—*Structures used:* Entire body. *Action:* Spider appears dorsoventrally compressed in one plane. All the legs are held at the sides of the body in typical latigrade position, i.e. the femora are directed posteriorly and the more distal segments directed anteriorly. *Context:* Diurnal resting or defensive posture.

Tap.—*Structures used:* Legs I (or II). *Action:* Leg is extended, metatarsus and tarsus then flex and re-extend. Contralateral legs alternate in tapping. *Context:* Initial localization of prey after it has touched the web or spider.

Spit.—*Structures used:* Chelicerae. *Action:* Spider is in slightly elevated posture by leg extension. Spitting is accompanied by a convulsive shudder and slight posterior movement of the body. Multiple spits occasionally occur. *Context:* After prey has been contacted and is roughly positioned between extended legs I and the spider's body.

Reach and Roll (RR).—*Structures used:* Legs I (or II). *Action:* Leg is extended, then tibia, metatarsus, and tarsus are flexed and slightly retracted, then elevated and re-extended. The movement describes a circular motion with contralateral legs moving in unison. *Context:* Immediately after spitting, RR is performed distal or lateral to prey and serves to entangle it in the drying spit. It may also help to localize the prey.

Bite.—*Structures used:* Chelicerae and pedipalpi. *Action:* Pedipalpi are extended as in PALP EX. As they palpate the prey and a suitable surface is found (e.g. an appendage) the spider leans forward and bites the prey with the chelicerae. *Context:* Occurs after spitting and as the prey is cut from the spit or during wrapping.

Nibbling.—*Structures used:* Chelicerae, pedipalpi, and legs I (or II). *Action:* Distal leg segments (metatarsi or tarsi) are brought to the mouth and held there by pedipalpi. Leg is pulled out dorsally as the chelicerae nibble proximo-distally. *Context:* After RR the same legs are nibbled as were used in RR. This behavior appears homologous with nibbling seen during grooming.

Pedipalp Reciprocal Scraping (RECIP).—*Structures used:* Pedipalpi and chelicerae. *Action:* Pedipalpi scrape ipsi- or contra- lateral chelicera then scrape against one another. *Context:* Often follows nibbling and cleans dried spit from the chelicerae. It also occurs during grooming.

Pedipalp extension (PALP EX).—*Structures used:* Pedipalpi, legs I (or II), and chelicerae. *Action:* Both pedipalpi are extended with slight lateral oscillation toward a thread (dried spit or silk) held by a leg. A single pedipalp pulls the thread to the chelicerae which cut it. *Context:* Freeing the prey from the substrate by cutting the dried spit around it.

Hind leg wrap (HLW).—*Structures used:* Legs IV. *Action:* Legs alternate wiping spinnerets. Each wipe is accompanied by a lateral movement of the abdomen toward the leg which pulls silk from the spinnerets and places it around the prey which is held by legs III. *Context:* After partially or completely freeing the prey from the substrate, the prey is bound into a silk package.

Dragline attachment (DGL).—*Structures used:* Spinnerets and legs IV. *Action:* Abdomen flexed toward the surface to which attachment disc is applied. When the surface is a web line it is pulled to the spinnerets with either leg IV. *Context:* 1. Disc is applied to substrate or web line upon initial contact of prey to spider or web. 2. During wrapping, especially near completion, discs are applied to the prey package, the substrate, web lines, or several of these structures.

Feed.—*Structures used:* Chelicerae and pedipalpi. *Action:* Prey is bitten with the chelicerae and held against the mouth with the pedipalpi. *Context:* At the conclusion of the predation sequence.

Typical prey capture is similar to that reported by Monterosso (1927, 1928) for *Scytodes thoracica* (Latr.). When prey first contacts the web lines or spider's legs, the spider assumes an alert posture and usually fastens its dragline to the substrate with its abdomen or to a web thread using its abdomen occasionally aided by a leg IV. The spider then orients toward the prey and approaches it slowly, tapping with legs I, occasionally touching the prey. When the prey is approximately centered between the forelegs and the spider, it spits a net of glue at the prey (Fig. 1). The spider steps quickly to the prey; we seldom observed the leisurely saunter reported by Gertsch (1979:222). As it approaches the prey, the spider uses legs I and sometimes II in the RR motion which further entangles the prey in the rapidly drying glue. The spider infrequently spits a second time. As the spit dries on the immobilized prey, the spider palpates and bites the prey, usually on an appendage. At this point the spider alternately nibbles legs I and II with the chelicerae. This behavior is similar to nibbling of the legs observed in grooming. After nibbling, the spider begins to free the immobilized prey from the net of spit. If the prey is not securely fastened, the spider simply bites it with the chelicerae and pushes down on the substrate with all eight legs, thus pulling the prey free from the net of spit. With more securely fastened prey the spider cuts through the securing threads around the prey by drawing them to its chelicerae using the pedipalps (PALP EX) and legs I and II. Once prey is freed or has only one side attached to the substrate the spider begins to wrap the prey.

The form of scytodid hind-leg wrapping is analogous to that of araneids, theridiids, and other spiders (e.g., Robinson 1975, Eberhard 1982, for further references see DISCUSSION). The prey is held with the short legs III, while legs IV alternate in distributing loops of silk, stripped from the spinnerets, over the prey. Occasionally one leg wraps several (3-5) loops over the prey before the opposite leg is used. During wrapping the abdominal apex repeatedly waggles from side-to-side toward the leg which will apply the next loop of silk. In *Scytodes* the strands of silk are fine and we could not determine whether strands
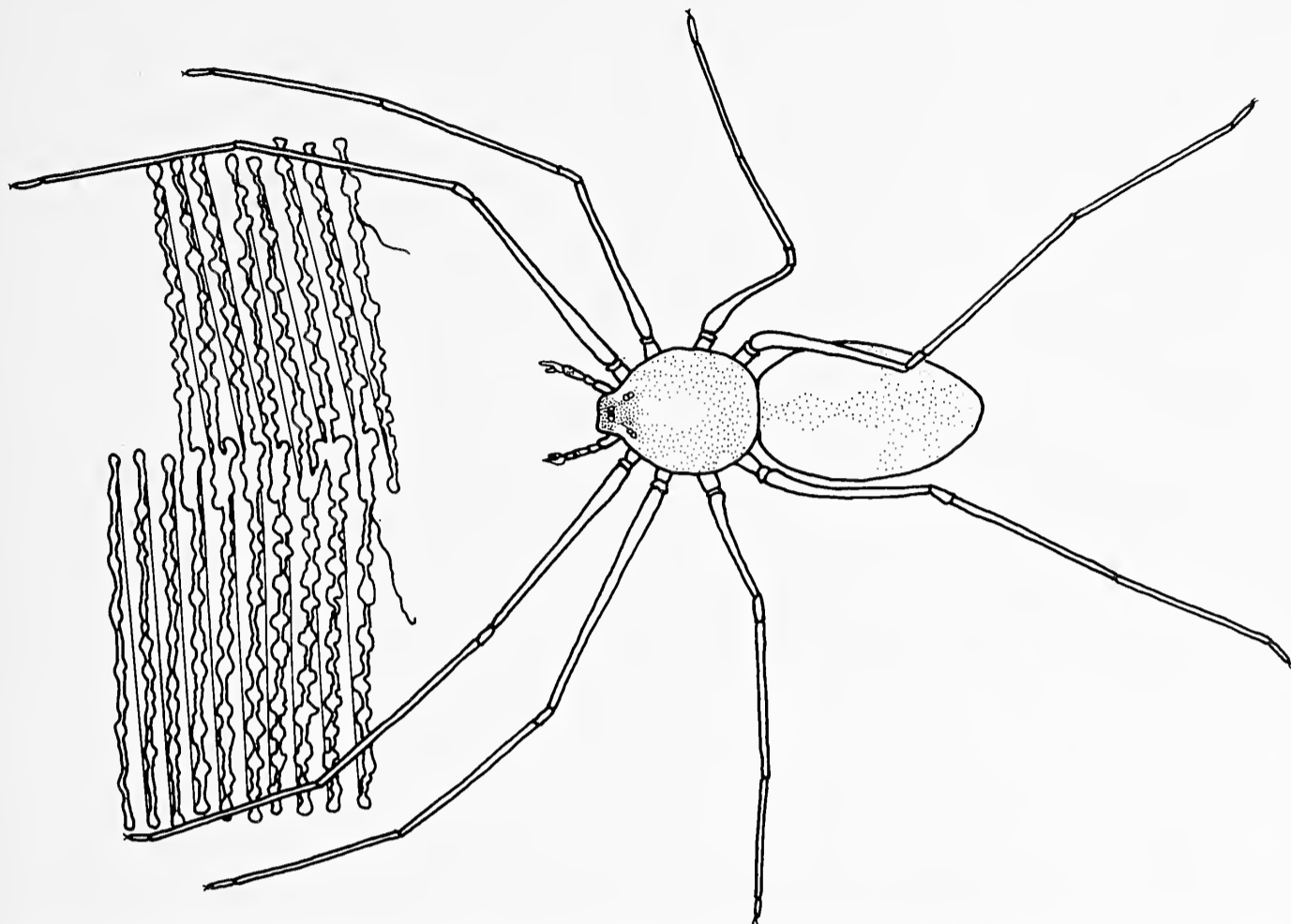
Fig. 1.—Dorsal view of *Scytodes* sp. to show the orientation of the spider and its spit immediately after spitting. Prey has been omitted for clarity.

were composed of multiple fibers. Nor could we determine from which spinnerets the silk was pulled. The strands are definitely not the swathing bands seen in *Argiope* Audouin and some other araneid genera (Robinson, Mirick and Turner 1969). The spider punctuates its wrapping by placing dragline attachment discs on the prey, the substrate, or the threads which the spider is contacting. Finally the spider holds the trussed prey in its chelicerae and begins to feed. Occasionally the spider carries the prey a short distance, but feeding generally occurs at the capture site. It is possible that the observed feeding at the capture site was an artifact of the small cages. One of us (LSR) has observed predation by *Scytodes longipes* Lucas in Costa Rica where it is found in association with human dwellings. *Scytodes longipes* typically bites its prey (in one case, a wolf spider twice its body size) and wraps it at the capture site, then carries it to its retreat before feeding.

Localization of the prey by tapping occurred prior to spitting (Fig. 2). Vision does not appear to play a role in prey localization. Prey were almost always bitten at least once before being wrapped. If prey continued to struggle, biting occurred intermittently with wrapping. A long period of feeding terminated a sequence. The sequence is not stereotyped even for the same individual capturing the same type of prey. There is variability in the number of acts per capture and in the components used. The mean number of acts per capture sequence is 19.5; the range in this study is 3 - 97. The lower bound is close to the minimum given the resolution of our component descriptions. A shorter sequence could be BITE-FEED, but this was never observed even for prey much smaller than the spider.
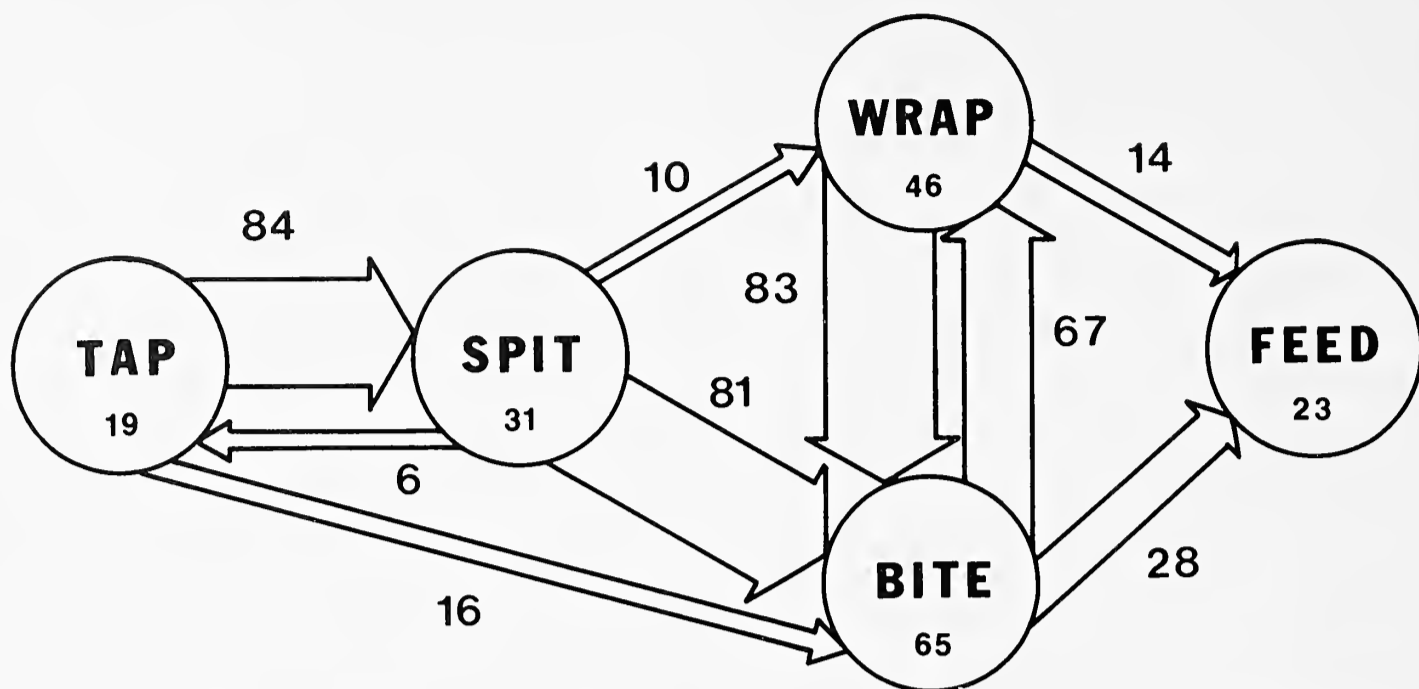
Fig. 2.—Predatory sequence of *Scytodes* sp. Main components are represented by circles; numbers within the circles are the number of occurrences of the behavior in the data set analyzed. The numbers beside the arrows and the width of the arrows represent the percentage of transitions in which a behavior was followed by the next. Transition percentages smaller than 4% have been omitted for clarity.

The upper limit may depend entirely upon the prey item. The 97 acts were used to subdue a pyralid moth 30% longer than the spider. In nature it is possible that even relatively larger prey are caught and require more acts to subdue.

Another source of variability in the predatory behavior is in the component composition of the sequence. Obviously, all the behavioral components listed in the ethogram cannot be present in a sequence of fewer acts. However, even several of the longer capture sequences did not display all behavioral components listed. We could not discern any systematic relationship between prey size and the extent of or position of wrapping in the sequence, although few large prey items were offered.

DISCUSSION

Prey capture by *Scytodes.*—Though our report of predation in this species of *Scytodes* agrees with previous general accounts, it differs significantly in one respect from the thorough study of *Scytodes thoracica* by Dabelow (1958) (see also Schaller 1956 and Kaestner 1963). The net of spit observed in *S. thoracica* reportedly consists of a single block oriented so that the parallel bands are parallel to the spiders's longitudinal axis. In the *Scytodes* sp. used in the present study, although the net itself is similar to that of *S. thoracica,* the parallel bands are perpendicular to the spider's longitudinal axis (Fig. 2). Further, the net seems always to consist of two discrete, yet often overlapping blocks of spit each composed of 5 - 17 parallel bands (mean = 10, N = 8). Typically the left and right blocks are composed of unequal numbers of bands. Similar orientations have been observed in *S. intricata* Banks (McAlister 1960), *S. venusta* (Thorell), *S. longipes* (= *marmorata* L.K.), and *S. fusca* Walkn. (= *domestica* Dol.) (Bristowe 1931).

Two other genera have recently been included in the family Scytodidae: *Drymusa* Simon and *Loxosceles* Heinecken and Lowe (Gertsch 1967, but see Gertsch and Ennik 1983). *Drymusa dinora* Valerio has not been observed to use spit during prey capture (Valerio 1974). *Loxosceles* has perhaps been observed to spit, for Kaestner (1963:579) says, "*Loxosceles* Lowe, greift aus viel geringerem Abstand als *Scytodes* durch Speien von Leim aus den Cheliceren an und erzeugt dabei viel weniger regelmassig angeordnete sehr zarte Faden." However numerous other authors (Hite et al. 1966, Kaston 1972, Gertsch 1979, Foelix 1982) did not report spitting in *Loxosceles,* and this agrees with our own observations of *L. reclusa* Gertsch and Muliak and *Loxosceles* sp. made with the help of a binocular microscope.

Although the actual components of predation differ among taxa, the form of these behaviors in *Scytodes* sp. are analogous to those reported in predation of many other labidognath spiders with one exception, the component termed reach-and-roll. This maneuver, performed with both legs I and occasionally legs II serves to entangle the prey in the drying spit. Further, the spider may be applying additional fine strands of spit with its legs as it alternates between reach-and-roll and nibbling during the pre-bite portion of the sequence.

Comparative prey wrapping.—Given the present understanding of the use of silk in the predatory behavior of *Scytodes,* the remainder of the discussion will focus on the evolution of prey wrapping as an adaptation accompanying the use of aerial webs. Primitive ground-dwelling spiders, such as liphistiomorphs, do not build trapping snares and do not wrap their prey (Bristowe 1976), whereas spiders in more derived groups with aerial snares or elevated cursorial habits do exhibit prey wrapping. This difference leads to the inference that prey wrapping is an adaptive response to the increased chance of losing contact with prey in an aerial habitat.

Descriptions of the predatory behavior of "vagrant" spiders which capture prey in an elevated setting support this interpretation (Table 1). In a study of spiders of four species in the family Lycosidae, Greenquist and Rovner (1976) reported that individuals of the ground-dwelling genus *Schizocosa* Chamberlin never wrapped their prey. On the other hand, individuals of *Lycosa punctulata* Hentz and *L. rabida* Walckenaer which spend significantly more time foraging on elevated foliage exhibit post-immobilization prey wrapping at the capture site. The spider immobilizes the prey with a bite then circles it and applies silk directly from the spinnerets. We designate this as the 'primitive' prey wrapping form. This method is equally efficient on the ground or on elevated substrates. In our view, it represents a form of prey wrapping that is adaptive for above ground prey retention, not just specifically adapted to use with aerial webs. Similar forms of circular prey wrapping, occasionally involving the application of silk by legs IV, have been reported for at least one species in the following, primarily vagrant, families: Theraphosidae (M. Teeter pers. comm.), Lycosidae (Rovner and Knost 1974, Greenquist and Rovner 1976) Gnaphosidae and Hersiliidae (Bristowe 1930), Uroctiidae (Crome 1937), Oecobiidae (Glatz 1967), Psechridae (Robinson and Lubin 1979), Theridiidae (Carico 1978), and Ctenidae (Melchers 1967).

Spiders which employ aerial capture webs tend to use a second form of prey wrapping which we designate as 'derived.' The spider hangs from its web and using legs IV applies silk to the prey which may be in contact with the spider, the web, or both. This method has been reported for species in the families:

Table 1.—Summary of capture and wrapping elements of predatory behavior of spider taxa at different stages in the evolution of prey wrapping. See text for details of elements.

Taxon	Web Structure	Method of Immobilization	Wrapping Location	Wrapping Form	Feeding Location	Source
Hypochilus gertschi (Hypochilidae)	Aerial inverted funnel	Bite	No Wrapping		Capture site	Shear 1969
Lycosa rabida *L. punctulata* (Lycosidae)	Elevated capture (no web)	Bite	Capture site	Primitive	Capture site	Greenquist and Rovner 1976
Fecenia angustata (Psechridae)	Aerial inverted funnel/ planar	Bite	Capture site	Primitive	Retreat	Robinson and Lubin 1979
Diguetia albolineata (Diguetidae)	Aerial inverted funnel	Bite	Retreat	Unique	Retreat	Eberhard 1974
Drymusa dinora (Scytodidae)	Aerial space-filling	Bite	Capture site	Primitive	Removed from capture site	Valerio 1974
Scytodes sp. (Scytodidae)	Aerial space-filling	Bite	Capture site	Derived	Capture site	Present study
Modisimus spp. (Pholcidae)	Aerial space-filling	Wrap	Capture site	Derived	Retreat	Eberhard and Briceño 1976

Diguetidae and Linyphiidae (Eberhard 1967), Theridiidae (Kaston 1965), Araneidae (Robinson 1975), Theridiosomatidae and Uloboridae (Eberhard 1982), Pholcidae (Eberhard and Briceño 1983), and Scyotdidae (present study).

There is relatively little variation in the derived form of prey wrapping employed by morphologically and phylogenetically diverse taxa. This is in contrast to the enormous variation in predatory technique and to the great variation in web structure, from primitively unstructured to highly derived and secondarily reduced, in these same taxa. This similarity of form of prey wrapping, though convergent, leads us to speculate that once a taxon moves into the aerial niche there is a greater evolutionary premium associated with efficient prey handling than is associated with the actual method of prey capture or details of web structure. Thus selection has not only favored some form of prey wrapping by spiders when they capture prey above ground, but selection has tended to channelize the form of this behavior in those species well adapted to prey capture in an aerial habitat.

Examination of primitive aerial-web weavers may reflect the early steps in the evolution of prey wrapping. Predatory behavior has been described for several taxa (Table 1) in the group Filistatides (sensu Lehtinen 1967) which includes the

Hypochilomorpha and Haplogynae of other authors (Simon 1892, Petrunkevitch 1933, Platnick 1977, Brignoli 1978). The hypochilids are the most primitive taxon in this group, sharing many characters with orthognaths (Gertsch 1958, Marples 1968). *Hypochilus gertschi* Hoffmann does not wrap its prey, but merely bites the prey, pulls it through the web, and feeds at the capture site. This represents a very early stage in the evolution of aerial webs and prey wrapping.

A slightly more advanced stage may be represented by species in the cribellate family Psechridae. "The [phylogenetic] position of Psechridae is enigmatic." According to Lehtinen (1967:383) who considers them closer to his Amaurobiides than Filistatides. The family, as delimited by Forster and Wilton (1973), includes both terrestrial vagrant genera and aerial-web building genera such as *Fecenia* and *Psechrus*. *Fecenia augustata* (Thorell) immobilizes its prey by biting, then binds it to the web by applying silk directly from the spinnerets. After this primitive wrapping of the prey, it is cut from the web, carried in the chelicerae to the retreat, and eaten immediately or re-attached to the substrate.

The next stages may be represented by primitive aerial-web building haplogyne spiders. *Diguetia albolineata* (O. P.-Cambridge) (Diguetidae), also bites its prey and pulls it through the web, then transports it to the retreat where it is wrapped and eaten. The wrapping however, has a form unique to this species (Eberhard 1967:179) and may represent an independent response to the selective pressures favoring prey wrapping.

Drymusa dinora (Scytodidae) does not wrap small prey, but after immobilizing larger prey with a bite, the prey is wrapped at the capture site. The form of prey wrapping is similar to that used by *Fecenia* and spiders in "vagrant" taxa. *Drymusa* applies silk directly from the spinnerets while moving around the prey. The spider then carries it a short distance before feeding. The situation reported for *Scytodes* is different. The form of prey wrapping it uses is the typical derived form of hind-leg wrapping: alternate use of opposite legs IV in casting loops of silk over the prey.

The Pholcidae is the only other family of haplogyne aerial-web building spiders for which we are aware of detailed accounts of predatory behavior. Prey wrapping in this group is advanced both in form and in position in the predation sequence. *Modisimus* spp. wrap their prey at the capture site using the derived from. Wrapping is the first means of prey immobilization. Prey are then bitten, carried into the retreat, and eaten.

We agree with previous authors (e.g. Eberhard 1967, Robinson 1975, Lubin 1980) that the use of wrapping as the primary method of prey immobilization is the most derived use of the behavior. We suggest that because of the selective pressures on aerial prey capture, post-immobilization wrapping at the capture site was one of the earliest stages in the evolution of prey capture in aerial webs. Spider phylogeny is poorly understood and it is reasonable to assume that just as aerial webs have evolved several times (Lehtinen 1967, Kullman 1972), prey wrapping also may have evolved independently in many taxa as their members adapted to an aerial niche.

ACKNOWLEDGMENTS

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REDESCRIPTIONS OF SOME POORLY KNOWN SPECIES OF THE *NITIDULUS* GROUP OF THE GENUS *VAEJOVIS* (SCORPIONES, VAEJOVIDAE)

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ABSTRACT

The *nitidulus* group of *Vaejovis* is defined on the basis of pedipalp chela morphology and dentition, trichobothrial patterns, and carinal structure of the pedipalp chela and the metasoma. Five species are treated herein: *V. mexicanus decipiens* Hoffmann is elevated to specific status and transferred to the *nitidulus* group; *V. intermedius* Borelli, *V. nigrescens* Pocock, and *V. nitidulus* C. L. Koch are all considered valid species and redescribed; and *V. minckleyi* Williams is transferred to the group and a revised diagnosis given.

INTRODUCTION

Vaejovis C. L. Koch, 1836, with over 90 described species and subspecies, is the largest and most widespread genus of scorpions in North America. Through the years, a number of distinct species groups have been established, largely through the efforts of Williams (1970a, 1970b, 1971, 1980) and Soleglad (1972, 1973). Several of these groups are now recognized as valid genera (i.e., *Paruroctonus* Werner and *Paravaejovis* Williams; Williams 1970c, 1972). Currently, four species groups remain in the genus: the *eusthenura, mexicanus* (with the *minimus* subgroup), *punctipalpi,* and *wupatkiensis* groups. The purpose here is to provide a preliminary definition of a fifth group, the *nitidulus* group, and to clarify the status of five poorly understood taxa within it.

The most important features of the *nitidulus* group are: (1) the pedipalps are long and slender with chela length/palm width ratios greater than 3.3 (in most species, greater than 4.0); (2) the pedipalp chela fingers are long and tenuous, and

each terminates in an enlarged clawlike denticle bearing distally a distinct white patch; (3) chela trichobothria *ib* and *it* are located at the base of the fixed finger; (4) the pectinal teeth of the female are subequal in size, never with the proximal teeth enlarged; (5) the primary row of denticles on the chela fixed finger is divided into five, six or seven distinct subrows: (6) the dorsointernal carina of the pedipalp chela is the strongest and usually bears enlarged, sharp granules; and (7) the ventral submedian carinae of the metasoma are usually obsolete (but in some species are weak to moderate). The following described species are referable to the *nitidulus* group: *V. carolinianus* (Beauvois), *V. decipiens* Hoffmann (n. comb.), *V. gracilis* Gertsch and Soleglad, *V. intermedius* Borelli, *V. janssi* Williams, *V. jonesi* Stahnke, *V. minckleyi* Williams, *V. nigrescens* Pocock, *V. nitidulus* C. L. Koch, *V. peninsularis* Williams, and *V. spicatus* Haradon. A complete revision of this species group, with descriptions of new species, is in preparation by the senior author.

The status of three of these species, *V. nitidulus, V. nigrescens,* and *V. intermedius,* has been particularly confusing. Until now, each has been considered a subspecies of *V. nitidulus;* with the nominal subspecies in Oaxaca, *V. nitidulus nigrescens* in central and eastern Mexico, and *V. nitidulus intermedius* in northwestern Mexico (Hoffmann 1931). Examination of the primary types of these species and considerable material from pertinent areas indicates that all three taxa are distinct species, and that *V. nitidulus* has been continuously misidentified since its original description in 1843. A second source of confusion in the identification of these taxa is the occurrence in central and southern Mexico of the aforementioned new taxa. Some of these have almost certainly been called *V. nitidulus* or *V. nigrescens* in the past (e.g., Díaz Nájera 1964, 1975). Unfortunately, our attempts to obtain specimens from Mexican collections have failed, and we can neither confirm nor deny many of the old records for these species. To clarify the identity and taxonomic status of the three taxa, complete redescriptions are provided below.

Two other species are dealt with here. *Vaejovis mexicanus decipiens* Hoffmann is elevated to specific status and redescribed as a valid species of the *nitidulus* group based on examination of the types. *Vaejovis minckleyi* Williams, which has lately been considered a member of the genus *Paruroctonus* (Stahnke 1974), is returned to *Vaejovis* and placed in the *nitidulus* group. Because Williams' original description (1968) is largely adequate and the species is very distinctive, only a revised diagnosis and some comments are given below, emphasizing new characters of taxonomic importance.

Vaejovis nitidulus C. L. Koch
(Figs. 1-13)

Vaejovis nitidulus C. L. Koch 1843: 4, fig. 758; Peters 1861: 510; Karsch 1879: 135; *nec* Pocock 1902: 12; Borelli 1915: 7; Moritz & Fischer 1980: 320.

Vejovis nitidus (sic), Thorell 1876: 186.

Vejovis spinigerus, Kraepelin 1894: 202 (part).

Vejovis nitidulus, nec Kraepelin 1899: 186; Bücherl 1959: 271 (?), 1971: 329; Stahnke 1974: 135.

Vejovis nitidulus nitidulus, nec Hoffmann 1931: 371, *nec* 1937: 204, *nec* 1939: 318; *nec* Gertsch 1958:5; Díaz Nájera 1964: 20 (part?), 1975: 7 (part?).

Type data.—Of four syntypes of *Vaejovis nitidulus* used by Koch (1843) in his original description, only two remain (Moritz and Fischer 1980). Both are adult females, and represent two different taxa. Koch's description is too general to determine whether he based it on either specimen or all four; likewise, his measurements cannot be assigned with certainty to either specimen (Although his measurements, which are few and general, are similar to those of the smaller female, it is not certain that they indeed belong to that female; it is equally possible that the measurements refer to one of the missing syntypes).

We hereby select the larger female from Mexico (Deppe, coll.), bearing the label ZMB 10a, as the lectotype for *V. nitidulus*. We have identified conspecific material from Hidalgo and eastern Querétaro, Mexico, and the coloration of these specimens match very well the description by Koch and his color plate (Koch 1843: fig. 758).

The lectotype, originally a dry, pinned specimen, is in very poor condition. The pedipalps, metasoma, and most of the legs are detached from the body; some of the legs themselves are broken into separate segments, as is one pedipalp. Some damage by dermestid beetles is evident. The carapace is also detached from the body, and the specimen is strongly discolored. However, in spite of its poor condition, no body parts are missing and taxonomic characters are readily observable.

The identity of specimen ZMB 10 is unknown. It is definitely not referable to *V. nitidulus,* and we have not yet seen any material which is conspecific with it. In the vial containing this specimen is a label written by H. L. Stahnke, selecting this specimen as lectotype. Dr. Stahnke has never published this designation, and therefore, it is not valid according to the International Code of Zoological Nomenclature, Art. 74(a)(i). The reference to Stahnke's invalid lectotype by Moritz & Fischer (1980) also does not constitute proper designation, as it was not intended as such [ICZN 74(c)]. Stahnke's paralectotype label in the vial containing ZMB 10a should likewise be disregarded.

Both specimens are deposited in the Zoologisches Museum of Humboldt Universität in Berlin.

Distribution.—Known from Hidalgo, and eastern Querétaro, Mexico.

Diagnosis.—Adults 45-65 mm in length. Base color yellow brown, without conspicuous underlying markings. Sternite VII with lateral keels weak, granular. Metasoma with ventral submedian carinae obsolete on I-IV; ventrolateral carinae moderate to weak, smooth; distalmost granules of dorsolateral and lateral supramedian carinae enlarged, spinoid. Pedipalp: tibia with 15 trichobothria (3 *et*, 1 *est*, 2 *em*, 3 *esb*, 5 *eb*, 1 *v*) on external face; fixed finger with primary row divided into seven subrows by six larger granules; keels of chela developed. Pectinal tooth count 24-28 in males, 21-27 in females.

Vaejovis nitidulus, in possessing an extra *esb* trichobothrium on the tibia and high pectinal tooth counts, is most similar to *V. minckleyi.* It is easily distinguished from that species by possessing seven subrows of denticles on the pedipalp chela fixed finger (instead of six subrows), by having smooth or obsolete keels on the dorsal and external surfaces of the pedipalp chela (instead of granulose keels), by having obsolete ventral submedian keels on the metasoma (rather than weak, granular keels), and by having metasomal segments I-II wider than long (instead of longer than wide).

Redescription.—The following redescription is based on adults. Parenthetical statements refer to females. Measurements of the female lectotype and an adult male appear in Table 1.

Coloration (in alcohol). Carapace and tergites yellow brown. Metasomal segments I-III yellow brown to light orange brown, IV-V orange brown to reddish brown. Telson yellow brown to light orange brown; aculeus dark brown.
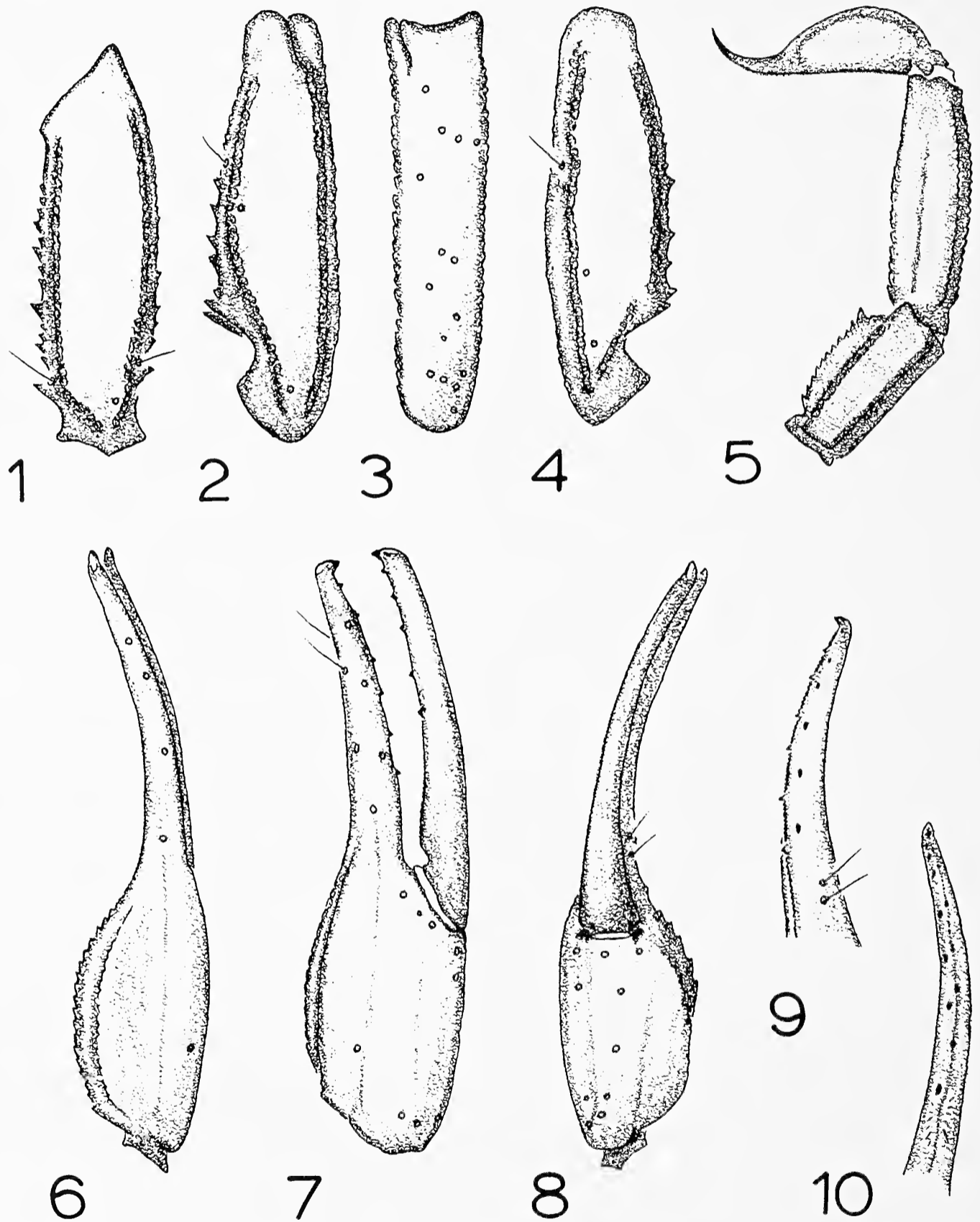
Figs. 1-10—*Vaejovis nitidulus* Koch, male from Hidalgo, Mexico: 1, dorsal aspect of pedipalp femur; 2, dorsal aspect of pedipalp tibia; 3, external aspect of pedipalp tibia; 4, ventral aspect of pedipalp tibia; 5, lateral aspect of metasomal segments IV and V, and telson; 6, dorsal aspect of pedipalp chela; 7, external aspect of pedipalp chela; 8, ventral aspect of pedipalp chela; 9, dentition pattern on fixed finger of pedipalp chela; 10, dentition pattern on movable finger of pedipalp chela.

Pedipalps: femur and tibia yellow, lighter than body; chela orange brown, darker at base of fingers with yellowish fingertips; denticles of dentate margin brown. Legs yellow with some faint dusky markings; tarsi yellowish. Venter: coxosternal region yellow brown; pectines yellowish white; sternites light yellow brown; third sternite in male with whitish patch along posteromedial margin (absent).

Prosoma. Carapace approximately as long as wide. Median ocular prominence moderately raised above carapacial surface. Three pairs of lateral eyes. Anterior carapacial margin obtusely emarginate; median notch shallow, narrow. Median longitudinal furrow deep, wide at anterior margin; deep, narrow posteriorly. Posterior lateral furrow curved, deep, wide. Entire carapacial surface densely granular.

Mesosoma. Tergites I-VI: median carina on I obsolete, on II-VI weak, granular; submedian carinae vestigial. Tergite VII: median carina weak, finely granular, present on anterior one-third to one-half; submedian and lateral carinae strong, serratocrenulate. Genital operculi distinctly lobed posteriorly; without median longitudinal membranous connection (with short basal connection, one-half length of genital operculum). Genital papillae well developed (absent). Pectinal teeth numbering 24-28 (21-27). Sternites III-VI smooth, stigmata about three times longer than wide. Sternite VII with median pair of carinae obsolete; lateral carinae weak, granular.

Metasoma. Segments I-IV: Segments I-II, occasionally III, wider than long, others longer than wide. Dorsolateral carinae on I-III strong, serrate; on IV strong, irregularly crenulate to serrate; distalmost denticle distinctly enlarged, spinoid (Fig. 5). Lateral supramedian carinae on I strong, serrate; on II-III strong, finely crenulate to finely serrate; on IV moderate, smooth to finely serrate; distalmost denticle distinctly enlarged, spinoid on I-III; flared and winglike on IV (Fig. 5). Lateral inframedian carinae on I complete, strong, crenulate to serrate; on II present only on posterior one-third, crenulate to serrate; on III present on posterior one-fourth, granular to crenulate; on IV absent. Ventrolateral carinae on I moderate, smooth, sometimes with few posterior serrations; on II-IV weak, smooth, posterior serrations sometimes present. Ventral submedian carinae on I-IV obsolete. Intercarinal spaces irregularly granular, lustrous. Segment V (Fig. 5): slightly more than twice as long as wide. Dorsolateral carinae weak, granular. Lateral median carinae present on anterior three-fourths, weak, granular. Ventrolateral and ventromedian carinae moderate, finely serrate. Intercarinal spaces irregularly granular, lustrous.

Telson (Fig. 5.). Dorsal surface flattened, smooth; ventral surface with irregularly spaced granules and punctations.

Chelicera. Movable finger internally with well developed serrula.

Pedipalp. Femur (Fig. 1) tetracarinate. Dorsointernal, dorsoexternal, and ventrointernal carinae strong, crenulate. Ventroexternal carina strong, with irregularly spaced, large rounded granules. Internal face with large, conical granules; dorsal face coarsely granular; ventral and external faces with granulation on basal portion. Orthobothriotaxia C (Vachon 1974).

Tibia (Fig.s 2-4) tetracarinate. Dorsointernal and ventrointernal carinae strong, crenulate. Dorsoexternal carina moderate, granular to crenulate. Ventroexternal carina moderate, crenulate. Internal face with moderate basal tubercle and large, sharp granules. Dorsal face smooth; ventral face with few scattered, coarse

granules; external face with weakly granular, longitudinal series of granules. Neobothriotaxia C (Vachon 1974), with three *esb* trichobothria; *esb*$_2$ petite (Fig. 3). Positions of *em*$_1$ and *em*$_2$ variable (see Figs. 11-13).

Chela (Figs. 6-10): Dorsal marginal carina weak, granular. Dorsal secondary and digital carinae weak, smooth. External secondary carina obsolete. Ventroexternal and ventromedian carinae weak, smooth. Ventrointernal carina weak, granular. Dorsointernal carina moderate, with large sharp granules. Dentate margin of fixed finger with primary row broken up into seven subrows by six larger granules; six internal accessory granules of which all but distal one paired with larger granule in primary row (Fig. 9). Dentate margin of movable finger with primary row broken up into seven subrows by six enlarged granules; apical row consisting of one or two small granules; seven internal accessory granules of which distal granule not paired with larger granule of primary row, basalmost granule distinctly basal to corresponding granule in primary row (Fig. 10). Both fingers terminating in large, sharp, claw-like tooth bearing distally an oblong elongate whitish cap. Orthobothriotaxia C (Vachon 1974).

Legs. Tarsomere I on legs I-II with one retrolateral and two ventrolateral rows of spinules; ventral rows complete, interrupted at irregular intervals by large spines. Retrolateral row present on distal one-half, interrupted by one or two spines. Tarsomere I spinule rows rudimentary on legs III-IV, with spines well developed. Tarsomere II on all legs with single ventromedian row of spinules, procurved basally, terminating distally between single pair of medium-sized spines. Spinule rows flanked by pairs of setae as in Soleglad (1975: Fig. 17); seta formula given in Table 3.

Variation.—Although only a small number of specimens have been located and examined, pectinal tooth counts varied as follows: among males, 5 combs with 24 teeth, 3 combs with 25 teeth, 3 combs with 26 teeth, 2 combs with 27 teeth, and 3 combs with 28 teeth; among females, 2 combs with 21 teeth, 3 combs with 22 teeth, 4 combs with 23 teeth, 4 combs with 24 teeth, 4 combs with 25 teeth, 3 combs with 26 teeth, and 2 combs with 27 teeth. As is typical of the group, adult males have relatively shorter, wider chelae than females and slightly longer and narrower metasomal segments. No other significant variation was observed.
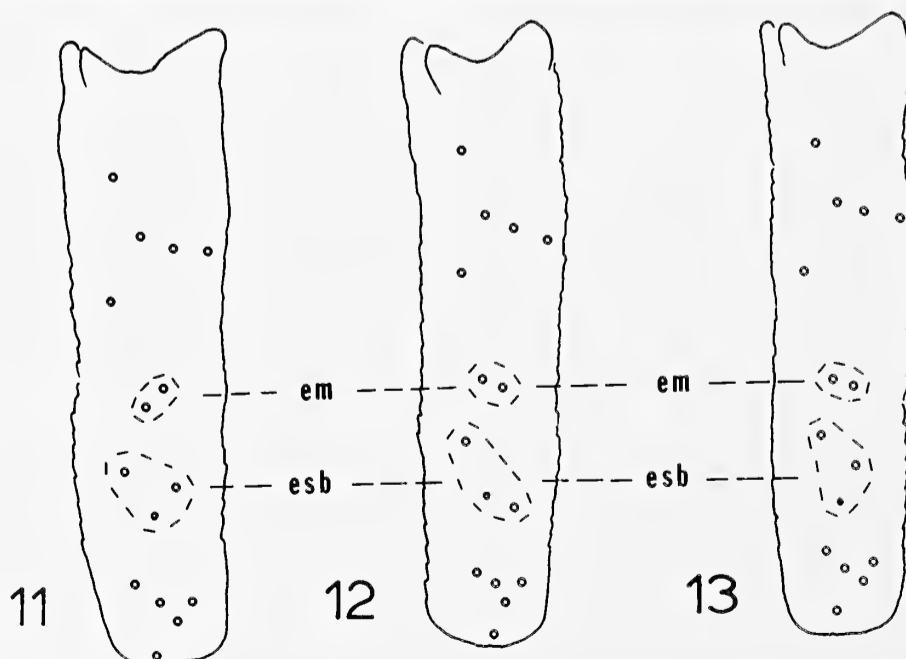
Figs. 11-13.—*Vaejovis nitidulus* Koch, males from Hidalgo, Mexico: external aspect of pedipalp tibia showing variability in position of *em* and *esb* trichobothria.

Remarks.—*V. nitidulus* and its relationship to other species in the group have been poorly understood since the original description. Hoffmann (1931), in his treatment of the scorpions of Mexico, considered *V. nitidulus* to be polytypic, containing three subspecies: *V. n. nitidulus, V. n. intermedius,* and *V. n. nigrescens.* The new characters established by examination of the types of the three nominal taxa (i.e., number of subrows in the dentate margin of the chela fingers, structure of pedipalp chela keels, trichobothrial pattern of the tibia, pectinal tooth counts, and morphometrics) show conclusively that each is a good species. Problems in identifying these taxa were compounded by the fact that Hoffmann (1931) misidentified *V. nitidulus.* We have examined some of Hoffmann's specimens from Cuicatlán, Oaxaca, and they are not referable to *V. nitidulus* (actually they represent a new species being described by the senior author). All records of *V. nitidulus* from Guanajuato and western Querétaro (Díaz Nájera 1975) need to be confirmed.

Specimens examined.—MEXICO: no specific locality or date (Deppe), 1 lectotype female (ZMB) *Hidalgo:* Jacala (east side), W99.11: N21.01, 27 July 1966 (J. & W. Ivie), 1 female (AMNH), 1 juv (AMNH); 18 July 1963 (R. E. Woodruff) (under cow dung), 1 female (FSCA); Jacala, W99.12: N21.01, 20 April 1963 (W. J. Gertsch & W. Ivie), 1 female (AMNH); Taxquillo (Tzindejeh), W99.19: N20.33, 29 July 1966 (J. & W. Ivie), 1 male (AMNH), 1 juv (AMNH): 1 mi SE Danghu (3 mi S Taxquillo), 22 Aug 1984 (W. D. Sissom, C. Myers, L. Born) (N slope of rocky hillside, UV light), 5 males, 2 females (WDS), 1 male, 1 female (OFF); *Querétaro:* Mountains near San Joaquin, July 1976 (S. Minton), 1 female (SAM); Mission Bucareli, 31 Dec 1981 (S. Minton), 1 female (SAM), 1 juv female (MEB).

Vaejovis nigrescens Pocock
(Figs. 14-23)

Vaejovis nigrescens Pocock 1898:396.
Vejovis nitidulus, Kraepelin 1899: 186 (part); 1901: 274 (part).
Vaejovis nitidulus, Pocock 1902: 12.
Vejovis nitidulus nigrescens, Hoffmann 1931: 365, 1937: 204, 1939: 318; Gertsch 1958: 5.
Vaejovis nitidulus nigrescens, Díaz Nájera 1964:20, 24, 25, 29; 1975: 7, 22, 25, 26, 30, 34.

Type data.—Adult female holotype from Mexico (no date or collector); deposited in the British Museum (Natural History); examined. The holotype, formerly a pinned specimen, is in poor condition: metasomal segments II-V and the telson are detached from the body and held together with a pin; the right pedipalp, its movable finger, and most of the legs are also detached; the pectines are shriveled and broken; and the specimen is strongly discolored.

Distribution..—The specimens we have examined are from the central Mexican states of Aguascalientes, Distrito Federal, and Guanajuato. Hoffmann (1931, 1937) and Díaz Nájera (1964, 1975) record *V. nigrescens* additionally from Hidalgo, Querétaro, and adjacent parts of Jalisco, Michoacan, San Luis Potosí, and Zacatecas. As in the case of *V. intermedius,* these records need to be verified. We have also examined a series of specimens from Dinamita, Durango collected by Duges; this record is far outside the range of *nigrescens* (including the records of Hoffmann and Díaz Nájera) and may possibly be the result of a labeling error.

Diagnosis.—Adults 42-68 mm in length. Base color orange brown to reddish brown with variable faint underlying dusky markings. Sternite VII with submedian keels obsolete; lateral keels weak to moderate, granular. Metasomal

segments I-II wider than long, III as long as wide, V less than twice as long as wide; ventrolateral carinae of I-IV weak, smooth to finely granular; ventral submedian carinae obsolete. Pedipalp: tibia with 14 trichobothria (3 *et*, 1 *est*, 2 *em*, 2 *esb*, 5 *eb*, 1 *v*) on external face; fixed finger of chela with primary row of denticles broken into six subrows by five enlarged denticles; femur as long as carapace; dorsointernal carina of chela with weak to moderate, rounded granules. Pectinal tooth count 19-21 in males; 17-21 in females.

Vaejovis nigrescens is most similar to *V. intermedius*. For comparisons between these two species, see the diagnosis of the latter species.

Redescription.—The following redescription is based on adult males and females. Parenthetical statements refer to females. Measurements of the female holotype and an adult male appear in Table 1.

Coloration. Base color of carapace and tergites orange brown to reddish brown, with faint underlying dusky markings. Venter yellow brown to orange brown; third sternite in males with whitish patch along posteriomedial margin (absent). Metasomal segments I-III orange brown to reddish brown, IV-V dark reddish brown. Telson reddish brown, with dark brown aculeus. Chelicerae yellow brown at base, mottled with brown distally; teeth brown. Pedipalps: Femur and tibia yellow brown to orange brown with carinae somewhat darkened; chela manus reddish brown to dark orange brown; fingers dark brown basally, reddish brown to dark orange brown distally. Legs yellow to orange brown, usually lighter than body. Pectines whitish.

Prosoma. Carapace slightly longer than wide. Median ocular prominence only slightly raised above carapacial surface. Three pairs of lateral eyes, diameter of

Table 1. Measurements in mm and meristic characters of *Vaejovis nigrescens* Pocock and *Vaejovis nitidulus* C. L. Koch.

| Character | V. nitidulus | | V. nigrescens | |
	lectotype ♀	adult ♂ (AMNH, Taxquillo)	holotype ♀	adult ♂ (MNHN, RS-0671)
Total length	64.8	50.4	61.8	49.5
Carapace length	7.7	5.8	7.4	5.9
Mesosoma length	20.8	14.8	20.6	14.4
Metasoma length	27.5	23.1	25.9	22.0
I length/width	3.6/4.8	3.0/3.6	3.4/4.4	2.8/3.8
II length/width	4.0/4.8	3.6/3.5	3.9/4.5	3.4/3.8
III length/width	4.5/4.8	3.9/3.5	4.3/4.4	3.8/3.8
IV length/width	6.2/4.6	5.1/3.4	6.0/4.4	5.0/3.9
V length/width	9.2/4.6	7.5/3.4	8.3/4.4	7.0/3.8
Telson length	8.8	6.7	7.9	7.2
Vesicle length/width/depth	5.8/3.4/2.8	4.3/2.4/1.9	5.1/3.4/2.6	4.7/2.8/2.2
Aculeus length	3.0	2.4	2.8	2.5
Pedipalp length	26.7	22.2	27.3	21.3
Femur length/width	7.2/2.2	6.0/1.6	7.2/2.0	5.6/1.6
Tibia length/width	7.5/2.3	6.2/1.5	7.5/2.2	6.0/1.7
Chela length/width/depth	12.0/2.6/3.0	10.0/2.2/2.8	12.6/2.8/3.2	9.7/2.9/2.9
Movable finger length	8.0	6.6	8.6	6.0
Fixed finger length	6.5	5.5	7.1	4.7
No. primary rows (FF/MF)	7/7	7/7	6/6	6/6
Int. accessory granules (FF/MF)	6/7	6/7	6/7	6/7
Pectinal teeth (l/r)	27-26	26-24	18-19*	24-23

*as reported by Pocock (1898).

posteriormost pair approximately one-half the diameter of the preceding pairs. Anterior carapacial margin obtusely emarginate, median notch distinct, shallow, wide. Median longitudinal furrow deep, wide at anterior margin; deep, narrow posteriorly. Posterior lateral furrows curved, deep, wide. Entire carapacial surface coarsely granular.
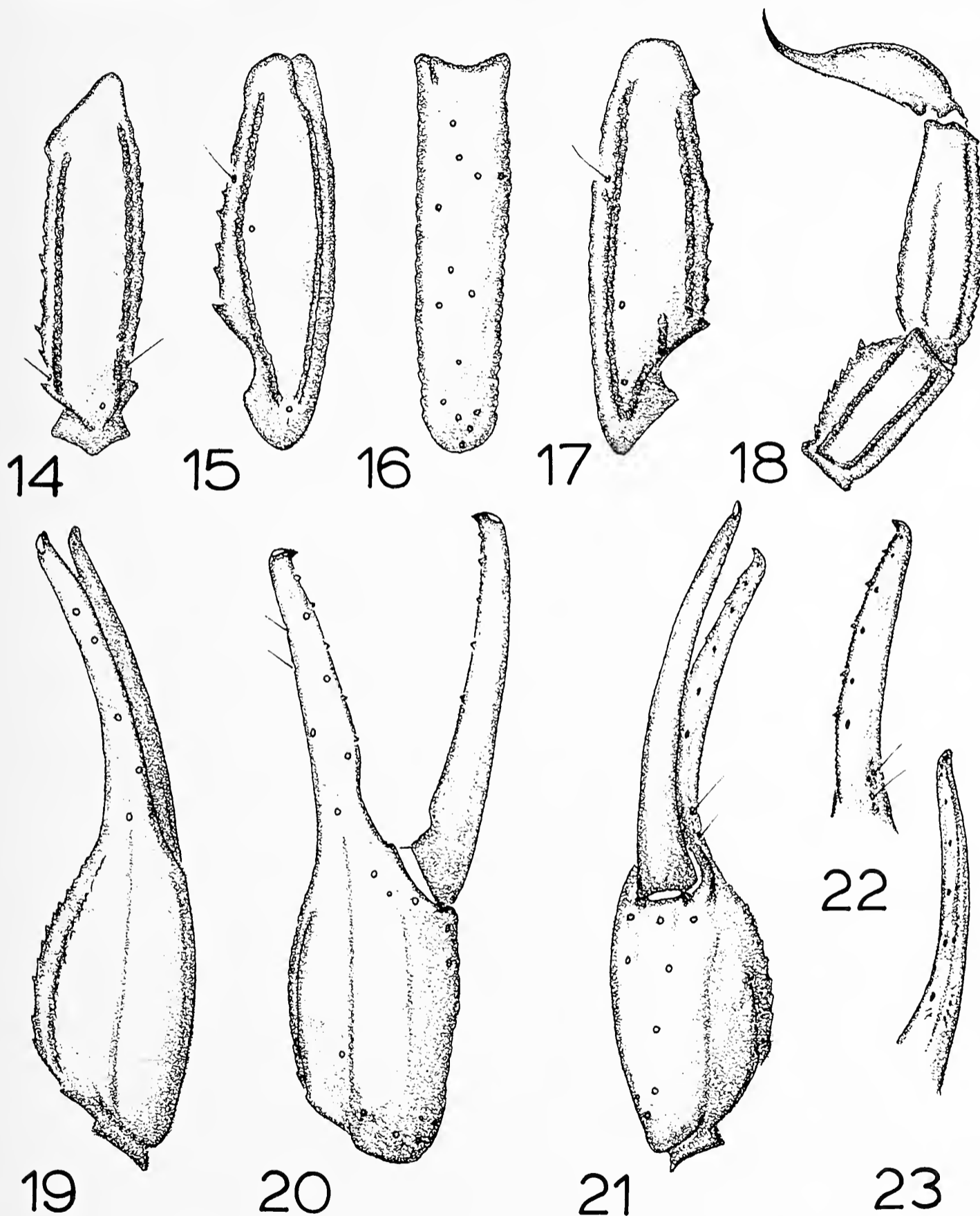
Figs. 14-23.—*Vaejovis nigrescens* Pocock, male from Guanajuato, Mexico: 14, dorsal aspect of pedipalp femur; 15 dorsal aspect of pedipalp tibia; 16, external aspect of pedipalp tibia; 17, ventral aspect of pedipalp tibia; 18, lateral aspect of metasomal segments IV and V, and telson; 19, dorsal aspect of pedipalp chela; 20, external aspect of pedipalp chela; 21, ventral aspect of pedipalp chela; 22, dentition pattern on fixed finger of pedipalp chela; 23, dentition pattern on movable finger of pedipalp chela.

Mesosoma. Tergites I-VI: Median carina on I obsolete, on II-VI weak, granular; submedian carinae vestigial. Tergite VII: median carina weak, granular, present on anterior one-half to two-thirds; submedian and lateral carinae strong, crenulate. Genital operculi distinctly lobed posteriorly, without median longitudinal membranous connection (with basal connection two-thirds length of genital operculum); genital papillae well developed (absent). Pectinal teeth numbering 19-21, mode = 21 (17-21, mode = 18). Sternites III-VI smooth, with slit-like stigmata. Sternite VII with one pair of lateral carinae, these weak to moderate, granular.

Metasoma. Segments I-IV: Segments I-II shorter than wide, III as long as or longer than wide, IV longer than wide. Dorsolateral carinae on I-III strong, crenulate; on IV strong, irregularly crenulate; distalmost denticle on I-IV distinctly enlarged, spinoid (Fig. 18). Lateral supramedian carinae on I-III strong, crenulate to finely crenulate; on IV strong, granular to finely crenulate; distalmost denticle on I-III distinctly enlarged, spinoid, on IV widely flared (Fig. 18). Lateral inframedian carinae on I complete, strong, crenulate; on II present on posterior one-half, strong, crenulate; on III present on posterior one-third, moderate, crenulate; on IV absent. Ventrolateral carinae on I weak, finely granular; on II-IV weak, smooth to finely granular. Ventral submedian carinae obsolete. Intercarinal spaces dorsally and laterally with scattered, coarse granules. Segment V (Fig. 18): Averaging 1.95 (1.84) times as long as wide. Dorsolateral carinae weak to moderate, granular. Lateromedian carinae weak, finely granular. Ventrolateral and ventromedian carinae weak, finely serrate. Intercarinal spaces with scattered coarse granules.

Telson (Fig. 18). Dorsal surface smooth, flattened; ventral surface with irregularly spaced granules and punctations; subtle subaculear tubercle sometimes present.

Chelicera. Dentition typical of genus, with well developed serrula on ventral margin of movable finger.

Pedipalp. Femur (Fig. 14) tetracarinate: Dorsointernal, ventrointernal, and dorsoexternal carinae strong, granulose. Ventroexternal carina strong, composed of large irregularly spaced, sharp granules. Internal face with about 15 large, subconical granules; dorsal face with scattered coarse granules; ventral face with coarse granulation proximally. Femur as long as or slightly longer than carapace. Orthobothriotaxia C (Vachon 1974).

Tibia (Figs. 15-77): Dorsointernal and ventrointernal carinae strong, granulose. Dorsoexternal carina moderate, granular. Ventroexternal carina moderate, somewhat crenulate. Internal face with about 10 large, sharp, subconical granules; dorsal and ventral faces with scattered coarse granules; external face with vestigial, granular external keel. Orthobothriotaxia C (Vachon 1974); trichobothrium em_2 consistently basal to em_1 (Fig. 16).

Chela (Figs. 19-23): Dorsal marginal carina moderate, granular. Dorsal secondary keel weak, smooth. Digital carina weak basally, moderate distally, smooth. External secondary and ventromedian carinae weak, smooth. Ventrointernal carina weak, finely granular. Dorsointernal carina weak to moderate, with medium-sized granules more rounded than sharp. Dentate margin of fixed finger with primary row divided into six subrows by five larger denticles; six internal accessory granules, of which distalmost not paired with larger granule

in primary row (Fig. 22). Dentate margin of movable finger with primary row divided into six subrows by five larger granules; apical subrow with only one or two granules; seven internal accessory granules, of which distalmost and basalmost not paired with larger granule in primary row (Fig. 23). Both chela fingers terminating in large, sharp, clawlike tooth bearing distally an oblong whitish cap. Fingers. of male with weak scalloping. Orthobothriotaxia C (Vachon 1974).

Legs. Arrangement of setae, spines, and spinules as in *V. nitidulus;* seta formula given in Table 3.

Variation.—Male pectinal tooth counts varied as follows: 6 combs with 19 teeth, 11 combs with 20 teeth, and 12 combs with 21 teeth. Female pectinal tooth counts varied as follows: 12 combs with 17 teeth, 22 combs with 18 teeth, 7 combs with 19 teeth, 3 combs with 20 teeth, and 1 comb with 21 teeth. Pectinal tooth counts of males and females are statistically different ($F_{1,75} = 71.0$, p < 0.001).

Sexual dimorphism occurs in body size and morphometrics of the pedipalp chela and metasoma (see Table 4). Adult males range from 42-52 mm in length; adult females from 46-68 mm.

Specimens examined.—MEXICO: no specific locality, date, or collector, 1 holotype female (BM); no specific locality, date or collector, 1 female (MCZ), 3 males, 1 female (MCZ); no date, 1 female (AMNH); *Aguascalientes:* Rio de Pirules (no date or collector), 1 female (AMNH); *Mexico, D.F.:* Mexico City, no date (Bononsea), 4 males, 2 females (Sc516, ex. 617) (TOR); *Durango:* Dinamite (no date or collector), 3 males, 1 female (Sc 517, ex. 656) (TOR); *Guanajuato:* Guanajuato, no date (Duges), 4 females (RS-0668) (MNHN), 2 females (RS-0678) (MNHN), 1 female (RS-0684) (MNHN), 1 male, 5 females, 7 first instars (RS-0671) (MNHN), 1 female (BM); Guanajuato, no date (Duges) (in houses) 3 males, 4 females (Sc 515, ex. 616) (TOR), 2 females (BM), 1 female (BM), Guanajuato, June 1963 (S. A. Minton), 1 female (SAM).

Vaejovis intermedius Borelli
(Figs. 24-33)

Vaejovis intermedius Borelli 1915: 6.
Vejovis nitidulus intermedius, Hoffmann 1931: 368, 1937: 204, 1939:318; Gertsch 1958: 5.
Vaejovis nitidulus intermedius, Díaz Nájera 1964: 20, 24, 25; 1975: 7, 22, 25, 26.

Type data.—The type series consists of three adult males and three adult females taken from Dinamita, Durango, Mexico (collector and date unknown). From this type series we designate one adult male, clearly labeled as lectotype and the remaining specimens as paralectotypes. One of the female syntypes has been labeled as a lectotype by H. L. Stahnke; however, this designation is not valid as it has never been published [International Code of Zoological Nomenclature, Art. 74 (a) (i)]. We have chosen to select the male as lectotype because it is intact; the female is broken into three parts.

The lectotype and five paralectotypes are permanently deposited in the Museo ed Istituto di Zoologia Sistematica della Universita di Torino; Torino, Italy (cat. no. Sc 508, ex. 799).

Distribution.—*Vaejovis intermedius* is known from southwestern Texas (Brewster, Crockett, Presidio, Terrell, and Val Verde Counties), U.S.A. and the state of Durango in Mexico. Hoffmann (1931) reports the species also occurs in the Sierra de Guadalupe, Distrito Federal, Mexico. Díaz Nájera (1964, 1975)

reports additional records from Hidalgo and Jalisco. We have been unable to obtain these specimens, and, in light of the confusion previously surrounding the species of the *nitidulus* group, we must consider these records as tentative.

Diagnosis.—Adults 40-57 mm in length. Base color yellowish to reddish brown; pedipalps and metasoma dark reddish brown distally. Sternite VII with submedian keels obsolete; lateral keels moderate, smooth to crenulate. Metasoma: segments I-II wider than long, III as wide as long; IV-V longer than wide; ventrolateral carinae moderate, smooth to finely granular; ventral submedian
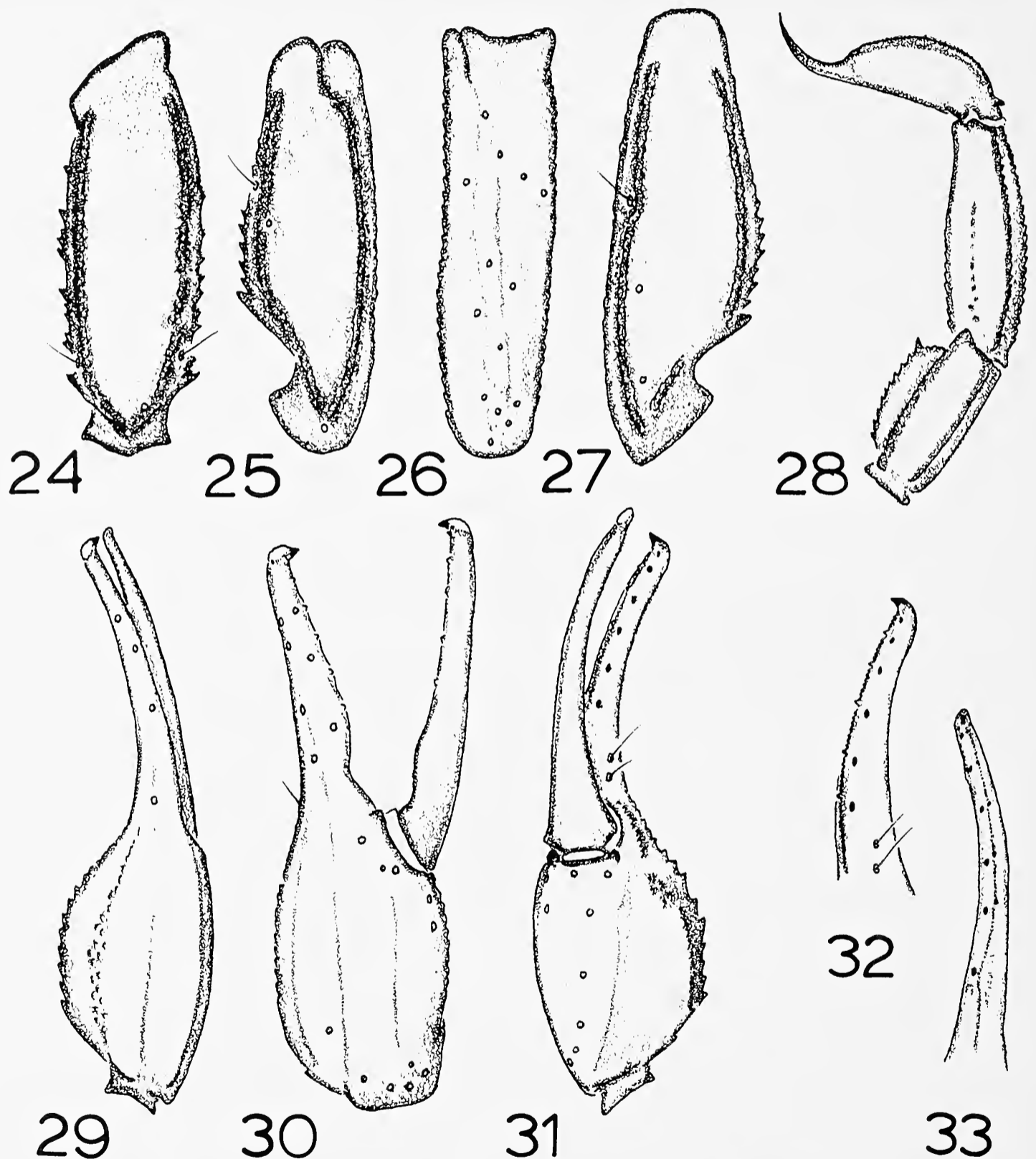
Figs. 24-33.—*Vaejovis intermedius* Borelli, lectotype male from Durango, Mexico: 24, dorsal aspect of pedipalp femur; 25, dorsal aspect of pedipalp tibia; 26, external aspect of pedipalp tibia; 27, ventral aspect of pedipalp tibia; 28, lateral aspect of metasomal segments IV and V, and telson; 29, dorsal aspect of pedipalp chela; 30, external aspect of pedipalp chela; 31, ventral aspect of pedipalp chela; 32, dentition pattern on fixed finger of pedipalp chela; 33, dentition pattern on movable finger of pedipalp chela.

carinae on I-IV obsolete; distalmost denticle of dorsolateral and lateral supramedian carinae of I-IV distinctly enlarged, spinoid. Pedipalp: tibia with 14 trichobothria (3 *et*, 1 *est*, 2 *em*, 2 *esb*, 3 *eb*, 1 *v*) on external face; fixed finger of chela with primary row of denticles broken into six subrows by five enlarged denticles; pedipalp femur distinctly shorter than carapace; keels of dorsal and external faces of chela faint to weak, smooth. Pectinal tooth count 21-26 in males, 19-23 in females.

Vaejovis intermedius is most similar to *V. nigrescens* Pocock from central Mexico. The most significant differences between the two are as follows: (1) male pectinal tooth counts range from 21-26 (mode = 23, 24) in *V. intermedius*, 19-24 (mode = 21) in *V. nigrescens*; (2) female pectinal tooth counts range from 19-23 (mode = 21) in *V. intermedius*, 17-22 (mode = 18) in *V. nigrescens;* (3) the pedipalp chela is proportionately wider and deeper in *V. intermedius*, with shorter fingers (see Table 4); (4) the dorsointernal carina of the pedipalp chela possesses strong, sharp granules in *V. intermedius*, but weak, more rounded granules in *V. nigrescens;* and (5) metasomal segment V length/width is distinctly greater in both males and females of *V. intermedius* than in *V. nigrescens* (Table 4).

Redescription.—The following redescription is based on adult males and females. Parenthetical statements refer to females and indicate sexual differences. Measurements of the lectotype male and a paralectotype female appear in Table 2.

Coloration. Base color of carapace and tergites yellowish to orange brown, with variable underlying dusky markings; in some specimens, dusky markings appear as faint submedian stripes on tergites. Venter yellow to yellow brown; third sternite in males with whitish patch along posteriomedial margin (absent).

Table 2.—Measurements in mm and meristic characters of *Vaejovis decipiens* Hoffmann and *Vaejovis intermedius* Borelli.

Character	*V. intermedius* lectotype ♂	*V. intermedius* paralectotype ♀	*V. decipiens* holotype
Total length	46.3	51.6	53.7
Carapace length	5.5	6.5	6.4
Mesosoma length	12.7	16.0	14.9
Metasoma length	21.7	22.3	25.1
I length/width	2.9/3.4	3.1/3.8	3.5/3.6
II length/width	3.4/3.4	3.4/3.7	4.0/3.5
III length/width	3.6/3.3	3.8/3.6	4.3/3.6
IV length/width	4.8/3.2	5.0/3.5	5.6/3.4
V length/width	7.0/3.1	7.0/3.5	7.7/3.4
Telson length	6.4	6.8	7.3
Vesicle length/width/depth	4.1/2.4/1.8	4.4/2.8/2.1	4.8/2.6/2.0
Aculeus length	2.3	2.4	2.5
Pedipalp length	18.9	21.1	24.9
Femur length/width	5.0/1.6	5.7/1.9	6.7/1.7
Tibia length/width	5.2/1.7	5.8/2.1	7.0/1.8
Chela length/width/depth	8.7/2.5/2.7	9.6/2.4/2.6	11.2/2.6/3.2
Movable finger length	5.5	6.1	7.2
Fixed finger length	4.5	5.1	6.1
No. primary rows (FF/MF)	6/6	6/6	6/6
Int. accessory granules (FF/MF)	6/7	6/7	6/7
Pectinal teeth	25-25	21-21	24-24

Pectines whitish. Metasomal segments I-III (sometimes IV) yellowish brown; IV-V dark reddish brown; ventral submedian and ventrolateral carinae usually with faint underlying dusky pigment. Telson reddish brown; aculeus dark reddish brown. Chelicerae yellowish brown; teeth dark reddish brown. Pedipalps: femur yellowish brown; tibia yellowish brown, often reddish brown distally; chela reddish brown, with palm somewhat lighter than fingers. Legs yellow brown.

Prosoma. Carapace slightly longer than wide. Median ocular prominence only slightly raised above carapacial surface. Three pairs of lateral eyes, diameter of posteriormost pair approximately one-half the diameter of preceding pairs. Anterior carapacial margin obtusely emarginate; median notch distinct, shallow, narrow. median longitudinal furrow deep, wide at anterior margin; deep, narrow posteriorly. Posterior lateral furrow curved, deep, wide. Entire surface of carapace moderately granular, shagreened (less granular, lustrous).

Mesosoma. Tergites I-VI: Median carina on I obsolete, on II-VI weak, granular; lateral carinae vestigial. Tergite VII pentacarinate: median carina weak, granular, present on anterior one-third to one-half; submedian and lateral carinae strong, serrate. Genital operculi distinctly lobed posteriorly; without median longitudinal membranous connection (with short basal connection, one-half length of genital operculum); genital papillae well developed (absent). Pectinal teeth numbering 21-26, mode = 23, 24 (19-23, mode = 21). Sternites III-VI smooth, agranular; stigmata approximately three times longer than wide. Sternite V with submedian carinae obsolete; lateral carinae moderate, smooth to crenulate (smooth).

Metasoma. Segments I-II (occasionally III) wider than long, III-IV longer than wide. Dorsolateral carinae strong, serrate; distalmost denticle on I-IV distinctly enlarged, spinoid (Fig. 28). Lateral supramedian carina on I-II strong, serrate; on III strong, finely serrate (finely crenulate); on IV moderate, granular (granular to finely crenulate); distalmost denticle distinctly enlarged, spinoid on I-III, flared and winglike on IV (Fig. 28). Lateral inframedian carinae on I complete, moderate, irregularly serrate (crenulate); on II-III present on posterior one-half, moderate, crenulate; on IV absent. Ventrolateral carinae moderate; on I-II smooth anteriorly, finely granular posteriorly; on III-IV smooth to finely serrate. Ventral submedian carinae obsolete. Intercarinal spaces dorsally and ventrally with faint luster, all faces with scattered small granules. Segment V (Fig. 28): Dorsolateral carinae moderate, anteriorly serrate, posteriorly granular. Lateral median carinae present on anterior three-fifths, weak, smooth to granular. Ventrolateral carinae moderate, finely serrate (crenulate). Ventromedian carina moderate, finely crenulate to finely serrate. Intercarinal spaces as on I-IV.

Telson (Fig. 28). Dorsal surface smooth, flattened; ventral surface with irregularly spaced punctations. Subtle subaculear tubercle present.

Chelicera. Dentition typical of genus, with well developed serrula on ventral margin of movable finger.

Pedipalp. Femur (Fig. 24) tetracarinate: Dorsointernal and ventrointernal carinae strong, serratocrenulate. Dorsoexternal carina strong, serrate. Ventroexternal carina strong, with irregularly spaced, large serrate granules. Internal face with numerous, large conical granules; dorsal and ventral faces granular; external face with few proximal granules. Orthobothriotaxia C (Vachon 1974).

Tibia (Figs. 25-27) tetracarinate: Dorsointernal carina strong, serratocrenulate. Ventrointernal carina serratocrenulate to serrate. Dorsoexternal carina moderate, granular (smooth). Ventroexternal carina moderate, granular to crenulate. Internal face with moderate basal tubercle and short row of enlarged conical granules; external face granular; dorsal and ventral faces smooth. Orthobothriotaxia C (Vachon 1974). Trichobothrium em_2 consistently basal to em_1.

Chela (Figs. 29-33): Dorsal marginal carina moderate, with medium sized sharp granules. Dorsointernal carina strong, composed of large, serrate granules. Ventrointernal carina weak to moderate, granular. Ventroexternal carina weak, granular (smooth). Ventromedian carina weak, smooth. Other carinae faint, smooth. Dentate margin of movable finger with primary row divided into six subrows by five larger granules; six internal accessory granules, of which distalmost not paired with larger granule in primary row (Fig. 32). Dentate margin of movable finger with primary row divided into six subrows by five larger granules; distal subrow with only one or two granules; seven internal accessory granules, of which distalmost and basal most not paired with larger granules in primary row (Fig. 33). Chela fingers moderately (weakly) scalloped. Both chela fingers terminating distally in large, clawlike tooth bearing distally an oblong whitish cap. Orthobothriotaxia C (Vachon 1974).

Legs. Arrangement of setae, spines, and spinules as in *V. nitidulus;* seta formula given in Table 3.

Variation.—Male pectinal tooth counts varied as follows: 1 comb with 21 teeth, 8 combs with 22 teeth, 25 combs with 23 teeth, 25 combs with 24 teeth, 9 combs with 25 teeth, and 4 combs with 26 teeth. Female pectinal tooth counts varied as follows: 2 combs with 19 teeth, 12 combs with 20 teeth, 68 combs with 21 teeth, 37 combs with 22 teeth, and 4 combs with 23 teeth. Pectinal tooth counts of males and females are statistically different ($F_{1,193} = 340.3$, $p < 0.001$).

Coloration varies with age. Juveniles (including subadults) tend to be light yellow with more prominent dusky markings on the body. The distal segments

Table 3.—Seta formulae and variation in setal counts of the ventral surface of the tarsi of legs I-IV in *Vaejovis* spp. The numerator of the fractions indicates the number of setae in the prolateral row; the denominator indicates the number in the retrolateral row. The number outside the parentheses is the mode (=most common observation); the numbers within parentheses indicate the range.

SPECIES	I left	I right	II left	II right	III left	III right	IV left	IV right
nitidulus	2(1-2)	2(1-2)	4	4(3-4)	4(4-5)	4(4-5)	5(4-5)	5(4-5)
	1(0-1)	1(0-1)	2(2-3)	2(2-3)	3	3(3-4)	4(3-4)	4(3-4)
nigrescens	3(2-4)	3(2-4)	4	4	4(4-5)	4(4-5)	5(4-5)	5(4-5)
	1	1(1-2)	3	3(3-4)	3-4	3(3-4)	4(3-5)	4(3-5)
intermedius	2(1-2)	2	4(3-4)	4(3-4)	4(4-5)	4(4-5)	5(4-5)	5(4-5)
	1(1-2)	1(1-2)	2(2-3)	2(2-3)	3(3-4)	3	4(3-5)	4(3-4)
*decipiens**	2	2	3-4	3-4	4	4-5	4-5	4-5
	1	1-2	2-4	2	3-4	3-4	4	3-4
*minckleyi**	2	2	3	3	3	3-4	4	4
	1	1	2	2	3	3	3	3

*Only the range of observations is given due to the small sample sizes (i.e., n<10).

Table 4.— Morphometric and meristic characteristics (mean and standard deviation) of *Vaejovis inter-medius* Borelli and *V. nigrescens* Pocock. For *V. intermedius*, morphometrics are based on 20 ♂♂ and 20 ♀♀; for *V. nigrescens*, 8 ♂♂ and 13 ♀♀. Pectinal tooth counts are taken from 36 ♂♂ and 62 ♀♀ *V. intermedius*; and 4 ♂♂ and 23 ♀♀ of *V. nigrescens*.

Character		V. intermedius		V. nigrescens	
		males	females	males	females
Slenderness of pedipalp chela					
1. chela length/width	$\bar{x}$	3.78	4.35	3.94	4.54
	s	0.20	0.25	0.31	0.29
2. chela length/depth	$\bar{x}$	3.10	3.70	3.70	4.04
	s	0.21	0.16	0.32	0.31
Relative length of pedipalp					
3. fixed finger length/carapace length	$\bar{x}$	0.79	0.81	0.84	0.88
	s	0.02	0.03	0.01	0.04
4. femur length/carapace length	$\bar{x}$	0.91	0.88	1.02	0.99
	s	0.02	0.03	0.03	0.03
Slenderness of metasoma					
5. I length/width	$\bar{x}$	0.81	0.76	0.81	0.75
	s	0.03	0.02	0.04	0.03
6. III length/width	$\bar{x}$	1.05	1.00	1.03	0.98
	s	0.03	0.04	0.05	0.04
7. V length/width	$\bar{x}$	2.05	2.00	1.95	1.89
	s	0.09	0.07	0.08	0.05
Relative length of metasoma					
8. carapace length/met V length	$\bar{x}$	0.88	0.90	0.84	0.90
	s	0.03	0.03	0.04	0.03
Meristics					
9. Pectinal tooth counts	mode	23,24	21	21	18
	range	21-26	19-23	19-21	17-21

of the pedipalps and metasoma are light orange brown, rather than dark reddish brown as in adults.

Sexual dimorphism also occurs in body size and morphometrics of the pedipalp chela and metasoma (see Table 4). Adult males range from 40-48 mm in length; adult females from 50-57 mm.

Specimens examined.—MEXICO: *Durango:* Dinamita (no date or collector), 1 lectotype male, 2 paralectotype males, 3 paralectotype females (Sc. 508, Ex. 799) (TOR). USA: **Texas:** *Brewster Co.:* NE rim of Chisos Basin, Chisos Mts., Big Bend National Park (5600'), 6 Sept 1969 (Cazier, Bigelow), 1 male, 1 female (OFF); Chisos Mts., Juniper Canyon, Big Bend National Park, July 1921 (no collector), 1 female (AMNH); Chisos Mts., The Basin, Big Bend National Park, 1-10 Aug 1937 (K. P. Schmidt), 1 female (FMNH); Chisos Mts., The Basin, Big Bend National Park, 6 Aug 1937 (K. P. Schmidt), 1 female (FMNH); *Crockett Co.:* 14.3 mi E Sheffield, 11 October 1972 (T. R. VanDevender), 1 female (FSCA); *Presidio Co.:* no specific locality, 2 Dec 1978 (under rock) (W. W. Dalquest), 1 female (OFF); 9 mi E Bandera Mesa, 11 Mar 1975 (W. W. Dalquest), 1 female (OFF); *Terrel Co.:* 5 mi N Sanderson, 15 June 1974 (L. Draper, M. A. Cazier, O. F. Francke), 2 females (OFF); *Val Verde Co.:* 1 mi SSE Langtry, 7 June 1974 (L. Draper, M. A. Cazier, O. F. Francke), 1 female (OFF); 0.5 mi S Langtry, 14 June 1974 (L. Draper, M. A. Cazier, O. F. Francke), 18 males, 19 females (OFF); Langtry, 21 Apr 1973 (no collector), 1 female (OFF); 10 mi W Comstock, E side of Pecos River Bridge on US Highway 90 (among large rocks), 2 Sept 1983 (W. D. and J. C. Sissom), 1 female (WDS); Amistad Reservoir, railroad cuts off US Highway 90 (1000'), 6 Sept 1969 (Cazier, Bigelow), 12 males, 26 females (OFF); Amistad Reservoir, 11 June 1974 (L. Draper, M. A. Cazier, O. F. Francke), 3 males, 5 females (OFF).

Vaejovis decipiens Hoffmann
(Figs. 34-43)

Vejovis mexicanus decipiens Hoffmann 1931: 349, 399-401; 1939: 318.
Vaejovis mexicanus decipiens, Díaz Nájera 1975: 7, 19; *nec* Vásquez 1960: 219-221; Williams 1980: 105-107.

Type data.—Hoffmann's (1931) original description was based on nine specimens: three males, four females, and two juveniles from Batopilas, Chihuahua, Mexico (no date or collector). We have been able to locate and examine only two males permanently deposited in the American Museum of Natural History. One of these, carrying Hoffmann's label, "#1, ♂ type", is considered to be the holotype, and the other a paratype.

Both the holotype and paratype are in good condition. However, the holotype has the left pedipalp loosely articulated at the femur-tibia joint, and leg II loose at the coxa-trochanter joint. The paratype has the right pedipalp loosely articulated at the tibia-chela joint, right leg I loose at the trochanter-femur joint, right leg II loose at the patella-tibia joint, left leg III loose at the coxa-trochanter joint, and left leg IV completely detached.

Distribution.—Known only from the type locality.

Diagnosis.—Adults 50-60 mm in length. Base color dark brown to dark reddish brown with variable underlying dusky markings. Sternite VII with submedian keels obsolete; lateral keels strong, granular to crenulate. Metasoma with ventral submedian carinae on I obsolete or weak, smooth; on II-IV weak, smooth with fine posterior granulation. Pedipalp: tibia with 14 trichobothria (3 *et*, 1 *est*, 2 *em*, 2 *esb*, 5 *eb*, 1 *v*) on external face; fixed finger of chela with primary row of denticles broken into six subrows by five enlarged denticles. Pectinal tooth count 22-25 in males, 21-22 in females.

V. decipiens is most similar to *Vaejovis janssi* Williams from Isla Socorro (Revillagigedo Islands). It may be distinguished from *V. janssi* by pectinal tooth counts of 22-25 in males and 21-22 in females, rather than 21-22 in males and 18-21 in females; and by having the ventral submedian carinae on metasomal segments II-IV smooth with fine posterior granulation, rather than crenulate. Morphometric differences cited by Williams (1980) apparently based on Hoffmann's (1931) measurements of *V. decipiens,* are not consistent or cannot be evaluated due to lack of adult females of *V. decipiens.*

Redescription.—The following redescription is based on adult males. Measurements of the holotype appear in Table 2.

Coloration. Carapace, tergites, and metasoma brown to dark reddish brown with variable underlying dusky markings. Pedipalp femur and tibia same color as body; chela dark reddish brown, usually lighter than body, with yellow brown fingertips. Chelicerae yellow brown with teeth dark brown. Legs yellow brown to brown with variable underlying dusky markings. Venter light brown to medium brown with dusky markings; third sternite with conspicuous yellowish white patch posteromedially. Pectines yellowish white.

Prosoma. Carapace slightly longer than wide. Median ocular prominence slightly raised above surface of carapace. Three pairs of lateral eyes, diameter of posteriormost pair approximately one-half the diameter of preceding pairs.

Anterior carapacial margin obtusely emarginate; median notch distinct, shallow, narrow. Median longitudinal furrow deep, wide at anterior margin; deep, narrow posteriorly. Posterior lateral furrow curved, deep, wide. Entire carapacial surface coarsely granular.

Mesosoma. Tergites I-VI with median carina weak, granular; lateral carinae vestigial. Tergite VII pentacarinate: median carina weak, granular, present on anterior one-third; submedian and lateral carinae strong, serrate. Genital operculi distinctly lobed posteriorly; without median longitudinal membranous connection.
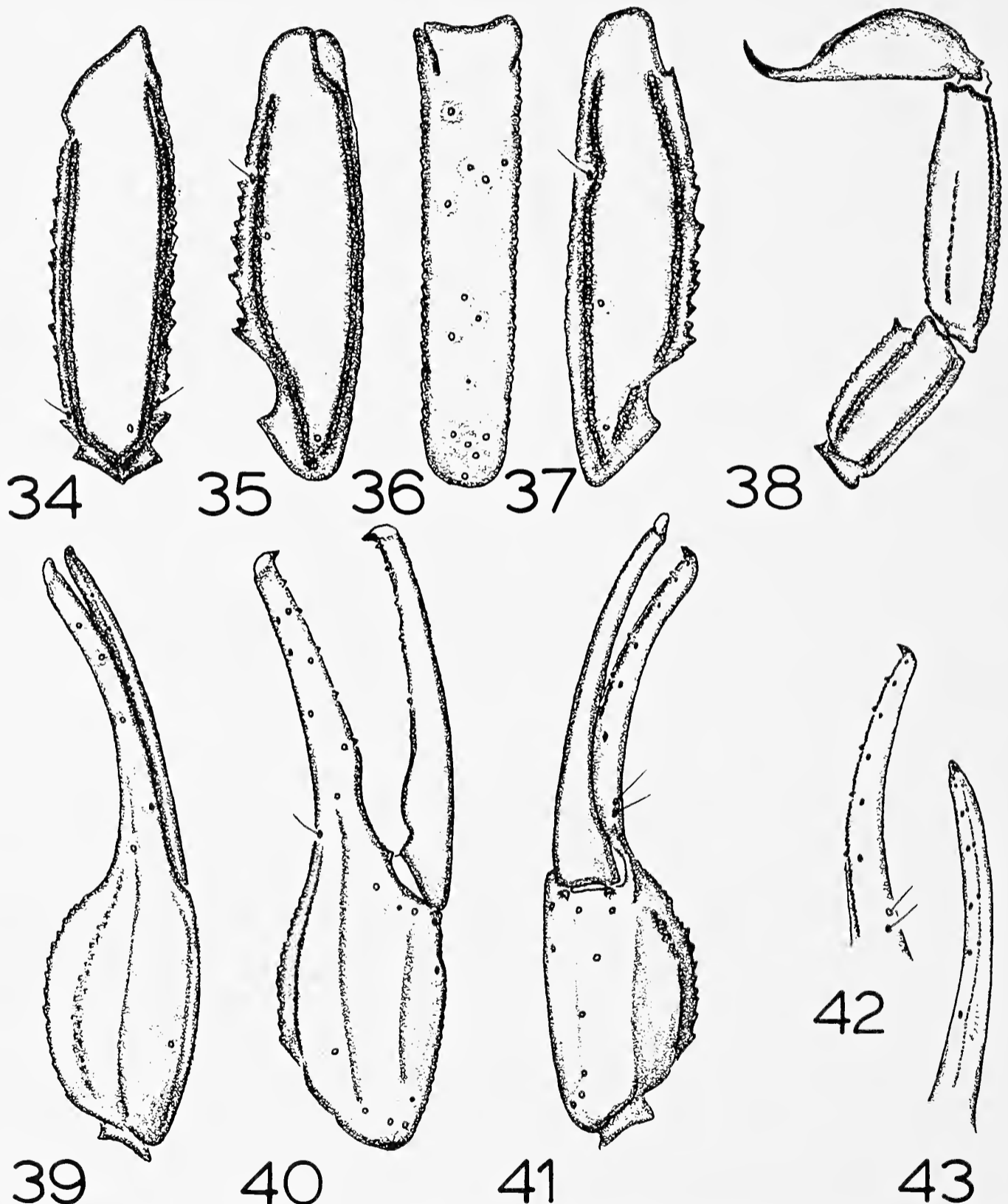
Figs. 34-43.—*Vaejovis decipiens* Hoffmann, holotype male from Chihuahua, Mexico: 34, dorsal aspect of pedipalp femur; 35, dorsal aspect of pedipalp tibia; 36, external aspect of pedipalp tibia; 37, ventral aspect of pedipalp tibia; 38, lateral aspect of metasomal segments IV and V, and telson; 39, dorsal aspect of pedipalp chela; 40, external aspect of pedipalp chela; 41, ventral aspect of pedipalp chela; 42, dentition pattern on fixed finger of pedipalp chela; 43, dentition pattern on movable finger of pedipalp chela.

Genital papillae well developed. Pectinal teeth numbering 22-25. Sternites III-VI smooth, agranular; stigmata approximately 2.5 to 3 times longer than wide. Sternite VII with submedian carinae obsolete; lateral carinae strong, granular to crenulate.

Metasoma. Segments I-IV longer than wide (except sometimes I). Dorsolateral carinae strong, serrate; distalmost denticle distinctly enlarged and spinoid (Fig. 38). Lateral supramedian carinae on I strong, serrate; on II-III strong, serrate to finely serrate; on IV strong, granular to finely serrate; distalmost denticle distinctly enlarged and spinoid on I-III, flared and winglike on IV (Fig. 38). Lateral inframedian carinae on I complete, strong, serrate; on II present on posterior one-third, strong, serrate; on III present on posterior one-fourth, strong, crenulate to serrate; on IV absent. Ventrolateral carinae on I-III strong, finely serrate; on IV strong, finely crenulate to finely serrate. Ventral submedian carinae on I obsolete or weak, smooth; on II-IV weak, smooth, usually with fine serrations on posterior portion. Intercarinal spaces with scattered coarse granules, primarily on dorsal surfaces. Segment V (Fig. 38): Dorsolateral carinae strong, granular. Lateromedian carinae present on anterior three-fourths of segment, strong, granular to finely serrate. Ventrolateral carinae strong, finely serrate (sometimes finely crenulate posteriorly). Ventromedian carina strong, finely crenulate to finely serrate. Intercarinal spaces essentially agranular.

Telson (Fig. 38). Dorsal surface smooth, flattened; ventral surface with irregularly spaced fine granules and punctations.

Chelicera. Dentition typical of genus, with well developed serrula on ventral margin of movable finger.

Pedipalp. Femur (Fig. 34) tetracarinate: Dorsointernal and ventrointernal carinae strong, serratocrenulate. Dorsoexternal carina strong, serrate. Ventroexternal carina strong, composed of large, irregularly spaced sharp granules. Internal face with large, scattered, conical granules; ventral face with moderate granulation basally; dorsal face smooth. Orthobothriotaxia C (Vachon 1974).

Tibia (Figs. 35-37) tetracarinate: All keels strong, crenulate to serratocrenulate. Internal face with moderate basal tubercle plus series of large, conical granules; external face granular; dorsal and ventral faces smooth. Orthobothriotaxia C (Vachon 1974). Trichobothrium em_2 basal to or in juxtaposition with em_1.

Chela (Figs. 39-43). Dorsal marginal carina strong, granular. Dorsal secondary carina weak, smooth to finely granular. Digital carina moderate, smooth to finely granular. External secondary carina weak, smooth to finely granular. Ventroexternal carina moderate, granular. Ventromedian carina weak, smooth. Ventrointernal carina weak to moderate, finely granular. Dorsointernal carina strong, composed of large, sharp granules. Dentate margin of fixed finger with primary row divided into six subrows by five larger granules; six internal accessory granules, of which distalmost not paired with larger granule in primary row (Fig. 42). Dentate margin of movable finger with primary row divided into six subrows by five larger granules; distal subrow with only one or two granules; seven internal accessory granules, of which distalmost and basalmost not paired with larger granule in primary row (Fig. 43). Both chela fingers terminating in large, sharp, clawlike tooth bearing distally an oblong whitish cap. Orthobothriotaxia C (Vachon 1984).

Legs. Arrangement of setae, spines, and spinules as in *V. nitidulus;* seta formula given in Table 3.

Variation.—Male pectinal tooth counts varied as follows: 1 comb with 22 teeth; 3 combs with 23 teeth; 3 combs with 24 teeth; 1 comb with 25 teeth. Only a single female (a juvenile) was available for study; its pectinal tooth count is 21-21. Hoffmann (1931) reported pectinal tooth counts of 22 for the females he studied.

Juveniles differ from adults in general coloration. In juveniles the body is yellow brown with dusky underlying markings: the tibia and chela of the pedipalp are orange brown; the metasoma is yellow brown basally (segments I-III) and gradually becomes orange brown distally (segments IV-V); the telson is orange brown.

Remarks.—Hoffmann (1931), in his original description, noticed the similarity between *V. decipiens* and the *V. nitidulus* group, but was reluctant to group it with those taxa because its ventral submedian keels were distinctly developed (not obsolete). As a result, he considered it to be a subspecies of *V. mexicanus.* In possessing the enlarged terminal denticles on the pedipalp chela fingers (each with a distinct whitish cap), it is clear that *V. decipiens* is a member of the *nitidulus* group and not a subspecies of *V. mexicanus.*

Specimens examined.—MEXICO: *Chihuahua:* Batopilas (no date or collector), 1 male holotype (labeled "#1, male type" by Hoffmann), 1 male paratype (AMNH); Barranca de Rio Batopilas, 120 km S Creel (approx. 1000 m), 26 Feb. 1966 (W. Bell, J. Reddell), 2 males, 3 juvs. (AMNH).

Vaejovis minckleyi Williams
(Figs. 44-53)

Vejovis minckleyi Williams 1968: 21-24, figs. 11-12; Soleglad 1972: 180, 1973:357.
Paruroctonus minckleyi, Stahnke 1974: 138.

Type data.—Holotype male from 5.3 km NW Cuatro Cienegas, Coahuila, Mexico, 3 January 1965 (W. S. Parker). Paratype male from second canyon from the eastern tip of San Marcos Mountain, 12 km SW Cuatro Cienegas, 3 January 1965 (W. L. Minckley, W. S. Parker, and W. K. Taylor). Deposited in the California Academy of Sciences; not examined.

Distribution.—*Vaejovis minckleyi* is apparently endemic to the Cuatro Cienegas Basin, Coahuila, Mexico. This remarkable intermontane valley in the Sierra Madre Oriental contains a highly diversified biota with a conspicuous percentage of endemic taxa, a considerable portion of which are Pleistocene relicts or older (Minckley 1969).

Diagnosis.—Adults 60-70 mm in length. Base color yellow; pedipalp chelae yellow orange with reddish brown fingers. Sternite VII tetracarinate: submedian keels faint, smooth; lateral keels strong, crenulate. Metasoma: all segments distinctly longer than wide; ventrolateral carinae on I-IV strong, serrate; ventral submedian carinae on I-III weak to vestigial, smooth, on IV weak, granular. Distalmost denticle of dorsolateral carinae of I-IV not distinctly larger than others or spinoid (Fig. 48). Pedipalp (Figs. 44-47; 49-53): tibia with 15 trichobothria (3 *et,* 1 *est,* 2 *em,* 3 *esb,* 5 *eb,* 1 *v*) on external face (Fig. 46): fixed finger of chela with primary row of denticles broken into six subrows by five enlarged denticles (Fig. 52); fixed finger distinctly longer than carapace; keels of

dorsal and external surfaces of chela strong in males (moderate in females), granulose (Figs. 49-51). Pectinal tooth count 31-32 in males, 28-29 in females.

Vaejovis minckleyi is a very distinctive member of the *nitidulus* group. In pectinal tooth counts and tibial trichobothrial pattern, it most closely resembles *V. nitidulus*. However, it may be easily distinguished from that species by having six subrows of granules on the chela fingers rather than seven subrows; by having distinct ventral submedian carinae on metasomal segments I-IV, rather than
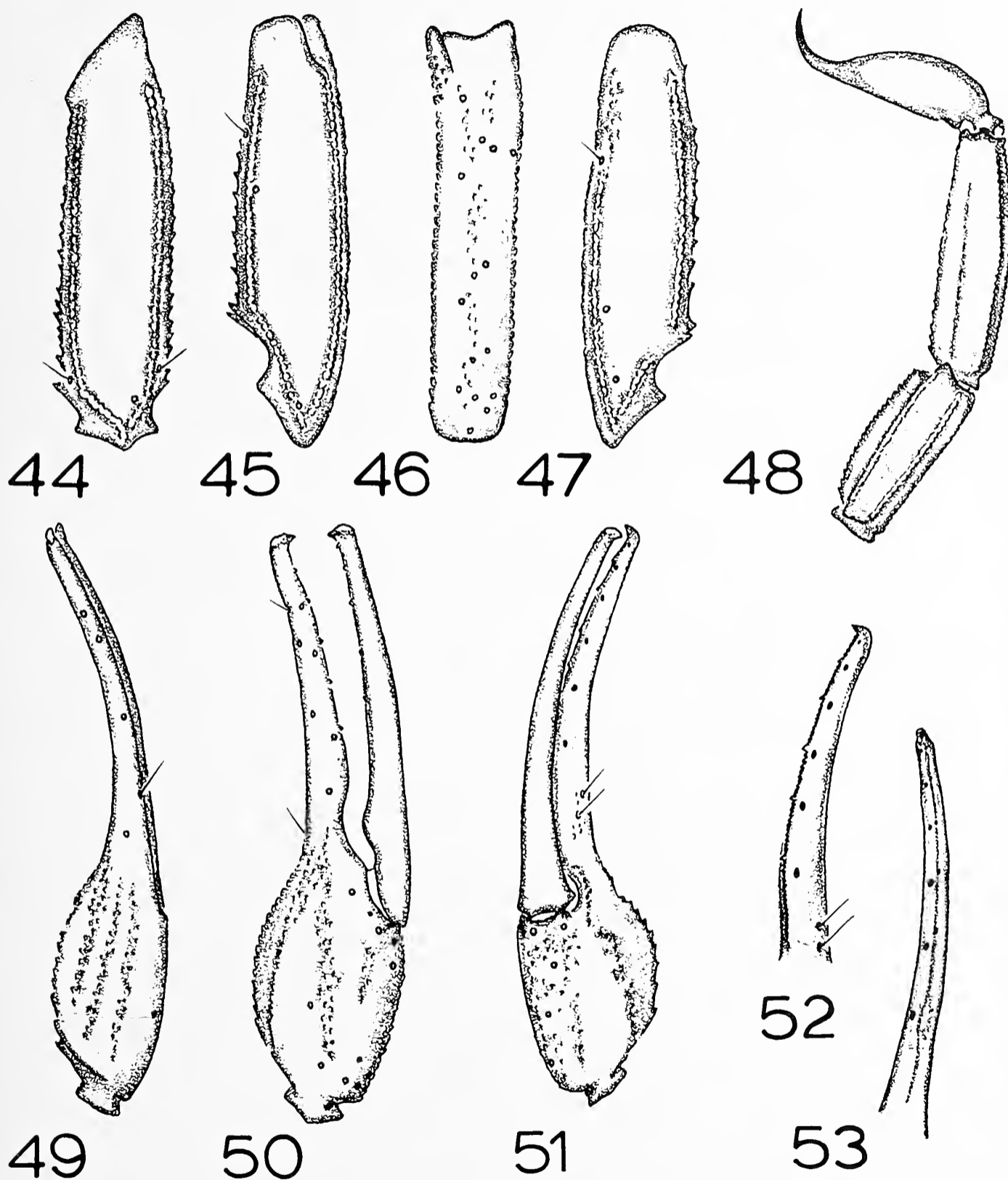
Figs. 44-53.—*Vaejovis minckleyi* Williams, male from Coahuila, Mexico: 44, dorsal aspect of pedipalp femur; 45, dorsal aspect of pedipalp tibia; 46, external aspect of pedipalp tibia; 47, ventral aspect of pedipalp tibia; 48, lateral aspect of metasomal segments IV and V, and telson; 49, dorsal aspect of pedipalp chela; 50, external aspect of pedipalp chela; 51, ventral aspect of pedipalp chela; 52, dentition pattern on fixed finger of pedipalp chela; 53, dentition pattern on movable finger of pedipalp chela.

obsolete carinae; by having all metasomal segments longer than wide; and by having granulose carinae on the dorsal and external surfaces of the chela, rather than weak, smooth carinae.

Variation.—Only one male and one female (both topotypes) were studied.

Remarks.—Stahnke (1974) considered *V. minckleyi* to be a member of the genus *Paruroctonus,* apparently because the distalmost denticles of the dorsolateral carinae of metasomal segments I-IV are not enlarged and spinoid (Fig. 48). We interpret this condition to result from the elongation of the metasomal segments (as seen in other *nitidulus* group species and also in *Syntropis*), and it does not indicate phylogenetic affinity with *Paruroctonus.* In addition, *V. minckleyi* lacks denticles or scallops on the inferior margin of the movable cheliceral finger and has the anterior margin of the carapace distinctly notched. Both of these characteristics exclude it from *Paruroctonus.* The structure of the pedipalp chelae and the trichobothrial pattern of the tibia and chela, however, indicate that *V. minckleyi* is a member of the *nitidulus* group of *Vaejovis.*

Specimens examined.—MEXICO: *Coahuila;* Cuatro Cienegas Basin, large canyon ½mi E of W tip of Sierra San Marcos, 12 May 1968 (S. C. Williams, M. Bentzien), 1 male, 1 female (OFF).

ACKNOWLEDGMENTS

Parasitology, University of California, Berkeley; W. H. Hutchinson, University of Mississippi Medical Center, Jackson, for information about the collection of the late H. L. Keegan; James R. Reddell, Texas Memorial Museum, the University of Texas, Austin; C. Carlton, University of Arkansas Agricultural Experiment Station; and M. Alvarez del Toro, Instituto de Historia Natural, Tuxtla Gutierrez, Chiapas, Mexico.

For correspondence and cooperation during the course of this study, we wish to acknowledge Max Vachon and M. E. Soleglad. James C. Cokendolpher provided stimulating taxonomic discussions for the senior author, and his comments are sincerely appreciated. For reviewing the manuscript we are grateful to M. E. Soleglad and S. C. Williams. To the friends and colleagues who assisted in the field, we express our warmest appreciation: Mont A. Cazier, Linda Draper (neé Welch), Joe Bigelow, Neal McReynolds, Chris Colwell, Chris Myers, Lynne Born, and John Sissom.

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RESEARCH NOTES

STICKY BALLS IN WEBS OF THE SPIDER
MODISIMUS SP. (ARANEAE, PHOLCIDAE)

Sticky or viscid balls have been found on thread of the webs of araneid, theridioso-matid, anapid, symphytognathid, theridiid, nesticid and linyphiid spiders; these families are all in the superfamily Araneoidea, and it has recently been proposed that the balls represent a synapomorphy for this group [Coddington, J. in press, In: Orb Webs (W. Shear, ed.). Stanford University Press; see this article also for a review of evidence].

This note documents the presence of balls in the webs of *Modisimus* sp. of the family Pholcidae, which is not related to the araneoids. It also shows that they are liquid and water-soluble and that they are produced during a particular stage in web construction.

Web construction was elicited by damaging webs. Some samples ("controls") were taken from undisturbed webs (presumably built the night before), whereas others were taken after interrupting spiders which were at various stages of web construction. The edges of a glass microscope slide were covered with vaseline, and the slide was held against one sector of the web which was cut free from the rest with scissors. Only one sample was
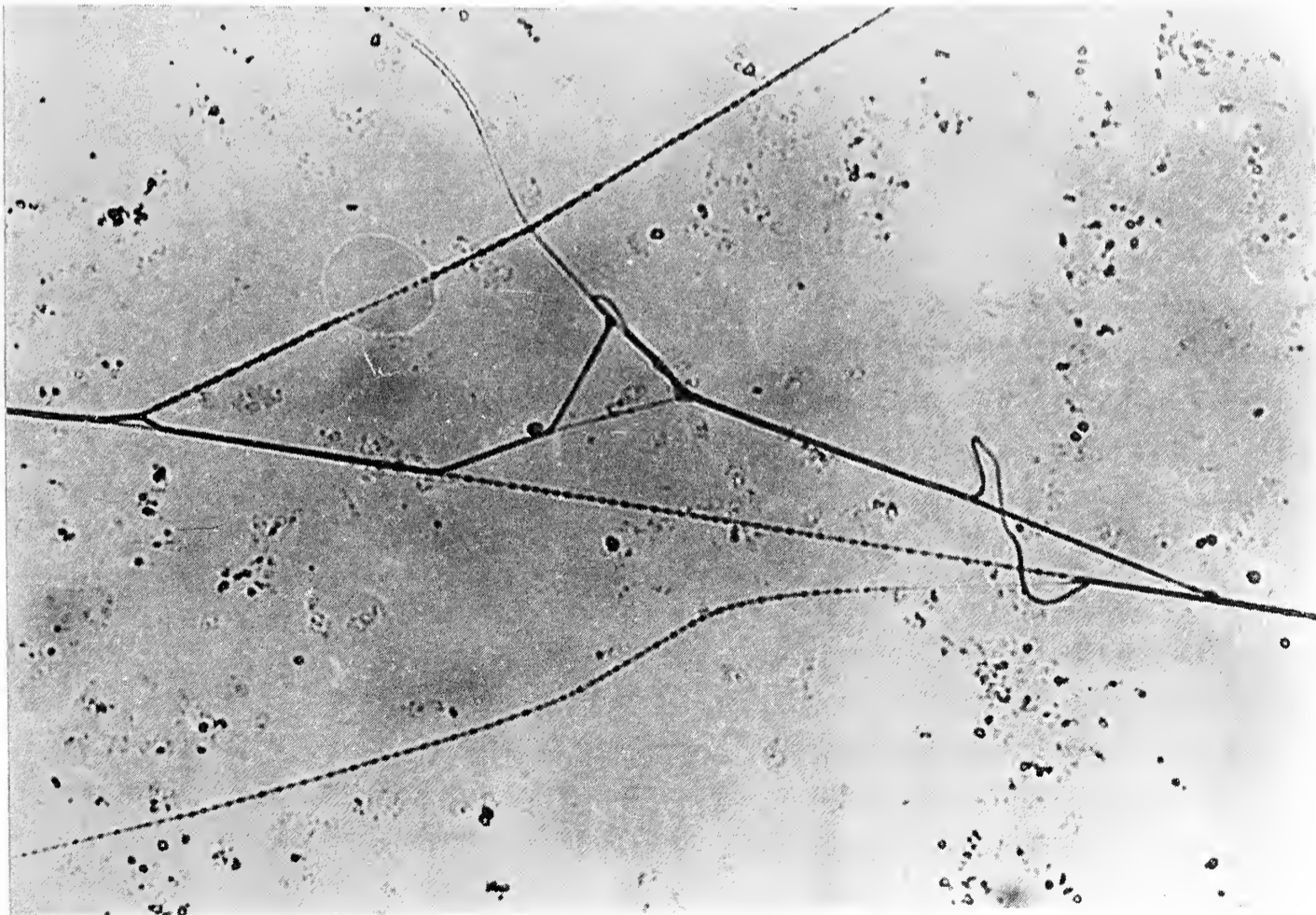
Fig. 1.–Photograph of a line with globules, from a mature female of *Modisimus* sp.

taken per web. The threads were observed under a compound microscope, in some cases several days after the web was built.

Voucher specimens of the spiders are deposited in the collection of the Escuela de Biología of the Universidad de Costa Rica, and in the Museum of Comparative Zoology in Cambridge, Mass.

In order to determine the relative numbers of different kinds of lines present on each, five surveys were made from left to right across the entire width of the slide at a magnification of 40X. Each time a new line was encountered it was placed at the extreme left of the field and all lines present in the field were classified into four categories: (a) thick without balls; (b) thin without balls; (c) thick with balls; and (d) thin with balls (see Fig. 1). The slide was then moved on until the thread at extreme right was at the left of the field. Then the slide was moved onward until the next thread was encountered, and the process was repeated. A total of 14 sample fields was examined in each pass across the slide, giving a total of 70 samples (5 x 14) per slide.

At least four types of line were seen in finished webs. In some cases an apparently "thick" line split into thin lines, so "thick" means, at least sometimes, several thin lines together.

The spiders' construction behavior had tow distinct stages: (1) " Frame lines." The spider laid most lines at the edge of the web, expanding the area covered. Every attachment of the line being laid to other lines was made just posterior to the point where one leg III held it. (2) "Fill In." The spider walked back and forth across the area already covered, using its legs IV to push the line it was producing upward against the network of lines already in place. Only when it reached the edge of the web did it attach as above, using one leg III and touching the other line with its spinnerets. Once stage 2 had begun the spider did not return to stage 1 behavior. The lines laid in two stages were different, thick lines without balls being more common in stage 1 (Table 1).

The liquid nature of the balls was demonstrated by pressing lines with balls into contact with the slide, and noting that they spread out to form puddles.

The balls were shown to be water soluble just like those of at least some araneoid spiders (Kavavaugh, E. S. and E. K. Tillinghast. 1979. J. Morph., 160:17-31) by placing drops of water on slides; all of the balls were gone from the threads when the droplet evaporated.

The wrapping thread of some theridiid spiders is covered with viscous balls, but samples of wrapping thread of *Modisimus* sp. showed no balls.

The liquid nature of the balls and the fact that they had not evaporated even days after being produced suggest that they are viscous and function by causing prey to adhere

Table 1.–Percentage of types of threads present during different stages of web construction in webs of *Modisimus* sp.

	Thin Thread		Thick Thread	
	with balls	without balls	with balls	without balls
Stage 1. (<25 lines)	0	15.0	0	85.0
Stage 2. (>25 lines)	40.7	48.7	6.9	3.7
Web repair completed	3.8	73.4	3.5	29.4
Completed webs (control)	41.8	48.4	4.9	4.9

to spider's web. The stickiness is only slight however, and attempts to localize ball-bearing threads in completed webs by dusting the webs with talcum powder and then jarring the web to knock the powder from non-sticky lines resulted in the powder being dislodged from nearly all the threads. The relative small sizes of the balls and their often relatively dispersed nature may account for this. The attack behavior of *Modisimus* sp. is extremely rapid, and perhaps only relatively brief retention is necessary to insure prey capture.

The prevalence of thick lines in the first stage of web buildings suggests that this stage serves to establish a scaffolding or frame for the rest of the web. The high frequency of thin threads both with and without balls in finished webs suggest that the webs may trap prey by entanglement as well as by adhesion.

The reason for the lower frequency of sticky balls in repaired webs as compared to controls is not clear. Possibly it is related to a lack of material from which sticky balls are made, or the control webs may contain threads that have accumulated over a period of days.

The question of whether the pholcid balls are homologus with those in araneoid webs cannot be answered at the moment. The pholcid *Pholcus phalangioides* is known to possess two pairs of ampullate (non-sticky silk) glands (Kovoor, J. 1977. Ann. Biol., 16:7-171) but their other silk glands are difficult to homologize with the silk glands of other spiders (Apstein, C. 1889. Arch. Naturgesch., 55:29-74) so the glandular source of the balls cannot be determined.

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ARBORINE AND METHAQUALONE ARE NOT SEDATIVE IN THE WOLF SPIDER *LYCOSA CERATIOLA* GERTSCH AND WALLACE

Glomerin and homoglomerin, two quinazolinone alkaloids in the defensive secretion of the pill milliped, *Glomeris marginata*, produce delayed sedation of prolonged duration in wolf spiders (*Lycosa* spp.). The compounds are sedative at small doses (1-7 μg per spider), representing but a fraction of the total secretory output of a medium sized milliped (Carrel and Eisner 1984). Glomerin and homoglomerin are structurally related to arborine, a plant natural product, and to methaqualone, a synthetic drug. Both arborine and methaqualone are sedative to vertebrates (Dey and Chatterjee 1967, Inaba et al. 1973), which suggests that they might also be sedative to spiders. We here present evidence indicating that this hypothesis is incorrect, since neither arborine nor methaqualone given in large doses produced sedation (= hypnosis) in the wolf spider, *Lycosa ceratiola* Gertsch and Wallace.

Arborine, also known as glycosine, was synthesized using the procedure described by Kametani et al. (1977). Chromatography of the reactant residue on a silica gel column eluted with ethylacetate-ethanol (4:1, v/v) yielded pure arborine, whose melting point and UV, IR, NMR, and mass spectral data were identical with published values (Chakravarti et al. 1961, Kametani et al. 1977). Methaqualone hydrochloride (Parest-200®, Parke-Davis and Co., Detroit, Michigan) was locally purchased. Dosages of methaqualone were calculated as the HCl-free base (0.875 times the weight of the methaqualone-HCl).

Lycosa ceratiola, stemming from the same population at the Archbold Biological Station near Lake Placid, Florida, as those used to test glomerin and homoglomerin, were maintained as described by Carrel and Eisner (1984). As before, spiders were of relatively uniform body size ($\bar{x}$ ± S.E.M.; body mass = 344 ± 13 mg).

The sedative potencies of arborine and methaqualone in spiders were measured by injection. In these tests (N = 140, including 20 controls), essentially the same as in those for glomerin and homoglomerin (Carrel and Eisner 1984), injection (5 μl) was accomplished with a micrometer-activated syringe into the abdomen of the spider. Arborine and methaqualone as sonified suspensions were injected at six dosages (N = 10 spiders per dosage) in the range of 1-50 μg per spider. Spider saline (Rathmayer 1965) containing 1% (w/v) methylcellulose was used as sample carrier and was itself tested as the control. Spiders were checked for sedation at 4, 12, 24, and 48 hours after injection. The criterion for sedation, as in earlier tests, was the spider's inability to right itself promptly when flipped on its back with a curved glass rod.

None of the *L. ceratiola* became sedated and none died within 48 hours after injection of 1-50 μg of arborine or methaqualone. Control spiders also showed no behavioral abnormalities. Maximum doses of either compound used in our study ($\sim$ 150 mg/kg spider body weight) were large compared with doses of these compounds that are sedative/ hypnotic in humans, mice, and rats (Gujral et al. 1955, Swift et al. 1960, Wheeler 1963, Dey and Chatterjee 1967, Mukherjee and Dey 1970, Hardtmann et al. 1971, Ochiai et al. 1972, American Medical Association 1980). Hence, the absence of sedation in wolf spiders treated with arborine or methaqualone definitely did not result from using dosages of the compounds below their established pharmacological ranges.

Our findings cannot be explained by a general insensitivity of spiders to sedative drugs. Phenobarbital (Luminal) and diazepam (Valium), two sedatives commonly used by humans, each in low doses (10-100 mg/kg) cause the cross-spider, *Araneus diadematus,* to curtail construction of its orb web (Reed and Witt 1968). Both phenobarbital and diazepam bear little structural resemblance to the quinazolinones we tested and preliminary evidence indicates that, at least in mammals, they act *via* different neurobiochemical mechanisms to depress the central nervous system (Mukherjee and Dey 1970, Smith 1977, Martin 1982). We think the ineffectiveness of some, but not all sedative drugs in spiders likely is explained by basic and as yet undescribed neurophysiological differences between spiders and mammals more than it is by the vagaries of various drug bioassays.

Our study confirms the long standing view of pharmacologists (Witt 1968, 1971) that spiders are imperfect substitutes for humans for the characterization of psychoactive drugs. Our findings also illustrate how little is known about the short and long term responses of spiders to pure substances, especially natural products contained in their prey. We suspect that many dietary chemicals may alter a spider's physiological state, causing changes—ranging from profound to subtle ones—in feeding, reproduction, or maintenance activities. The chemical ecology of spiders, an emerging field of study, is bound to be diverse and complex, perhaps rivaling that of herbivorous insects, about which so much has recently been written (Rosenthal and Janzen 1979, Harborne 1982).

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PARASITIC FUNGI AS A MORTALITY FACTOR OF SPIDERS

Several times during arachnological studies in Panama I found dead spiders covered with fungi. As the notes which record fungi attacking spiders are scattered and few in number, my observations are reported here in detail.

The field studies were carried out in Panama (Province of Panama) at three locations: On Pipeline Road near Gamboa; on Cerro Galera, a hill at the Pacific coast near Arraijan; on the road from El Llano to Carti, km 13. The first two areas represent typical tropical moist lowland forest, the third premontane moist forest. In Panama, there is a distinct seasonality with a dry season (January to April), and a wet season (May to December). Annual rainfall is more or less restricted to the wet season and amounts to 2000-3000 mm per year. Fungus-covered spiders were found only from August to October, i.e. in the second and wetter part of the wet season, though field-work was carried out during the whole year.

Immature specimens of the deuteromycete *Nomuraea*, probably *N. atypicola* (Yasuda), were found on the araneids *Argiope argentata* (F.) (three observations), *A. savignyi* Levi (one observation) and *Nephila clavipes* (L.) (two observations). A compact white mycelial stroma was observed on the opisthosoma of the spiders but fruiting structures (conidiophores) were lacking (Fig. 1). Fungal colonies are initially white but typically become purple as a powdery spore bloom develops. The heavy overgrowth of a mucoraceous fungus ("bread mould") is characteristic of recently invaded or badly dried immature (= non-mummified) specimens (Evans, pers. comm.). On the araneid *Eriophora fuliginea* (C. L. Koch) and an unidentified web building spider (one observation each) the fungus overgrowth was also immature but could tentatively be identified as the *Granulomanus* state of a *Gibellula* sp. (Deuteromycetes).

All araneids were found hanging with their legs in a relatively normal position on the hub of the orb web. The web, however, was always reduced to a silken platform with a network of irregular threads, similar to the moulting webs of orbweavers (Fig. 2). Because old spiders build orb webs of increasing irregularity but never without sticky spiral (Nentwig, unpubl.) this web type indicates that the fungi probably did not attack a dead spider but rather killed a living one. The period between infection and death of the spider must have been at least two days to enable the spiders to build this specific type of web. It is not possible that these webs represented real moulting webs since no exuviae were found and all the spiders were full-sized adult females.

An overview of insect-parasitism among fungi has been presented by Madelin [1968, pp. 227-238, *In:* The Fungi (G. Ainsworth and A. Sussmann, eds.). Academic Press, New York, Vol. 3]. Most ectoparasites are Laboulbeniales (Ascomycetes), only a few dozen are Deuteromycetes, most records originate from tropical and subtropical countries. These include the *Nomuraea (= Spicularia)* and *Gibellula* species which are mentioned here and are well-known to parasitise spiders [Samson and Evans 1977, Proc. Konink. Nederland. Akad. Wet., Amsterdam, ser. C, 80(2):120-133]. Further records of fungi which infect spiders include *Engyodontium* species (Hyphomycetes) (Gams, De Hoog and
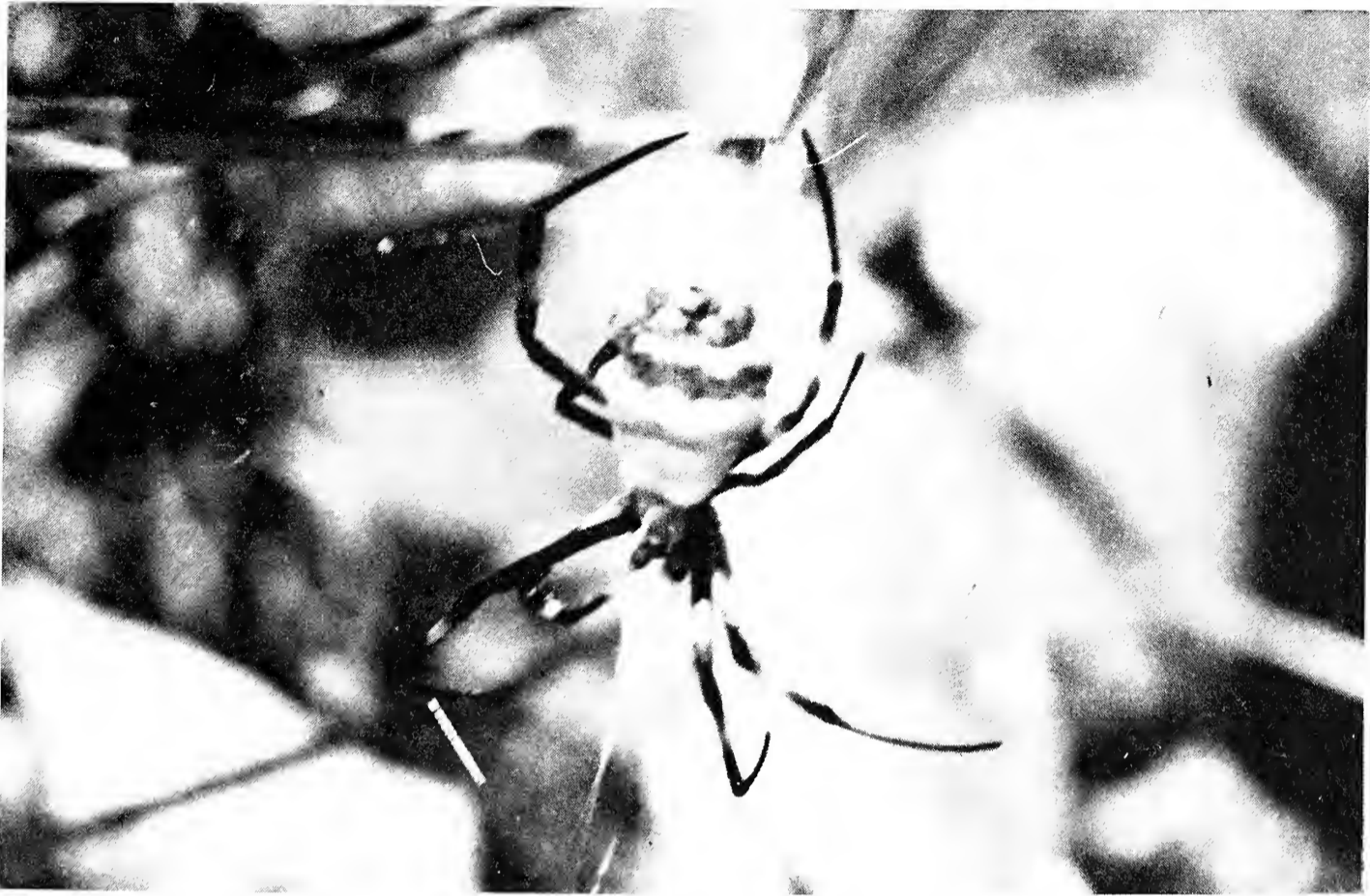
Fig. 1.—A dead *Argiope argentata* (Araneidae) covered with the white mycelial stroma of the deuteromycete *Nomuraea* cf. *atypicola.*
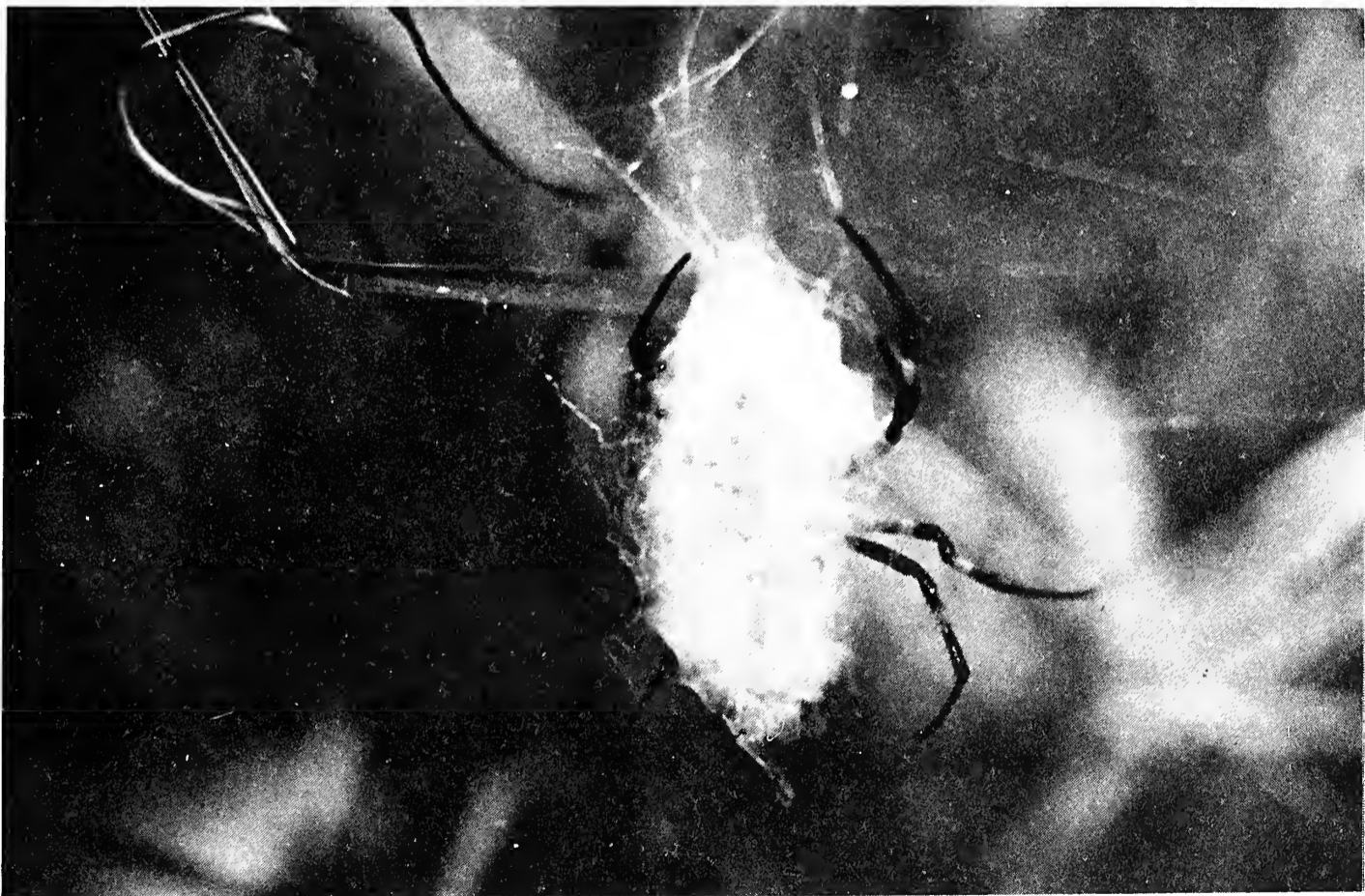
Fig. 2.—The web of a dead *A. argentata*, infected by *N.* cf. *atypicola*, is reduced to a silken platform and irregular suspension threads.

Samson 1984, Persoonia, Leiden, 12:135-147) and the ascomycete *Cordyceps* sp. which had been found on dead linyphiids on the arctic island Jan Mayen (Bristowe 1941, The comity of spiders, London, The Ray Society, vol. 2:332-333). In India, the endoparasitic deuteromycete *Beauveria alba* has been found in a theridiid (Chandrashekhar, Suryanarayanan and Narasimham 1981, Curr. Sci., Bangalore, 50:248). Apart from the last two cases, none of the several dozen records in the mycological literature mentioned here gives an identification of the spiders, with the exception of one reference to an ant-mimicking Salticidae by Samson and Evans (1977) and one reference to an "Opilionid spiders" by Gams et al. (1984). It is possible that the exposed posture of the araneids mentioned here facilitates infection by airborn fungus spores. This indicates perhaps that entomophagous fungi are an important mortality factor among spiders, especially web building species in the tropics.

I thank Dr. H. C. Evans, Commonwealth Mycological Institute, Kew, England, for the identification of the fungi and for helpful comments.

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NOMENCLATURAL NOTES

On 2 April 1985 the Commission gave six months notice of the possible use of its plenary powers in the following cases:

Z. N. (S.) 1481—*Argyrodes* Simon, 1864 and *Robertus* O. Pickard-Cambridge, 1879 (Arachnida, Araneae): proposed conservation by the suppression of *Argyrodes* Guénée, 1845 and *Ctenium* Menge, 1871.

Z. N. (S.) 2484—*Olpium* L. Koch, 1873 (Arachnida, Pseudoscorpionida, Olpiidae): proposed designation of type species and related problems.

Z. N. (S.)2480—*Erigone* Audouin, 1826 (Arthropoda, Araneae): proposed designation of type species.

The Commission welcomes comments and advice from interested Zoologists (Bull. Zool. Nomencl., vol. 42 pt. 1).

BOOK REVIEW

Roberts, M. J. 1985. The Spiders of Great Britain and Ireland. Harley Books, Martens, Great Horkesley, Colchester, Essex, C06 4AH England. Vol. I, £45.00, 229 pp. 100 textfigs., 1985. Vol. III, £55.00, 256 pp., 237 plates of colored drawings, 1985.

Besides a similarity in titles between Blackwall's great work and that of Roberts' there is also the similarity in page size, both being much larger than the usual. The 212 by 290 mm page of Roberts' is just about twice that of the usual manual size. The recently published "Spiders of the Britain and Northern Europe" by Jones, and the "Spiders of the World" by the Preston-Mafhans are each about half the page size of the Roberts' work.

In volume I the first 30 pages are devoted to spider morphology, followed by general information about spiders. The rest of the volume is devoted to descriptions of those spiders belonging to the 27 families: Atypidae to Theridiosomatidae. The description of the remaining family, the Linyphiidae *(sensu lato)* is reserved for volume II, due to appear in 1986.

Most of the keys are of the standard dichotomous type. However, the key to the families is not a completely dichotomous one, e.g., there are 12 alternatives in "couplet" 7, and four each in "couplets" 6 and 10. There is merely a statement of the chief characters for these taxa. Moreover, there is no key to the genera of Lycosidae, but rather a listing of the nine genera and the characters of each to be noted.

Interspersed throughout the text the author has included some "Taxonomic notes" from which the reader can see that the author is well versed in current and recent literature. For example, in these notes he explains why he does not use either of the names *Trachyzelotes* and *Urozelotes* both accepted recently by Platnick and Shadab. For the most part he does not follow Lehtinen (1967) but does accept the latter's generic name *Nigma* in the Dictynidae. The three orb-weavers, originally in *Araneus* (or *Epeira*) referred to by Emerton as the three house *Epeira's*, but more recently shown to belong to *Nuctenea* Simon are by Roberts placed, following Grasshoff, in *Larinoides* Caporiacco.

For each genus a section is given over to "distinguishing the species," followed by a section indicating the distribution in the British Isles. For those spiders in which there are intraspecific variations in body size, carapace markings, and in genitalia, such as in *Pardosa*, the author supplies lengthy comments in his "taxonomic notes." There may also be an assortment of illustrations. All this, together with the excellent drawings should facilitate identification. Although most of these drawings appear as black and white textfigures of genitalia, three of the latter are in color, and some are of bodies, legs, and abdominal patterns.

In volume III all of the plates are in color. Most show a dorsal view including the legs of both sides, of one spider. But a few plates show at a smaller scale the bodies only of four different spiders. Accompanying each of these figures is an inked outline showing the spider's actual size. The plates 1-157 belong with the descriptions given in volume I; the remaining 80 plates are of the Linyphiidae. The author's stated intent is to facilitate identification of specimens and he succeeds admirably. Although the author is not an araneologist of long standing any Britisher using this fine work will find himself deeply in Roberts' debt.

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GRANTS-IN-AID FOR RESEARCH

Grants-in-Aid for research on Arachnida (excluding Acarina) and Myriapoda are made available to students and researchers through the *"Exline-Frizzell Fund for Arachnological Research"* of the California Academy of Sciences. Applications, which will be evaluated by the American Arachnological Society and the Department of Entomology, California Academy of Sciences (Golden Gate Park, San Francisco, California 94118-9961, phone [415] 221-5100), may be submitted to the latter at any time. Application forms may be obtained upon request. Awards will be made upon the approval of the Academy's Director shortly after March 1 and September 1 yearly. Grants will normally not exceed $750. The *Exline-Frizzell Fund* may be used for fieldwork, museum research (including travel), expendable supplies, and costs of publications (including artwork).

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.

Manuscripts for *THE JOURNAL OF ARACHNOLOGY* are acceptable only from current members of the Society, and there are no page charges. Detailed instructions for the preparation of manuscripts appear in the Fall issue of each year, and can also be obtained from the Editor and the Associate Editors. Manuscripts that do not follow those instructions will be returned to the author(s) without benefit of review. Manuscripts and all related correspondence must be sent to Dr. William B. Peck, Associate Editor, Department of Biology, Central Missouri State University, Warrensburg, Missouri 64093, U.S.A.

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THE JOURNAL OF ARACHNOLOGY

PREY CAPTURE AND STINGING BEHAVIOR IN THE EMPEROR SCORPION, *PANDINUS IMPERATOR* (KOCH) (SCORPIONES, SCORPIONIDAE)

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ABSTRACT

Prey capture behavior in the emperor scorpion, *Pandinus imperator,* is described and an ontogenetic change in prey capture behavior reported. Young scorpions up to 6 cm in length stung nearly all prey items. At 10 cm in length these scorpions stung only large, violently struggling prey items. Adult scorpions never used the sting, dispatching prey with the pedipalps and apparently refusing prey too large to subdue with the pedipalps alone. Prey capture behavior in *P. imperator* is compared with other species and the possible survival values of sting use is discussed.

INTRODUCTION

The stinging behavior of scorpions is well known as a means of prey capture and defense. However, the willingness to use the sting appears to vary greatly with the species. The emperor scorpion, *Pandinus imperator* (Koch), is one of the largest living scorpions, reaching a total length of over 17 cm. Inhabiting tropical west Africa, it is a forest dwelling species (Cloudsley-Thompson 1958).

During feeding captive adult emperor scorpions were never observed to sting their prey (usually common house crickets, *Acheta domesticus* Linnaeus). In the fall of 1980 one of the scorpions gave birth to six young. Interesting was the fact that the mother scorpion had been individually caged, without contact with other scorpions, for at least two years prior to giving birth. This suggests that sperm retention or some type of developmental interruption can occur in this species. The mother died of unknown causes soon after giving birth and subsequently only two young survived. The young scorpions, in direct contrast to the adults of their species, stung their prey at every opportunity, often stinging crickets 2 or 3 times. As they grew larger this behavior waned, until at some 6-8 cm in length they no longer used their sting on crickets.

Having observed this declining use of the sting with growth, it was decided to explore under what, if any, conditions the sting would be employed in prey subdual. Various sizes of prey items were offered to the scorpions, to test the idea that prey over a certain size threshold would stimulate sting use.

METHODS

Seven individuals of *P. imperator* were maintained in 32 cm X 7 cm terraria with 1-2 cm sanitary processed ground clay (Hartz® cat litter) as substrate. A bottle cap containing water was the only cage furnishing. Five individuals were adults at least four years of age and ranging form 14 cm to 17 cm in length (measured from tip of chelicerae to tip of telson). Adults were housed individually. Two individuals were 2.5 years of age and 10 cm in length. These were sibling littermates and were housed together. Temperatures during the three month study period ranged from 16-26° C, varying with outside temperature. No artificial sources of heat or light were provided. Various sizes of the common house cricket, *A. domesticus,* and the common house mouse, *Mus musculus* Linnaeus, were offered to the scorpions as prey. Time between feedings was generally one week.

RESULTS

Table 1 shows the results of 35 feeding trials with mice. In four trials the sting was used, in one trial there was an unsuccessful attempt to sting, in 24 trials the prey was subdued without using the sting, and in six trials the scorpion refused to feed. All four instances of sting use were by the smaller, younger scorpions. In no instance did the large adult scorpions attempt to sting. Moreover, none of these scorpions stung crickets of any size, generally devouring them alive. Mice which were not stung were killed by the crushing action of the pedipalps, except in two instances where very small mice were devoured alive.

A typical encounter was as follows (terminology after Bub and Bowerman 1979). Upon opening the terraria the scorpion would either back into a corner with the legs and pedipalps retracted, making itself as small as possible, or would assume an alert stance in which the scorpion is supported above the substrate by the legs, the pedipalps are extended anteriorly, and the metasoma is curled over the back. Initially the pedipalps would often be raised 1-2 cm above the substrate. Upon introducing the mouse and closing the terraria the alert stance would usually be modified by placing the movable fingers of the pedipalpal chelae and the pectines in contact with the substrate. If the scorpion had cowered in a corner an alert stance would be assumed a minute or two after the terraria was closed with the mouse inside.

Next the scorpion orients, directing its anterior aspect towards the prey. Orientation occurred only when the prey was active, the scorpion seemingly being unable to orient if the mouse remained motionless. The scorpion would next approach to within 5-10 cm of the prey. During orientation and approach the pedipalpal chelae and the pectines are raised off the substrate, only to be lowered again when the scorpion halts its progress.

Finally there occurs the attack and grasp attempt, in which the scorpion rushes at the prey with the pedipalps extended and held widely apart, so as to form a sort of corral. Contact is often made seemingly by accident, the scorpion apparently bearing down on the general vicinity of the prey with the extended pedipalps sweeping a wide enough area to make contact likely. The attack culminates in the grasp attempt, in which the scorpion attempts to obtain a firm

Table 1.—Feeding response of *P. imperator* to *Mus musculus*. Scorpion lengths measured from tip of chelicera to tip of telson. Mice: Group A-3.0 cm (snout to vent length), hairless, eyes closed; B-3.8 cm, furred, eyes closed; C-4.0 cm, furred, eyes closed; D-5.0 cm, furred, eyes open; E-5.1 cm, furred, eyes open.

Scorpion	Mouse group	Sting use	Remarks
1-10 cm	A	no	devoured alive
	B	no	killed by pedipalps
	C	yes	stung once midbody
	D	yes	stung once midbody
	E	—	refused
2-10 cm	A	no	devoured alive
	B	no	killed by pedipalps
	C	unsuccessful attempt	attempted sting in head but did not penetrate, subsequently killed by pedipalps
	D	yes	stung once midbody
	E	yes	stung once at shoulders
3-14 cm	A	no	killed by pedipalps
	B	no	killed by pedipalps
	C	no	killed by pedipalps
	D	—	refused
	E	—	refused
4-14 cm	A	no	killed by pedipalps
	B	no	killed by pedipalps
	C	no	killed by pedipalps
	D	no	killed by pedipalps
	E	no	killed by pedipalps
5-15 cm	A	no	killed by pedipalps
	B	no	killed by pedipalps
	C	no	killed by pedipalps
	D	—	refused
	E	—	refused
6-15 cm	A	no	killed by pedipalps
	B	no	killed by pedipalps
	C	no	killed by pedipalps
	D	no	killed by pedipalps
	E	no	killed by pedipalps
7-17 cm	A	no	killed by pedipalps
	B	no	killed by pedipalps
	C	no	killed by pedipalps
	D	no	killed by pedipalps
	E	—	refused

hold on the prey with at least one pedipalp. If the prey at any time runs away or otherwise eludes the scorpion or manages to free itself from a successful grasp, the scorpion performs the sequence of orientation, attack, and grasp attempt all over again.

Once the prey is successfully grasped by one pedipalp the scorpion immediately obtains a hold with the other pedipalp as well. At this point the prey is held well away from the mouthparts and often slightly elevated, so as to prevent purchase on the substrate which might facilitate its struggling. Biting and clawing by the prey is also thus restricted to attacks on the pedipalps, the cuticle of which is sufficiently durable to withstand any damage. Should the prey struggle violently it may be subdued by one or both of two methods.

In the first method, the scorpion may use the pedipalps as killing or maiming weapons. Often this entails obtaining new and more effective holds on the prey than those found with the initial grasp. Consequently one pedipalp may release its grip and regrasp elsewhere. Usually the scorpion will grasp the prey at either end, thereby obtaining a head grip with one pedipalp that is frequently lethal when force is applied. Violently struggling prey is often repeatedly passed from pedipalp to pedipalp in an attempt to find an effective grip. Scorpions will occasionally intentionally release and retreat from violently struggling prey, only to attack again. Larger prey items often escaped during regrasping attempts, necessitating reorientation and a new attack by the scorpion.

In the second method, the sting may be used to subdue prey after a successful grasp attempt. This only occurred if the prey struggled violently. In the four instances of stinging observed, struggling ceased almost immediately upon aculeus penetration, with cessation of breathing and apparent death from 90 to 180 seconds later. In the four instances observed the prey was stung only once. Rather than a quick jab, the metasoma was leisurely arched over the back and the telson used to probe the prey for a soft spot if one was not immediately encountered. The aculeus was inserted for 5 to 15 seconds, presumably injecting venom. The sting was always preceded by attempts to subdue the prey with the pedipalps. A firm grip was maintained by the pedipalps during stinging.

Once the prey is subdued ingestion begins. The pedipalps bring the prey in contact with the chelicera, which tear off pieces of flesh and convey them to the oral cavity. *P. imperator* may feed for two days on a carcass before leaving it, apparently disdaining stale food. The prey is often alive when ingestion commences.

DISCUSSION

Notes on sting employment in prey subdual are very scarce in the literature. McDaniel (1968) divided California scorpions into two groups on the basis of their habits and morphology. Errant types are characterized by long legs, a slender body, a large thick cauda with a large telson, and chelae with a long slender tarsus and tibia. These are described as actively pursuing prey and having rapid stinging reflexes. *Paruroctonus sylvestrii* (Borelli) is of this type. The second type is the obligate burrower, with a stouter body, shorter and more slender cauda, and broad chelae with short, sturdy tarsus and tibia. These are described as waiting for prey to come to them rather than pursuing it and relying on the pincers rather than the sting. Here *Anuroctonus phaiodactylus* (Wood) is an example. Williams (1966) also discusses burrowing activities in the scorpion *A. phaiodactylus* and again notes that the pedipalps are distinctively thick, heavy, and powerful; they are the primary means of catching and immobilizing prey.

Stahnke (1966) notes that the sting is used as an offensive weapon "when the prey is obstreperous and will not quietly submit to being devoured alive" and that "scorpions with powerful chelae depend largely upon their pinching and crushing ability for both offensive and defensive action." Fabre (1923), in working with *Buthus occitanus* (Amoreux), noted that the sting was frequently employed to subdue struggling insects. Southcott (1955) found that *Urodacus manicatus* (Thorell) invariably stings its prey as soon as it is captured. By contrast, Schultze

(1927) recorded that he had never seen the large Philippine forest scorpion, *Heterometrus longimanus* (Herbst), sting its prey. Schultze believed that "the poisonous stinger us used only as a defensive weapon against its enemies." In Schultze's experiments the prey (cockroaches) was held clear of the ground and eaten while still struggling. Vachon (1953) writes that in capturing its prey the scorpion "moves slowly forward, supported on its hind legs, with claws open and extended and tail raised and pointing forwards. Often the scorpion will then hesitate, and the final act of capture seems almost accidental, the scorpion may even withdraw for a time, but it waits patiently and finally achieves its aim. Then, especially if the victim struggles, it inserts its sting where best it can, often without any delay."

Hadley and Williams (1968) made observations on *Vaejovis confusus* Stahnke, *Paruroctonus mesaensis* Stahnke, *Paruroctonus baergi* (Williams and Hadley), *Hadrurus arizonensis pallidus* Williams, and *Centruroides exilicauda* (Wood). They found that "scorpions generally used their venom apparatus at the time of prey capture." They note that several species of mice and lizards preyed upon by *H. a. pallidus* appeared immune to the venom, however. Although the scorpions observed by Hadley and Willliams usually grasped the prey in the pedipalps before employing the sting, this was not always so. If the prey fought back aggressively, the scorpion sometimes stilted on its walking legs with the mesosoma and metasoma arched in almost a vertical position, from which posture the scorpion could strut slowly or twirl around in small circles, stinging blindly at its target.

Bub and Bowerman (1979) studied prey capture in *Hadrurus arizonensis* Ewing and found that the prey was stung at least once in all sequences observed. Baerg (1961) points out that scorpions with large pedipalps and reduced metasomas probably do not use the sting to immobilize their prey. Burton (1975) writes that scorpions will only use the sting if the prey offers resistance. Cloudsley-Thompson (1951) notes that *Euscorpius italicus* (Herbst) seldom, if ever, uses the sting to subdue prey. On the other hand, *Scorpio maurus* Linnaeus, *Buthus occitanus* (Amoreaux), and *Androctonus australis* (Linnaeus) will lash out with their sting at the slightest provocation (Cloudsley-Thompson 1958).

In sum, accounts in the literature tend to state generally that the sting is only used in prey subdual if the prey struggles excessively. However, when species are individually examined some tend never to use their sting and others always use their sting. There appears to be an inverse relationship between the size of the pedipalps and the frequency of stinging behavior. Those species with large powerful pedipalps appear to rarely use their sting (for example *P. imperator, H. longimanus,* and *A. phaiodactylus*), while those species with small slender pedipalps use the sting frequently (*H. arizonensis, U. manicatus, B. occitanus, Vaejovis* spp.).

STING USE IN *P. IMPERATOR*

Pandinus imperator is a species with large powerful pedipalps. The metasoma is also well developed. Although the sample size was too small for statistical analysis, the present observations indicate that *P. imperator* seldom, if ever, uses the sting in prey subdual as an adult. In this respect *P. imperator* is similar to

E. italicus and *H. longimanus* (Cloudsley-Thompson 1951, Schultze 1927). *Heterometrus longimanus* is also a large species with well developed pedipalps. (Information on the morphology of *E. italicus* was not available.)

An ontogenetic change in prey capture behavior was evident in the present study. The young *P. imperator* used their stings on crickets frequently as they grew. At 6-8 cm in length these scorpions changed their prey capture behavior and dispatched crickets with the pedipalps or devoured them alive. These scorpions were then entered into the feeding trials with mice, where they reverted to their earlier stinging behavior to subdue mice larger than 4 cm in length but continued to dispatch smaller mice via pedipalpal action alone or by devouring them alive.

Why use of the sting in prey capture should be phased out as *P. imperator* matures is an interesting question. Possibly the use of the sting increases the prey capture success of the young scorpions, thereby imparting a survival advantage. No information on the natural prey items of *P. imperator* was available, but it is likely that by using the sting the young scorpions make available a greater variety of prey, obtain prey more efficiently, and consequently grow rapidly during a period of life when mortality is undoubtedly high. But if use of the sting is advantageous in capturing prey, why is its use lost in the adults? Possibly, once the scorpion has attained a certain size its pedipalps alone are large enough and powerful enough to dispatch any normal prey item, and prey items large enough to necessitate stinging are rejected in favor of smaller items which pose less of a risk of injury to the scorpion. Also, venom production may be costly from an energetics standpoint. Whether or not this is so, it was clear in the present experiments that the use of the sting would have saved much energy in struggling with the prey item. In fact, if not for the confines of the terraria it is unlikely that the scorpion could have caught the mouse in the first place, much less be able to make a second attempt after the mouse escaped an initial grasp. Clearly, further investigations will be necessary to explain the biological significance of this ontogenetic behavioral change.

CONCLUSION

An ontogenetic change in prey capture behavior, involving loss of stinging behavior in prey subdual, was observed in two captive born *P. imperator*. At 6-8 cm in length these scorpions abandoned sting use in prey subdual, but at 10 cm in length were shown to revert to the juvenile stinging behavior if confronted with prey too formidable to be subdued via pedipalpal action alone. Wild caught adult scorpions at least 14 cm in length refused to utilize the sting in prey subdual, apparently rejecting prey too large to subdue with the pedipalps alone. The ontogenetic change in prey capture behavior demonstrated in *P. imperator* may occur in other scorpions as well, and needs to be investigated especially in those species noted for infrequent or absent stinging behavior (*H. longimanus, E. italicus, A. phaiodactylus*). The biological significance of this ontogenetic change is at present unknown.

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TWO NEW SPECIES OF *IXAMATUS* SIMON FROM EASTERN AUSTRALIA (NEMESIIDAE, MYGALOMORPHAE, ARANEAE)

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ABSTRACT

Two new species of *Ixamatus—I. lornensis* has a low, broad tarsal organ; *I. rozefeldsi* has a spinose cymbium—present characters previously unknown and probably plesiomorphic for the genus.

INTRODUCTION

Ixamatus was revised in a two-part study (Raven 1980, 1982) and includes eight species. Some initial confusion between species from eastern Australia and apparently similar species in the south and west resulted in a much wider distribution being ascribed to the genus than is actually the case (see Main 1983). After the second revision, new material of *Ixamatus* was found. Because the changes required in the diagnosis of *Ixamatus* are cladistically noteworthy I have chosen to describe both the species and the changes prior to making a general biogeographical history (in prep.) of *Ixamatus* and other Australian mygalomorphs that have been revised.

The terminology, methods, and abbreviations are consistent with my previous studies and any of the larger studies (e.g., Raven 1982) will provide a full list.

Ixamatus Simon

Ixalus L. Koch 1873:469. Type species by monotypy: *Ixalus varius* L. Koch 1873.
Ixamatus Simon 1887:195 (*nomen novum* for *Ixalus* L. Koch 1873); Raven 1982:1036.

Diagnosis.—*Ixamatus* differs from *Xamiatus* in the absence of plumose hairs on the palpal trochanters of adults, and from the remaining nemesiid genera by the elevated tarsal organ.

Remarks.—A full synonymy and description are given in Raven (1982, 1985). Males described here require two modifications of that description. First, in most species of *Ixamatus,* the tarsal organ is high and raised and the cymbium is not spinose. In contrast, the tarsal organ of *I. lornensis* is short and broad, and the

cymbium of *I. rozefeldsi* is spinose. The cladistic implications will be discussed elsewhere. Suffice it to say here that both of these newly described conditions are plesiomorphic in the Nemesiidae.

Ixamatus lornensis, new species
Figs. 1-7, Table 1

Type.—Holotype male, Lorne State Forest, N. S. W., 31°35′ S—152°38′ E (11.v-19.vi.1978, D. Milledge), Australian Museum No. KS 1562.

Diagnosis.—Differs from *I. caldera* Raven by the low tarsal organ, spinose cymbium, and the absence of megaspines on tibia I. Medium-sized spiders, carapace ca. 5-6 long. Dorsal abdomen anteriorly mottled. Maxillary serrula group of about 15 low teeth. Tibia I of male unmodified; metatarsus I with slight retrolateral excavation proximally; palpal bulb spherical with short embolus, tarsus with several distinct spines apically. Tarsal organ low, broad. Female unknown.

Etymology.—The specific epithet refers to the type locality.

Description.—Holotype male. Carapace 5.69 long, 4.63 wide. Abdomen 5.00 long, 2.88 wide. Total length 11.88.

Color in alcohol: carapace, chelicerae, and legs orange brown; abdomen dorsally brown with white mottling anteriorly forming two irregular lines, ventrally almost entirely white with brown areas medially.

Carapace: fovea broad, slightly procurved; lateral margins with silver hairs on dorsal coxae, caput, and interstrial ridges; sparsely clothed; 3 pairs of foveal bristles. Eyes: tubercle low but distinct; group 0.4 of head-width, 1.82 times wider than long; back row recurved; ratio MOQ back width: front width: length, 35:26:23; ratio AME:ALE:PME:PLE, 11:10:7:8; eye interspaces: AME-AME, 4; AME-ALE, 1; PME-PLE, 1; ALE-PLE, 1. Chelicerae: with brown bristles and silver hairs on prodorsal surface; 2 depressions in anterolateral surfaces; promargin of furrow with 12 teeth; basally with 8 fine teeth.

Maxillae: front length, 1.56; back length, 2.16; width, 1.04, with about 40 blunt cuspules on inner mound; serrula consisting of about 15 low teeth. Labium: 1.08 wide, 0.48 long. Sternum: 2.92 long, 2.44 wide; shape, length, and distance from margin of sigilla: posterior, oval, 0.32, 0.28; middle, oval, 0.20, 0.08; anterior, circular, 0.12, 0.04.

Palp: bulb spherical; embolus short; with eight spines and three stout bristles on apical tarsi.

Legs: (Table 1). 1423; tibia I unmodified; metatarsus I with slight retrolateral excavation and mid-distal retrolateral cuticular point; retroventral metatarsus IV

Table 1.—Leg measurements of *Ixamatus lornensis.* Values are for holotype male.

	I	II	III	IV	Palp
Femur	4.75	4.06	3.69	4.63	3.13
Patella	2.81	2.19	1.94	2.06	1.61
Tibia	3.31	2.69	2.06	3.25	2.56
Metatarsus	3.19	2.94	3.19	3.81	-
Tarsus	1.63	1.50	1.56	1.88	1.00
Total	15.69	13.38	12.44	15.63	8.30
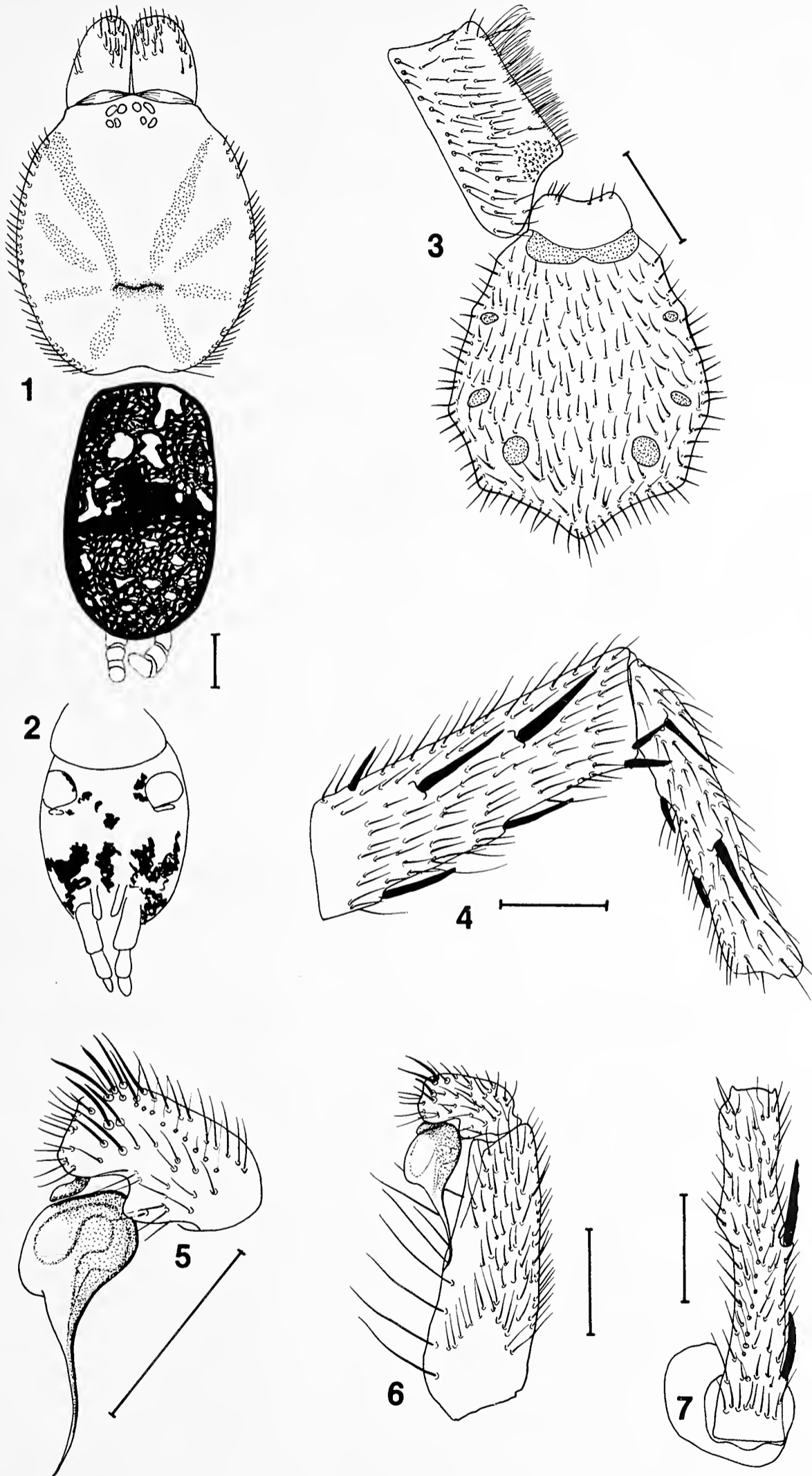
Figs. 1-7.—*Ixamatus lornensis,* holotype male: 1, carapace, chelicerae, and abdomen, dorsal view; 2, abdomen and spinnerets, ventral view; 3, sternum, maxilla, and labium; 4, tibia and metatarsus I, prolateral view; 5, bulb and cymbium, retrolateral view; 6, palpal bulb, cymbium, and tibia, retrolateral view; 7, metatarsus I, dorsal view. All scale lines = 1 mm.

with two close setae-like preening combs; silver hairs on femora I-IV; scopulae entire but thin on metatarsi and tarsi I. Spines: no spines on leg tarsi. First leg: femur, pl d4; patella, p2; tibia, p2 d1 v9; metatarsus, p2 v4. Second leg: femur, p2 d3; patella, p2; tibia, p2 v8; metatarsus, p3 v7. Third leg: femur, p3 d3 r3; patella, p2 r1; tibia, p2 d1 r2 v6; metatarsus, p5 r3 v7. Fourth leg: femur, p3 r3; patella, r1; tibia, p2 d1 r2 v7; metatarsus, p3 d1 r3 v9. Palp: femur, pl d3; patella, p1; tibia, p1 v2; tarsus, 9 apical. Claws: STC of legs I, II with 10 teeth in each of two rows; STC of legs III, IV with 8-9 teeth per row; ITC without teeth. Trichobothria: two rows, each of 9 for full length of tibiae; 12 on metatarsi; 18 on tarsi; tarsal rod low, broad.

Spinnerets: PMS 0.23 long, 0.18 wide, 0.40 apart; lengths of basal, middle, apical, and total segments of PLS, 1.05, 0.93, 1.18, 3.16, respectively.

Distribution and Habitat.—*Ixamatus lornensis* is known only from the rainforest of Lorne State Forest, New South Wales.

Material Examined.—Only the type.

Ixamatus rozefeldsi, new species
Figs. 8-14, Table 2

Type.—Holotype male, Byfield near Rockhampton, Q., 22°51'S — 150°39'E (27.vi.1982, A. Rozefelds). Queensland Museum No. S1314.

Diagnosis.—Differs from all other *Ixamatus* species by the distinct process on retrolateral metatarsus I of males. Large spiders, carapace ca. 8 long. Dorsal abdomen with large white area anteriorly. Maxillary serrula absent. Tibia I of male with three large megaspines on raised bases; metatarsus I with excavation proximal to retrolateral cuticular process; cymbium not spinose; bulb pyriform with short embolus. Female unknown.

Etymology.—The specific epithet in a patronym in honor of Mr. Andrew Rozefelds, an enthusiastic and fearless collector of mygalomorphs.

Description.—Holotype male. Carapace 8.25 long, 8.13 wide. Abdomen 9.70 long, 6.00 wide.

Color in alcohol: carapace, chelicerae, and legs red brown; abdomen dorsally brown with large white area anteriorly and three pairs of irregular areas forming broken chevrons, ventrally cream with brown areas between PMS and laterally.

Carapace: fovea deep, recurved; several paired bristles in front of fovea; uniformly covered with black bristles and pile of silvery hairs on interstrial ridges and caput. Eyes: tubercle low but distinct; group 0.31 of head-width, 2.07 times wider than long; back row slightly recurved; ratio MOQ back width: front width: length, 44:31:26; ratio AME:ALE:PME:PLE, 13:14:9:12; eye interspaces: AME-AME, 8; AME-ALE, 2; PME-PLE, 3; ALE-PLE, 3 (PME and PLE of one side

Table 2.—Leg measurements of *Ixamatus rozefeldsi*. Measurements are for holotype male.

	I	II	III	IV	Palp
Femur	8.13	7.19	6.69	8.25	5.00
Patella	4.44	4.06	3.38	3.88	2.69
Tibia	5.38	4.75	4.19	6.31	3.94
Metatarsus	5.56	5.00	5.31	7.06	-
Tarsus	2.94	2.75	2.63	3.13	1.75
Total	26.45	23.75	22.02	28.63	13.38

˙ fused). Chelicerae: with silver hairs and long black bristles; promargin of furrow with 11 teeth; basally with 8 fine teeth.

Maxillae: front length, 2.48; back length, 3.52; width, 1.60, with about 50 stout, pointed cuspules on inner edge; serrula absent. Labium: 1.52 wide, 1.04 long.
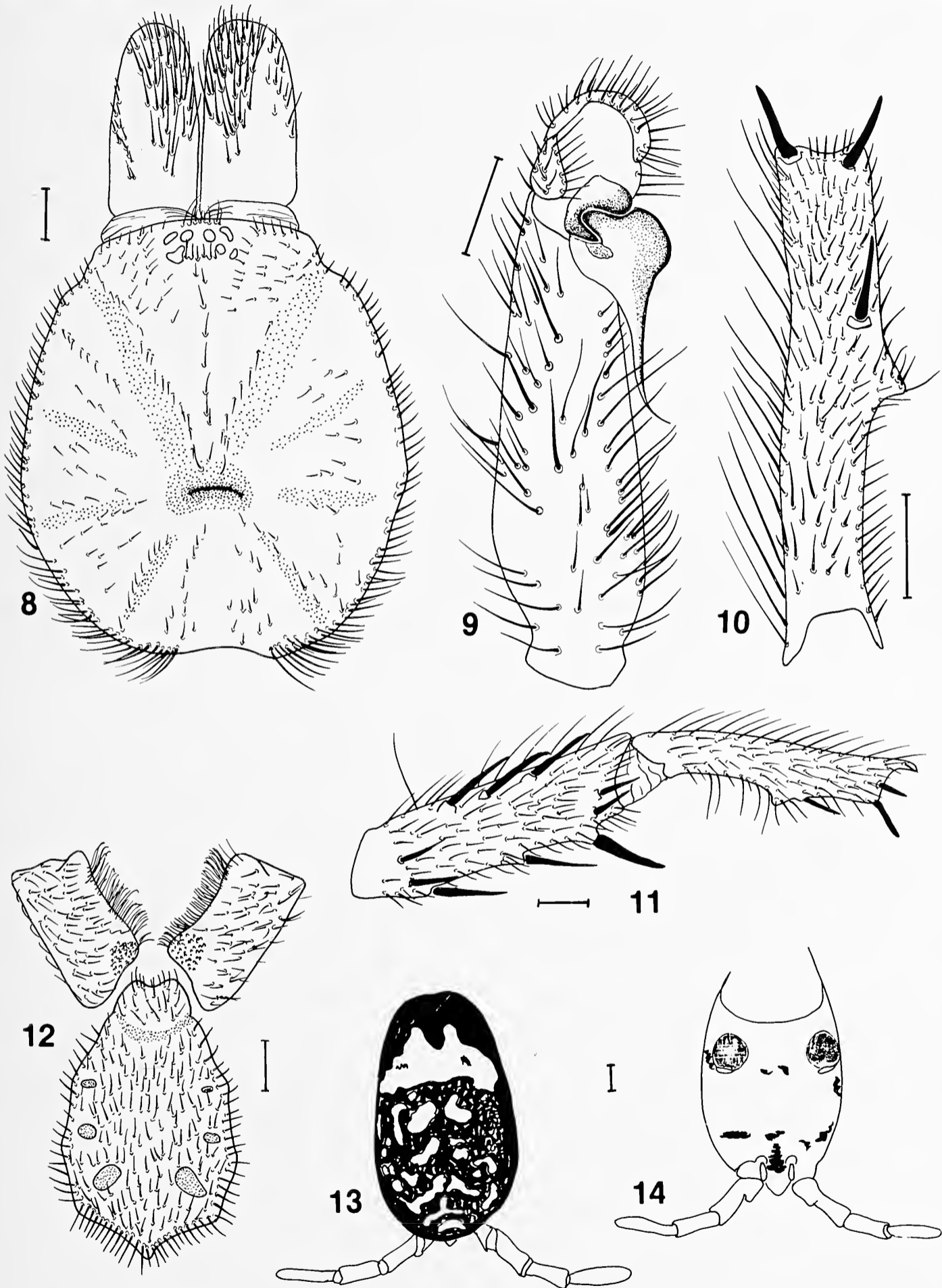
Figs. 8-14.—*Ixamatus rozefeldsi*, holotype male: 8, carapace and chelicerae, dorsal view; 9, palpal bulb, cymbium, and tibia (right), ventral view; 10, metatarsus I (right), ventral view; 11, tibia and metatarsus I, prolateral view; 12, sternum, maxillae, and labium; 13, 14, abdomen and spinnerets, dorsal view (13), ventral view (14). All scale lines = 1 mm.

Sternum: 4.88 long, 3.56 wide; all sigilla oval. Length and distance from margin of sigilla: posterior, 0.63, 0.40; middle, 0.40, 0.28; anterior, 0.15, 0.20.

Palp: bulb pyriform with short embolus.

Legs: (Table 2). 4123; tibia I with 3 large megaspines on raised bases, most distal thickest; metatarsus I with excavation proximal to retrolateral cuticular process; preening combs absent; scopulae on tarsi I, II; fine brown hairs on femora; no modified hairs anywhere. Spines: no spines on leg tarsi. First leg: femur, p2 d2; patella, p1; tibia, p3 v7; metatarsus, v3. Second leg: femur, p3 d2; patella, p2; tibia, p2 v8; metatarsus, p1 v7. Third leg: femur, p1 d3 r2; patella, p1 r1; tibia, p2 r2 v7; metatarsus, p2 r1 v8. Fourth leg: femur, p3 r2; patella, 0; tibia p2 r3 v7; metatarsus, p2 r2 v8. Palp: femur, p2; patella, 0; tibia, v1; tarsus, 0. Claws: STC with 10 teeth in each of two rows; ITC without teeth. Trichobothria: two rows, each of 11 extending to ¾ length of tibiae; 16 in straight line on metatarsi; 23 in slightly irregular line on tarsi; tarsal rod large, elevated, distal.

Spinnerets: PMS 0.96 long, 0.32 wide, 0.88 apart; lengths of basal, middle, apical, and total segments of PLS, 2.40, 1.88, 2.80, 7.08, respectively.

Distribution and Habitat.—*Ixamatus rozefeldsi* is known only from Byfield, near Rockhampton, Queensland. The holotype was found in a small temporary web under a log in a gully that is part of a small area of low "poor" rainforest.

Material examined.—Only the type.

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BALLOONING MYGALOMORPHS: ESTIMATES OF THE MASSES OF *SPHODROS* AND *UMMIDIA* BALLOONERS (ARANEAE: ATYPIDAE, CTENIZIDAE)

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ABSTRACT

The masses of *Sphodros atlanticus* and *Ummidia* sp. spiderlings capable of ballooning, and of *Antrodiaetus unicolor* spiderlings believed not to balloon, were estimated by means of a volume-mass regression developed with data from five araneomorph families, and compared with the mass frequency distribution of a sample of 216 aerially dispersing araneomorphs trapped over a one week period in a soybean field. Mean estimated masses of the *Sphodros* and *Ummidia* spiderlings were 1.25 mg and 3.45 mg, respectively. Although these were in at least the 95th percentile of masses of the trapped araneomorphs, larger araneomorphs were trapped. These results and the finding that *A. unicolor* spiderlings were intermediate in estimated mass (mean = 2.02 mg) between *S. atlanticus* and *Ummidia,* indicate that mass is not the only constraint on ballooning behavior in mygalomorphs. Habitats of the three species support the habitat predictability hypothesis of ballooning, *A. unicolor* tending to be found in more predictable habitats than the other two species. Live mass measurements of ballooning *Ummidia* spiderlings indicate that the volume-mass regression estimates of mygalomorph spiderling masses are consistently slightly high. This may be due to tissue density differences between araneomorphs and mygalomorphs.

INTRODUCTION

Although the great majority of mygalomorph spider species do not appear to disperse aerially, observations of ballooning *Sphodros atlanticus* (Gertsch and Platnick) and *Ummidia* spiderlings (Coyle 1983, 1985) and of pre-ballooning behavior in spiderlings of *Sphodros rufipes* (Latreille) (Muma and Muma 1945), *Atypus affinis* Eichwald (Enock 1885, Bristowe 1939), *Ummidia carabivora* (Atkinson) (Baerg 1928), and *Conothele malayana* (Doleschall) (Main 1957) show that some species in two mygalomorph families (Atypidae and Ctenizidae) are aerial dispersers. Although *Sphodros* and *Ummidia* ballooning (which involves dropping and hanging from a dragline that is lifted and lengthened by a breeze,

breaks near the attachment substrate, and serves as the ballooning thread) is a more primitive (and probably less effective) form of ballooning than that practiced by most araneomorphs, it appears to increase significantly the vagility of these animals (Coyle 1983). The water gaps bridged by the distribution ranges of *A. affinis* (Kraus and Baur 1974; Locket, Millidge, and Merrett 1974), *C. malayana* (Main 1957), and by other *Atypus* and *Ummidia* species in Japan (Yaginuma 1970) and the Florida Keys (G. B. Edwards, pers. comm.) also suggest that mygalomorph ballooning can significantly increase vagility.

Because spiders are not capable of active flight, there must be some upper limit to the mass at which they can disperse aerially. Ballooning in mygalomorphs has therefore been an arachnological curiosity, since average mygalomorph adults and spiderlings (data presented in this paper) are far more massive than the corresponding stages of araneomorphs. This study was designed to estimate the masses of ballooning mygalomorph spiders and to compare them with the masses of typical ballooning araneomorphs, so that the following questions can begin to be addressed: is ballooning rare in mygalomorphs primarily because of large spiderling size? In those mygalomorph species which do balloon, to what degree is large mass a handicap which has been overcome by special adaptations?

METHODS AND STUDY SITES

Sphodros atlanticus spiderlings were collected on 9 October 1980 with their mother in her burrow on a grassy roadbank 6.5 km south of Cullowhee in Jackson County, North Carolina. These were third instar spiderlings which overwinter in the maternal burrow and disperse in the spring (see Coyle and Shear 1981, for a description). Spiderlings of an undetermined species of *Ummidia* were collected while performing pre-ballooning behavior (climbing around in the top of a boxwood shrub about 1 m above ground) on 19 April 1982 near Apex in Wake County, North Carolina, by J. M. Ragan. Twenty dispersal stage (second instar) spiderlings of *Antrodiaetus unicolor,* collected on 16 January 1973, eight km south of Cullowhee in Jackson County on the Wolf Creek Biological Preserve, were included in the study to provide mass estimates for a mygalomorph which is believed not to balloon (Coyle 1971, Reagan and McGimsey pers. comm.). All spiderlings were preserved in 70% ethanol.

Ballooning araneomorphs were collected on vertical sticky traps set out between 30 and 200 cm high in an eleven ha. soybean planting at the University of Missouri South Farms, eight km SE of Columbia in Boone County, Missouri, during the seven-day period ending 9 August 1983. Details of the trapping procedure have been presented elsewhere (Greenstone 1984). Briefly, the trap supports were banded with adhesive to prevent spiders from walking onto them, and all vegetation was cleared from within 3 m of the traps to reduce the probability that spiders would be inadvertently trapped while "rappelling" (J. E. Carico, personal communication) or "bridging", i.e., floating silk "lines on the wind to establish paths to distant objects" without releasing hold of the substrate (W. G. Eberhard, personal communication). The traps were returned to the laboratory and examined with a Wild M5 stereomicroscope to locate all trapped spiders. The spiders were removed from the adhesive (Tacktrap®, Animal Repellents, Inc., Tifton, Ga) and placed for three days each in paint thinner and toluene before final preservation in 70% ethanol.

Mass estimates for both the mygalomorphs and sticky-trapped araneomorphs were made by use of a volume-mass regression developed with 101 araneomorph specimens ranging in mass from 0.7 to 19.5 mg. Briefly, previously massed animals were preserved in 70% ethanol and their volume estimated by treating them as cylindrical solids having diameter equal to the mean of greatest carapace and abdominal widths and height equal to total length (anterior edge of carapace to posterior end of abdomen, exclusive of spinnerets). Measurements were made with the Wild M5 stereomicroscope with ocular micrometer at 12X magnification. Separate regressions for five araneomorph families do not differ significantly in slope and intercept, and the overall regression combining the data for those five families provides a good fit for limited data from two other araneomorph families (Greenstone et al., in press, a). This regression is valid for sticky-trapped as well as directly ethanol preserved specimens (Greenstone et al., in press, b). As the seven families include spiders of varying proportions and shapes, we assumed that mygalomorphs would also fit the overall regression (they certainly do not resemble tetragnathids, the one family which did have a significantly different volume-mass regression).

On April 7, 1984, we were presented with an opportunity to check this assumption partially, when F.A.C. located a group of ballooning *Ummidia* spiderlings near Cullowhee in Jackson County, North Carolina (Coyle 1985). Twenty of these were weighed within 48 h of collection, preserved in 70% ethanol, and mailed to A.-L.H. for measurement. Because these mass determinations and those for the araneomorph volume-mass regressions were made at different times and places, special care was taken in the calibration of both microbalances (a Mettler M5 and Mettler 160, respectively). The twenty *Ummidia* were measured four months after preservation, to ensure that the preserved volumes had come to equilibrium [Araneids require six weeks (Greenstone et al., in press, b)].

RESULTS AND DISCUSSION

Comparison of Estimated Masses of Araneomorphs and Mygalomorphs.—Two hundred sixteen araneomorphs were collected off the soybean field sticky traps and measured. The frequency distribution of their estimated masses is shown in Fig. 1. Means (and standard errors) for mass estimates of the Wake County *Ummidia* and the *S. atlanticus* spiderlings are 3.45 mg (0.13 mg), and 1.25 mg (0.03 mg), with N =9, and 15, respectively, and are indicated by arrows in Fig. 1. Although the araneomorph mass frequency distribution appears representative of other weeks in the summer and fall of 1983 (Greenstone et al., unpublished data), it would be premature to characterize the shape of this distribution in order to derive a parametric assessment of the deviation of mygalomorph ballooner masses from those of araneomorphs. However it is clear that the ballooning mygalomorphs studied here are more massive than most other ballooners, and will probably turn out to be in the ninetieth percentile or higher (they are in the ninety-fifth and ninety-eighth in Fig. 1). On the other hand they are not the most massive spiders ballooning. Although we cannot entirely rule out the possibility that some of the larger trapped animals were "rappelling", spiders ranging in mass from 4.8 to 19.2 mg have been trapped by nets suspended more than 100 m above the ground (animals collected by R. A. Farrow in New

South Wales, Greenstone et al., MS in preparation). This suggests that in many mygalomorph taxa ballooning may not be precluded solely or even primarily by large mass.

Although the *Sphodros* and *Ummidia* spiderlings used in this study were not caught in the act of ballooning, we have strong evidence that they were capable of doing so. The age (third instar), time of collection, and behavior of the *S. atlanticus* spiderlings indicate that the animals were overwintering prior to dispersal (see Coyle and Shear 1981 for observations on the phenology of other *Sphodros* spp). Twenty-five of their siblings were kept alive in a glass-topped terrarium containing humid soil. They wandered freely over the soil for a few days and performed pre-ballooning behavior (climbing up the corners of the terrarium and depositing large amounts of silk at the upper ends of the corners just under the glass lid) before finally excavating burrows and constructing their pursewebs. Furthermore the *Sphodros* spiderlings seen ballooning by F.A.C. (Coyle 1983) were almost certainly *S. atlanticus*. The behavior and location of the *Ummidia* spiderlings at the time of collection were also indicative of pre-ballooning behavior.

The twenty spiderlings of *A. unicolor,* the non-ballooning species, had an estimated mean mass of 2.02 mg (standard error =0.19 mg), which is intermediate between those of the two ballooning mygalomorph species. This demonstrates that mass is not the only constraint on ballooning behavior in mygalomorphs and suggests that for at least some species, other factors may be more important than mass in determining whether ballooning occurs. One of us (Greenstone 1982) has suggested that the predictability of the habitat will be the major selective factor in the evolution and maintenance of ballooning behavior, with less predictable habitats selecting for higher rates of ballooning. The habitats of the three species studied here support that hypothesis. *A. unicolor* is most often found in mesic forests (Coyle 1971), whereas the other two species, while sometimes found in forests, are as apt to be found in forest edge habitats, lawns and old fields. Mesic forests are inherently longer lived and hence more predictable than successional habitats like lawns and old fields (Southwood 1962), and they also provide better buffered and hence more predictable microclimates for their inhabitants. It is also possible that the kinds of air currents conducive to mygalomorph ballooning are prohibitively rare in forest habitats.

Comparison of Actual and Estimated Masses of Mygalomorphs.— Measurement of the twenty *Ummidia* spiderlings collected on April 7, 1984, while their siblings were ballooning (Coyle 1985) indicated that the araneomorph volume-mass regression may not be entirely accurate for mygalomorphs. The mean (and standard error) measured mass of this sample was 2.48 mg (0.02), whereas the mean estimated mass was 2.93 mg (0.06). All measured masses were between two and 35% less than those estimated from the volume-mass regression, with a mean deficit of 17.4% (arc-sine transformation of original percent data). If this is representative of the equation's overestimation for all mygalomorphs of this volume range, the arrows in Fig. 1 should be moved to the left one mass class for *Sphodros* and four for *Ummidia:* this does not change their percentile ranks.

The consistent overestimation of *Ummidia* mass by the volume-mass regression is counterintuitive, since the volume estimate does not include the chelicerae and legs, which look more massive in mygalomorphs than in araneomorphs. We can

think of three possible explanations for the overestimation: 1) the regression consistently overestimates the masses of all spiders in this volume range; 2) mygalomorph body shape differs sufficiently from araneomorph body shape that the araneomorph mass-volume regression is not valid for them; 3) mygalomorphs, at least in this volume range, do in fact have lower density than similar sized araneomorphs.

The first possibility was ruled out by comparison of the actual and estimated masses of eight animals (six araneids and two thomisids) from among the 101 used to construct the regression which happened to fall in the same volume range (2.2 to 2.9 mm^3) as the twenty *Ummidia:* exactly half of the estimates were overestimates and half underestimates.

The second possibility will have to be determined by further research. The third is most interesting. If in fact mygalomorph spiderlings are less dense than araneomorphs of the same volume, it may simply reflect some unknown physioanatomical difference unrelated to ballooning. On the other hand such a capacity to be less massive at a given volume could be a preadaptation for the evolution of still lower density to permit ballooning at larger sizes, an ability that might permit the transport of larger energy stores, reduce the rate of body water loss, and enhance colonizing potential by allowing older animals to balloon (MacArthur and Wilson 1967). Given sufficiently strong winds and very long or
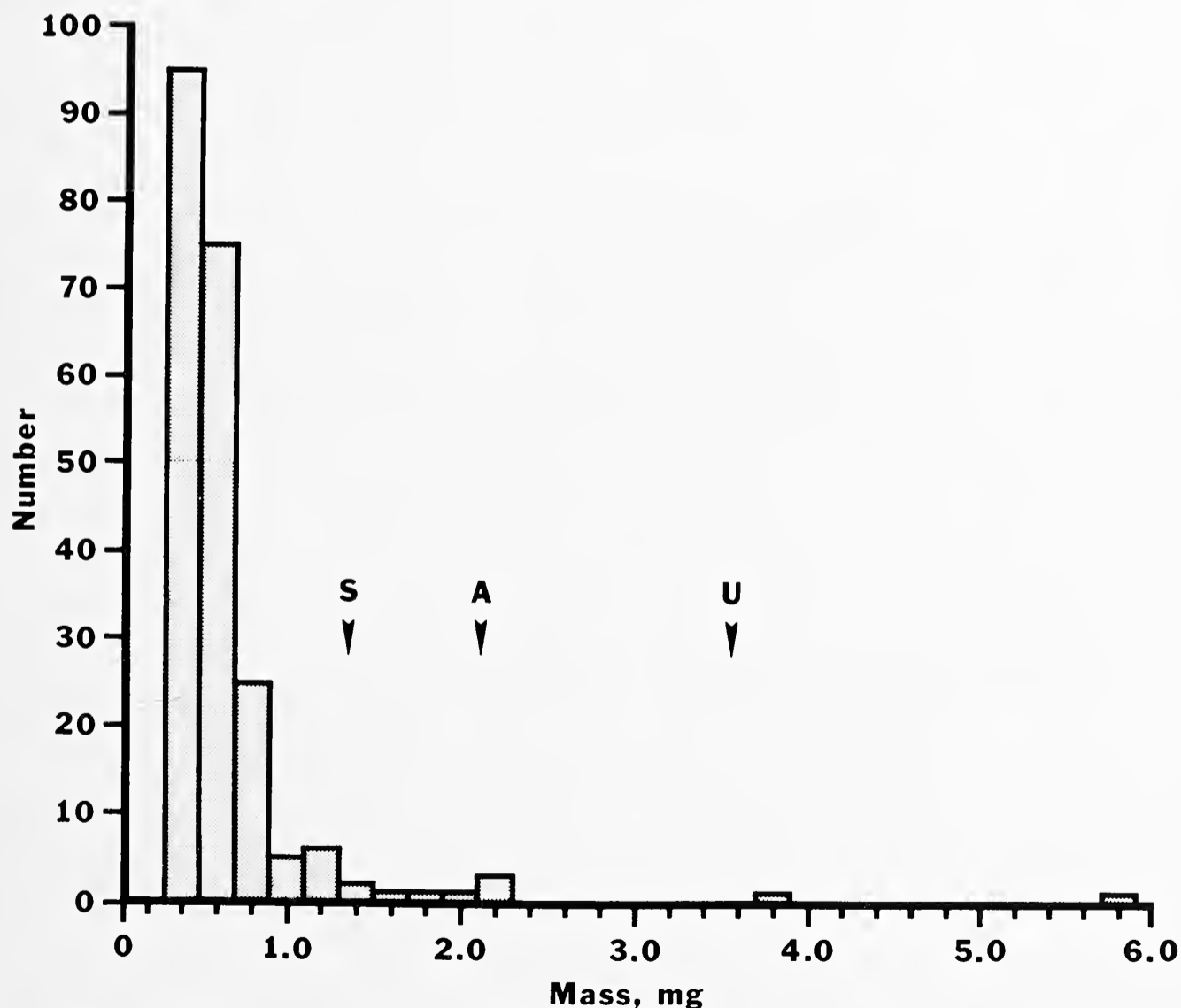
Fig. 1.—Frequency distribution of estimated masses of ballooning araneomorphs collected in a soybean field near Columbia, Missouri, with approximate mean masses of *S. atlanticus* (S), Wake County *Ummidia* (U) and *A. unicolor* (A) spiderlings indicated (arrows). Mass classes are 0.2 mg wide. Class labels designate upper bound of each class.

multi-stranded balloons, spiders much larger than those studied here should be capable of ballooning (R. Buskirk and R. B. Suter, pers. comm.). However, since large spiders seldom balloon, perhaps there is selection against ballooning at large sizes due to such disadvantages as decreased lift resulting from a decreased surface to volume (or mass) ratio, dangerously high terminal velocities, or enhanced visibility to aerial predators. At this point we really do not understand why the distribution of aeronaut masses is so heavily skewed to the light end.

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LABORATORY INFECTION OF SPIDERS AND HARVESTMEN (ARACHNIDA: ARANEAE AND OPILIONES) WITH *NEOAPLECTANA* AND *HETERORHABDITIS* NEMATODES (RHABDITOIDEA)

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ABSTRACT

Specimens of the aerial spiders, *Pholcus phalangiodes* and *Latrodectus mactans,* a ground spider, *Pirata* sp., and a harvestman, *Phalangium* sp., were placed on damp filter paper containing the entomogenous nematodes, *Neoaplectana carpocapsae* and *Heterorhabditis heliothidis.* Representatives of all four hosts were killed by the above nematodes. In *Pholcus, Pirata* and *Latrodectus,* the nematodes developed to the adult stage but did not multiply. In the case of *Phalangium,* the nematodes reproduced and formed infective juveniles. The present report establishes that under ideal conditions, neoaplectanid and heterorhabditid nematodes are capable of infecting, killing and with one host, reproducing in arachnids.

INTRODUCTION

With the commercialization of nematodes belonging to the genera *Neoaplectana* and *Heterorhabditis* for insect control, studies are being undertaken to determine what effect these nematodes may have on non-insect arthropods. *Neoaplectana carpocapsae* and *Heterorhabditis heliothidis* are known to infect a range of insects under laboratory conditions but have never been tested against members of the class Arachnida. The host range and biology of these nematodes are summarized by Poinar (1979).

The present paper reports infectivity tests made with *N. carpocapsae* and *H. heliothidis* in the laboratory against three species of spiders and a harvestman.

MATERIALS AND METHODS

For the present tests, the aerial spiders, *Pholcus phalangiodes* (Pholcidae) and *Latrodectus mactans,* a ground spider, *Pirata* sp. (Lycosidae), and a harvestman, *Phalangium* sp. (Phalangidae) were used.

The nematodes employed were the 42 strain of *Neoaplectana carpocapsae* Weiser and the NC strain of *Heterorhabditis heliothidis* (Khan, Brooks and Hirschmann).

The infection chambers for *Pholcus, Pirata* and *Latrodectus* were plastic vials (65 mm long by 25 mm in diameter) which were lined with filter paper. The inner area of the exposed filter paper was 65 mm x 80 mm or 52 cm.[2] A single spider was placed in each vial. The inoculum consisted of 0.5 cc of infective stage nematodes applied in an aqueous mixture to the filter paper in each vial. The spiders were exposed to nematodes over most of the surface (except for the bottom and top of the vial). The nematode concentrations consisted of 10.7 x 10^4/cc for *H. heliothidis* and 12 x 10^4/cc for *N. carpocapsae,* making the dosage rate approximately 1028 nematodes/cm^{2} for *H. heliothidis* and approximately 1150 nematodes/cm^{2} for *N. carpocapsae.* Fifteen adult specimens of each spider were used in these experiments. Six were challenged with *N. carpocapsae,* six with *H. heliothidis* and three served as controls. In the controls, only 0.5 cc of water was added to the filter paper.

Because of their larger size the harvestmen were placed together in containers measuring 140 mm x 190 mm x 90 mm containing filter paper in the bottom. The area of the filter paper was 266 cm[2]. Approximately 10 cc of the nematode mixtures were added to the filter paper making the nematode concentration approximately 4022 nematodes/cm^{2} for *H. heliothidis* and approximately 4511 nematodes/cm^{2} for *N. carpocapsae.* Ten harvestmen were placed in a container with *H. heliothidis,* ten with *N. carpocapsae* and nine served as controls (with water only).

The experiments lasted for 20 days. Water was periodically added to the filter paper to keep the nematodes viable. At the time of death, the arachnid was removed and a sample of blood drawn and plated out on Tergitol 7 plus TTC (triphenyltetrazolium chloride) agar. The symbiotic bacteria that are carried by the nematodes and released when they enter the host's hemocoel (*Xenorhabdus* spp.) (Thomas and Poinar 1979) turn a characteristic blue color on Tergitol 7 plus TTC agar. A positive color reaction from blood samples indicates a successful infection and the probable cause of death. This test is especially useful to determine infections when the nematode is not able to reproduce or perishes after entering the host.

RESULTS

The results of challenging three species of spiders and a harvestman with *N. carpocapsae* and *H. heliothidis* nematodes are summarized in Table 1. In every category, mortality as a result of nematode activity was obtained. The controls of *Pholcus, Pirata* and *Latrodectus* were all alive at the end of the experimental period, yet 67% of the control harvestmen perished. None of the controls showed evidence of nematode infection and death of the harvestmen was attributed to possible cannibalism.

With all hosts, those that died showed the presence of *Xenorhabdus* bacteria in their hemocoel shortly after death and later also exhibited mature nematodes in their body cavities (Figs. 1-4). However, although both *N. carpocapsae* and *H. heliothidis* were able to penetrate and develop to the adult stage in the hemocoel of the test spiders, reproduction and the production of infective stages occurred only in the phalangid host. With the latter, six harvestmen infected with *N. carpocapsae* produced a total of 43,000 infective juveniles (ca. 7,200 per host) and five harvestmen infected with *H. heliothidis* produced a total of 130,000 nematodes (26,000 per host).
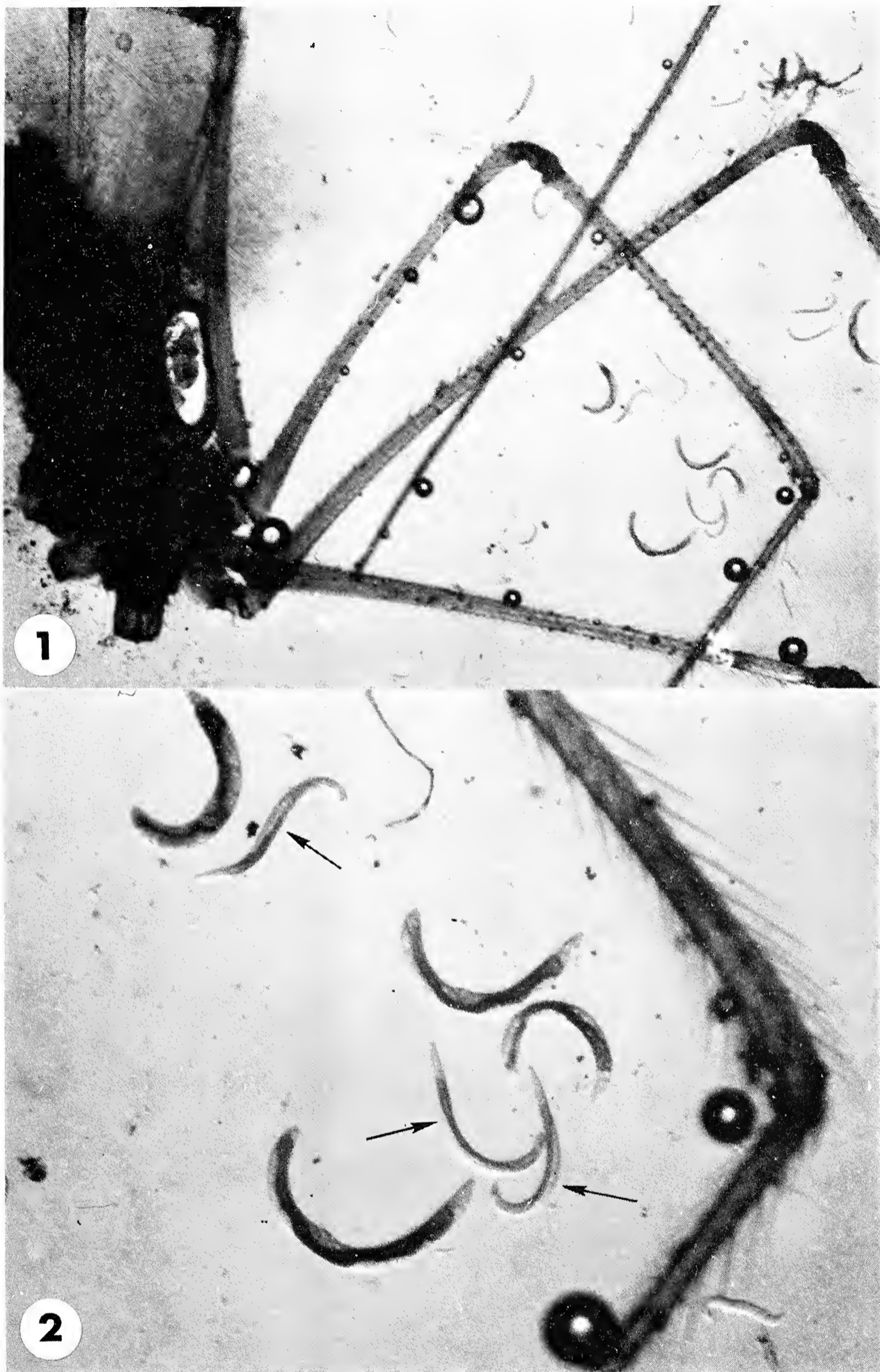
Fig. 1.—*Pholcus phalangiodes* killed by *Neoaplectana carpocapsae*. Adult nematodes removed from the spider's body are on the right side of the figure.

Fig. 2.—Detail mature females and males (arrows) of *Neoaplectana carpocapsae* removed from the body cavity of an infected *Pholcus phalangiodes*.
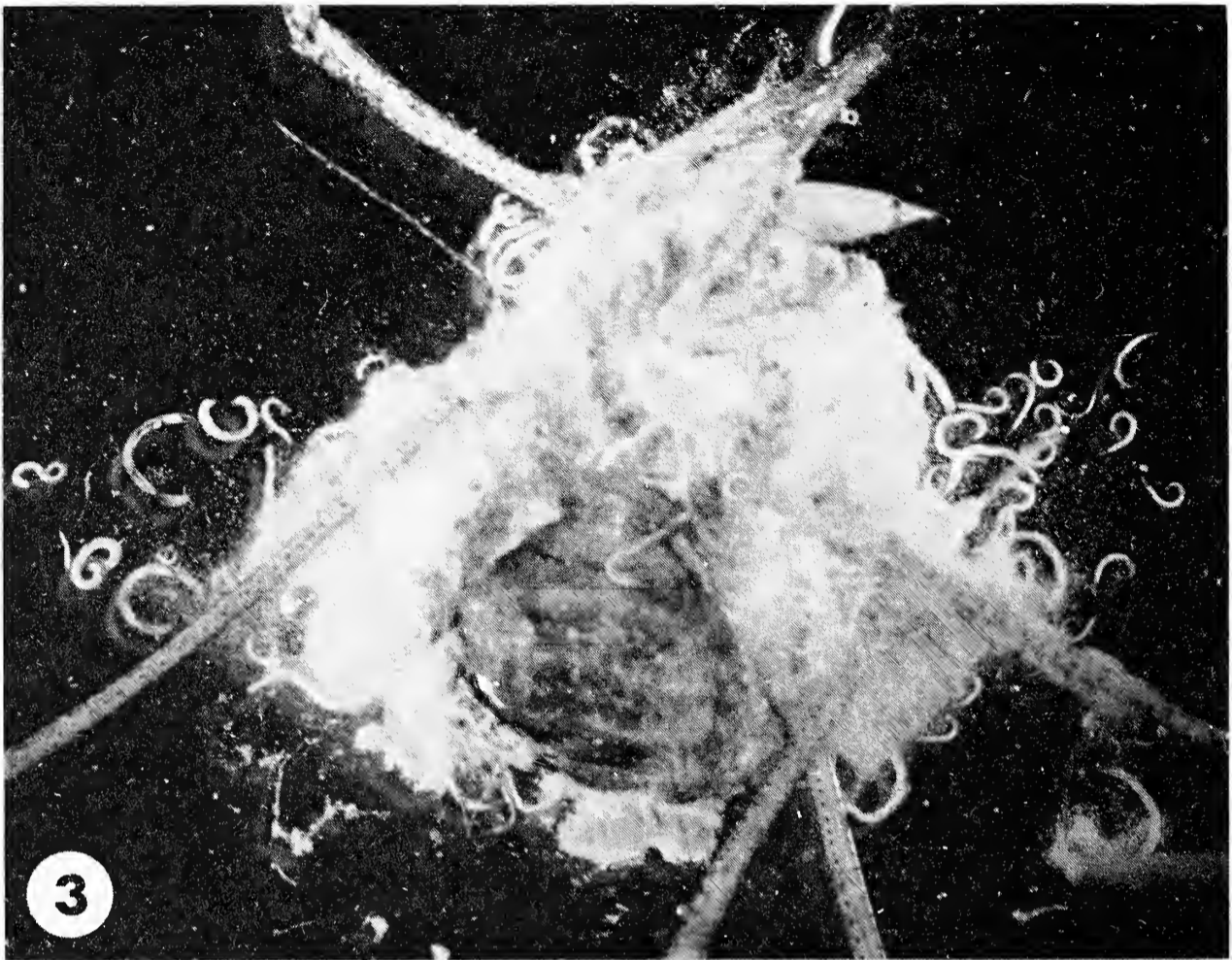
Fig. 3.—A *Phalangium* sp. killed by *Neoaplectana carpocapsae*. Note developing nematodes adjacent to the opened body.

Fig. 4.—Detail of developing female *Neoaplectana carpocapsae* removed from the body cavity of a *Phalangium* sp. Note juvenile nematodes developing inside a mature female (arrow).

Table 1.—Results of challenging three spiders and a harvestman with *N. carpocapsae* and *H. heliothidis.*

| Host | Number of Individuals Dead After 20 Days[1] | | |
	with *N. carpocapsae*	with *H. heliothidis*	control
Pholcus phalangiodes	6(100%)	3(50%)	0
Pirata sp.	3(50%)	4(66%)	0
Latrodectus mactans	6(100%)	6(100%)	0
Phalangium sp.	6(60%)	5(50%)	6(67%)

[1] The number in parenthesis refers to the percentage of those exposed that died.

DISCUSSION

The present tests are interesting because they show that some members of the class Arachnida are subject to infection by neoaplectanid and heterorhabditid nematodes.

These nematodes are able to invade and develop to the adult stage in the aerial spiders *Pholcus phalangiodes,* and *Latrodectus mactans,* a ground spider(*Pirata* sp.), and a harvestman (*Phalangium* sp.). However, only in the harvestmen was nematode reproduction complete and infective juveniles formed.

One reason for the lack of reproduction in the spider hosts could be due to the presence of foreign bacteria. In many hosts, a strain of *Pseudomonus aeruginosa* appeared soon after the spider died. This bacterium was noted to reproduce rapidly and fill the cadaver, thus competing with the symbiotic bacteria (*Xenorhabdus* sp.) which are necessary for nematode reproduction (Poinar 1979).

In conclusion, although spiders and harvestmen can be infected by neoaplectanid and heterorhabditid nematodes, they are only slightly susceptible in comparison with most insects. There is no record of a spider parasitized by these nematodes in nature, though there are reports of spider parasitism by mermithid nematodes (Poinar 1985).

Most spiders would normally not become infected during the mass release of nematodes on the soil surface for insect control. The aerial spiders would be protected by the nature of their habitat. The rapid movement of many ground spiders would be detrimental for nematode attachment and during periods of activity the phalangids would normally carry their bodies too high for the nematodes to reach. Such forms could be infected only during periods of quiescence.

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UPTAKE OF LEUCINE AND WATER
BY *CENTRUROIDES SCULPTURATUS* (EWING)
EMBRYOS (SCORPIONES, BUTHIDAE)

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ABSTRACT

In vitro radiotracer studies using tritiated leucine revealed that *C. sculpturatus* embryos accumulated leucine by a process that is characterized by a rate constant of approximately 0.02 min^{-1}. Cyanide inhibits leucine uptake, indicating that active transport is probably involved. Leucine is incorporated into embryonic proteins, and uptake is more rapid during early developmental stages when growth is most rapid. Although leucine uptake continues throughout development, dry mass of embryos does not increase during the later stages. These stages are characterized by differentiation, maturation, and by accumulation of water. Total body water increases from 53% of body mass in embryos with unpigmented median eyes to more than 80% at birth.

INTRODUCTION

The data on embryology and parturition in scorpions was recently reviewed by Francke (1982), who concluded that the term ovoviviparous could not justifiably be applied to scorpions (see also Williams 1969). Instead, he argued that the terms katoikogenic and apoikogenic, first suggested by Laurie (1896), were more appropriate. Katoikogenic scorpions (Diplocentridae and Scorpionidae) are characterized by relatively small eggs, lack of persistent extraembryonic membranes, long parturition times, and nutrition of the embryos via a placenta-like interaction between the uterine wall and the oral cavity of the embryos. Apoikogenic scorpions (Buthidae, Chactidae, Iuridae, and Vaejovidae) are characterized by well-developed extraembryonic membranes (the amnion and serosa) that fuse to enclose completely the embryo, short parturition times, and relatively large eggs. It has generally been assumed that apoikogenic scorpion embryos receive no nourishment from the mother, and thus the term ovoviviparous has been applied, in spite of the fact that embryonic growth in apoikogenic scorpions results in considerable increase in size (Laurie 1896).

Preliminary work in my laboratory had revealed that tritium-labelled leucine (^{3}H-leucine) injected into the hemolymph of gravid female *Centruroides sculpturatus* could be detected in the embryos within 72 hours. The experiments described in this paper were undertaken to analyze the kinetics of leucine entry into the embryos and to determine whether the leucine is actually incorporated

into the embryonic proteins. Data on mass changes during development were also gathered.

MATERIALS AND METHODS

Gravid female *C. sculpturatus* were collected from a population occupying cobblestone beaches along the Salt River approximately 50 km east of Phoenix, Arizona and returned immediately to the laboratory. All scorpions were maintained at 25°C and given *ad libitum* access to food (crickets) and drinking water.

Uptake of Radiolabeled Leucine (^{3}H-leucine).—Embryos were obtained from females that had been sacrificed by severing their anterior mesosoma. Embryos were dissected from the ovariuterus and placed in scorpion ringers (pH 7.4, 25°C) solution (Ahearn and Hadley 1976). Only embryos with intact extraembryonic membranes and, with one exception (see "^{3}H-leucine Uptake by Early Embryos," below), pigmented median eyes were used.

Kinetics of ^{3}H-leucine Uptake.—The time-course of ^{3}H-leucine penetration into the embryos was determined by placing three embryos into each of seven tubes containing 2.0 ml aliquants of scorpion ringers to which had been added ^{3}H-leucine and ^{131}I-albumin (ICN Radiochemicals). At intervals (see Table 1), the embryos in a tube were removed and their extraembryonic membranes were dissected free and discarded. The embryos were briefly washed with a gentle stream of distilled water and then homogenized in a known volume (1.88-2.20 ml) of distilled water. The ^{3}H and ^{131}I activity in a 1.0 ml aliquant of each homogenate was determined by liquid-scintillation counting. The total ^{3}H activity for each set of 3 embryos was then calculated by correcting the observed counting rate for the total volume of the respective homogenates.

Two replicate experiments were performed, the first one day, and the second two days after collection.

Effect of Metabolic Inhibition of Embryos.—To determine if the uptake of ^{3}H-leucine was energy-dependent, during each replicate experiment an additional tube containing 2.0 ml of radiolabeled scorpion ringers and sufficient NaCN (aqueous solution) to yield a CN⁻concentration of 1 mM was set up. Three embryos were placed in the tube and after 120 min incubation (at 25°C) the embryos were homogenized and ^{3}H activity was determined as described above.

Incorporation of ^{3}H-leucine into Embryonic Proteins.—As part of the second replicate experiment, a tube containing 2.0 ml of ^{3}H-leucine ringers and three embryos was incubated (at 25°C) for 48 h. The embryos were then homogenized in 0.5 ml distilled water and the proteins in a 40 μl aliquant of the homogenate were precipitated with 10% trichloroacetic acid (TCA). The precipitated proteins were washed with 5% TCA and ethanol/ether (50/50, v/v). The washed proteins were solubilized and ^{3}H⋅ activity was determined. Total ^{3}H activity in the proteins of the three embryos was then estimated as described above.

^{3}H-leucine Uptake by Early Embryos.—One of the females sacrificed for the first replicate contained embryos that were at a very early developmental stage as evidenced by their small size and the lack of visible differentiation of a metasoma or appendages. Three of these embryos (with intact extraembryonic

membranes) were placed into 2.0 ml of ^{3}H-leucine ringers and uptake was determined after 60 min incubation.

Mass Changes During Embryogenesis.—Seven of the gravid females were sacrificed by exposure to CN$^-$, and their embryos were removed and dissected free of their extraembryonic membranes. Each female's clutch of embryos was assigned to one of two developmental classes, based on whether or not the median eyes were pigmented (metasomal and appendage development was evident in all embryos). The total mass of each clutch was immediately determined to the nearest 0.1 mg, after which the embryos were freeze-dried to a constant mass.

Five females were allowed to deliver broods. After all of the young had climbed to their mother's dorsum, the total wet and dry masses of the newborn scorpions and their mothers were determined as described above.

Statistical comparisons involving the data were accomplished with appropriate non-parametric and parametric tests.

RESULTS

^{131}I counting rates did not significantly exceed background counting rates in any set of embryos, indicating that the extraembryonic membranes were intact and that large molecules were unable to penetrate the membranes at significant rates.

The time-course of entry of ^{3}H-leucine into *C. sculpturatus* embryos is indicated in Table 1. In both replicates, embryo counting rates (CPM) increased rapidly during the first 5 minutes, with a declining rate of increase thereafter. The presence of the metabolic inhibitor cyanide in the incubation medium significantly reduced the rate of leucine entry; even after 120 min incubation, embryo CPM were less than 1/3 those of the normal embryo 45 min CPM (t = 5.20, p $\ll$ 0.001). Leucine entry into the early embryos was more rapid, as evidenced by the more than two-fold higher CPM in the earlier embryos.

After 48 h incubation in medium containing ^{3}H-leucine, the embryonic proteins are definitely labelled with ^{3}H, indicating that the ^{3}H-leucine is incorporated into the embryonic proteins.

Estimates of rate constants for entry of leucine into the embryos may be obtained from the data in Table 1. The time-dependent increase in concentration of a solute entering a reservoir is described by the equation:

$$\ln \frac{c_\infty - c_t}{c_\infty} = -kt \qquad \text{Equation 1}$$

where c_∞ and c_t are, respectively, the solute concentrations in the reservoir at time $= \infty$ (i.e., at equilibrium) and at time t after initiation of the experiment, and k is the rate constant (Kotyk and Janacek 1975). Equation 1 also describes the time-dependent increase in counting rate (CPM) when radiotracers are used to monitor transport processes. In the present context, k is a measure of how rapidly the amino acid concentration in the embryos approaches equilibrium with the incubation medium. Numerically, it equals the proportion by which the difference between c_t and c_∞ is reduced each minute. Because c_t approached c_∞

Table 1.—Uptake of ^{3}H-leucine by *C. sculpturatus* embryoes. CPM = [3]H counts per minute for 3 embryos.

Incubation Time (min)	First Replicate		Second Replicate	
	CPM	% of Medium CPM[1]	CPM	% of Medium CPM[2]
2.5	273	0.32	380	0.53
5.0	408	0.48	702	0.97
10.0	701	0.83	618	0.86
20.0	942	1.12	842	1.17
30.0	848	1.01	997	1.38
45.0	1182	1.40	1182	1.64
60.0	1348	1.60	—[3]	—
CN⁻ (120 min)	369	0.44	375	0.52
Protein Incorporation (48 h)	—	—	13,238	18.34
Early Embryos (60 min)	2972	3.53	—	—

[1]Medium CPM = 42,125 CPM ml⁻[1]
[2]Medium CPM = 36,084 CPM ml⁻[1]
[3]Sample destroyed during processing

asymptotically, I used an iterative approach to estimate the value of c_∞ that maximized the r^2-value when Equation 1 was fitted to the data in Table 1 by least-squares regression. The CPM values for t = 2.5 min were not used in the regression analysis, because the data suggested the presence of a rapidly exchanging compartment that resulted in anomalously high CPM at t = 2.5 min. The results of this analysis are presented in Table 2.

Similarly, estimates of k for CN⁻-poisoned embryos may be obtained from Equation 1. Here, however, the estimates are biased somewhat by the fact that the effects of the rapidly-exchanging compartment cannot be factored out, and the values of k in Table 2 are probably somewhat larger than they should be.

In a strict sense, the fact that the leucine is incorporated into proteins requires use of a more complicated model (Kotyk and Janacek 1975). The consequence of not including the incorporation process in the model is that the estimated values of k for 'uninhibited' embryos (Table 2) are somewhat too high. The r^2-values suggest, however, that the errors are not large enough to preclude use of the k-values for purposes of discussion.

Wet and dry masses of different ontogenetic stages are presented in Table 3. Dry mass did not change significantly during the developmental stages listed, but

Table 2.—Kinetic analysis of ^{3}H-leucine uptake by *C. sculpturatus* embryos. Parameters were derived by iterative fitting of the data in Table 1 using Equation 1 as a model for least-squares regression.

	C_∞ (CPM)	k(min⁻¹	r^2	k(CN⁻)
First Replicate	1660	0.023	0.94	.0021
Second Replicate	1700	0.018	0.95	.0021

Table 3.—Ontogenetic changes in wet and dry mass of individual *C. sculpturatus* embryos. Values are presented as $\bar{x}$ ± S.D.. Total number of offspring in the litters is given in parentheses below the number of litters. Litter sizes ranged from 19 to 34 ($\bar{x}$ = 26.6, S.D. = 5.30).

Development stage	Number of litters	Average Dry Mass (mg)	Average Wet Mass (mg)	% H_2O
Median eyes unpigmented	3 (78)	2.70 ± 0.46	5.77 ± 1.04	53.1 ± 0.6
Pigmented median eyes	4 (121)	2.65 ± 0.64	9.99 ± 2.29	73.3 ± 1.5
Newborn	6 (147)	2.50 ± 0.15	12.72 ± 1.45	80.8 ± 0.7
Adults	—	—	—	71.2 ± 1.2

wet masses increased significantly (Kruskal-Wallis single factor ANOVA; H =9.45, p <0.01). This reflected a greater than 3-fold increase in the water content of embryos, from an average of 3.07 mg H_2O in embryos with unpigmented median eyes to 10.22 mg H_2O at birth.

DISCUSSION

Leucine not only penetrates the extraembryonic membranes of *C. sculpturatus* embryos, but is also incorporated into the proteins of the embryos at a fairly rapid rate (Table 1). Presumably, other amino acids and nutrients such as lipids and carbohydrates are also accumulated and utilized by the embryos. In the case of leucine, at least, the accumulation is energy-dependent, as evidenced by the order of magnitude decrease in k, the rate constant for leucine uptake, brought about by the addition of cyanide to the incubation medium (Table 2). These findings suggest that *C. sculpturatus* embryos are not metabolically isolated from their mother, but rather, are adapted to utilize nutrients provided by her throughout embryonic development. From that perspective, *C. sculpturatus* (and probably other apoikogenic scorpions) is not qualitatively different from the katoikogenic scorpions, in spite of the lack of obvious morphological specializations for embryo nutrition.

Ontogenetic changes in amino acid uptake are also suggested by the data in Table 1. It is not possible to calculate a rate constant for leucine transport in the "Early Embryo" stage, but the 60 min CPM is significantly greater than the corresponding CPM for the embryos whose median eyes have become pigmented (i.e., the stage used for all other uptake measurements listed in Table 1). This indicates that leucine uptake during the early stages of embryonic development is more rapid than during later stages. As is discussed below, the early developmental stages of *C. sculpturatus* are characterized by considerable increase in dry mass, while the later stages grow very little, if at all. The higher leucine uptake rate in the "Early Embryos" undoubtedly reflects this.

The nature of the energy-dependent process responsible for leucine uptake is unclear. The energy-dependence could result from active transport across the extraembryonic membranes, active transport into the embryonic tissues,

incorporation of leucine into the embryonic proteins, or a combination of these. The data presented here do not allow discrimination among the possibilities. In mammalian small intestine, transmembrane flux of alanine (like leucine, a neutral, lipophilic amino acid) results from a combination of passive diffusion along concentration gradients and active transport. At low luminal alanine concentrations, active transport is essential for amino acid uptake, whereas at higher concentrations, passive diffusion becomes the predominant uptake mode (Stevens, Kaunitz and Wright 1984).

The presence of ^{3}H-leucine in the embryos that had been incubated with cyanide indicates that leucine can diffuse through the extraembryonic membranes and into the embryonic tissues (Tables 1 and 2). However, the large effect of cyanide on the value of k (Table 2) makes it seem unlikely that the energy dependence of leucine uptake stems solely from the incorporation of leucine into proteins. Active transport through the extraembryonic membranes is probably involved, although further work is necessary to test this hypothesis.

Accumulation of dry mass is essentially completed by the time most of the characteristic features of scorpion external morphology (metasoma, pedipalps, etc.) have developed (Table 3). Growth during stages is considerable. If we assume that *C. sculpturatus* oocytes are spherical and similar in dimension to those reported for *C. vittatus* (approximately 0.5 mm; Francke 1982), and have a specific gravity of 1.0, then an oocyte would have a total (wet) mass of approximately 65 μg. By the earliest developmental stage listed in Table 3, even dry mass has increased by at least 40-fold. Dry mass changes very little during the later stages, indicating that differentiation and maturation, rather than growth, predominate.

There is, however, a marked increase in water content of embryonic *C. sculpturatus* during the final phase of development. Water content of the average embryo increases by more than 7 mg prior to birth. This results in an increase in the % H_2O from 53.1% to more than 80% at birth. Comparable data for earlier developmental stages of other arthropods do not appear to be available, so the generality of the increase in water content cannot be assessed. Water absorption, apparently energy-dependent, does occur in insect eggs, however (Edney 1977). The mechanism of H_2O accumulation in embryonic *C. sculpturatus* is unknown, but the constancy of dry mass of the embryos suggests an extraembryonic source.

The water content of newborn *C. sculpturatus* is higher than that of most other arthropods, being comparable to levels reported for lepidopteran larvae (Edney 1977). The increase in water content prior to birth may be adaptive. Newborn scorpions are, in many respects, extrauterine embryos: the sting is enclosed in a 'sheath', the cuticle is not sclerotized or tanned, and the young apparently do not feed while on the mother's back. The cuticle of newborn scorpions is probably relatively ineffective at retarding water loss. Prior to leaving the mother and beginning independent existence, the young molt. Molting scorpions seem to be very susceptible to relative humidity (O. F. Francke, personal communication), and successful completion of molting may be impossible if the scorpion desiccates too much prior to molting. The relatively high water 'stores' of newborn scorpions may thus increase the probability of completing the first molt.

The water stores could also be critical to the survival of the first instar larvae after leaving the mother. Organisms as small as first instar *C. sculpturatus* have

high surface:volume ratios, which makes the danger of fatal desiccation particularly acute. Because of their flattened shape, scorpions have relatively large surface areas for a given mass (Toolson and Hadley 1977), which would tend to exacerbate the susceptibility of the first instar young to transcuticular water losses. I suspect that desiccation is a leading cause of mortality for immature scorpions, particularly during the first instar. Although I do not have evidence that the high water content of the newborn scorpions is maintained through the molting to first instar, if it were this would certainly enhance the probability of surviving.

The data presented in this paper are consistent with Francke's contention that the term ovoviviparous should not be applied to the Buthidae or other apoikogenic families of scorpions. Although the details of the uptake processes remain to be worked out, it is apparent that the embryos of *C. sculpturatus,* at least, are not nutritionally isolated from their mother. Embryos accumulate leucine at the expense of energy, particularly during the earlier developmental stages (when most of the increase in embryonic mass occurs), and incorporate the leucine into proteins. Even during the later developmental stages, leucine uptake continues but at reduced rates. Moreover, during the final developmental stages, the embryos accumulate large amounts of water, which must necessarily be derived, at least in part, from the water stores of the mother.

The demonstration that 'large-egged' apoikogenic scorpions provide nutrients to the embryos raises some interesting questions about the evolution of viviparity in the order. Little work has been done on the metabolism of gravid females or of embryos. In the katoikogenic scorpion, *Heterometrus fulvipes* (C. L. Koch), a member of the family Scorpionidae, gravid females exhibit enhanced glycolytic activity in the hepatopancreas and "reproductive tissues" (Jayaram et al. 1978). In the same tissues, total lipid content and total protein content decrease significantly during embryogenesis apparently to meet the metabolic demands of the embryos. Comparable work on apoikogenic scorpions does not appear to have been done. Comparative studies on several species should be undertaken. The resulting data should provide insights into the reason(s) why the two markedly different 'approaches' to embryogenesis have been maintained during the evolution of the Scorpiones.

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OPILIONES FROM THE CAPE HORN ARCHIPELAGO: NEW SOUTHERN RECORDS FOR HARVESTMEN

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ABSTRACT

Previous subantarctic and extreme southern cold temperate island localities for harvestmen are reviewed. The record of *Spinicrus tasmanicum* (Hogg) from South Georgia is questioned. *Thrasychirus dentichelis* Simon and *Thrasychirus modestus* Simon are now recorded from Isla Deceit (55°49'S latitude), and *T. dentichelis* alone from Isla Bayly (55°37'S) and Isla Wollaston (55°44'S), Cape Horn Archipelago.

RESUMEN

Se revisan las localidades ya conocidas de los Opiliones recolectados el las islas del extremo sur templado-frío e islas subantárticas. Se pone en duda la validez del registro de *Spinicrus tasmanicum* (Hogg) en Georgia del Sur. *Thrasychirus dentichelis* Simon y *Thrasychirus modestus* Simon se citan aquí por primera vez de la isla Deceit (55°49'S) y *T. dentichelis* se cita además de la isla de Bayly (55°37'S) e isla Wollaston (55°44'S), en el archipiélago del Cabo de Hornos.

INTRODUCTION

Although Opiliones are reported (Marx 1892) as far north as 81°44' (Fort Conger, Ellesmere Island, Canada), there are few reports from extreme southern latitudes. There are no reports of harvestmen from Antarctica proper and there

Table 1.—Opiliones reported from subantarctic and extreme southern cold temperate islands.

Family/species	Occurrence	Latitude South	Climate	Literature
TRIAENONYCHIDAE				
Neonucia campbelli Forster	Campbell Islands	52°33'	cold temperate	Forster 1954, 1964
Neonuncia eastoni Forster	Auckland Islands	50°32'	cold temperate	Forster 1954, 1964
Neonuncia enderbyi (Hogg)	Auckland & Campbell Islands	50°32', 50°33'	cold temperate	Forster 1954, 1964
Nuncia unifalculata (Enderlein)	Crozet Islands	46°30'	subantarctic	Tambs-Lyche 1954, Hickman 1939
GONYLEPTIDAE				
Lycomedicus planiceps (Guerin)	Isla Hoste	55°10'	cold temperate	Soares & Soares 1954
Haversia defensa (Butler)	Islas Malvinas	52°	cold temperate	Soares & Soares 1949
Hoggellula vallentini (Hogg)	Islas Malvinas	52°	cold temperate	Soares & Soares 1949
MEGALOPSALIDIDAE				
Pantopsalis distincta Forster	Auckland Islands	50°32'	cold temperate	Forster 1964
Pantopsalis johnsi Forster	Auckland Islands	50°32'	cold temperate	Forster 1964
Pantopsalis mila Forster	Auckland Islands	50°32'	cold temperate	Forster 1964
Pantopsalis rennelli Forster	Campbell Island	52°33'	cold temperate	Forster 1964, Gressitt et al. 1964
Pantopsalis snaresensis Forster	Snares Island	48°	cold temperate	Forster 1964
NEOPILIONIDAE				
Thrasychirus dentichelis Simon	Isla de los Estados, Isla Hoste	54°50', 55°30'	cold temperate	Ringuelet 1959
	Cape Horn Archipelago	55°37'-49'	cold temperate	present paper
Thrasychirus gulosus Simon	Isla de los Estados, Isla Hoste	54°50', 55°30'	cold temperate	Ringuelet 1959
Thrasychirus modestus Simon	Isla Hoste, Isla Navarino	55°10'-30'	cold temperate	Cekalovic K. 1976
	Isla Deceit	55°49'	cold temperate	present paper

are only two species reported from true subantarctic habitats (one record of which is probably in error). The known records of Opiliones from subantarctic and southern cold temperate localities are listed in Table 1.

Roewer (1956) reported *Spinicrus tasmanicum* (Hogg), family Megalopsalididae, from "Süd-Georgien — 3♂, 3♀." Although South Georgia lies at 54°00'-50', it is within the Antarctic Convergence and is a true subantarctic island. As the only other records of *S. tasmanicum* are from Tasmania (Roewer 1956, Hickman 1957), South Georgia is an unlikely locality for this species. We suspect the South Georgia collections are mislabeled. Further support for our suspicion comes from the knowledge that numerous specimens from the Roewer collection are believed to be mislabeled (see Cokendolpher and Cokendolpher 1984, Levi 1983, and citations contained therein). Furthermore, no other collections of Opiliones are known from South Georgia (Tambs-Lyche 1954, Gressitt 1970), making Roewer's collection of three pairs appear unrealistic.

Until now no harvestmen have been reported from the Cape Horn Archipelago. The most southern records from South America were previously reported from Isla Navarino and Isla Hoste by Simon (1884, 1902). We have two species of neopilionid harvestmen which were collected from the Cape Horn Archipelago: *Thrasychirus dentichelis* Simon and *Thrasychirus modestus* Simon. Our records not only extend the known ranges for these species, but also set a new southern latitude for the Order.

THE STUDY AREA

The eight main islands making up the Cape Horn Archipelago are situated between 55°S-67°W and 56°S-68°W. Despite their extreme southern latitude they lie north of the Antarctic Convergence and have a relatively mild climate compared to other islands of similar latitudes (Figs. 1, 2). The Cape Horn Archipelago has been included in the Magellanic Tundra Complex because of its climatic, floristic and vegetational characteristics (Pisano V. 1977, 1983).

There are no meteorologic stations on this archipelago. The nearest stations are located at Isla Navarino (Puerto Williams) and at Islas Diego Ramírez (Isla Gonzalo). The climate of the Cape Horn Archipelago is similar to that of Diego Ramírez. However, the latter supports an Isothermic Tundra clime with a high oceanic influence, which is more moderate at the area studied (Zamora and Santana 1979, Pisano V. 1980). Nevertheless the most reliable data registered from nearby the Cape Horn Archipelago are those obtained from October 1882 to August 1883 by the French Scientific Mission to Cape Horn at Bahía Orange, Isla Hoste (Lephay 1887). From interpolation of these data, Pisano V. (1983) reported 1,357 mm of annual rain and 5.2°C of mean annual temperature for the area. The relative humidity fluctuates from 87 to 93%. Another important climatic factor is the wind, especially that from the SW. This element has a high constancy in the archipelago and a mean monthly speed of approximately 30km/hr, with maximal squalls of over 100km/hr during any season.

Because of these characteristics the area of Cape Horn can be included in the Isothermic Tundra type of climate, with the notation ETi(w')k'c, from the Köppen classification (Llorente 1966). It is snowy during winter (E); supports a Tundra vegetation type (T); is isothermic with a difference between the warmest
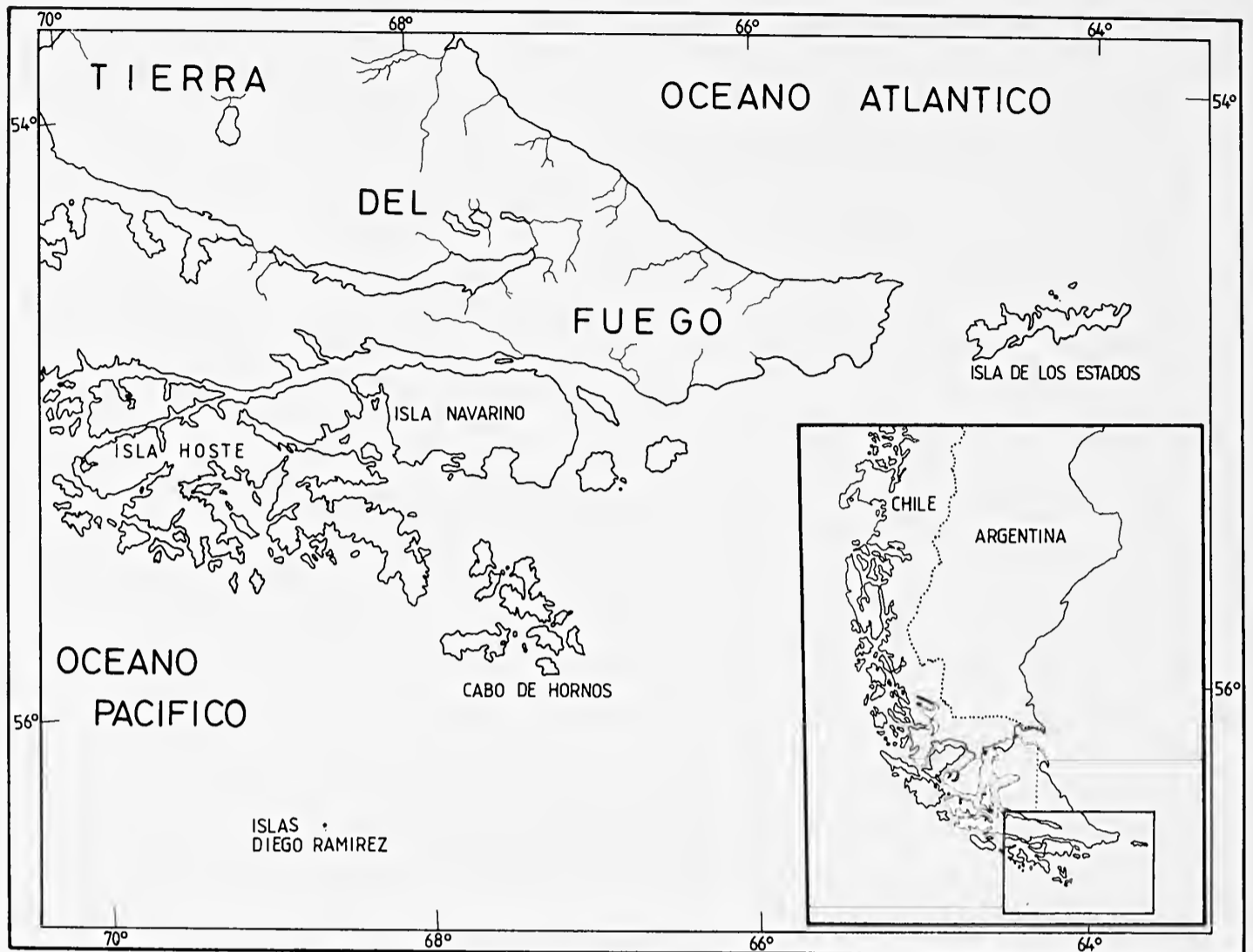
Fig. 1.—Map of southern tip of South America, showing Cape Horn Archipelago and other localities where opilionids have been reported.

and the coldest month medium temperatures of 5°C (i): its rainiest season, although not so marked, is autumn (w′); it is very cold, with a mean monthly temperature lower than 18°C, but those of the coldest months are higher than -18°C (k′) and during the four warmest months the mean is lower than 10°C (c).

The distribution and floristic composition of the vegetational communities depends primarily on the edaphic characteristics, such as the low availability of organic nutrients, the differential capacities of the soils to retain water, and high organic acidity. In the study area, the dominant vegetational formations are moorlands and dwarf forests communities. Bogs can be found at low or high elevations, in flat or slightly undulating sites with poor drainages. There are three basic types of bogs based on floristic composition: cyperoideus, cushion and mossy. Intermediate forms are frequently encountered and were sampled on Bayly, Wollaston and Deceit islands. The cyperoideus bog develops mostly at low elevations, with dominant species such as *Schoenus andinus* (Phil.) Pfeiffer being associated with *Carpha alpina* R. Br. var. *shoenoides* (Banks & Sol. ex Hooker f.) Küken, *Schoenus antarcticus* (Hooker f.) Dusén and the Juncaceae *Marsippospermum grandiflorum* (L. f.) Hooker f. In the lower stratum cushion growing species predominate. They form large convex cushions of low height with caespitose species such as *Astelia pumila* (Forster f.) Gaudich. (which dominates), *Donatia fascicularis* Forster & Forster f., *Caltha dionaefolia* Hooker f., *Drapetes muscosus* Banks ex Lam., *Gunnera lobata* Hooker f., *Phyllachne uliginosa*
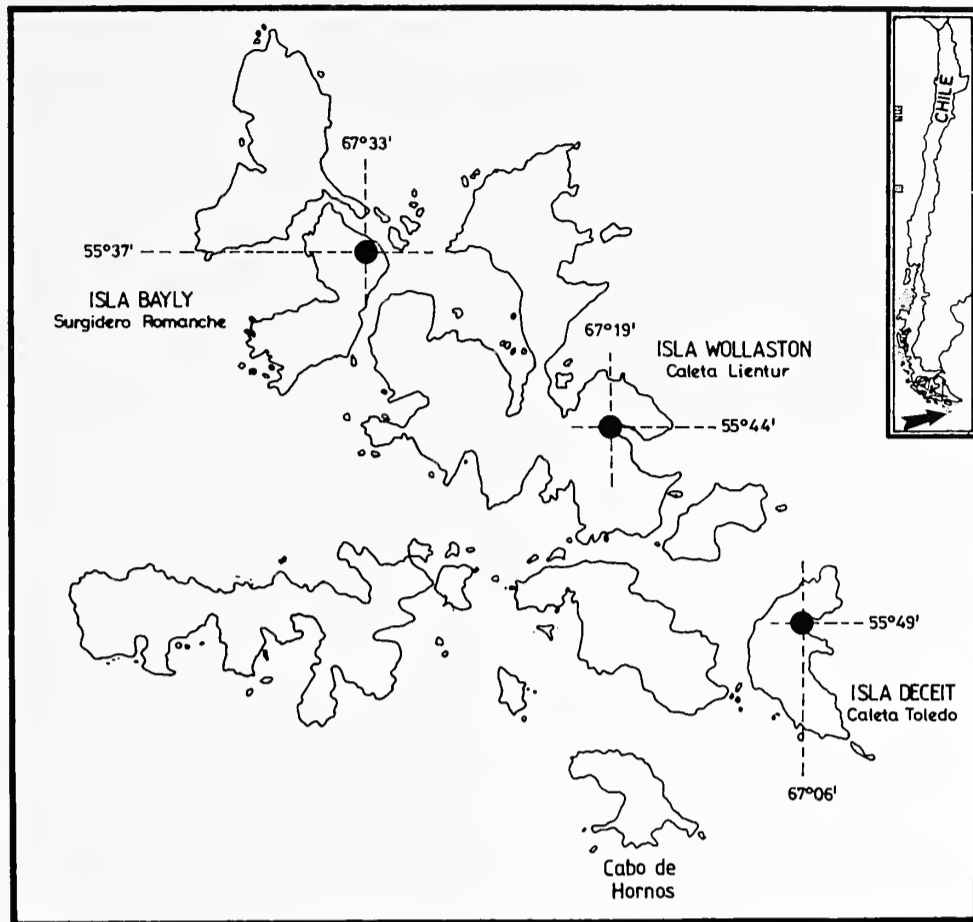
Fig. 2.—Map of Cape Horn Archipelago, showing collection sites of Opiliones.

Forster & Forster f., *Tetroncium magellanicum* Willd, *Tapeinia pumila* (Forster f.) Baillon, *Gaimardia australis* Gaudich and *Oreobolus obtusangulus* Gaudich. Mosses, ferns and liverworts form a very dense cover in moist areas with high humidities. At drier sites, herbaceous species (mostly cyperoideus) dominate.

The forest communities grow in wind protected places like gorges, hill slopes and the fringes of the valleys. The floristic composition and physiognomy changes depend upon the wind exposure (Pisano V. 1980). The arboreal level is formed almost exclusively by *Nothofagus betuloides* (Mirbel) Oersted, associated in some sectors with a few specimens of *Drimys winteri* Forster & Forster f. These species form a semidense stratum with tortuous trees of low height and flat treetops (due to effects of winds). The forest shrub layer is composed by *Berberis ilicifolia* L. f., *Pernettya mucronata* (L. f.) Gaudich. ex G. Don. and a few specimens of *Berberis buxifolia* Lam., *Chiliotrichium diffusum* (Forster f.) Kuntze, *Empetrum rubrum* Vahl ex Willd. and *Escallonia serrata* J. E. Sm. Several species of ferns, lichens, mosses and liverworts constitute the basal level. The ground cover of dead leaves does not exceed 7 cm in depth.

THE OPILIONID FAUNA

Pitfall Barber traps with 7% formaldehyde, without attractive fats, were used. The traps, in each of the studied islands, were located in two sectors of forest and bog communities. All of the material captured was stored in 70% isopropyl alcohol. The localities and dates samples, and number of traps used were: (1) Isla Bayly, Surgidero Romanche (55°37'S-67°33'W) 28 Feb.-4 March 1980, 20 traps; (2) Isla Wollaston, Caleta Lientur (55°44'S-67°19'W) 15-25 Feb. 1980, 20 traps;

(3) Isla Deceit, Caleta Toledo (55°49′S-67°06′W) 18 Nov.-3 Dec. 1982, 80 traps (Lanfranco L. 1980, 1981, in press).

Specimens were identified by the use of taxonomical keys by Ringuelet (1959) and Cekalovic K. (1976). Species identifications were verified by comparisons to type specimens (as part of a generic revision). Identified specimens are deposited at the Instituto de la Patagonia, American Museum of Natural History and in the senior authors personal collection.
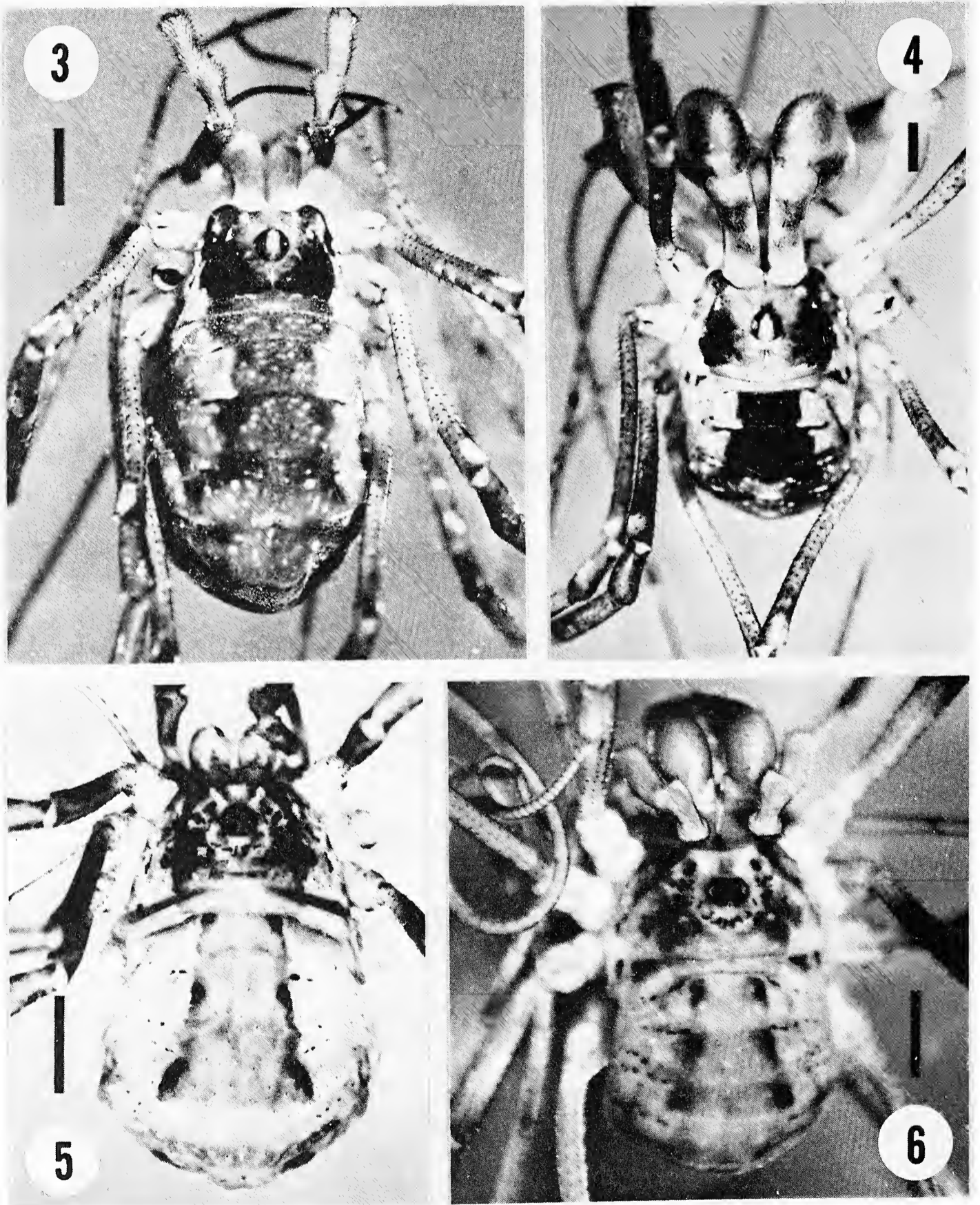
Fig. 3-6.—*Thrasychirus* spp.: 3, *T. dentichelis* female; 4, *T. dentichelis* male; 5, *T. modestus* female; 6, *T. modestus* male. Scale lines = 1 mm.

Thrasychirus dentichelis Simon
Figs. 3, 4

This species was described by Simon (1884) from specimens collected from Isla Hoste and it has been reported from several more northern localities in Argentina and Chile (Ringuelet 1959, Cekalovic K. 1976). Recent studies of museum specimens reveal that the specimens reported as *T. dentichelis* from Valdivia and Santiago provinces of Chile and the Nahuel Huapi region of Argentina are representatives of two different undescribed species of *Thrasychirus* Simon. *Thrasychirus dentichelis* is restricted to the cold forest of the Magallanes province (Chile), the Argentinean Territory of Tierra del Fuego and Islands of Cape Horn Archipelago. The northern limit for this species is from a specimen collected at about 50°50'S.

Thrasychirus dentichelis can be separated from *T. modestus* (the only other species of harvestmen from Cape Horn Archipelago) by the differences in size and dorsal body color patterns. The dorsum of *T. dentichelis* is covered with numerous white spots which are absent on *T. modestus*. The wedge shaped pattern on the dorsum is generally sharply defined posteriorly on *T. modestus*. The pattern is weakly defined posteriorly or absent on *T. dentichelis* (compare figs. 3 and 6). Adults of *T. dentichelis* are noticeably larger than those of *T. modestus*. The males of *T. dentichelis* also differ from those of *T. modestus* by having enlarged chelicerae and a large apophysis on the mesal margin of each palpal tibia distally. The genitalia of these species differ greatly. Illustrations showing these differences will be published elsewhere in the context of a generic revision.

New records.—CHILE: *Magallanes,* Isla Wollaston, Caleta Lientur, from both bog and forest habitats (15-25 Feb. 1980, D. Lanfranco L.), 4 females, 25 juveniles. Isla Bayly, Surgidero Romanche, coastal mixed forest, transitional scrub and moorland communities (28 Feb.-4 March 1980, D. Lanfranco L.), 8 females, 19 juveniles. Isla Deceit, Caleta Toledo, from bog and forest communities (majority from forests) (18 Nov.-3 Dec. 1982, D. Lanfranco L.), 7 males, 22 females.

Thrasychirus modestus Simon
Figs. 5, 6

This species was described by Simon (1902) from specimens collected in southern Tierra del Fuego and Isla Navarino. Cekalovic K. (1976) reports other localities in southern Magallanes province. The northern record appears to be Punta Arenas at about 53°10'S (Cekalovic K. 1976).

New record.—CHILE: *Magallanes,* Isla Deceit, Caleta Toledo, forest communities (single specimen from moorlands) (18 Nov.-3 Dec. 1982, D. Lanfranco L.), 4 males, 17 females.

Thrasychirus sp.

Among the collections already mentioned were numerous examples of early instar juveniles that could not be identified. The majority of these, if not all, probably represent examples of *T. dentichelis* as they lack the characteristic dark, sharply-defined pattern on the abdomen. As the lack of a pattern on the abdomen could also be due to the animal being recently molted we prefer not to attach specific names.

New Records.—CHILE: *Magallanes,* Isla Wollaston, Caleta Lientur, bog and forest habitats (15-25 Feb. 1980, D. Lanfranco L.), 2 juveniles. Isla Deceit, Caleta Toledo, forest and moorlands (18 Nov.-3 Dec. 1982, D. Lanfranco L.), 74 juveniles.

ACKNOWLEDGMENTS

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STAGE-BIASED OVERWINTERING SURVIVAL
OF THE FILMY DOME SPIDER
(ARANEAE, LINYPHIIDAE)

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ABSTRACT

Overwintering success of the filmy dome spider *Prolinyphia marginata* (Koch) [= *Neriene radiata* (Walckenaer) and *Linyphia marginata* Koch] was observed with respect to stage of development and differences in body weight within a stage. Studies conducted in three different areas measured winter survivorship rates of 60 spiders housed in outdoor cages (Michigan), 243 spiders in outdoor jars (Maryland), and 245 spiders in a combination of cages and jars (New York). The overall proportion of spiders successfully overwintering was 0.31 in New York, 0.69 in Maryland, and 0.75 in Michigan. All three studies showed that older stages (instars) had substantially higher survival rates than younger stages. Comparison between the autumn weights of overwintering survivors and non-survivors indicated that differences in spider weight within a stage had no significant influence on winter survival.

These experimental studies suggest that overwintering mortality may be significant in natural populations of *P. marginata,* and that different overwintering survival rates among stages can alter the composition of the population.

INTRODUCTION

Not much information is available on overwintering mortality in spiders. Schaefer (1977) studied the winter ecology of several species and found that winter mortality was not correlated with overall generation mortality. Buche

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(1966, cited by Toft 1976) discovered that the smaller stages (instars) of linyphiids do not survive cold temperatures as well as later stages. On the other hand, Schaefer found that only adults of the linyphiid *Centromerita bicolor* suffered substantial winter mortality. Other information is available (e.g. Kirchner 1973, Edgar and Loenen 1974), though we lack much basic data, especially considering the potential importance of winter mortality as a key factor in the dynamics of spider populations. Not much is known about the relative susceptibility of the younger stages to winter conditions, despite the fact that populations of over 70% of temperate spider species overwinter, at least partially, in juvenile stages (Schaefer 1977).

The filmy dome spider, *Prolinyphia marginata* (C. L. Koch) [= *Neriene radiata* (Walckenaer) = *Linyphia marginata,* C. L. Koch], is a sheet-web building linyphiid common in North America. The species overwinters in forest leaf litter (J. Martyniuk and D. H. Wise, pers. obs.), as do many temperate linyphiids (Schaefer 1977, Aitchison 1978). Census data for a Michigan population of *P. marginata* indicate that winter disappearance is significant in this population (Wise 1976). The complex phenology of the filmy dome spider produces an overwintering population that is a mixture of subadult stages, ranging from recently emerged spiderlings to large, late-stage juveniles (Wise 1976, 1984). This mixture of stages reflects within-season differences in the timing of reproduction and development patterns of young spiders, and also reflects the effects of variable prey abundance upon rates of growth and development (Wise 1975, submitted, Martyniuk 1983).

This paper reports the results of three separate studies, each with a different population of *P. marginata.* Considered together, the studies examined the relative overwintering survival of different stages and the influence of weight differences within a stage on winter mortality. Study I was conducted by J. Martyniuk, and Studies II and III by D. H. Wise.

STUDY I

Methods.—The population that was studied occurred on the Nature Preserve of the State University of New York at Binghamton, Broome Co., New York. During February 1981, leaf-litter samples were collected and examined in order to document the presence of *P. marginata* in the leaf litter during the winter. Five 30 cm x 30 cm forest floor plots were excavated and removed (10 cm depth) from known *P. marginata* habitat and transported to the laboratory in plastic bags. Three viable, immature *P. marginata* were found in the samples. It was not possible to determine the exact location of the spiders in the litter due to the disruption of excavation and transportation.

To determine overwintering mortality in *P. marginata,* 145 spiders in 1981-82 and 55 spiders in 1982-83 were individually housed in 400 ml glass jars containing ca 5 cm of leaf-litter and soil. The jars were securely covered with fabric netting and placed next to a wall on an open terrace. A sheet of plywood was suspended 10 cm above the top of the jars, minimizing snow accumulation and possible drainage problems. As a control for this artificial situation, in 1981-82 three 30 cm x 30 cm x 30 cm net cages, each containing soil and leaf-litter with 15 spiders, were embedded 10 cm into the ground in an area known to harbor *P. marginata.*

The mesh size of the cages was large enough to allow snow to accumulate inside. Leaf litter and soil used in the jars and cages were collected from the field and examined for resident *P. marginata* prior to use in experimental containers. Jars were placed outside and spiders were introduced into the cages with the final disappearance of *P. marginata* in the field, 1 November 1981 and 5 November 1982. Likewise, jars and cages were examined for survivors with the reappearance of spiders in the field, 18-28 April 1982 and 15-25 April 1983. Following these monitoring periods, the soil and leaf-litter were inspected in the laboratory for further survivors.

To investigate further the degree of similarity of the jar environment to that of field conditions, jar leaf-litter temperatures were compared to actual leaf-litter temperatures measured in the field. The leaf-litter temperature and snow covered in 13 previously identified *P. marginata* web-sites were monitored from 23 January 1981 to 24 February 1981. Glass-encased mercury thermometers, which had been calibrated with a total emersion, mercury/nitrogen thermometer over a range of temperatures including those encountered in the field, were placed ca 5 cm down in the litter. Litter temperatures and snow covered at these sites were recorded daily (1200 hours), and the total emersion, mercury/nitrogen thermometer was used to record the daily ambient air temperature. Similarly, from 13 January 1983 to 24 February 1983 the litter temperature of a sample jar was recorded every six days (1200 hours) using the total emersion mercury/nitrogen thermometer.

Spiders used in the study were collected one week prior to the start of the experiments. For each collection period (1981 and 1982), a 20 m x 20 m plot was marked in *P. marginata* habitat and all observed individuals were captured. The cephalothorax width of the collected spiders was measured so as to identify the particular stage of development for each individual (Martyniuk 1983). Thus samples for both years reflect the composition of stages in the population entering the winter. No stage I, II or III spiders were found in 1982, whereas 15 stage III spiders were collected in 1981, but escaped shortly after the start of the experiment. Fifteen stage I and 15 stage II individuals, captured in 1981, were combined into one group to increase the sample size. Such variation in population structure is characteristic of this species (Wise 1984). None of the stage VI spiders used in these studies were mature.

To determine if there was a difference in average weight between entering and surviving spiders within a stage, 20 spiders in 1981, and 10 spiders in 1982, all stage V, were individually weighed to provide a direct comparison of the autumn weight between survivors and non-survivors.

Results.—Overwintering survival rates for the various developmental stages of *P. marginata* are presented in Table 1. The combined data for all three experiments indicate an average overwintering survival rate of 0.31 (76/245). However, mortality was not evenly distributed among stages. Older stages, V and VI, had a much higher success rate than younger stages ($\chi^2 = 37.03$, $p < 0.001$, 2 X 4 contingency table).

Differences in spider weight within stage V seem to have had little influence on overwintering success. Analysis of Variance shows no significant difference (F = 1.25, $p > 0.05$) between the average autumn weight of 19 stage V survivors, 2.6 ± 0.6 mg.

Table 1.—Overwintering survivorship of *P. marginata* in jars and cages, Study I.

| Stage | 1981-82 (jars) | | 1981-82 (cages) | | 1982-83 (jars) | |
	n	Proportion Surviving	n	Proportion Surviving	n	Proportion Surviving
I, II	30	0.03	-	-	-	-
IV	35	0.06	15	0.13	20	0.25
V	55	0.42	15	0.47	20	0.65
VI	25	0.44	15	0.40	15	0.33
TOTAL	145	0.26	45	0.33	0.42	

The overwintering field parameters of leaf-litter temperature, snow cover, and ambient air temperature from 23 January 1981 to 24 February 1981 are depicted in Figure 1. Comparison of survival rates in jars and cages, in conjunction with the recording of leaf-litter temperatures, suggests that conditions in the jars adequately mimicked overwintering field conditions. Analysis of variance showed no significant difference (F = 4.05, p > 0.05) between the average temperature of litter in the field, -2.6 ± 2.3 °C, and the average temperature of litter in the jars -0.1 ± 5.7°C. Elimination of stage I and II data from the 1981-82 jar study, since they were not included in the cage study, produces a survival rate of 0.31 compared to the 0.33 rate found for the field cages and 0.42 in the 1982-83 jar study. Z-score comparisons show no significant differences (p > 0.05) between the 1981-82 survival frequencies in cages and jars for stages IV, V and VI.

STUDY II

Methods.—A total of 242 immature spiders was collected from two Maryland populations at the end of October 1982. One population inhabited an oak forest on the Liberty Watershed, 40 km northwest of Baltimore. The second site was a predominately oak forest located 35 km south of Liberty on the Patuxent Wildlife Research Center, near Laurel. Details on the phenology and size structure of both populations appear elsewhere (Wise 1984).

The spiders were assigned to stage based upon the relationship between length of the fourth tibia and developmental stage (unpubl. data). The two youngest stages have been combined for the analysis since only two Stage I spiderlings were collected. Stages V and VI were pooled because many spiders cannot be assigned unambiguously to one or the other of these stages when tibia length is the criterion. The spiders were kept in the laboratory until 10 November, when they were placed individually in 240 ml glass jars containing a layer of vermiculite, crumpled tissue paper to mimic leaf litter and a wire framework for web attachment. The top of each jar was covered tightly with fine-meshed nylon cloth. The jars were placed on shelves on a screened porch in the forest at Patuxent. On 11 November each spider was given three (stages I-II) or six (stages III-VI) fruit flies. On this date all spiders were alive and many were in small webs.

The jars were left on the porch through the winter, and were examined for living spiders on 20 March 1983. By this date *P. marginata* had appeared on webs in the forest at Patuxent.
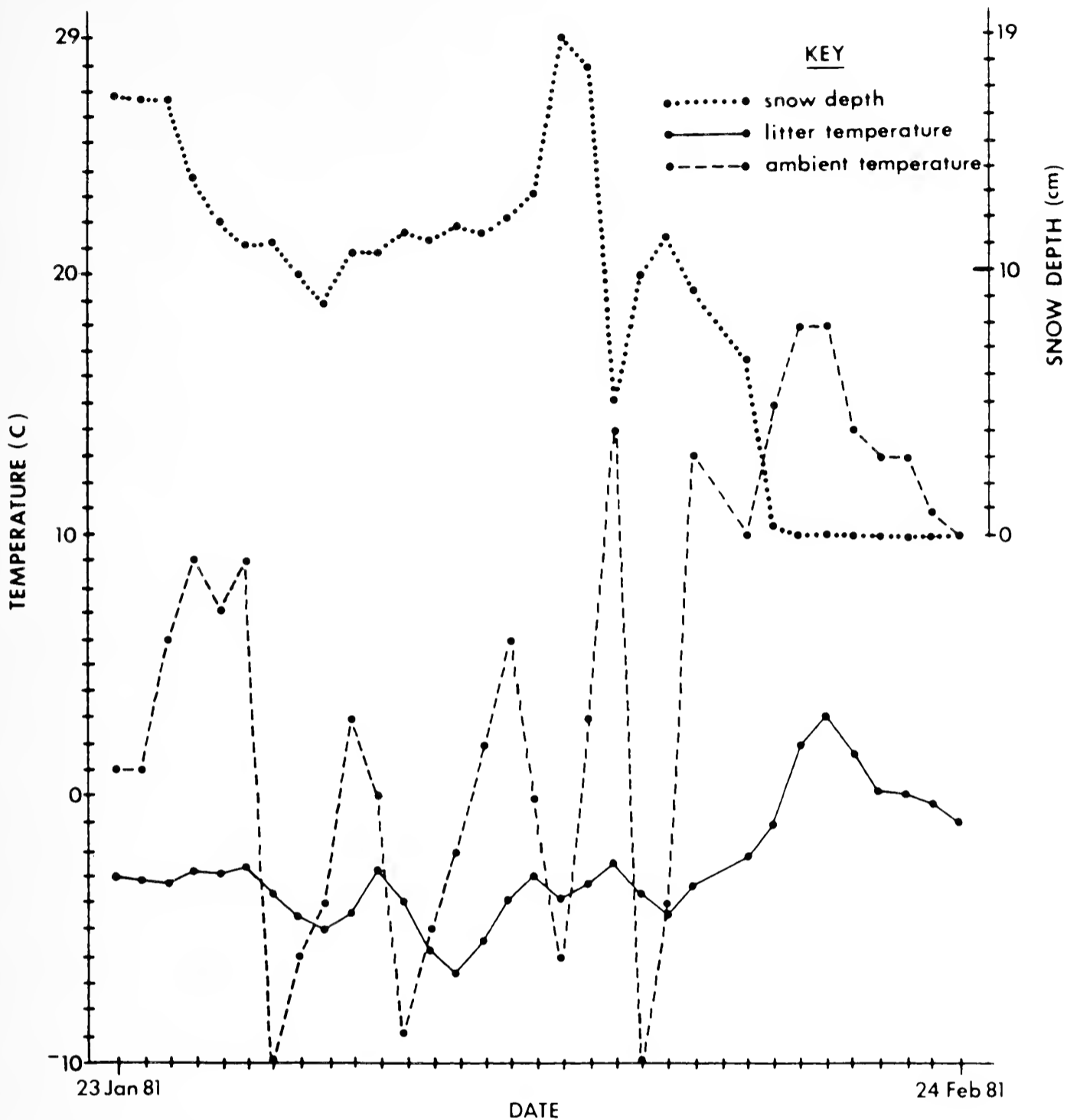
Fig. 1.—The overwintering field environment of *Prolinyphia marginata* from 23 January 1981 to 24 February 1981. Average daily leaf litter temperature, snow cover, and ambient air temperature for 13 sites, Study I.

Results.—The overall survival rate (stages I-VI combined) was 0.69 (168/242). Probability of surviving the winter was not the same for all stages ($\chi^2 = 42.8$, $p < 0.001$, 2 x 4 contingency table). The youngest stages (primarily stage II) suffered a markedly higher winter mortality than the larger stages (Fig. 2).

STUDY III

Methods.—The third study was conducted 1972-73 in an oak forest on the E.S. George Reserve, Livingston County, Michigan, in *P. marginata*'s natural habitat. Detailed information on this population of the filmy dome spider appears elsewhere (Wise 1975, 1976).
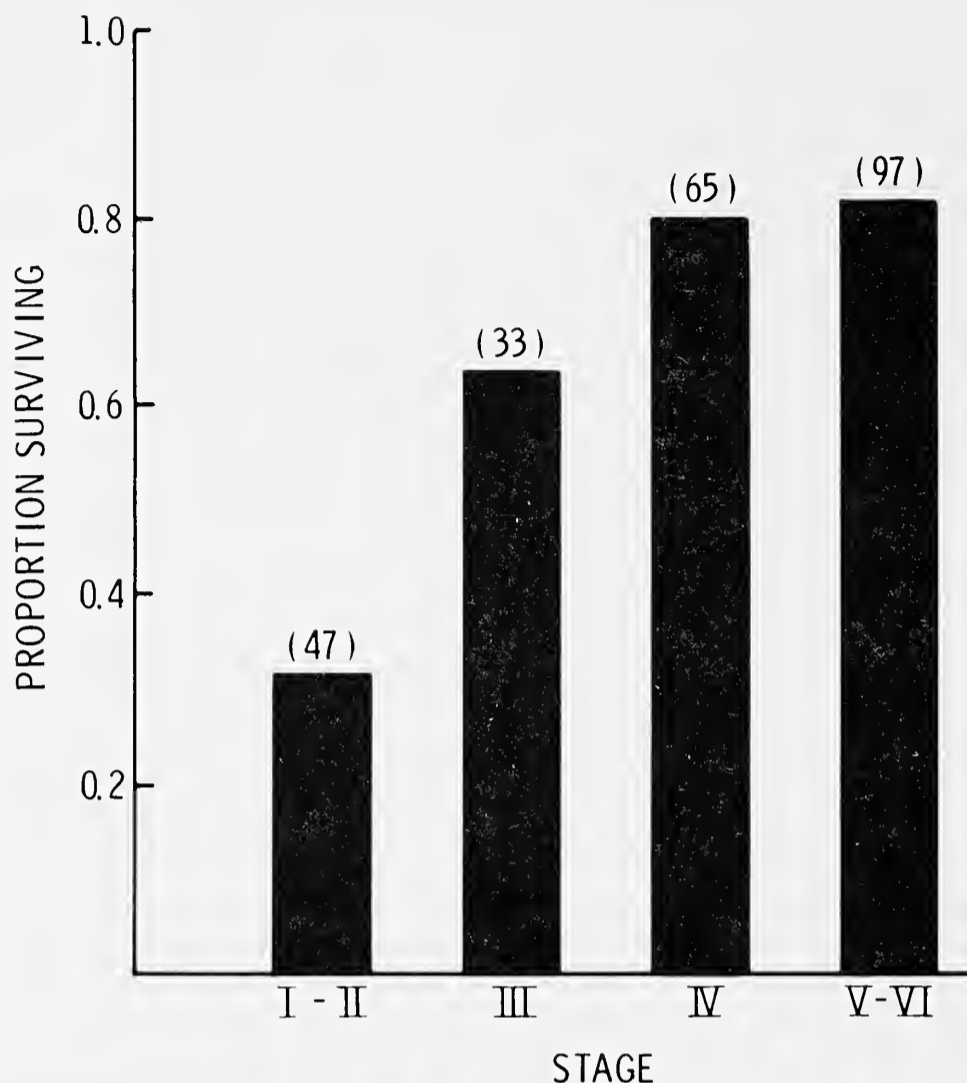
Fig. 2.—Overwinter survival of different stages, Study II.

The overwintering study was part of an experiment to determine the influence of feeding rate on rate of development. Sixty immature *P. marginata* were collected from various sites in the forest, weighed and placed individually in cylindrical cages ca 15 cm high and 10 cm in diameter, made of hardware cloth with openings small enough to retain fruit flies. The tops were covered with nylon cloth. The cages, which contained a layer of soil and leaf litter, were placed in leaf litter on the forest floor. Levels of soil and leaf litter were the same inside and outside the cages.

Each spider was randomly assigned to one of three feeding treatments: High (60 fruit flies/3 days), Medium (6 fruit flies/3 days), and Low (0 fruit flies/3 days); the only prey available to these spiders were very small insects that penetrated the screening, or insects that emerged from the soil). The spiders were fed from 3 August through 27 September. On 6 October they were removed, weighed and returned. Filmy dome spiders are found in webs through the end of October in this part of Michigan (Wise 1976); however, supplemental feeding was not continued through October, primarily because by then the weather is cold enough that feeding and growth in natural populations are probably minimal. The cages were searched for living spiders on 30 March, when *P. marginata* began to appear in webs on natural vegetation.

Results.—The overall survival rate over the winter was 0.75 (41/55). The smaller spiders suffered a significantly higher winter mortality rate (Table 2; $\chi^2 =$ 24.4, p < 0.001, 2 x 3 contingency table). Apparently the size within a stage did not affect survival, since within the Low feeding treatment the October weight

Table 2.—Results of study III.

Feeding treatment	Low	Medium	High
August 3			
No. alive	20	20	20
Weight (mg)	0.90 ± 0.05	0.97 ± 0.06	0.91 ± 0.06
October 6			
No. alive	18	18	19
Weight (mg)	1.59 ± 0.16	6.04 ± 0.26	5.86 ± 0.33
No. Molts 3 Aug.-6 Oct.	0.7 ± 0.3	2.0 ± 0.3	1.8 ± 0.4
March 30			
No. alive	6	16	19
Weight (mg)	1.32 ± 0.14	4.71 ± 0.21	4.50 ± 0.26
Winter survival (%)	33	89	100

of those that survived the winter did not differ significantly from that of the spiders that died before spring (1.50 ± 1.8 mg and 1.63 ± 0.60 mg, respectively; t = 0.42 p > 0.5).

The rate of feeding clearly affected growth rate and rate of development, as measured by weight gain and by the number of molts from August through September (Table 2). In addition to being heavier, spiders in the High and Medium feeding treatments were 1-2 stages more advanced than those in the Low feeding group. Since linear dimensions were not recorded, it is not possible to assign the spiders to a particular stage. However, it is clear that the larger spiders in October were more advanced developmentally i.e., they had completed more molts and were closer to adulthood than the smaller spiders.

DISCUSSION

Depth of the snow cover and condition of the litter affect the microclimate experienced by overwintering spiders (Aitchison 1978). We used outdoor cages in Studies I and III in order to mimic natural conditions as much as possible. Spiders overwintering in jars in studies I and II did not benefit from the insulative effects of snow, and thus their mortality rates may have been higher than in natural populations. However, comparison of survival rates in outdoor cages with those in jars (Study I) suggests that mortality rates in the jars did adequately reflect those under entirely natural conditions. No such comparison is possible for Study II, but there is usually no significant snow cover for most of the winter for the part of Maryland in which this study was conducted. Thus it is unlikely that the physical conditions in the jars in this study caused higher mortality rates than would have been observed in the natural population inhabiting the surrounding forest.

Overall winter survival rates varied between the three studies, from a low of 0.26 in Study I (jars, 1981-82) to a high of 0.75 in Study III. This variation likely reflects both differences in experimental technique and differences in severity of winters between years and sites. Similar variation appears in rates estimated from census data of natural *P. marginata* populations. For example, two estimates of juvenile survival from the first week in October to the middle of April in the Liberty population in Maryland range from 0.24 (115/473; 1980-81) to 0.62 (190/306; 1981-82) (calculated from census data presented in Wise 1981). Direct

comparisons of survival in these three studies with census data of natural populations are of course not justified, because estimates in natural populations 1) encompass a longer time span than the period of winter stress; 2) include disappearances due to predation and dispersal; and 3) are subject to sampling error, particularly with the smaller stages. Taken as a whole, though, these experimental results and censuses of natural populations suggest that winter mortality may be a significant factor in the dynamics of *P. marginata* populations.

The markedly lower winter survival of the younger stages, a result consistent with the finding of Buche (1966), is a striking pattern that was found in all three studies. This differential survival increases the homogeneity of the size structure of the population after the winter. For example, in the New York population (Study I) representation in the experimental population decreased from 12% (autumn) to 1% (spring) for stages I and II, and from 29% to 12% for stage IV. Contrastingly, the proportion of stage V spiders increased from 37% to 57%, and stage VI from 23% to 29%. In this situation overwintering mortality not only reduces the overall population density, but also produces a more homogeneous population in developmental stage.

Higher winter mortality rates among the smaller stages may have led to selection against females that mature and reproduce late in the season. *P. marginata* populations display two peaks in adult abundance, one in spring and a second in August. The latter results from progeny of spring adults that develop rapidly (Wise 1976, 1984). These rapidly developing spiders usually mature no later than August. They deposit egg sacs during September and October and die by winter. Maturation and reproduction too close to the onset of winter has likely been selected against, because progeny of late-maturing spiders would face the winter as smaller stages [this aspect of *P. marginata*'s phenology is discussed in more detail in Wise (1984)].

Results of Study I and III suggest that within a stage, differences in weight do not influence overwintering survival. Perhaps physiological changes occurring during development affect the physiology of cold resistance. Alternatively, differences in the relative amount of food reserves, or differences in the surface area-to-volume ratio, may better explain the lower overwintering survival of the younger stages. More experimentation is required to answer these questions. Particularly fruitful would be a detailed examination of the effects of size differences within the smaller stages. The lower survival rate of the smaller spiders in Study III may have resulted at least partly from their feeding history. Perhaps they had fewer energy reserves at the start of the winter than the better fed spiders.

In summary, these three experimental studies suggest that overwintering mortality in natural populations of the filmy dome spider may be particularly important for the smaller stages. Such stage-biased mortality rates have consequences for population structure, and for individual fitnesses of spiders with particular feeding histories and reproductive patterns.

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EVIDENCE OF INSEMINATION OF MULTIPLE FEMALES BY THE MALE BLACK WIDOW SPIDER, *LATRODECTUS MACTANS* (ARANEAE, THERIDIIDAE)

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ABSTRACT

In a series of laboratory matings, adult *Latrodectus mactans* males were allowed to mate with up to three virgin females. The results demonstrate that *L. mactans* males are capable of successfully inseminating at least three females and that the tip of the embolus (apical sclerite) is not required for sperm transfer.

An escape mechanism used by the male involving possible spatial disorientation of the female in her web during courtship and mating is described.

INTRODUCTION

Courtship and mating in *Latrodectus* has been studied by a number of workers (Ross and Smith 1979, Kaston 1970, Abalos and Baez 1963, Bhatnagar and Rempel 1962, Baerg 1959, Smithers 1944, D'Amour et al. 1936, Burt 1935, Herms et al. 1935, Blair 1934). Despite myths to the contrary, it is well documented that the male need not be killed by the female after mating. The incidence of escape by the male has been correlated with the degree of hunger in the female (Ross and Smith 1979, Kaston 1970). In addition, the ability of the male black widow to successfully inseminate a number of females has been discredited (Foelix 1982, Abalos and Baez 1963, Bhatnagar and Rempel 1962). As Foelix (1982) stated of *Latrodectus* "the lengthy emboli often break off during copulation and remain stuck in the epigynum of the female preventing either sex from mating again." Abalos and Baez (1963) noted of *Latrodectus* "the breaking of the apical element (sclerite) of the male palpus is a mutilation that renders the male unable to carry out further matings." They claimed that if the male is not killed by the female after mating, it perishes after a few days. They explained away as mistaken observation reports by Herms et al. (1935) and Montgomery (1903) of males mating more than once. Bhatnagar and Rempel (1962) conceded that in *Latrodectus curacaviensis* (Muller) (= *Latrodectus hesperus* Chamberlin and Ivie, Kaston 1970) the female could perform multiple matings unlike the males. They further noted "males that have copulated can be identified on the basis of a broken embolus, a male individual can copulate only once, for two reasons.

Firstly, an embolus with a broken tip cannot penetrate a bursa, secondly, the whole structure of the palpal organ is such that, after the first copulation, it will not return to its original position and the organ may not be stimulated to enact copulation again."

To test the validity of these statements, a series of matings were staged where males were given the opportunity to copulate with two or three virgin females.

METHODS

Spiderlings from three eggsacs spun by a laboratory reared *Latrodectus mactans* (Fabricius) female that had been mated with a wild male (College Station, Texas) were used. The spiderlings were reared to adulthood individually from the second instar (third true instar) to ensure virginity. The group consisted of thirty females and eighteen males. Eight males were allowed to mate once, eight twice and two males were allowed to mate three times using the virgin females. Once introduced into the female's snare, the male was permitted to remain until all courtship and mating behavior ceased, usually between three and ten hours. Between matings, the males were placed into fresh containers where (as with every male in which this was done) they built a normal web, and behaved similarly to immature or unmated adult males in captivity. The males were killed and checked for the presence of the apical sclerite following their last mating. All eggsacs spun by the mated females were collected as they were made and attached to the foam top of 100 ml glass vials until emergence of the spiderlings or until the eggsac was found to be infertile. Insemination of a female was considered successful only when living, active spiderlings emerged or were dissected out of an eggsac spun by the female, and not by inspection of the epigynum for traces of semen. As a result, more females were probably inseminated than the data would account for, but this insures that only a parthenogenetic event would provide false positive data. Parthenogenesis is unknown in *Latrodectus,* although Kaston (1968) reports numerous examples of infertile eggsacs being spun by virgin females.

RESULTS

No apical sclerite (the tip of the embolus) remained on either palpus of the first group of males allowed to mate once. Five of the eight females of this first group later spun eggsacs from which active spiderlings emerged. The second group of eight males were allowed to mate with virgin females, then removed after copulation and rested for a few days to two weeks before being allowed to mate with another group of virgin females. One male of this second group retained both apical sclerites, another had the left sclerite still present and the six others were missing both apical sclerites. The male that had retained both sclerites was also the only male unsuccessful in inseminating a female in both attempts based on data from spiderling emergence from ensuing eggsacs. Two of the eight males in the second group were successful in inseminating females in both matings, three males only in the first, and one male only in the second. The third and final group consisted of two males that were allowed to mate with three separate

virgin females each. The apical sclerites were missing on both males and all six females involved later spun eggsacs from which active spiderlings emerged.

DISCUSSION

The males allowed to mate once had both of their apical sclerites missing and this loss after the first copulation is probably normal in the majority of males. The male's success in inseminating a second virgin female might have been due to retention of at least one of the apical sclerites which they then used in the
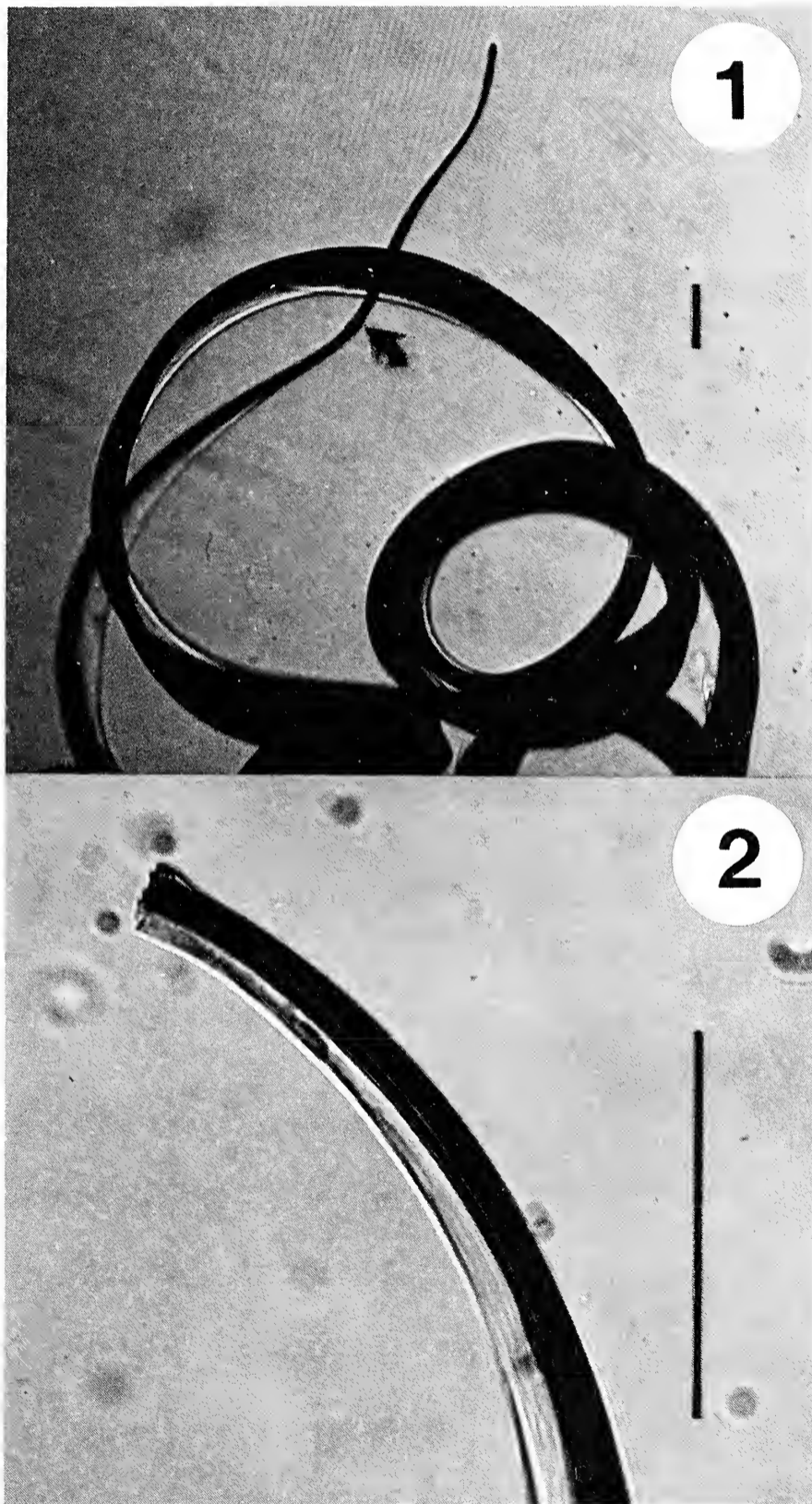
Figs. 1-2.—*Latrodectus mactans,* male genitalia: 1, Left palpus of unmated male, apical sclerite intact; 2, Condition of embolus after removal of apical sclerite, right palpus of mated male. Arrow indicates the point of attachment of the apical sclerite to the balance of the embolus. Scale line = 0.05 mm.

second copulation. However, the two males which inseminated three virgin females each demonstrates that not all *L. mactans* males require the presence of an apical sclerite to successfully transfer sperm. The gross morphology of the apical sclerite appears insufficient to somehow discourage or obstruct a second male from copulating with a previously mated female, and indeed, multiple apical sclerites have been found lodged in the seminal receptacles of *Latrodectus* (Kaston 1970, Abalos and Baez 1963), nor does it serve as a cap or plug as in many species of *Araneus* (Levi 1974). Perhaps the apical sclerite functions in the initial charging of the palpal organs with sperm.

Courtship and mating can be divided into three sequences in *L. mactans*. The first sequence is one of initiation. Upon introduction to the female's web, the male apparently contacts female pheromone that is incorporated in her silk (Ross and Smith 1979), which serves as a set of instructions or prime releasers, triggering courtship behavior. Secondly is the cutting sequence. The period between initiation and the original approach to the female is the first cutting sequence. After initiation, the male starts cutting away and loosely wrapping sections of the female's web. Concentrated sheets and bands (Kaston 1970) as well as balls are the shapes commonly observed formed by the male from the female's snare. The cutting sequence ends when the male slows, then cautiously approaches the female. The mean duration of the first cutting sequence (n = 30) was 58.5 minutes. In all our observations, the male was repulsed on the first approach, after which he resumed a cutting sequence. If rejected a second time, he began a third cutting sequence, and so on. Throughout the cutting periods the male vibrates his abdomen, preparing the female for mating by putting her in a trance (see Kaston 1970). The third sequence is the copulatory one. The female lets the male approach, spin the "bridal veil" and inseminate her, however, copulation can be interrupted by the female at any point, sending the male into another cutting sequence. We suggest that the cutting behavior of the male black widow prior to mating may serve to spatially disorient the female in her own web, especially if the male's silk, as is probable, contains pheromone that placates the female (Ross and Smith 1979). This behavior could effectively "blind" the female since her primary sensory contact with the environment is tactile and through her web. This "blinding" may serve to enhance the male's success in evading an attack by the female. We also propose that the "bridal veil" spun by the male prior to copulation, even though it may detain the female for a second or less, is sufficient to allow the male to escape by immediately dropping out of range, with little or no chance of successful pursuit by the female due to her disorientation in what is now the unfamiliar territory of her cut web. Ross and Smith (1979) working with *L. hesperus* suggested if the male could not successfully mate again, its reproductive success would be best served by providing the female with the energy of its body instead of wandering off to die as was generally believed. Only two of the eighteen males used were consumed by females. Both had inseminated a female in their first mating and both had apparently failed on their second and final mating to inseminate a female. These data, coupled with the surprising longevity and agility of the adult male black widow, lead us to suggest that the failure of an *L. mactans* male to escape the female after (or before) copulation may be due more to the physiological condition of the male at the time of mating than to the relative hunger of the

female. We further suggest that a larger study using the easily reared *L. mactans* might reveal more realistic frequencies of many different behavioral events observed in black widow spiders, including the number of copulations a male may participate in over his life span. A variety of useful methods for such a project can be found in Buskirk et al. (1984).

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SPIDER BALLOONING: DEVELOPMENT AND EVALUATION OF FIELD TRAPPING METHODS (ARANEAE)

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ABSTRACT

Sets of two types of sticky traps, horizontal wires and vertical panel traps, the latter including clear polyester, ½" hardware cloth, and ¼" hardware cloth substrates, were run concurrently for eighteen weeks in a Missouri soybean field to see which gave the best taxonomic- and mass-frequency representations of the aeronaut fauna. The wire traps significantly underrepresented the largest family (Linyphiidae) and mass class (≤ 0.6 mg) in the fauna. Of the three panel trap substrates, there were no differences between the two hardware cloth meshes but the polyester trap catches declined significantly during cold periods in late fall. An estimate is given of the number of hardware cloth traps needed for an effective sampling program.

INTRODUCTION

Spiders are among the most abundant and consistently present arthropod predators in crop fields and may contribute significantly to biological control of pests (Riechert and Lockley 1984). As with other natural enemies there may be a time lag between their population buildup and that of their prey, due in part to the need to recolonize fields following harvest or diapause. Spiders may recolonize either by walking or by ballooning [passive aerial dispersal, or aeronautic behavior (Richter 1967, Greenstone 1982)].

The composition of the aeronaut fauna has been assessed by mechanical suction traps (Taylor 1974), by kite-borne nets (Farrow and Dowse 1984), and by sticky traps of various designs. These have been mounted on airplanes (Glick 1939) or on ground level supports (Duffey 1956, Yeargan 1975, Van Wingerden and Vugts 1976). The purpose of the present investigation was to compare the efficacy and convenience of two simple and inexpensive sticky trap types, horizontal wires (Van Wingerden and Vugts (1976) and vertical panels (Yeargan 1975), and to see whether there were detectable differences among various substrates for the panel traps. We also wished to know whether height above the ground or compass direction affected the catches.
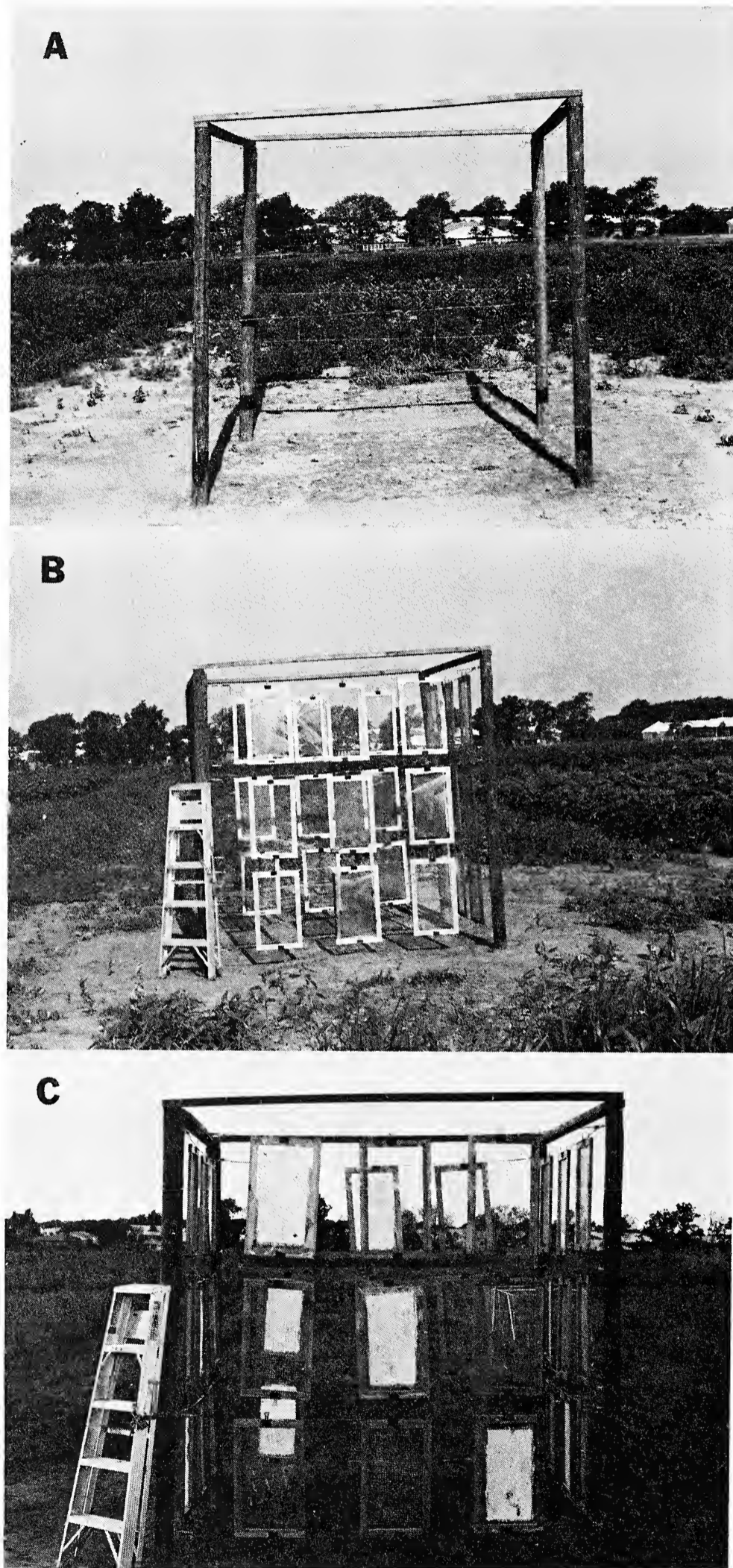
Fig. 1.—A, Wire trap setup in the field; B, Panel trap setup in the field. Note random arrangement of Mylar, ½″ hardware cloth and ¼″ hardware cloth at each of three heights (Photograph was taken in mid-summer); C, Panel trap setup photographed in late fall. Compare near opacity of Mylar traps with their translucence in mid-summer (Fig. 1B).

MATERIALS AND METHODS

The studies were performed in a 2.0 ha field at the University of Missouri South Farms, 9.7 km SE of Columbia in Boone County, Missouri. The field was planted in 18.3 m x 22.9 m plots of soybeans with admixtures of sunflowers ranging from 60 to 240 plants per plot. The placement of sunflower treatments among plots was determined by a randomized complete block design, as part of a study on the influence of cropping scheme on natural enemy diversity (N. L. Marston, personal communication). The treatments were set out in a three column by four row array, separated by 18.3 m wide alleyways, which produced six intersections in which the traps could be set up. Two of these were selected by use of a table of random digits (Rohlf and 1B 1969) and the wire traps set in one and the panels in the others. The two set-ups were 50-m apart.

Each set of traps was supported by a structure comprising four vertical posts set into the ground and braced with 2 x 4's at the top, forming a cube 2.5 m on a side with its vertical faces perpendicular to the cardinal compass directions. For the wire traps, six 2 mm diameter horizontal wires were nailed to the posts at heights of 35, 75, 115, 155, 195 and 235 cm (Fig. 1A). The central 2.0 m of each stretch of wire was coated with adhesive (Tack Trap,® Animal Repellents, Inc., Griffin, GA) to form the trapping surface. For the panel traps, pulleys were placed on the inside corners of the four posts at heights of 20 and 84, 95 and 160, and 170 and 235 cm, and a plastic coated three-wire clothesline run through each set of four pulleys and secured with a turnbuckle. Wooden frames holding the traps were attached to adjacent pairs of clotheslines using standard one-inch binder clips. The frames were 38 cm x 64 cm rectangles made up by gluing and nailing together lap-jointed 1 x 2's. They were dipped twice in varnish before use. Stapled to each frame was one of the following three panel substrates: 0.076-mm (.003 in) clear polyester (Mylar®) (Air Plastics, Inc., Mt. Vernon, NY), 12.7-mm (½″) galvanized hardware cloth, or 6.35-mm (¼″) galvanized hardware cloth. In order to facilitate coating the panels without fouling the wooden frames, an aluminum template having a 25-cm x 50 cm cutout in the center was placed over the panel, and prewarmed adhesive was painted on the unmasked area with a brush. The frames were hung from the clotheslines in three rows of three traps on each face (Fig. 1B), one of each substrate type, with position (left, right, or middle) determined by consulting the table of random digits. For transport to and from the field, the panel traps were stacked in groups of 18 on a wooden pallet with 1.8-cm diameter vertical pipes cemented into the corners to prevent shifting.

The two sets of traps were run concurrently for eighteen consecutive 1-wk periods beginning on June 15, 1983, and the panel traps for an additional five. (The wire traps were discontinued after it became clear that the panel traps were easier to handle and sampled the most important family more effectively [see below]). After each collection the panel traps were replaced with a fresh set and returned to the laboratory for microscopic examination at 6X with a Wild®M-5 stereo microscope. The wire traps were examined in the field with the aid of a 2½ X magnifying glass. Mylar traps were renewed by disposing of and replacing the Mylar. Hardware cloth traps were renewed by removing and soaking the hardware cloth panels overnight in Stoddard's solvent, cleaning them

with a wire brush, and drying, restapling and recoating them with prewarmed adhesive. The wire traps were cleaned in the field with paint thinner and paper towels and recoated each week.

To ensure that animals caught by the traps were ballooning and not crawling or "rappelling" (i.e., travelling via bridge lines, J. Carico, personal communication) onto the traps, all vegetation was cleared from within 3.0-m of all trap faces (see Figs. 1A and 1B) by three applications of Roundup® (Monsanto Chemical Co., St. Louis, MO), and 10 cm barrier bands of adhesive were placed encircling the tops and bottoms of all posts and the ends of all wire (trapping and clothesline) segments. These were checked for stickiness and renewed as needed.

The spiders collected were placed for three days each in paint thinner and toluene before final preservation in 70% ethanol. They were identified to family and the individual masses estimated using volume-mass regressions from previously live-massed and measured preserved animals (Greenstone et al., 1985). Because of the tedium of these measurements, a subset of seven samples, chosen to span the season and include a range of catches from very low to very high, was selected.

The numbers of spiders caught were subjected to multi-way analysis of variance of the factors date, height, compass direction, and, for the panel traps, substrate, using the SAS general linear models procedure at the University of Missouri, Columbia, Computing Center. The date x height x direction mean square was used to provide an error term for the wire trap ANOVA's, and the sums of squares for the four- and all three-way interactions were pooled to produce an error mean square for the panel trap ANOVA's.

RESULTS

Results of the ANOVA's are given in Table 1. All factors except compass direction show significant main effects, but all are also involved in significant interactions. The results are most easily understood if the two sets of comparisons are taken separately.

Comparison of Hardware Cloth and Mylar Panel Trap Substrates.—There were no obvious trends in any of the interactions except for that of date x type.

Table. 1—Results of F Tests.

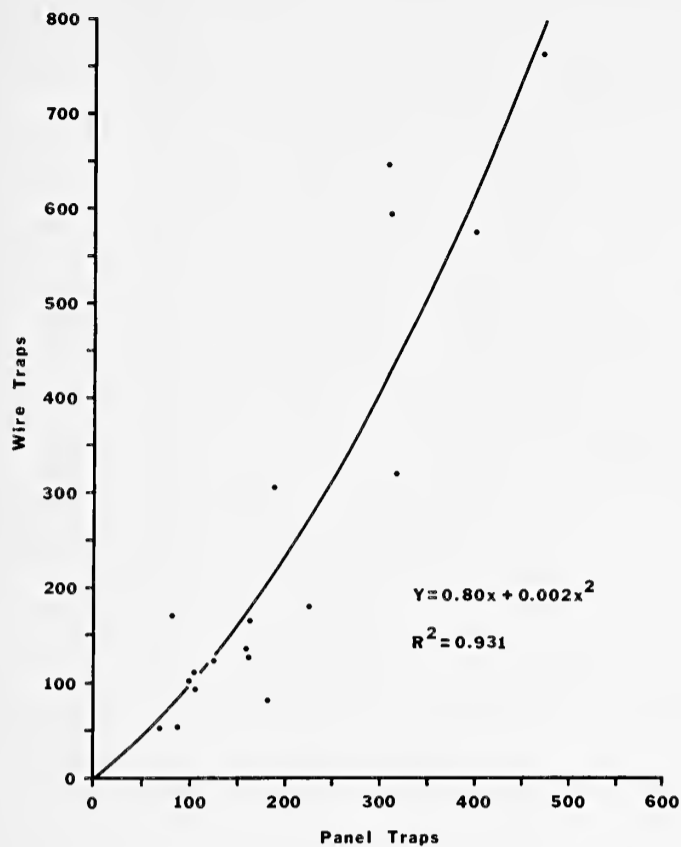| Source	PANEL TRAPS			WIRE TRAPS		
	F	*d.f.*	*P*	*F*	*d.f.*	*P*
Date	73.6635	22,628	***	150.1029	17,255	***
Height	6.0902	2,628		5.6602	5,255	*
Date x Height	1.2563	44,628		1.3965	85,255	*
Type	20.1498	2,628	*	—	—	
Date x Type	3.8025	44,628	***	—	—	
Height x Type	3.9545	4,628		—	—	
Direction	6.8794	3,628		1.8818	3,255	
Date x Direction	1.6339	66,628	**	1.4478	51,255	
Height x Direction	0.3480	6,628		2.7032	15,255	*
Type x Direction	1.4564	6,628		—	—	

***p<.001; **p<.01; *p<.05

Fig. 2.—Relationship between total number of spiders caught on the hardware cloth traps and wire traps on the eighteen concurrent dates.

$Y = 0.80x + 0.002x^2$

$R^2 = 0.931$

All six significant F's for panel trap type occurred toward the end of the season (the last week of September, the last two weeks of October, and the first and third week of November). We noticed a tendency for the Mylar traps to be more visible from a distance when we picked up the traps during this period (compare Figs. 1B and 1C). Close inspection showed that the adhesive, which is usually translucent, had become a nearly opaque white. Directions on the Tack Trap can indicate that it will not work consistently at temperatures below 35° F. There were eight weeks in which the temperature at the site fell to 35° F or below at least once. Five of these were included among the six weeks for which the F-test on trap type was significant, while the other three fell among the seventeen non-significant F-tests. This difference is highly significant by the log-likelihood ratio test (Sokal and Rohlf 1969, G = 8.47, p. < 0.01).

In order to determine where the differences among the panel substrates lay, Student-Newman-Keuls tests (Sokal and Rohlf 1969) were run on the data of the significant dates. In all six cases the ½″ and ¼″ hardware cloth means were not significantly different, while the Mylar traps were always significantly (p < 0.05) less than the ½″ hardware cloth and in all but one case significantly less than the ¼″ hardware cloth as well. The mean numbers on the hardware cloth panels on these dates ranged between 1.8 and 2.4 times those on the Mylar panels.

Comparison of Wire Traps and Panel Traps.—The relationship between the total numbers of spiders trapped on the wire traps and the ½″ plus ¼″ hardware cloth panel traps for the eighteen dates on which they were operated concurrently is shown in Fig. 2. These data were fitted to simple linear and polynomial regressions forced through zero. Both regressions were significant (p < 0.0001) but the polynomial gives a significantly better fit to the data ($F_{2, 12}$ = 5.27, p. < 0.025). This is the curve which has been fitted to the data in Fig. 1. It describes 93.1% of the variance in wire trap catches.

The wire and panel traps were compared further in their representations of the mass-frequency and taxonomic-frequency distributions of trapped spiders. Five
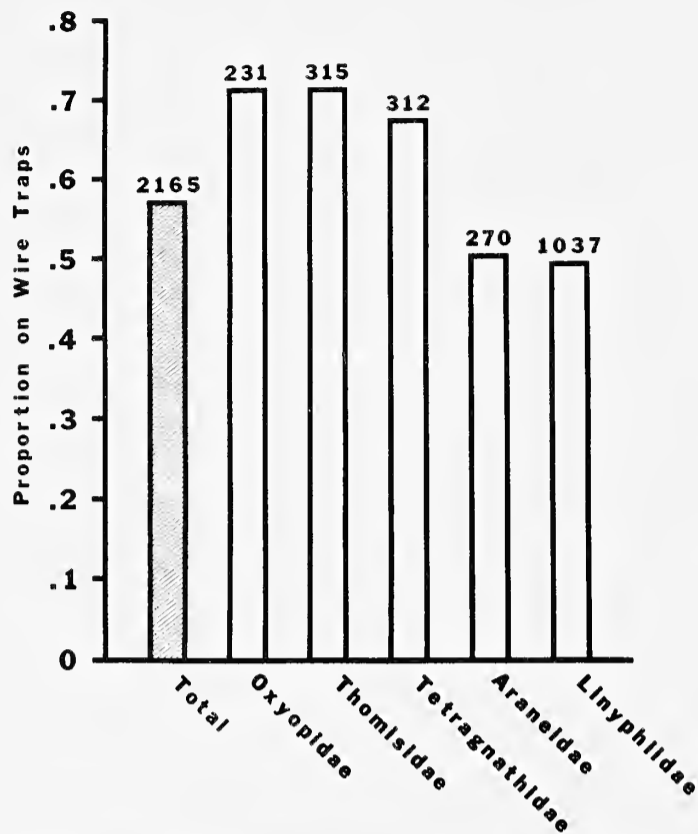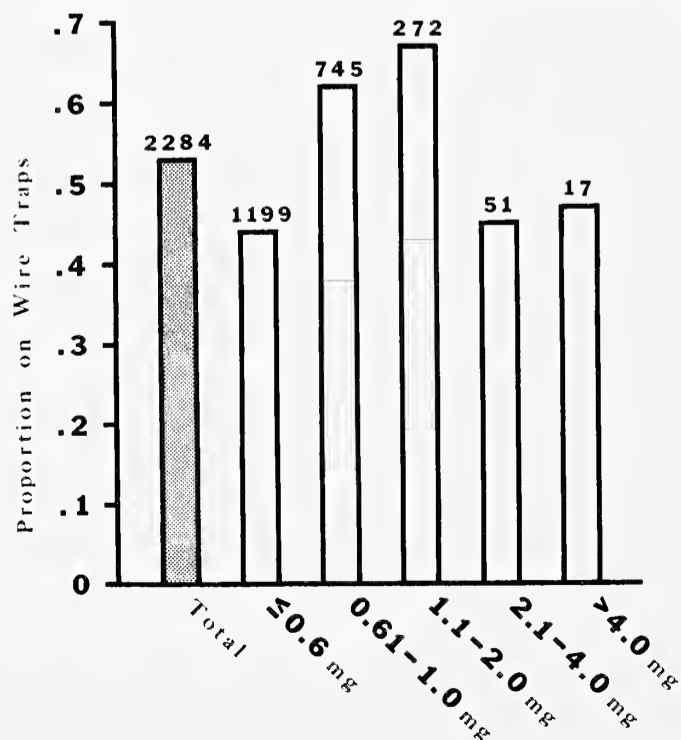
Fig. 3.—Proportions of the totals (heights of bars) and sample sizes (above the bars) for all spiders (hatched) and major families which were caught on the wire traps. See text for further explanation.

families each contributed at least five percent of all trapped individuals from the seven representative identified samples. Fig. 3 shows the proportions (heights of bars) of all spiders and of each family caught on the wire traps and the total numbers (above the bars) of all spiders and of each family caught on all traps. Of the 2165 animals in the sample, 1236, or 0.57 of the total, were caught on the wire traps. This is the expected proportion of animals on the wire traps for each family. The departures from expected are highly significant (G = 94.398, p < 0.0001). It can be seen by inspection that the family Linyphiidae, which makes up almost half of the total catch, is underrepresented on the wire traps.

Fig. 4 shows the proportions and totals for the mass classes of the same sample (the total sample size is slightly higher in Fig. 4 than in Fig. 3 because not all animals which could be measured could also be placed taxonomically). Again the departures from expected are highly significant (G = 86.296, p < 0.001). The largest mass class, animals 0.6 mg or less which make up slightly more than half the total, is underrepresented on the wire traps.

Fig. 4.—Proportions of the totals (heights of bars) and sample sizes (above the bars) for all spiders (stippled) and principal mass classes which were caught on the wire traps. See text for further explanation.

DISCUSSION

The curvilinear relationship depicted in Fig. 2 is partially explained by the data in Figs. 3 and 4. The smallest spiders tend to be linyphiids, so that Figs. 3 and 4 both reflect the tendency for the wire traps to undersample this family. There is a persistent, moderate to large number of linyphiids ballooning throughout the season. The other families are rare or absent early in the season, increase in numbers through early fall and then wane (Greenstone et al., unpublished data). This makes the wire traps appear to become more efficient as total numbers increase and the proportion of linyphiids, which they undersample, decreases (Fig. 2).

Our experience prior to data analysis led us to favor the panel traps since they can be brought into the lab and examined microscopically under uniform lighting conditions. Although all three authors seemed to get comparable counts on adjacent wires on the wire traps on any given day and compass direction, we did not feel confident about seeing the smallest spiders, particularly under changing lighting conditions in the field. The data in Fig. 4 bear this out. Whether the difference is due to actual differences in trapping efficiency or the difference in magnification and lighting used in scanning them is immaterial, because the wire traps must be checked in the field and therefore do not lend themselves to microscopic examination. At our site, where the linyphiids make up such a large proportion of the aeronaut fauna, wire traps can be expected to give a distorted picture of the taxonomic- and mass-frequency distributions of ballooners. In fact, the use of wire traps is probably not wise throughout mid to high latitudes in the Northern hemisphere, where linyphiids tend to be the largest family of ballooners.

Of the panel traps, Mylar is clearly at a disadvantage in cold weather. Furthermore, high winds destroyed two Mylar traps, so they are also less reliable. Because there were no significant differences between the ½" and ¼" hardware cloth, we recommend the ½", because, with less surface area they are easier to scan and require less adhesive.

We can think of two possible explanations for the halving of the catch on the Mylar traps in six of the late season samples. First, higher winds in the fall may tend to blow spiders around these solid traps more so than around the perforated, hardware cloth traps, a difference which may disappear at lower wind speeds (R. Suter, personal communication). Unfortunately we lack an *a priori* criterion for determining what windspeed is "high." The lowest mean windspeed recorded during the six significant weeks was 8.4 kph. If we take this as the threshold for a wind effect, then six of six significant weeks exceeded this threshold and 13 of the 17 non-significant samples also exceeded it. This difference is not significant ($G = 2.70$, $p > 0.1$). If we take as our threshold for a wind effect 12.2 kph, which was the next highest mean wind speed among the six significant dates, then five of six significant dates and five of twelve non-significant dates meet or exceed it. This difference is significant ($G = 5.49$, $p < 0.02$). We can look at the windspeed hypothesis in another way. If the drop in catches on the Mylar traps is indeed due to this wind effect, then the smallest animals should be most strongly affected (R. Suter, pers. commun.). The spiders caught on one of the significant dates, October 18, have been measured. Fig. 5
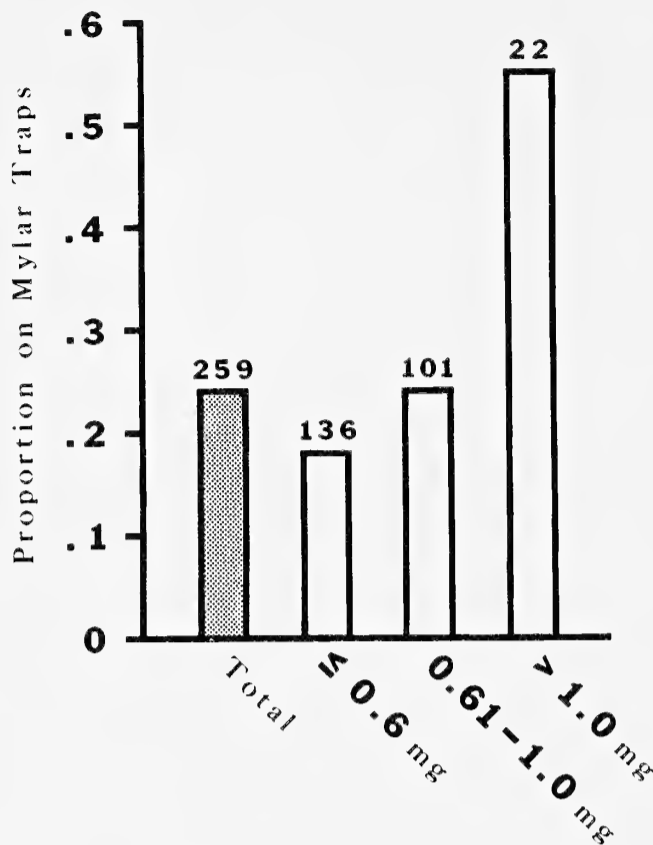
Fig. 5.—Proportions of the totals (heights of bars) and sample sizes (above the bars) for all spiders (stippled) and principal mass classes which were caught on the Mylar traps on October 18, 1983. See text for further explanation.

shows the proportions of the totals and sample sizes for all spiders (stippled) and principal mass classes which were caught on the Mylar traps. The departures from expected are highly significant (G = 11.89, p < 0.01) with the smallest spiders underrepresented and the largest overrepresented on the Mylar traps. These results are consistent with the wind-speed hypothesis.

One alternative explanation is that the spiders are better able to see the Mylar traps due to the large area of nearly opaque adhesive visible on cold days, and actively avoid them, e.g., by changing the length of the ballooning threads to rise above or drop below the traps. If correct, this would indicate that spiders may be at least partially able to guide their flight and thereby effect some degree of habitat selection before alighting (cf. Meijer 1977). This working hypothesis could be tested by setting up Mylar traps which are either clear or opaque and comparing the catches.

Our extensive trapping data can be used to estimate the number of traps required for a long-term ballooning study, using the formula presented by Sokal and Rohlf (1969, p. 247). In order to use this formula, the investigator must specify the size of difference between samples he or she wishes to detect, the probability that such a difference will be found if it exists, and the level of significance. There must also be an estimate of the variability of the data. The modal coefficient of variation for the hardware cloth trap data for this study was 44.9%. Taking 50% as a conservative expected coefficient of variation, α = 0.05 for rejection of the null hypothesis, P = 0.8 as our probability of finding a certain difference between two means, and d = 0.3 as that difference, we get n ≃ 16 traps. Given the absence of main effects of height and compass direction (Table 1), a four-sided trap with two traps at each of two heights on each side would support this number conveniently.

ACKNOWLEDGMENTS

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LEIOBUNUM LINEATUM: A SYNONYM OF *LEIOBUNUM CRETATUM* (OPILIONES, GAGRELLIDAE)

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ABSTRACT

The harvestman *Leiobunum lineatum* Edgar is synonymized with *Leiobunum cretatum* Crosby and Bishop. *Leiobunum cretatum* is rediagnosed, briefly compared to congeners, and numerous new records from central and eastern U.S.A. are provided. The labra and seminal receptacles are illustrated for the first time and the penis is redrawn.

INTRODUCTION

The original description of *Leiobunum lineatum* by Edgar (1962) mentions that this species may be confused with *Leiobunum aurugineum* Crosby and Bishop. Because *L. aurugineum* differs remarkably (leg and body relative lengths, body shape and microsculpturing, and genitalia) from *L. lineatum* no further comparisons need be made. Judging from the specific name, Edgar (1962) considered the silver lines on the abdomen to be diagnostic for the species. This character was used in his key (Edgar 1966) to separate *L. lineatum* from all congeners of the Great Lakes region. In his revision of *Leiobunum* Koch, Davis (1934) reports that *Leiobunum cretatum* Crosby and Bishop has the "dorsum golden-yellow, central marking obsolete." Presumably, Edgar (1966) was following Davis' description when he too reported no dorsal abdominal pattern on *L. cretatum*. This is indeed unfortunate, as in the original description of *L. cretatum* Crosby and Bishop (1924) described the species as having narrow longitudinal light lines on the abdomen. Furthermore, they used that character to separate their new species in a key to males of *Leiobunum*. Our examinations of the type materials and numerous other specimens of *L. lineatum* and *L. cretatum* reveal they are conspecific.

MATERIALS

The American Museum of Natural History, New York, is abbreviated "AMNH" in the text and specimens referred to as "JCC" and "WFR" are in the personal collections of the authors.
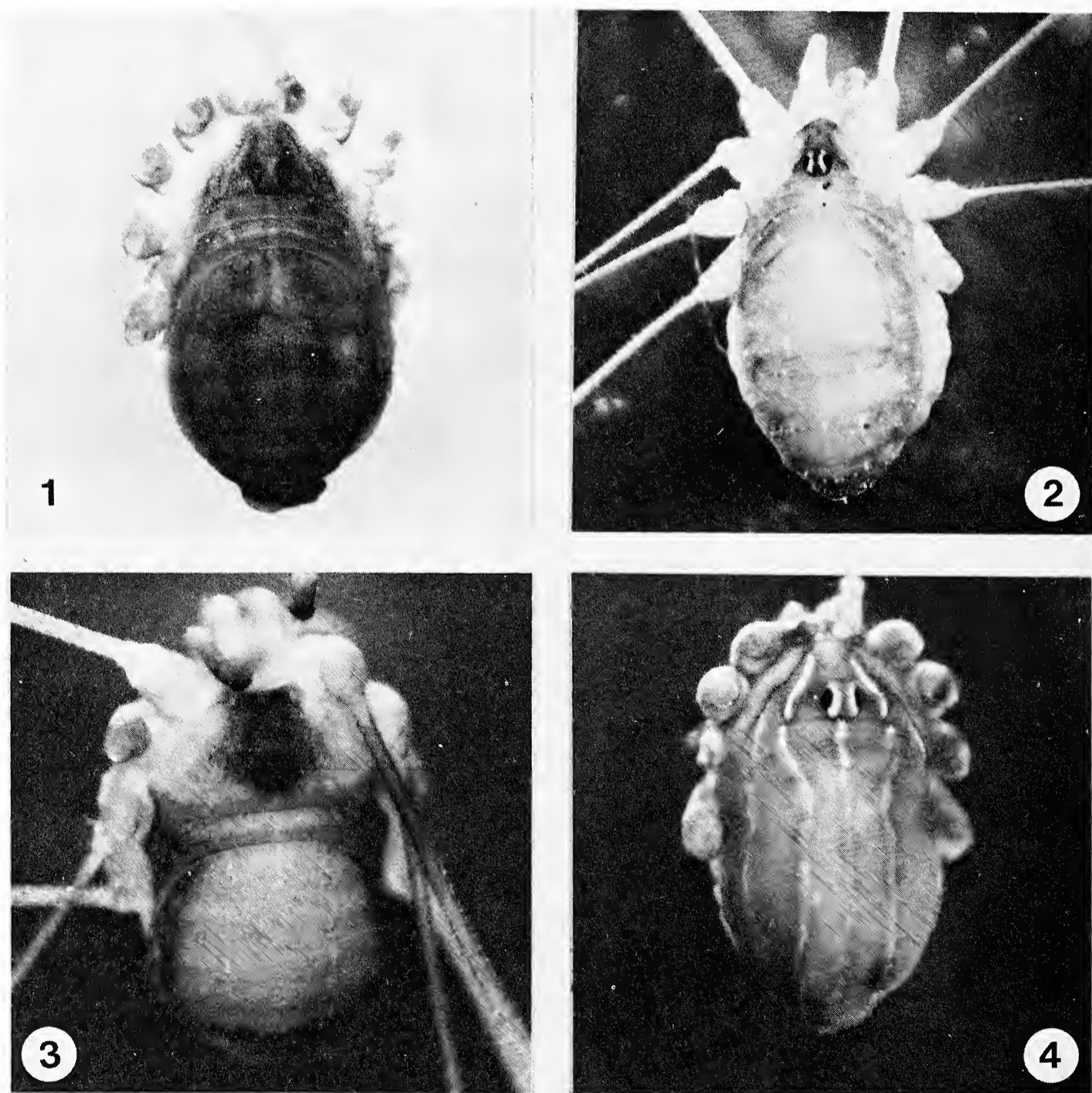
SYSTEMATICS

Leiobunum cretatum Crosby and Bishop
Figs. 1-12

Leiobunum cretatum Crosby and Bishop 1924:14, 19, 20, fig. 15; Davis 1934: 664, 673, figs. 14, 36; Goodnight and Goodnight 1942:12; Edgar 1966: 354, 361, 365.
Leiobunum lineatum Edgar 1960:377 (*nom. nud.*), 1962:146-149, figs. 1-3, 1966:6, 61, 62; Levi and Levi 1968:237, fig. (13-11); Cokendolpher 1982:89. **NEW SYNONYMY.**

Figs. 1-4.—*Leiobunum cretatum:* 1, female holotype from Georgia; 2, female from Tennessee; 3, male from Michigan; 4, juvenile paratype from Georgia.

Type data.—*Leiobunum cretatum* holotype female (reported "probably male" by Crosby and Bishop 1924) from Oglethorpe, Macon Co., Georgia (1 July 1910, J. C. Bradley), Cornell Collection in AMNH, examined, and two immature paratypes from Unadilla, Dolly Co., Georgia (28 June 1910, J. C. Bradley), one Cornell Collection in AMNH, examined—other juvenile not located. Holotype male and "allotype" female of *L. lineatum* from Locus Key T1N R5W S1, Eaton Co., Michigan (coll. 24 July 1959, reared to maturity/fixed 17 Aug. 1959, A. L. Edgar), in AMNH, examined.

Diagnosis.—Small species (body lengths: 2.3-3.5 mm for males, 2.6-5.25 mm for females) with femora I longer than body length. Dorsum with silvery-white longitudinal lines (Figs. 1-4). Ocular tubercle with several pointed spines over each eye. Male with alate penis (Fig. 5) and with only few weak teeth on palpal tarsi. Female seminal receptacles as in Figs. 6, 7. The labra of males are pointed and simple, similar to those of females (Figs. 8-10). All legs uniform in color, lacking white bands.

Comparisons.—The use of the shape of the labra is a relatively new taxonomic character in the study of *Leiobunum* (Suzuki 1976). The first North American species to be illustrated were by Tsurusaki (1985). Simple pointed labra, similar to those of *L. cretatum,* occur in European *Leiobunum* spp. and in U.S.A. *Leiobunum townsendi* Weed, *Leiobunum vittatum* (Say), and *Leiobunum relictum* Davis (Tsurusaki 1985: pers. obs.). The labra of the U.S.A. *Leiobunum aldrichi* Weed and *Leiobunum gordoni* Goodnight and Goodnight are unlike those of *L. cretatum* (see Tsurusaki 1985: figs. 3I and 3M).

Based on morphologies of penes (Davis 1934; Cokendolpher 1982; pers. obs.), *L. townsendi, L. vittatum,* and *L. relictum* can be eliminated as near kin to *L. cretatum.* The genitalia of *L. cretatum* appear similar to those of several European *Leiobunum* spp. (Martens 1978) and those of *L. aldrichi* and *L. gordoni* (Davis 1934; Cokendolpher pers. obs.).

Tsurusaki (1985) noted that most European *Leiobunum* spp. lack denticles on the palpal tarsi and that males of U.S.A. species have such denticles. Males of *L. cretatum* have only a few small denticles on the proximal end of the tarsi ventrally. Unlike European *Leiobunum* spp.; specimens of *L. cretatum, L. aldrichi,* and *L. gordoni* have several denticles over the eyes.

Variation.—Throughout the range of *L. cretatum* (Fig. 11), little variation in genital morphology, granulation of dorsa, spination of ocular tubercles, or coloration was noted. Obvious differences in leg lengths were noticed when comparing specimens from Michigan and Georgia. Femora II lengths for all adult specimens examined were plotted against latitude and longitude. The plots of lengths vs. longitude for both males and females showed no observed correlation, but the plots of lengths vs. latitude revealed variation in femora II lengths. Specimens from more northern localities have shorter legs than those from more southern localities (Fig. 12). North/south clines in leg lengths have been previously recorded in numerous Northern Hemisphere gagrellid opilionids (Weed 1892, 1893; Suzuki 1971, 1973; McGhee 1977) and the reverse cline has been reported in two gagrellid species from the Southern Hemisphere (Ringuelet 1960).

Unlike most studies on clines in harvestmen, we can not demonstrate a uniform decrease in body size with increase in latitude. Leg length clines were reported for the eastern U.S.A. *Leiobunum politum* Weed and *Leiobunum bracchiolum*
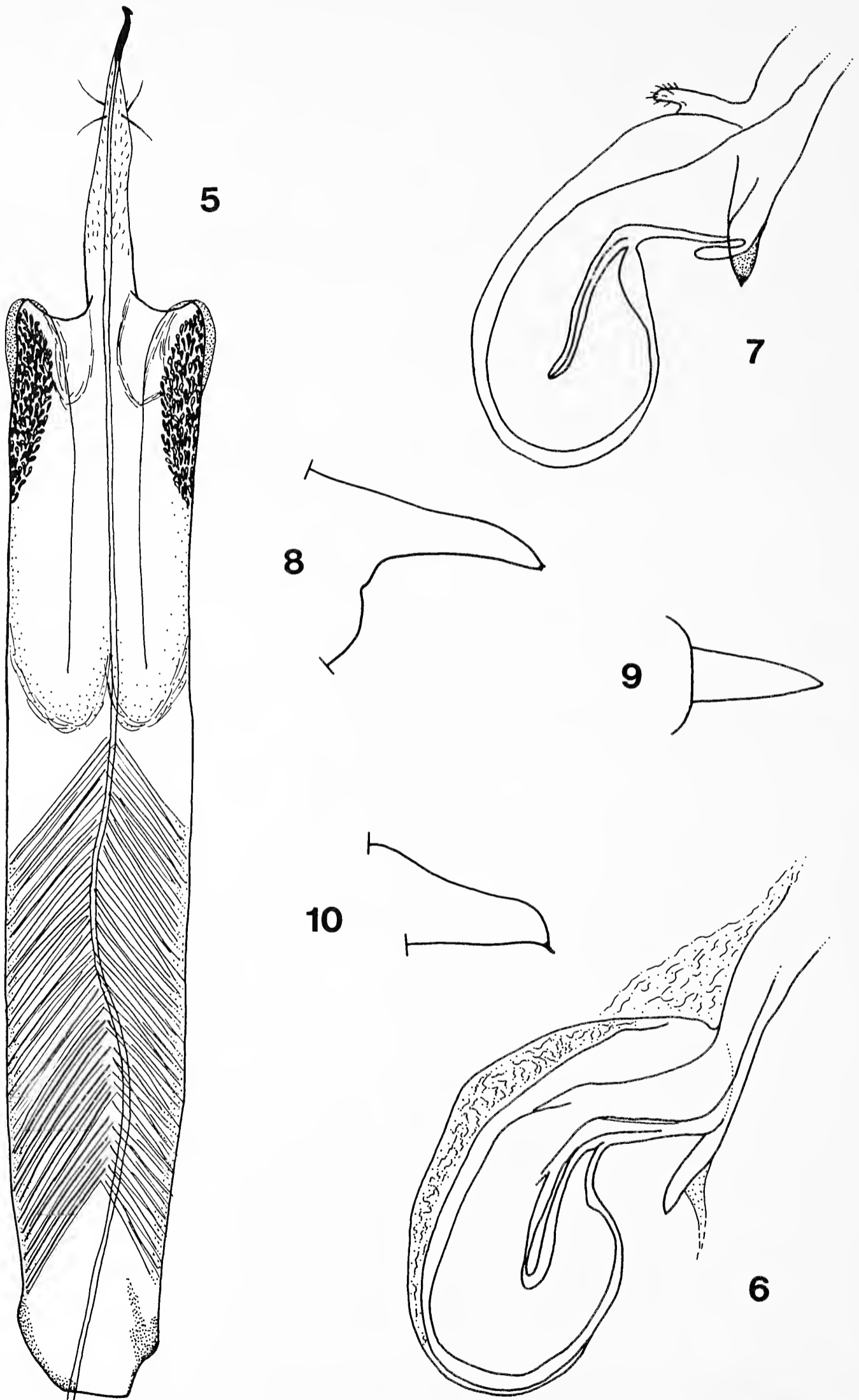
Figs. 5-10.—*Leiobunum cretatum:* 5, dorsal aspect of penis; 6, seminal receptacle of holotype from Georgia; 7, seminal receptacle of Tennessee female; 8, lateral aspect of male labrum; 9, ventral aspect of male labrum; 10, lateral aspect of female labrum.

McGhee by McGhee (1977). Plots of body lengths vs. latitude of adult males and females of *L. cretatum* revealed that: (1) males are smaller than females, (2) males do not vary with latitude, and (3) females from northern latitudes are generally larger than females from southern localities. These differences between females though are possibly due to the dates of capture. All females studied from southern localities were collected in summer and those from more northern localities were collected during late summer and fall. Unless females in the southern regions are gravid earlier than those from the north, we suggest that the noted differences in body sizes are due to the extended abdomen of egg-laying females.

Comments.—*Leiobunum cretatum* is one of the smaller members of the genus from North America. Due to this small size, it is possible specimens have been disposed of by collectors, thinking they were juveniles. This could account for the scarcity of specimens in museum collections.

Distribution and natural history.—*Leiobunum cretatum* is widely distributed in the eastern half of the U.S.A. (Fig. 11). It appears to be most abundant in

Fig. 11.—Distribution of *Leiobunum cretatum* in the eastern U.S.A., localities mapped by open circles are from Davis (1934) and Edgar (1962, 1971).

deciduous forest and does not appear to exist in the eastern coastal woodlands. It extends west into the Grassland Biome (Stipa-antilocapra biotic formation), but is not found in the grasslands, rather in the subclimax woodlands along streams. It is limited to floodplain woodlands where there is a heavy shrub and herb layer. From our observations it appears that there are no true grassland species of *Leiobunum*. However, in habitats which have high moisture content at least *Leiobunum vittatum* and *L. cretatum* can exist.

Specimens examined.—U.S.A.: MICHIGAN; *Eaton Co.,* 4 miles S. Charlotte, 4 Sept. 1979 (J. C. & J. E. Cokendolpher), 3 males, 1 female (1 male WFR, others JCC); *Washtenaw Co.,* 20 Sept. 1930 (J. S. Rogers), 1 male, 1 female (AMNH): MISSOURI; *Marion Co.,* Hannibal, 29 Sept. 1979 (W. F. Rapp), 1 female (JCC): NEBRASKA; *Brown Co.,* Long Pine, 10 Sept. 1975 (W. F. Rapp), 1 female

$$y = 54.46 - 1.54x$$
$$r^2 = 0.88$$
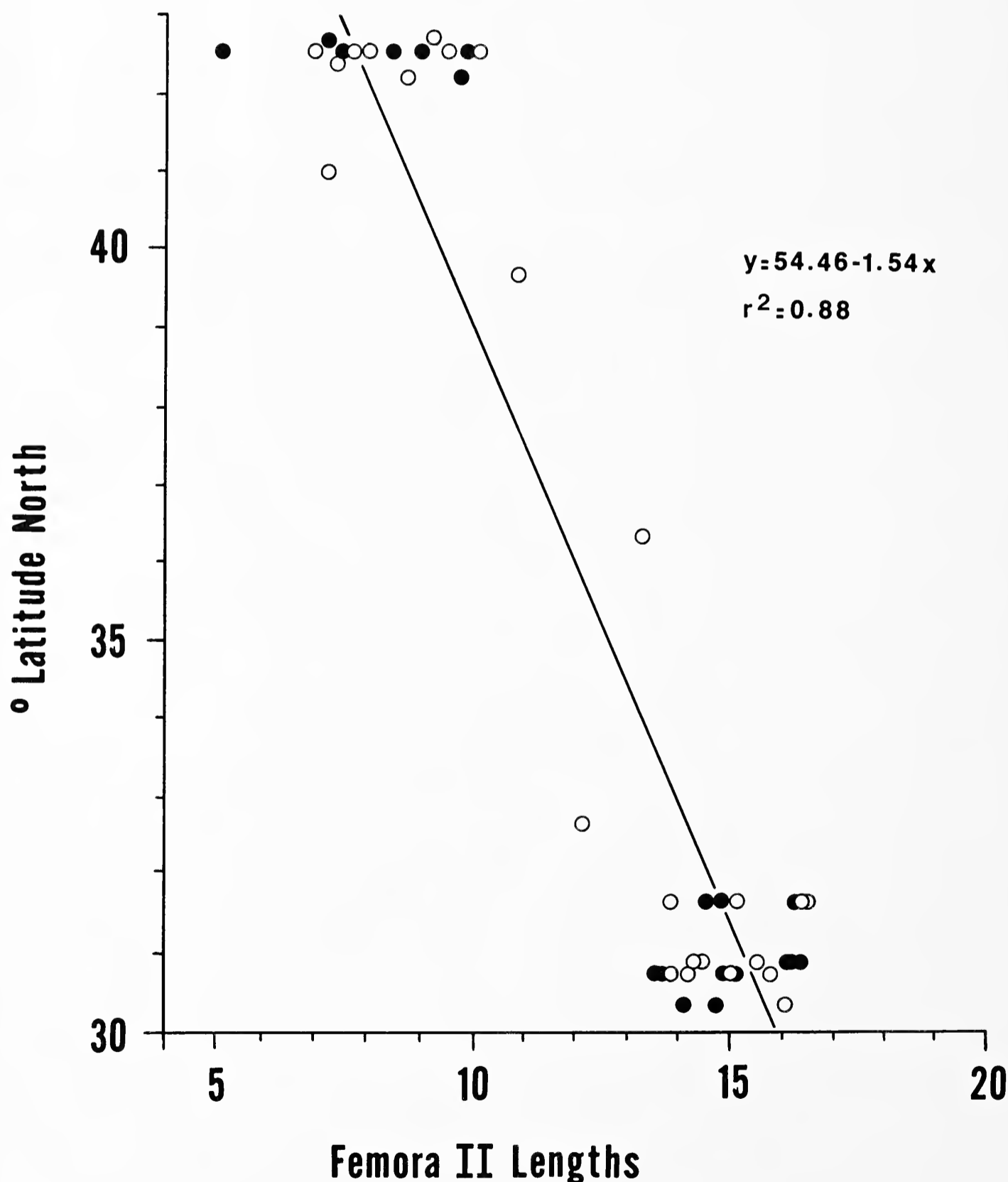
Fig. 12.—*Leiobunum cretatum* femora II lengths (in mm): male (solid circles), female (open circles).

(JCC), 11 Sept. 1979 (W. F. Rapp), 1 male (WFR); *Holt Co.,* O'Neill, 9 Sept. 1975 (W. F. Rapp), 2 males, 2 females (1 pair JCC, 1 pair WFR), Chambers, 10 Oct. 1979 (W. F. Rapp), 1 female (WFR), Swan Lake, 5 Sept. 1978 (W. F. Rapp), 1 female (JCC); *Merrick Co.,* Central City, 31 Aug. 1976 (W. F. Rapp), 1 female (WFR): TENNESSEE; *Williamson Co.,* 17 miles SW of Nashville, Mary Mount Campground, 20 Sept. 1981 (W. D. Sissom), 1 female (JCC): GEORGIA; *Lowndes Co.,* Valdosta, 1 Sept. 1940 (C. J. Goodnight), 4 males, 3 females (AMNH); *Turner Co.,* Ashburn, 31 Aug. 1940 (C. J. Goodnight), 3 males, 5 females (AMNH): FLORIDA; *Gadsden Co.,* Ochlochonee River and Marianna Road, 24 July 1930 (N. W. Davis), 3 males, 2 females, 3 juveniles (AMNH); *Jackson Co.,* Marianna, 24-29 July 1930 (N. W. Davis), 8 males, 7 females, 2 juveniles (AMNH); *Jefferson Co.,* Monticello (date & collector unknown), 1 male (AMNH).

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A NEW SPECIES OF *HETERONEBO* FROM JAMAICA (SCORPIONES, DIPLOCENTRIDAE)

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ABSTRACT

Heteronebo franckei, new species, is described from Jamaica and new Jamaican locality records are reported for *Heteronebo jamaicae portlandensis* Francke and *Heteronebo jamaicae occidentalis* Francke.

INTRODUCTION

The diplocentrid scorpion fauna of Jamaica was described by Francke (1978) and reviewed by Armas (1982). Two species (one with three subspecies) are known to occur on Jamaica: *Heteronebo elegans* Francke, *Heteronebo jamaicae jamaicae* Francke, *H. jamaicae occidentalis* Francke, and *H. jamaicae portlandensis* Francke. In the present paper, a newly discovered species of *Heteronebo* from Portland and St. Thomas Parishes is described and new locality records are reported for *H. jamaicae portlandensis* and *H. jamaicae occidentalis*.

METHODS

The description format and terminology follow that of Francke (1978) and Francke and Sissom (1980) except for the measurements of the chelicerae. In the present paper, the cheliceral chela length is measured along the dorsal surface of the chela from the posterior margin to the distal tip of the fixed finger. One hemispermatophore of the holotype was removed and examined in 100% lactophenol as described by Cokendolpher (1984) for opilionid genitalia. A Wild M7A dissecting microscope equipped with an ocular micrometer and a drawing tube was used to make all measurements (in millimeters) and drawings of the holotype. Acronyms for collections from which specimens were examined are given in the acknowledgments.

Heteronebo franckei, new species
Figs. 1-8

Type data.—Holotype male from near the mouth of Christmas River, Portland Parish, Jamaica, West Indies, 15 December 1969 (P. A. Drummond), deposited in FSCA. Seven paratypes are listed under specimens examined.

Etymology.—Named in honor of Dr. Oscar F. Francke in recognition of his contributions to scorpion biology and systematics.

Distribution.—Known from near the mouths of Christmas and Priestman's Rivers, Portland Parish, and the Horse Savanna and Crookshank Rivers, St. Thomas Parish, Jamaica, W. I. (Fig. 9).

Diagnosis.—*Heteronebo franckei,* new species, is placed in the *bermudezi* species group (Francke 1978) with *Heteronebo bermudezi* (Moreno), *Heteronebo caymanensis* Francke, and *H. jamaicae.* This group is characterized by dense, small and minute granulation on the lateral and ventral carinae of metasomal segment V. *Heteronebo franckei* is distinguished from other species of *Heteronebo* by the following combination of characteristics. Pedipalp chela length in adult males less than twice chela width, in females and immature males greater than twice chela width; pedipalp chelae weakly carinate; metasomal segment II wider than long; metasomal segment III in adult males slightly longer than wide, in females and immature males as wide or wider than long; setation on dorsal lateral carinae of metasomal segments I-IV, 1:1:1:1; metasomal segment V ventral median and ventral lateral carinae moderately strong with small to medium sized, low tubercles; pectinal tooth count in males 8, in females 7; prolateral pedal spurs large, well developed on all legs; tarsomere II spine formula 4-5/4:5/5:6/7:7/7.

Description.—With the characters of the genus (Francke 1978). Measurements of the holotype and a female paratype are given in Table 1. The following description is based on the adult male; parenthetical statements refer to females and immature males.

Prosoma: Carapace brown in color, median ocular tubercle and lateral ocular tubercles dark brown; carapace densely granular, weakly emarginate anteriorly; median anterior notch shallow (moderately deep), rounded (v-shaped). Venter brownish-yellow, moderately setate, densely punctate.

Mesosoma: Tergites brown in color, densely granular interspersed with small rounded tubercles. Tergite VII strongly bilobed posterolaterally; submedian carinae weak on posterior one-fourth, with single row of low, close tubercles; lateral carinae moderately strong on posterior half, with irregular row of low tubercles. Genital operculi yellow, subelliptical; pectinal tooth count in males 8, in females 7; sternites yellow, lustrous, densely punctate. Sternite VII submedian carinae weak on posterior one-half, crenate; lateral carinae moderately strong to weak on posterior half, crenate.

Metasoma: Reddish-brown in color, punctate, minutely coarsely granular; segments I and II wider than long, segment III slightly longer than wide (as wide as or wider than long). Ventral submedian carinae on segments I-III weak, crenate (with irregular rows of medium sized tubercles); on segment IV very weak with small, scattered tubercles. Ventral lateral carinae on segments I-IV weak, crenate (with irregular rows of medium sized tubercles) on I-III, with small scattered tubercles on IV. Lateral inframedian carinae weak on segment I, very weak on segments II and III, vestigal on segment IV; with a few small, scattered

Table 1.—Measurements (in millimeters) of *Heteronebo franckei*.

Character	Holotype male	Paratype female
Total length	31.20	37.10
Carapace length	4.95	5.85
Anterior width/posterior width	3.00/5.25	3.90/6.60
Width at median eyes	4.30	5.20
Mesosoma length	10.20	13.75
Metasoma length	16.05	17.50
I length/width	2.40/3.20	2.60/3.70
II length/width	2.70/2.90	2.95/3.30
III length/width	2.90/2.80	3.20/3.20
IV length/width	3.50/2.65	3.85/3.05
V lenght/width	4.55/2.50	4.90/2.90
Telson length	4.35	5.10
Vesicle length/width/depth	3.50/2.20/1.70	4.15/2.95/2.30
Aculeus length	0.90	0.90
Pedipalp length	15.65	19.15
Femur length/width/depth	3.50/1.65/1.80	4.05/1.95/2.20
Tibia length/width/depth	3.60/1.80/2.05	4.30/2.10/2.50
Chela length/width/depth	8.55/4.65/2.80	10.80/5.30/3.40
Movable finger length	5.40	7.00
Fixed finger length	3.60	4.80
Chelicera chela length/width	2.40/1.15	2.80/1.35
Movable finger length	1.50	1.80
Fixed finger length	0.90	1.10

tubercles. Lateral supramedian carinae on segments I-IV weak with small irregularly spaced tubercles. Dorsal lateral carinae weak on segments I-IV, irregularly granulose. Setation of dorsal lateral carinae on segments I-IV, 1:1:1:1:. Segment V ventral median carina moderately strong with wide row of small to medium sized tubercles and strong subterminal bifurcation with large tubercles (Fig. 5). Ventral lateral carinae moderately strong, irregularly tuberculate anteriorly; with a single row of large tubercles distally. Lateral median carinae very weak on anterior three-fourths with small scattered tubercles. Dorsal lateral carinae weak to vestigal, irregularly granulose. Anal arc rounded; subterminal keel weak to moderately strong with a row of close, medium sized tubercles; terminal keel obsolete, smooth. Telson slightly elongate (globular), moderately granulose, sparsely setate, densely punctate.

Pedipalps: Reddish-brown in color, orthobothriotaxia C, densely punctate. Femur trapezoidal in cross section, deeper than wide; dorsal internal keel obsolete; dorsal external keel weak with medium sized tubercles; ventral external keel obsolete; ventral internal keel moderately strong, coarsely granular; dorsal and internal faces densely and coarsely granular; ventral face minutely granular. Tibia much shorter than chela width (Fig. 4); dorsal internal keel obsolete; basal tubercle weak, represented by a few small tubercles; dorsal median keel moderately strong, weakly tuberculate; dorsal external keel moderately strong, weakly granular; external keel weak with obscure, scattered granules; ventral internal keel moderately strong, smooth to vestigally granulose; ventral external keel moderately strong, smooth; internal faces shagreened, dorsal external face moderately granular; other external and ventral faces very minutely shagreened.

Chela robust (Figs. 1-3) (inflated), moderately granulose, reticulate, densely punctate; digital keel weak (very weak), vestigally granulose (smooth); dorsal secondary keel vestigal, granular; external secondary keel obsolete; ventral external keel weak distally (vestigal distally), vestigally granular (smooth); ventral median keel weak, crenate (smooth); ventral internal keel weak (vestigal), smooth. Dentate margins of fingers densely tuberculate.

Legs: Yellow in color. All segments except tarsomeres shagreened. Prolateral pedal spurs large, well developed on all legs. Variation in tarsomere II spine counts shown in Table 2.

Hemispermatophore: See Figs. 6-8. Lamina length, 3.9 mm.

Habitat.—All specimens of *H. franckei* were collected from near the mouths of rivers in organic litter amid limestone pebbles.
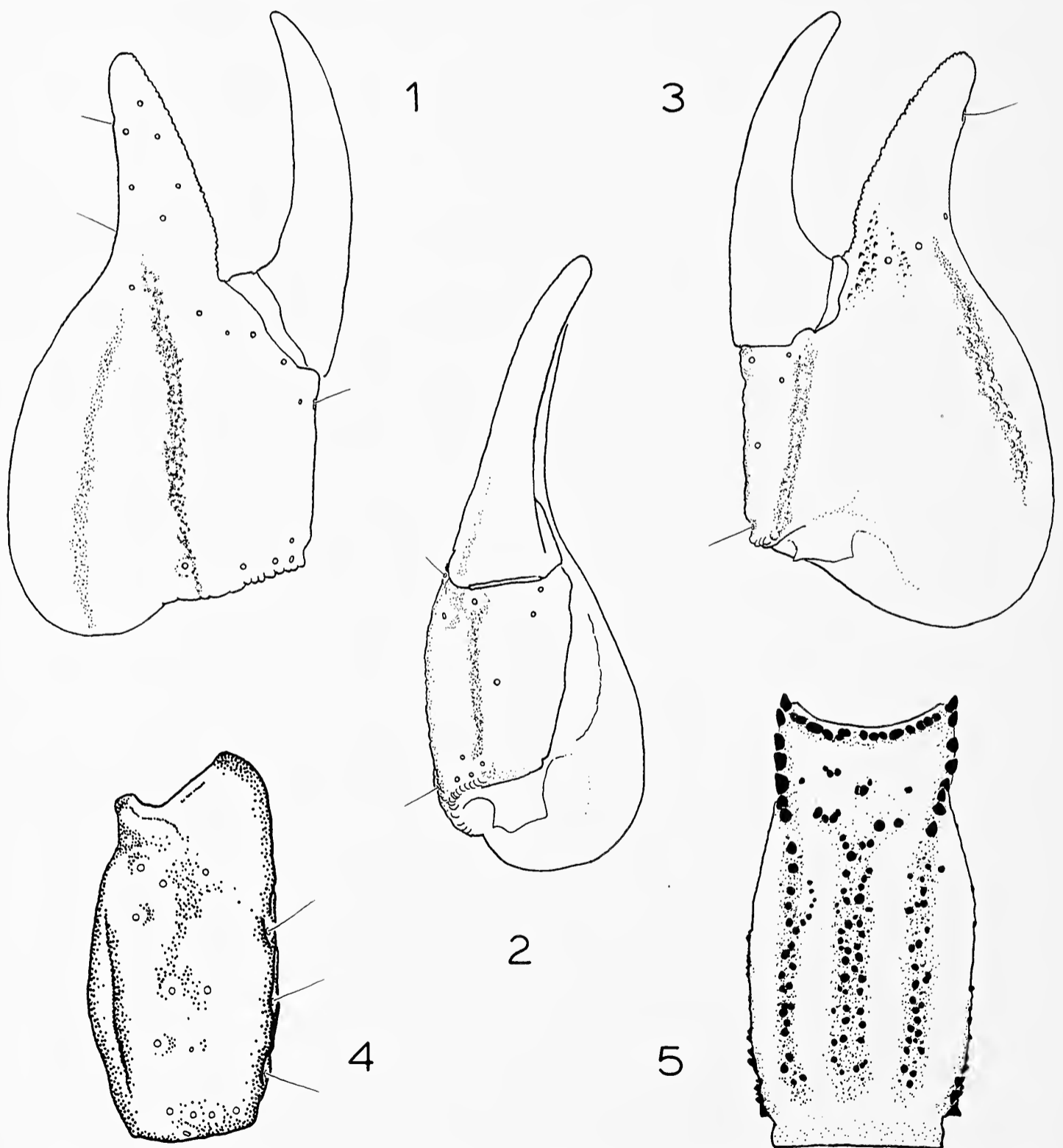
Figs. 1-5.—*Heteronebo franckei,* new species, male holotype: 1, right pedipalp chela, external aspect showing trichobothrial pattern; 2, right pedipalp chela, ventral aspect; 3, right pedipalp chela, internal aspect; 4, right pedipalp tibia, external aspect; 5, metasomal segment V, ventral aspect.

Table 2.—Variability in tarsomere II spine counts for *Heteronebo franckei*.

No. of spines in row	Leg I		Leg II		Leg III			Leg IV		
	4	5	5	6	3	6	7	6	7	8
Males										
Prolateral row	4	4	7	1	-	8	-	-	8	-
Retrolateral row	6	2	7	1	-	3	5	-	7	1
Females										
Prolateral row	2	6	7	1	1	6	1	1	7	-
Retrolateral row	6	2	8	-	-	2	6	1	5	2

Specimens examined.—JAMAICA: *Portland Parish,* mouth of Priestman's River, 15 December 1969 (P. A. Drummond), 1 adult female (FSCA), 1 immature female, 2 immature males (FSCA); *St. Thomas Parish,* along Crookshank River near sea, 16 March 1969 (P. A. Drummond), 1 subadult male (FSCA), just above mouth of Horse Savanna River, 16 December 1969 (P. A. Drummond), 1 immature female (FSCA), near N bank of mouth of Horse Savanna River, 15 June 1970 (P. A. Drummond), 1 adult female (OFF).

DISTRIBUTION OF *HETERONEBO* ON JAMAICA

This genus is represented on Jamaica by three species (one with three subspecies) (Fig. 9). *Heteronebo franckei* is known from the coastal regions of
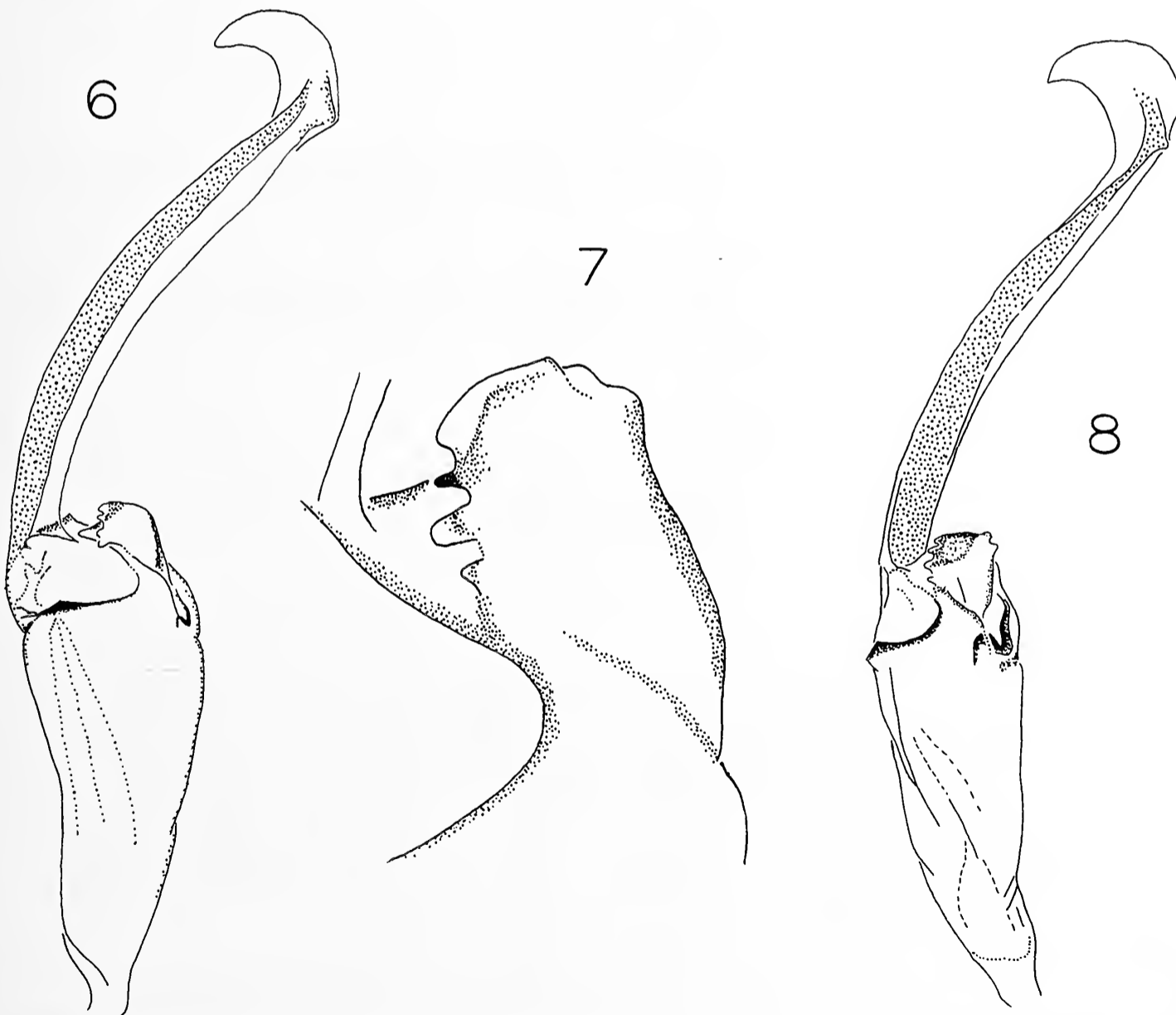
Figs. 6-8.—*Heteronebo franckei,* new species, male holotype, right hemispermatophore: 6, external (lateral) aspect; 7, detail of capsular region, dorsolateral aspect; 8, dorsal aspect.
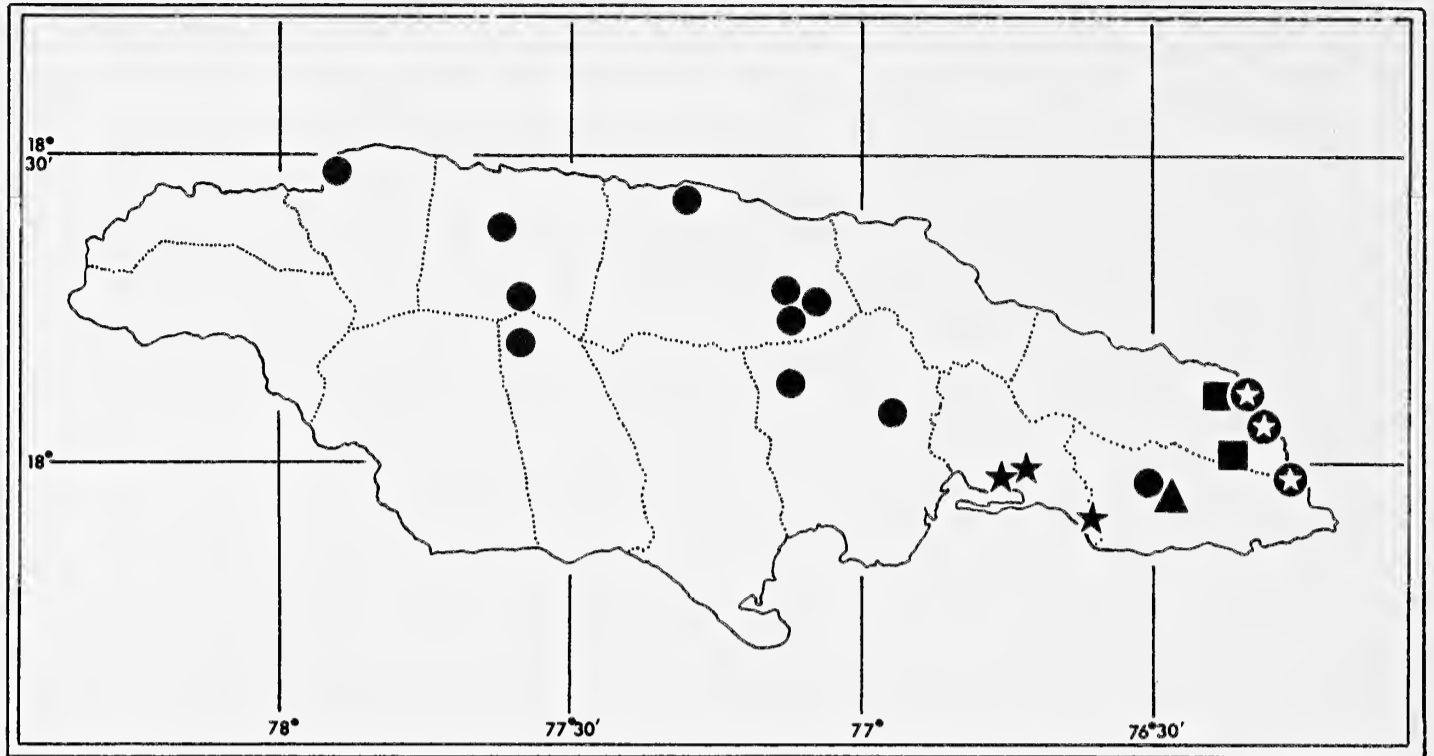
Fig. 9.—Map showing distribution of *Heteronebo* species on Jamaica, West Indies. Triangle = *H. elegans* Francke; star = *H. jamaicae jamaicae* Francke; solid circle = *H. jamaicae occidentalis* Francke; square = *H. jamaicae portlandensis* Francke; circled star = *H. franckei,* new species.

Portland and St. Thomas Parishes. *Heteronebo elegans* is known only from St. Thomas Parish and *Heteronebo jamaicae portlandensis* is known only form Portland Parish. *Heteronebo jamaicae jamaicae* is known from St. Andrews and St. Thomas Parishes and *H. jamaicae occidentalis* is known from the largely mountainous regions of Manchester, St. Ann, St. Catherine, St. James, St. Thomas, and Trelawny Parishes.

New locality records.—*Heteronebo jamaicae portlandensis* was previously known by a single specimen from the John Crow Mountains, Portland Parish. It is now known from the following locality. JAMAICA: *Portland Parish,* mouth of Priestman's River, 15 December 1969 (P. A. Drummond), 1 immature female (FSCA).

Heteronebo jamaicae occidentalis, formerly known only from St. James and Trelawny Parishes, is recorded from the following localities. JAMAICA: *Manchester Parish,* 2.4 mi. S. along road to Harry Watch of Craig Head, 27 March 1969 (P. A. Drummond), 1 female (FSCA); *St. Ann Parish,* 2.0 mi. along Hollymount Road from junct. with A1, 28 March 1969 (P. A. Drummond), 2 females (FSCA), 3.9 mi. along Hollymount Road from junct. with A1, 28 March 1969 (P. A. Drummond), 1 female (FSCA), 4.2 mi. along Hollymount road from junct. with A1, 28 March 1969 (P. A. Drummond), 1 male, 1 female (OFF), Rose Hill above Runaway Bay, 5 December 1969 (P. A. Drummond), 1 male, 1 female (FSCA); *St. Catherine Parish,* 0.2 mi. W of Sligoville, 18 March 1969 (P. A. Drummond), 1 female (FSCA), 2.2 mi. N of Worthy Park Crossroads, 19 June 1970 (P. A. Drummond), 1 female (FSCA); *St. Thomas Parish,* along path to Corn Puss Gap from S, 20 May 1969 (P. A. Drummond), 1 male (FSCA); *Trelawny Parish,* Tyre (2 mi. N of Troy), 16 May 1969 (P. A. Drummond). 1 male, 1 female (FSCA).

ACKNOWLEDGMENTS

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HABITAT USE BY COLONIES OF
PHILOPONELLA REPUBLICANA (ARANEAE, ULOBORIDAE)

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ABSTRACT

Philoponella republicana (Araneae, Uloboridae) is a communal orb-weaving spider. Colonies of this spider were found more frequently in interface forest than in high forest or mountain savannah forest. This does not appear to be due to differences in insect abundance among forest types, but is correlated with greater complexity of the understory in the interface forest. This may be due to the need for supports for colony attachment lines. Within the interface forest, the location of colonies is correlated with local insect abundance. When flying insects are excluded from colonies, individual spiders can respond by increasing the distance between orbs in the colony, and colonies can respond by abandoning the site and moving to a new location.

INTRODUCTION

Philoponella republicana (Simon) is a communal orb-weaving uloborid spider, found in Panama, Trinidad, and northern South America (Opell 1979). It occurs in the rainforest understory, frequently in small tree-fall gaps and other openings in the forest. It is a seasonal species, with as many as three discrete generations per year in Panama (Lubin 1980).

The colonies consist of attachment lines, individual prey capture orbs, and a central retreat area (Figure 1). The retreat is an irregular tangle of non-sticky threads; individuals leave their orbs and move to the retreat in the evenings and when disturbed. Females with egg-cases and adult males may also spend much of their time in the retreat (see also illustration in Simon 1891). Prey capture generally takes place in the orbs. The orbs are placed above and around the retreat, sometimes several layers deep (rarely directly below the retreat); orbs are occupied by one individual at a time. The body of the colony is suspended a short distance above the ground by the attachment lines. These are large conspicuous bundles of non-sticky threads running from the colony to objects in the environment used as supports (e.g., shrubs, herbs).

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The communal societies of *P. republicana* are simple compared with those of cooperative spider species such as *Agelena consociata* (Agelenidae; Kraft 1970), *Anelosimus eximius* (Theridiidae; Brach 1975, Christenson 1984, Vollrath 1982), or *Stegodyphus sarasinorum* (Eresidae, Jambunathan 1905). There is no maternal care of the young other than guarding the egg-case, and no cooperation in orb construction. Nor do females cooperate in prey capture: although several females may be attracted to a large struggling insect and help to wrap it, a short aggressive interaction ensues and one female claims the prey packet. There may, however, be more integration of colony members than this description implies, since colony mates share the support lines and the retreat, and there is some evidence (presented below) that the colony may respond as a group to unfavorable conditions.
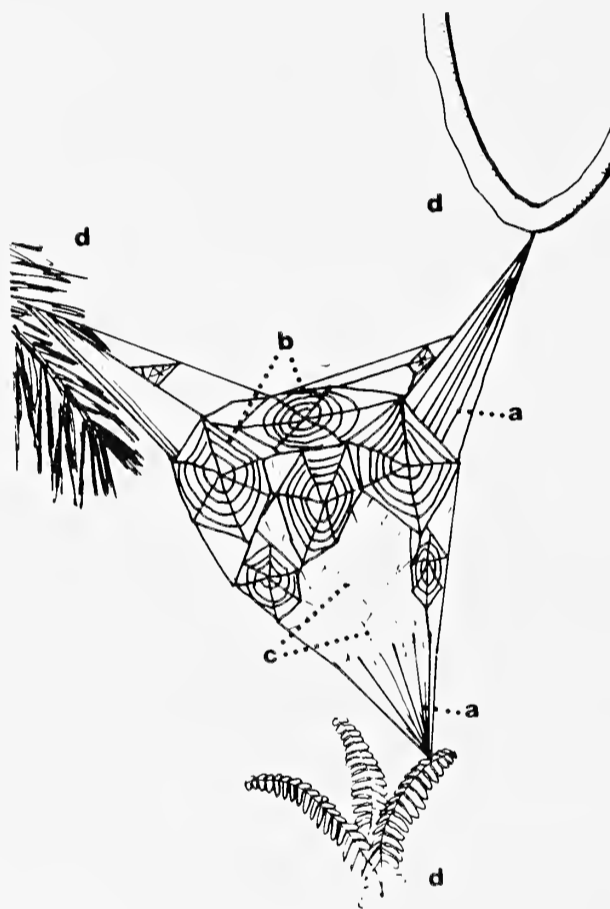
Fig. 1.—Sketch of a *Philoponella republicana* colony; a = support lines; b = individual prey capture orbs; c = central retreat area; d = objects used as supports (herbs, lianas, palms).

Study of the facultatively communal species *Philoponella oweni* in Arizona, U.S.A. (Smith 1982, 1983) showed that this species forms communal groups in response to several environmental factors. *Philoponella oweni* builds its long-lasting webs in protected sites, such as hollow trees or clefts among rocks. These sites may be scarce in some habitats, and the same sites are often used year after year by succeeding generations. Females are solitary if such sites are abundant, or if food is scarce. Communal groups form in areas where suitable sites for web construction are in short supply and insects are locally abundant, allowing several females to share a protected site and still obtain enough prey.

Lubin (1980) reports that new colonies of *P. republicana* are often founded by groups of immatures dispersing *en masse*. It is possible that *P. republicana*, with its larger and more complex groups, has evolved from an ancestor in which groups of immatures responded to patchily distributed resources in a way similar

to that of *P. oweni*. For instance, if food were abundant groups of siblings might remain together, whereas if food were scarce they would disperse. Later they might evolve the habit of remaining in groups even when local food supplies were low, moving as a group to a better location.

Here I examine the location of *P. republicana* colonies with respect to those environmental factors already known to be important to *P. oweni*—insect abundance and substrates for web attachment—and with respect to forest type. I also present natural history information on colony size and development.

METHODS

Forest type.—I carried out observations of *P. republicana* in the Voltzberg-Raleighvallen reserve, Saramacca Province, Suriname (04° 32′ N, 56° 32′ W) during February-April 1980 and February 1982. The Voltzberg reserve is located in primary lowland rainforest. The vegetation of Suriname is relatively well known and several forest types have been described from the Voltzberg region. The names used here for forest types, and the brief descriptions below follow Schultz (1960).

High forest is characterized by having two or three stories, the lower stories appearing very open. The main canopy is ca. 30 m tall, with emergent trees reaching about 40 m. Palms, particularly "*boegroe makka*" (*Astrocaryon sciophilum*), are abundant in the understory and form a fairly continuous layer at ca. 8 m. The understory is sparse.

Mountain savannah forest is a semi-deciduous forest which occurs on shallow stony soils, as on the edges of granite plates and bergs. It resembles true savannah somewhat in appearance (hence the name) but differs floristically. Trees are thin-stemmed and there is little stratification. There may be a dense herb layer.

I also included a third type: interface forest. Interface forest occurs where two or more forest types meet. This forest is characterized by a very dense understory of palms, lianas, shrubs, woody plants and herbs.

The forest in the Voltzberg reserve was essentially undisturbed except for trails, which passed through tracts of each of the three forest types mentioned here. I located colonies by searching along trails; because the trails did not pass through equal distances of each forest type, the amount of each forest type sampled was not equal. The understory in mountain savannah forest was much less dense than in either high or interface forest; although colonies a few meters off the trails in the latter two forest types might not be visible, one could easily see objects which were reasonable distances from the trail in mountain savannah forest.

Insect Abundance.—I measured insect abundance using sticky traps; my traps were fresh-cut leaves of *Heliconia* sp. (Because all equipment and food for two weeks at a time had to be backpacked into the study area, it was necessary to rely on natural materials as much as possible. I selected *Heliconia* leaves because they were large, abundant, and relatively uniform in size, and provided a smooth tough surface to spread the trap substance on.) I traced a 15 X 30 or 10 X 20 cm rectangle on the underside of the leaf, and coated an area larger than the rectangle with Stick'em Special. Insects which crawled onto the leaves would

presumably be caught before they reached the rectangle; insects captured inside the rectangle were assumed to be flying insects. By coating the underside of the leaf I ensured that the trapping surface would not be obscured if the leaf began to wilt. The leaf traps were suspended from trees and saplings.

I measured insect abundance at colony sites and at non-colony sites using a paired sampling scheme. I placed a *Heliconia* leaf trap next to each of seven colonies at the same height as the colony's prey capture surface, and a second trap at an arbitrarily chosen site 5 m due north, at the same height. Two trap sizes were used in different trials—10 X 20 and 15 X 30 cm. The traps in any paired comparison were the same size. In most cases the traps were examined after 24 hrs, but in some cases pairs were examined after 48 or 72 hours. I analyzed these data with the Wilcoxon signed rank test for paired comparisons (Seigel 1956) to allow for the variation in size and time among pairs. When traps were examined I recorded the number of insects captured, their size (length to the nearest mm; insects less than 1 mm were placed in one of two size classes: those less than 0.25 mm, and those greater than 0.25 mm and less than 0.5 mm), and taxonomic order.

I also compared insect abundance in the three forest types. I placed five *Heliconia* leaf traps with a 10 X 20 cm capture area in each forest type. Points for trap placement were randomly selected by laying a 50 m forester's tape along a trail passing through the appropriate forest type, and selecting two numbers from a random number table. The first number dictated how many meters I moved along the meter tape, the second how many meters I moved into the forest perpendicular to the tape, alternating left and right of the tape. I collected data on the number of insects captured as above, every 24 hours for five days.

Not all insects captured in sticky traps are potential prey for *P. republicana*. *Philoponella republicana* typically takes insects 5 mm or less in total body length, and usually does not take Orthoptera or Hemiptera (personal observation). I called the subset of insects captured that were 5 mm or less in length, exclusive of Orthoptera and Hemiptera the "small insects." The potential prey truly available to *P. republicana* probably consists of some of the "small insects" and also some insects not captured by the sticky traps at all. During data analysis I used four measures of insect abundance—total number of insects captured per trap per day, total number of "small insects" captured per trap per day, sum of the lengths of all insects captured per trap per day, and the sum of lengths of "small insects" per trap per day. Although watching actual prey capture is the best way to assess what a particular spider species is taking (Castillo L. and Eberhard 1983), this method cannot be used to compare insect abundances in habitats where spiders occur and where they do not. The sticky trap data can be useful to compare abundance of certain classes of insects among different locations, but cannot be used to calculate total insect prey available.

Forest understory.—I measured the structure of the forest understory at the sites of five *P. republicana* colonies and in each of the three forest types to find the relative numbers of potential supports for colony attachment lines. I randomly selected 10 points in each forest type using a meter type and random number table as described above. At 1 m north, south, east and west of each randomly chosen point I suspended a 160 cm plumb line and recorded the number of plant stems and leaves that intersected the line. At colony sites I took

measures 1 m north, south, east, and west of the center of the colonies. The total number of plant parts intersecting the four plumb lines for each point were summed for each point, since the four were not independent measurements. If a plumb line fell on a point occupied by a tree or boulder, that point was discarded.

Food Deprivation.—Orb-weaving spiders can respond in a number of ways to decreasing food supplies, for example by spinning larger orbs or by relocating the web. In communal groups spiders can also change the distance between orbs (a change in the diameter of the orb can also cause a change in orb spacing). I measured the response of colony members to food deprivation in terms of the distance between an orb and its nearest neighbor. I first gathered six days of baseline data on the nearest neighbor distances (NND) in three unmanipulated colonies (No. 1, 4, and 5). Each day I measured the distance (to the nearest cm, hub to hub) to the nearest neighboring orb for 10 to 22 orbs in each colony. If the orbs were readily accessible I measured the distance with a ruler. If direct measurement would have disturbed the spiders or the webbing I estimated the distance. To test the accuracy of my estimates I first estimated the NND's for a set of readily accessible orbs, and then measured the distance. My estimates were not significantly different from the direct measurements.

Next I built a large tent around colony 1. The tent consisted of a framework of saplings and rope covered with cheese cloth. The tent was left in place for five days, during which time it excluded most flying insects from the colony. After five days I measured NND for orbs in the experimental and two control colonies.

I repeated the experiment using colonies 3, 4, and 5. I gathered baseline data for one day and then built a cage around colony 3. After three days of insect exclusion I measured NND in the experimental and control colonies.

To test for the effect on NND of general disturbance during tent building I gathered baseline data for one day on colony 8 and then built a tent framework around it, consisting of poles and ropes without the cheese cloth. I recorded NND in this colony for three more days.

Colony growth and size.—I censused seven *P. republicana* colonies (No. 1 and 3-8) from 11 February to 10 April 1980. I classed the spiders in the colonies as adult males, adult females (7 mm or more in total body length) or one of four size classes of immatures: less than 1 mm, 1-2 mm, 3-4 mm, and 5-6 mm. When counting numerous tiny hatchlings much less than 1 mm in length I took three counts and used the average.

I measured the size of four colonies: height and horizontal diameter of the main body of the colony (retreat plus orbs) and number and length of attachment lines, all to the nearest 10 cm. I also noted the objects used as supports for the attachment lines.

RESULTS

Forest type.—In 1980 I located seven (or five—see the section on Food Deprivation below) large colonies of *P. republicana*. These colonies were in interface forest (five colonies) or in gaps in forest created by boulder fields (two colonies). The trails passed through large tracts of high forest and mountain

Table 1.—Mean number of insects of all types captured per sticky trap per day in three Suriname forest types. Trap sites are of three types: random sites were randomly selected points in each forest type; arbitrary sites were 5 m due north of *Philoponella republicana* colonies in interface forest; colony sites were next to colonies of *P. republicana*. Data from all trap sites were compared using the Mann Whitney U-test. Means with the same group letter do not differ significantly at the 0.05 level.

Forest type:	Trap site	Mean	SD	N	Group
High	random	3.6	2.5	25	A
Mt. Savannah	random	5.2	3.0	25	B
Interface	random	5.8	3.8	25	B
	arbitrary	5.3	3.5	28	B
	colony	7.9	4.2	28	C

savannah forest and only a small belt of interface forest. Because most of the colonies were found in interface forest, even though less of this forest type was sampled, this implies that *P. republicana* occurs more frequently in interface than in high or mountain savannah forest.

Insect abundance.—Insects were more abundant at colony sites than at arbitrarily selected sites 5 m north of colonies for all four measures of insect abundance: total number of insects ($p \ll 0.01$), total number of "small insects" ($p \ll 0.01$), sum of lengths of all insects ($p < 0.01$), and sum of lengths of "small insects" ($p \ll 0.02$) captured per trap per day (Wilcoxon signed rank test for paired samples, Seigel 1956).

A comparison of insect abundance in the three forest types is given in Table 1; these data were analyzed using three-way Analysis of Variance and Duncan's multiple range test (Barr et al. 1976). There is no difference in the mean number of insects captured per trap day in interface and mountain savannah forest, and significantly fewer captured per trap day in high forest than in the other forest types. It is also possible to compare insect abundance at these randomly selected points in the three forest types with insect abundance at colony sites and the arbitrarily chosen points 5 m north of colonies (Table 1). Data from 28 pairs of traps of the same size and duration of exposure as the forest samples (10 X 20 cm, 24 hrs) showed that there were significantly more insects captured per trap/day at colony sites (7.9 ± 4.2) than in any other site (Mann Whitney U-test, $p < 0.04$ or better). There was a mean of 5.3 ± 3.1 insects per trap/day at sites 5 m north of colonies, which is not significantly different from the values for randomly selected points in interface or mountain savannah forest ($p > 0.75$, Mann Whitney, U-test).

Understory structure.—Table 2 shows the complexity of the understory in three forest types and at sites occupied by colonies. There is no significant difference in the mean number of plant parts intersecting plumb lines in interface forest and at colony sites, and there is also no significant difference between high and mountain savannah forest in this respect. There are significantly more plant parts—potential web supports—in colony sites and in interface forest than in high and mountain savannah forest.

Food deprivation.—In replicates 1 and 2, in which functional insect exclusion tents were used, the NND increased when insects were excluded. In replicate 1

Table 2.—Structure of the forest understory: mean number of plant parts intersecting four 160 cm plumb lines in three forest types and at sites of *Philoponella republicana* colonies. Means with the same group letter do not differ significantly at the 0.05 level. Interface differs from High and Mountain Savannah forest at $p<0.002$; Colony sites differ from High and Mountain Savannah forest at $p<0.05$ (Mann Whitney U-tests).

Forest type:	Mean	SD	N	Group
High	2.3	1.6	10	B
Mt. Savannah	1.6	1.8	10	B
Interface	9.9	2.8	9	A
Colony	6.8	2.9	4	A

the NND in the experimental colony increased from 8.2 ± 1.5 cm (n = 19 orbs) on the day before insect exclusion to 11.1 ± 3.7 cm after exclusion (n = 17; p < 0.02, two-tailed Mann Whitney U-test; Seigel 1956). There was no significant change in the NND in the control groups. In control colony 4 the NND was 6.8 ± 1.7 cm (n = 20) before the experiment and 6.8 ± 1.5 after (n = 16; p > 0.10); in control colony 5 the NND was 6.1 ± 0.8 cm before (n = 20) and 6.4 ± 1.7 cm after (n = 20; p > 0.10).

In replicate 2 the NND in the experimental colony increased from 7.6 ± 2.1 cm (n = 16) on the day before insect exclusion to 11.2 ± 3.8 cm after (n = 18; p < 0.002, two-tailed Mann Whitney U-test). In control colony 4 the NND was 7.0 ± 1.7 cm before (n = 20), and 7.1 ± 1.0 after (n = 20; p > 0.10); control colony 5 the NND did increase significantly after the course of the experiment (p < 0.05) but the magnitude of the change was small (6.7 ± 1.6 cm before, n = 20, to 7.6 ± 0.9 cm, n = 20 after).

In colony 8 the NND did not increase after the sham tent was built. Before the tent was built NND was 12.1 ± 2.1 cm (n = 10 orbs). On the first day after the sham cage was built NND decreased significantly to 9.0 ± 1.5 cm (n = 7; p > 0.02). On the next two days NND increased back to values not significantly different from the original values: 11.8 ± 1.7 (n = 7) and 11.0 ± 2.2 (n = 5; p >0.10).

In addition, in replicates 1 and 2 the experimental colony abandoned its old site after the insect excluding tent was removed; apparently the colony moved as a group to a new location. Within a few days after removal of the tent the old site was abandoned and two new colonies, 6 and 7, appeared two to three meters away from the sites of the old colonies 1 and 3. The experimental colony 1 contained three marked individuals, one of whom was later seen in colony 6. In addition a female was seen walking on the ground from near the old site of colony 1 towards colony 6. This circumstantial evidence indicates that each colony moved as a group.

Colony Growth and Size.—Figure 2 presents the development of Suriname colonies over the period from 11 February to 10 April 1980. Hatchlings, i.e., spiderlings in their first post-emergence instar, are easily identified by their non-sticky "sheet" orbs (Eberhard 1971, Szlep 1961). All the hatchlings were found in the attachment lines of the colony, not in the body of the colony. Females with egg-cases often leave the colonies (Lubin 1980) perhaps in an attempt to avoid egg-case parasites. The hatchlings in the attachment lines may be the young
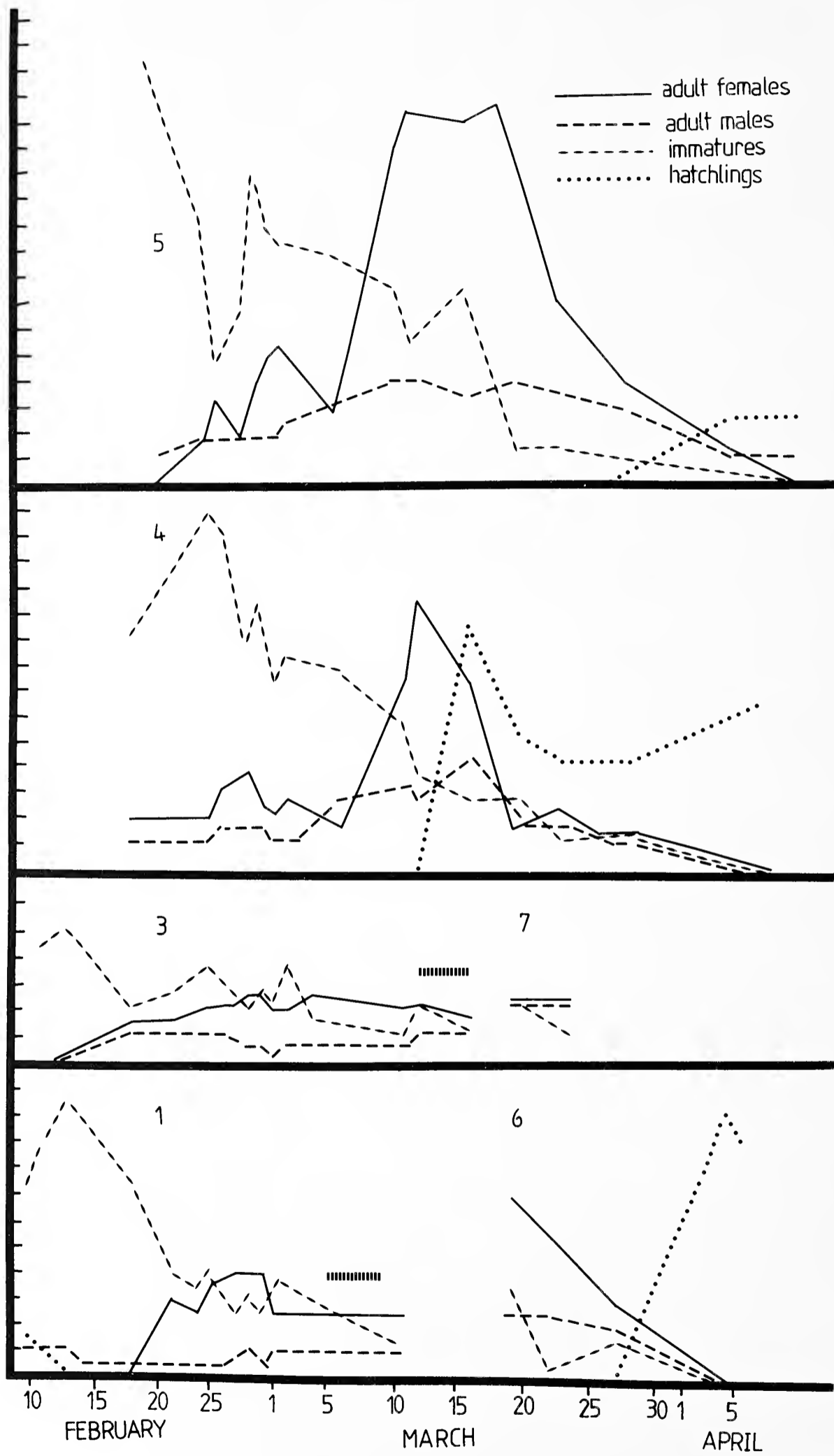
Fig. 2.—Census data from six colonies of *Philoponella republicana* (colonies no. 1, 3, 4, 5, 6, and 7). Horizontal axis, time in days; vertical axis, number of individuals in units of 10; striped horizontal bars, duration of insect exclusion experiments.

of females who left the colony along the attachment lines. The seven colonies were roughly synchronous in development, and most of the adults of a colony die or disappear before the young produced by their generation mature. Thus there is no overlap of adults between generations in these populations.

The four colonies measured to the nearest 10 cm were 85 ± 5 cm tall and 60 ± 0 cm in diameter. The retreats were 0 to 30 cm above the ground. There were an average of 8 ± 2.2 attachment lines per colony, each an average of 78.6 ± 41 cm long (range 40 to 200 cm). The attachment lines were fastened to lianas, leaves of hardwood trees, and most commonly, palms.

DISCUSSION

Colonies of *P. republicana* in Suriname were found more frequently in interface forest than high or mountain savannah forest. This does not appear to be a result of differences in insect abundance among the three forest types, since insects were no more abundant in interface than in mountain savannah or high forest. The size of *P. republicana* colonies, their height above the ground, and the length of their attachment lines means that they are using objects for support from ground level to 1.5 to 2.0 m above the ground. The understory in interface forest is denser than in high or mountain savannah forest and thus provides more potential supports for colony attachment lines.

Within interface forest the location of *P. republicana* colonies does appear to be influenced by insect abundance, inasmuch as colonies were found at sites where insects were locally abundant. (Considering insects caught in sticky traps as a measure of insect abundance.)

Individuals within colonies also respond to changes in insect abundance. If food supplies are reduced by building a cage around the colony, the individual spiders spin their orbs farther apart. When the cage is removed and the colony is given the opportunity to move the group abandons the old, "poor" site and relocates in a new site. Thus this species responds to environmental conditions at three levels: at the level of the forest type occupied, at the level of colony location within the chosen forest type, and at the level of individual spacing within colonies.

The responses of *P. oweni* and *P. republicana* to food supply and web building sites can be compared. *Philoponella oweni,* the facultatively communal species found in the southwestern United States, builds its webs in protected sites which may be in short supply in some habitats. Because the locations of these protected web sites do not change much from year to year, the location of *P. oweni* webs are also rather stable from year to year. Some immatures of *P. oweni* overwinter at their mother's web site and emerge the following spring to begin a new colony. Some sites were occupied by *P. oweni* colonies for at least six consecutive years. The number of adults which ultimately remain at a site appears to be largely governed by insect abundance at the site (Smith 1983). These results agree with those of Uetz et al. (1982), who found that the number of individuals in communal groups of *Metepeira spinipes* (Araneidae) and interindividual spacing within the colonies, varied in response to the abundance of prey.

Compared to *P. oweni,* colonies of *P. republicana* are more mobile. In habitat used by *P. republicana* (interface and second growth forest) suitable attachments for web building appear to be relatively abundant, and the results of the insect exclusion study indicate that a colony may move as a group in response to changes in food supply. Thus, whereas *P. oweni* remains at a web site and adjusts group size to food supply, *P. republicana* maintains its communal group and moves the colony in response to food shortages. This can only be done in habitats where potential web attachment sites are plentiful. *Philoponella republicana* could be derived from a species in which immatures dispersed in groups and responded to changes in food supply by moving the entire group to a better site rather than by breaking up the group into individuals.

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REPRODUCTIVE TACTICS AND FEMALE BODY SIZE IN THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE, OXYOPIDAE)

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ABSTRACT

Data collected on life history traits of *Peucetia viridans,* representing three generations, were analyzed. A total of 61 females and their clutches were examined to determine the following: female mass, female tibia length, clutch mass, clutch size, mean mass per young, egg sac mass, egg sac mass per young, and relative clutch mass (an estimate of reproductive effort). Clutch mass, clutch size and egg sac mass are strongly correlated with female mass. *Peucetia viridans* has the reproductive tactic of producing young of optimum size, with the number of young varying in response to environmental pressures that influence female size, thus producing optimal reproductive effort. Relative clutch mass is also optimized and apparently not influenced by the variation in female mass, clutch mass or size. Egg sac mass per young is similar in small clutches and large clutches. These findings are discussed in terms of the species' life history characteristics.

INTRODUCTION

Most information on reproductive tactics in spiders comes from literature dealing with spider taxonomy, where some observations of spider size (usually body length) and clutch size (number of eggs or young in an egg sac) have been reported (Bristowe 1939, Kaston 1948, Gertsch 1949). For *Peucetia viridans,* the green lynx spider, Brady (1964) gives the number of eggs from egg sacs taken from several geographical regions. There are very few studies that deal with the precise relationships between the size of female spiders, number and size of offspring, and estimates of reproductive effort.

Any reproductive event can be described in terms of a triumvirate: reproductive effort, expenditure of energy per progeny, and clutch size (Pianka, 1983). Though the concept of reproductive effort (the proportion of total energy allocated to a reproductive event) is very useful, it is often quite difficult to quantify. An operational estimate of reproductive effort that has been used is a ratio of clutch mass to female mass (Vitt and Congdon, 1978). This ratio, termed relative clutch mass, is used in this paper.

Though many authors have noticed the general trend that larger females produce larger clutches, few (Peterson 1950, Kessler 1973, Riechert and Tracy

1975, Eberhard 1979) have studied this relationship closely in spiders. Enders (1976) has shown, using published data from a variety of studies, that clutch size among species of spiders is positively correlated with length of female and that other life history traits (hunting manner, habitat selection) also appear to be related to clutch size. The energy content of spider eggs was studied by Anderson (1978). He included data on mass-specific energy content of *P. viridans* eggs from five clutches along with data from eleven other species. He discussed these data in relation to female mass and clutch mass and suggested that caution by used when selecting an estimator of reproductive effort.

Our three-year study of certain reproductive parameters of *Peucetia viridans* (Hentz) enables us to examine closely its reproductive tactics as they relate to the energetics associated with the reproductive biology of the species. We analyze the relationships between such parameters as clutch size, clutch mass, egg sac mass, mean egg mass, relative clutch mass, and female mass. We also examine how some parameters change significantly and others remain constant from one generation to the next.

STUDY AREA AND NATURAL HISTORY

Two study areas in east Texas were selected. One study area was an old field located 1.6 km northwest of the city of Whitehouse (Smith County) near the western edge of the Australoriparian Biotic Province. This 1.22 hectare field is surrounded by an Oak-Hickory-Pine Forest. In late summer and early fall the tallest herbaceous vegetation consists of composites (*Veronia* sp., *Lactuca* sp., *Ambrosia* sp.) and an euphorb (*Croton capitatus*), these being the most commonly encountered plants on which there are female *P. viridans* and their egg sacs. Samples were taken from this site in 1980 and 1981. The second study site was an old field very similar to the first, located approximately 11.2 km north-northeast of the first site, 0.8 km south of The University of Texas at Tyler. Samples were taken from this site in 1983.

The life history and phenology of *P. viridans* have been examined by Whitcomb, Hite and Eason (1966) and Turner (1979). In east Texas, there appears to be one reproductive period with a single clutch produced by a female between mid-September and late October. Though multiple clutches have been reported from other areas, none was observed during this study.

METHODS

Samples were taken from September 29 to October 12, 1980, and from September 17 to October 25, 1981, and on October 11, 1983. Twenty-one females with their corresponding egg sacs were taken in 1980, 14 were taken in 1981, and 26 were taken in 1983. The following information was determined for each specimen: female mass (mg) after egg sac construction, length of first tibia of female (mm), mass of egg sac (mg), mass of clutch (mg) and clutch size (number of eggs or juveniles). Relative clutch mass (RCM, clutch mass/female mass), mean mass of young (MMY, clutch mass/clutch size), and mean egg sac mass per young (MEY, egg sac mass/clutch size) were calculated.

These data were statistically examined using the computer-packaged Statistical Analysis System (Freund and Littell, 1981). The significance level chosen was α = 0.05. In addition to basic descriptive statistics the following were used: Duncan multiple range test to compare sample statistics by year; correlation; general linear regression, with coefficient of determination and test for homogeneity of slopes used to compare certain parameters to female size.

RESULTS

Tables 1 and 2 summarize sample statistics for each of the three years by parameter and for parameter totals.

Female mass and female tibia length were significantly different by year; the largest females were taken in 1981. Because the coefficients of variation (C.V.) did not vary greatly from year to year, the female size differences by year appear to be real.

Average clutch mass in 1980 was not significantly different form the other two years, but clutch mass in 1981 was significantly different from that of 1983. Note that in 1980 the C.V. is large compared to the other two years. Clutch mass appears to vary more than female size. There is a significant positive correlation of clutch mass and female mass by year and for the data combined. When clutch mass is regressed against female mass (Figure 1), 55.14% of the total variation in clutch mass is explained by the linear relationship to female mass in 1980, 58.12% in 1981, 63.38% in 1983, and 66.53% for the data combined. Regression coefficients are not significantly different for these data.

Clutch sizes in years 1980 and 1983 were not significantly different from each other, but clutch size in 1981 was significantly different from that of the other

Table 1.—Means (standard errors)/ranges of reproductive parameters of *Peucetia viridans*. Statistics underlined are not significantly different by year (P>0.05).

Year	1980	1981	1983	Total
Sample	21	14	26	61
Female mass (mg)	106.12(4.81)	226.07(14.30)	155.51(7.38)	154.70(7.45)
Range	77.10-164.10	168.10-335.40	85.90-214.10	77.10-335.40
Female tibia length (mm)	6.89(0.16)	9.07(0.17)	7.63(0.15)	7.70(0.14)
Range	6.66-8.21	7.92-10.18	6.22-8.86	5.66-10.18
Clutch mass (mg)	147.94(14.46)	266.78(21.82)	193.65(13.75)	194.70(10.66)
Range	42.10-360.10	131.60-403.60	66.70-375.00	42.10-403.60
Clutch size	98.38(9.64)	169.86(12.40)	114.08(7.66)	121.48(6.42)
Range	29-242	90-240	42-183	29-242
Mean mass per young (mg)	1.5.(0.03)	1.56(0.03)	1.70(0.04)	1.60(0.02)
Range	1.29-1.72	1.44-1.76	1.31-2.25	1.29-2.25
Egg sac mass (mg)	5.71(0.43)	13.16(0.75)	7.32(0.46)	8.11(0.47)
Range	3.60-11.90	9.60-18.40	3.40-12.20	2.40-18.40
Relative clutch mass	1.31(0.11)	1.18(0.07)	1.23(0.06)	1.27(0.04)
Range	0.49-2.23	0.69-1.50	0.55-1.91	0.49-2.23
Egg sac mass per young (mg)	0.06(0.01)	0.08(0.01)	0.07(0.00)	0.07(0.00)
Range	0.03-0.12	0.05-0.13	0.04-0.09	0.03-0.13

Table 2.—Coefficients of variation (coefficients of determination) of reproductive parameters of *Peucetia viridans*. Statistics underlined are not significantly correlated to female mass (P>.05); *=Regression coefficients for these parameters against female mass are not significantly different by year when compared to regression line of total.

Year	1980	1981	1983	Total
Female mass	20.75	23.67	24.19	37.62
Female tibia length	10.75	6.96	9.94	14.09
Clutch mass	44.80(0.5514)	30.60(0.5812)	36.22(0.6338)	42.77(0.6653)*
Clutch size	44.91(0.5735)	27.32(0.5419)	34.26(0.6802)	41.25(0.6435)*
Mean mass per young	8.10(0.0001)	6.17(0.1868)	13.16(0.0022)	11.80(0.0129)*
Egg sac mass	34.33(0.1601)	21.31(0.0160)	32.43(0.6486)	45.44(0.5883)
Relative clutch mass	30.88(0.1071)	21.84(0.0003)	24.62(0.0249)	27.09(0.0403)*
Egg sac mass per young	36.77(0.1766)	29.68(0.3476)	20.03(0.0462)	30.35(0.0006)*

two years. Clutch size also appears to vary more than female size. Significant positive correlation occurs between female mass and clutch size by year and for the data combined. Coefficients of determination indicate that 57.35% of the variation in clutch size is explained by a linear relationship to female mass (Figure 2) in 1980, 54.19% in 1981, 67.02% in 1983 and 64.53% for the data combined. Regression coefficients are significantly different for these data.

Mean mass of young was significantly different only in 1983. The C.V.'s are very small when compared to the C.V.'s of other parameters. There is no significant correlation of mean mass of young and female mass for any year nor for the data totals; neither is there a difference in regression coefficients by year.

Egg sac mass was significantly different by year. It was not significantly correlated to female mass in 1980 and 1981, though data from 1983 and the combined data show a significant correlation between these two parameters. Figure 3 shows the best-fit linear relationship between egg sac mass and female mass, with very little of the variation in egg sac mass being explained by female mass in 1980 and 1981, 16.01% and 1.6% respectively. The coefficients of determination are 64.86% in 1983 and 58.85% for the data combined. Slopes by year are significantly different from the slope of the composite regression line.

Relative clutch mass is not significantly different when compared by year. There is no significant correlation with female mass, and regression coefficients are not significantly different by year.

Egg sac mass per young is significantly different from other years only in 1981. There is no significant correlation between egg sac mass per young and female mass, nor are there significant differences in regression coefficients by year.

DISCUSSION

The results suggest that an analysis from two perspectives would be useful. First we examine the life history parameters as they relate to individual phenotypes, i.e., the expression of the parameters and their interactions. Next we consider the broader implications of these individual reproductive tactics as they relate to the species' life history characteristics.
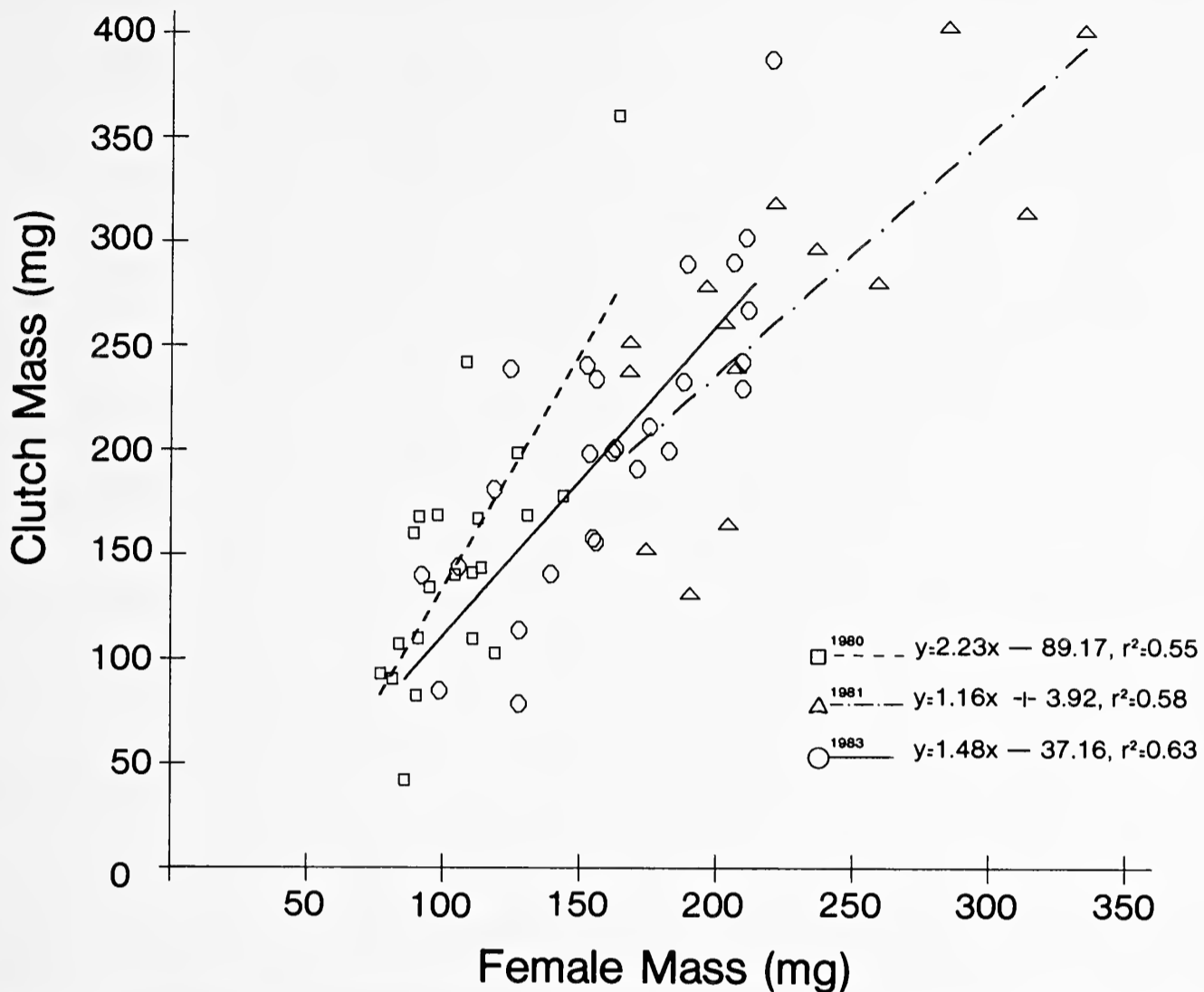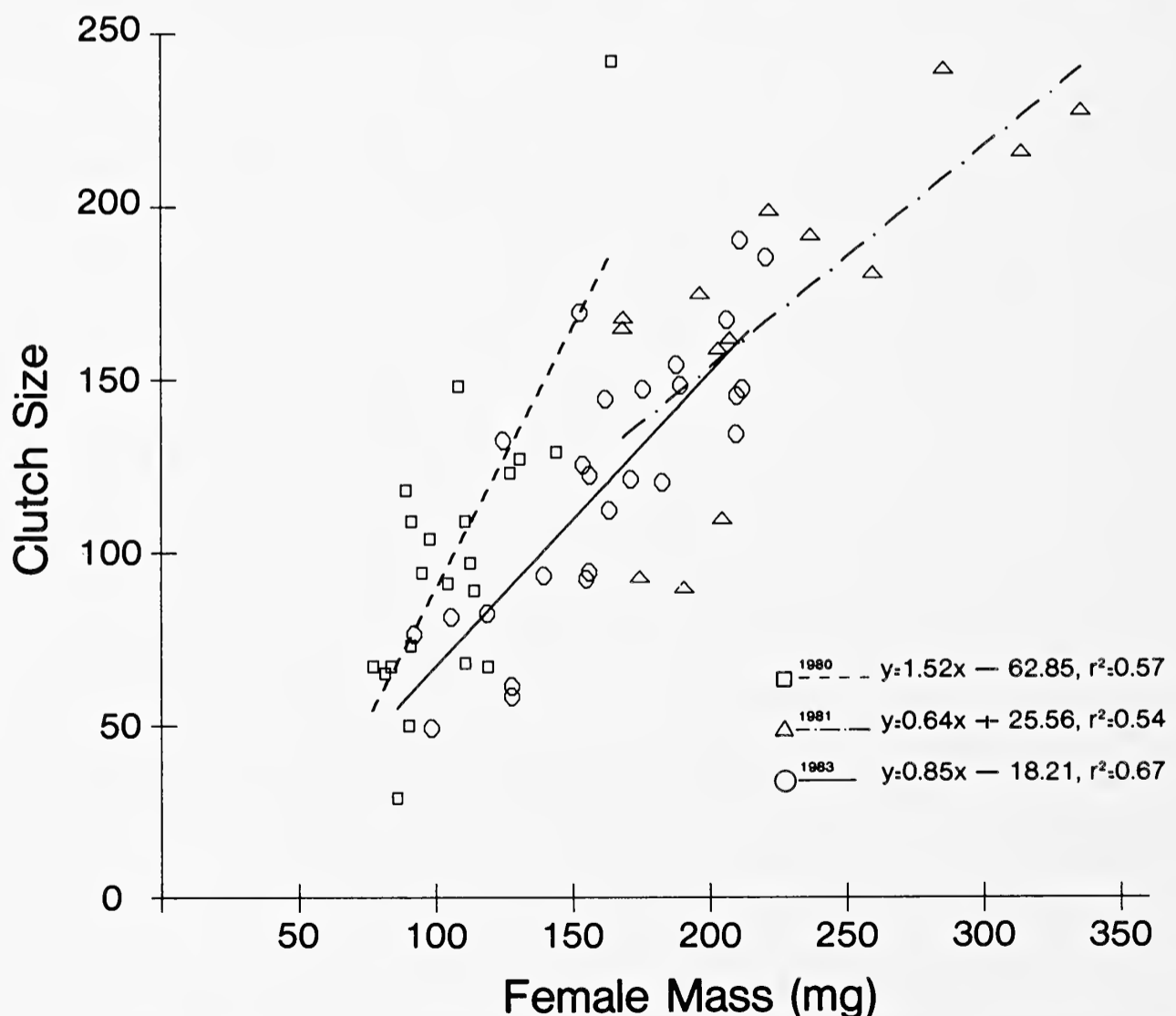
Fig. 1.—Regression of clutch mass against female mass of *Peucetia viridans* for three years. r^2 is the coefficient of determination.

It is clear that a reproductively successful female can vary greatly in size, the largest being some 4.4 times more massive than the smallest (Table 1). This allows for the exceptional range in clutch mass (42.10 - 403.60 mg) and clutch size (29 - 242) because these two parameters show high coefficients of determination when regressed against female mass (Figures 1 and 2). Although natural selection appears to favor individual variation in these three parameters, that variation does not affect reproductive effort. These data show that small females may have the same relative clutch mass as large females and that RCM does not change from one year to another (Table 1 and Table 2), implying an optimum RCM. This is striking, given that reproductive effort in some females is 4.5 times greater than in others. Since essentially none of this variation is explained by a linear relationship with female mass (or any other correlate of female mass) and since the two components of RCM covary so strongly, which would normally yield a constant RCM, we interpret the variation in RCM to be due to changes in female mass after oviposition. This effect is random in that, even though some females may have fed after oviposition, feeding frequency in the short time between oviposition and being collected is due to chance. This feeding effect is likely a minor component of variation in female mass, which is masked by the variation in female mass already existing at the time of oviposition. When the mass to mass ratio of RCM is calculated, the effect of variation due to post-oviposition feeding is exposed. We conclude that *P. viridans* has a reproductive tactic of optimal

reproductive effort regardless of the variation present in female mass, clutch size and clutch mass.

Another parameter that is important in understanding reproductive tactics is the energy allocation per spiderling. We utilized mean mass of young to estimate this element. MMY is not correlated with any parameter discussed thus far. Natural selection appears to produce an optimum MMY; in two of the three years, it is the same. MMY also has the smallest C.V. of any parameter. This leads to the conclusion that *P. viridans,* rather than having small females reduce their allocation of energy per young so as to have more but smaller young, has a reproductive tactic to produce fewer young of optimum size. Larger females likewise produce young of optimum size, but more than them. This explains how both clutch size and mass are strongly correlated with female mass.

Our findings are in agreement with those of Anderson (1978), who found that variation in mass-specific energy content in spiders was less than variation in clutch size, and there was no correlation between energy content per unit egg mass and size of the female parent, egg size, or clutch size. In the light of these findings and those of our study, RCM appears to be a valid estimate of reproductive effort and may be a useful operational tool in studies that require an indirect measure of the energy partitioned to reproduction by spiders.

In spiders, another quantitative reproductive parameter is important, namely egg sac mass. This parameter varies in a manner similar to clutch size and mass.

Fig. 2.—Regression of clutch size against female mass of *Peucetia viridans* for three years. r^2 is the coefficient of determination.
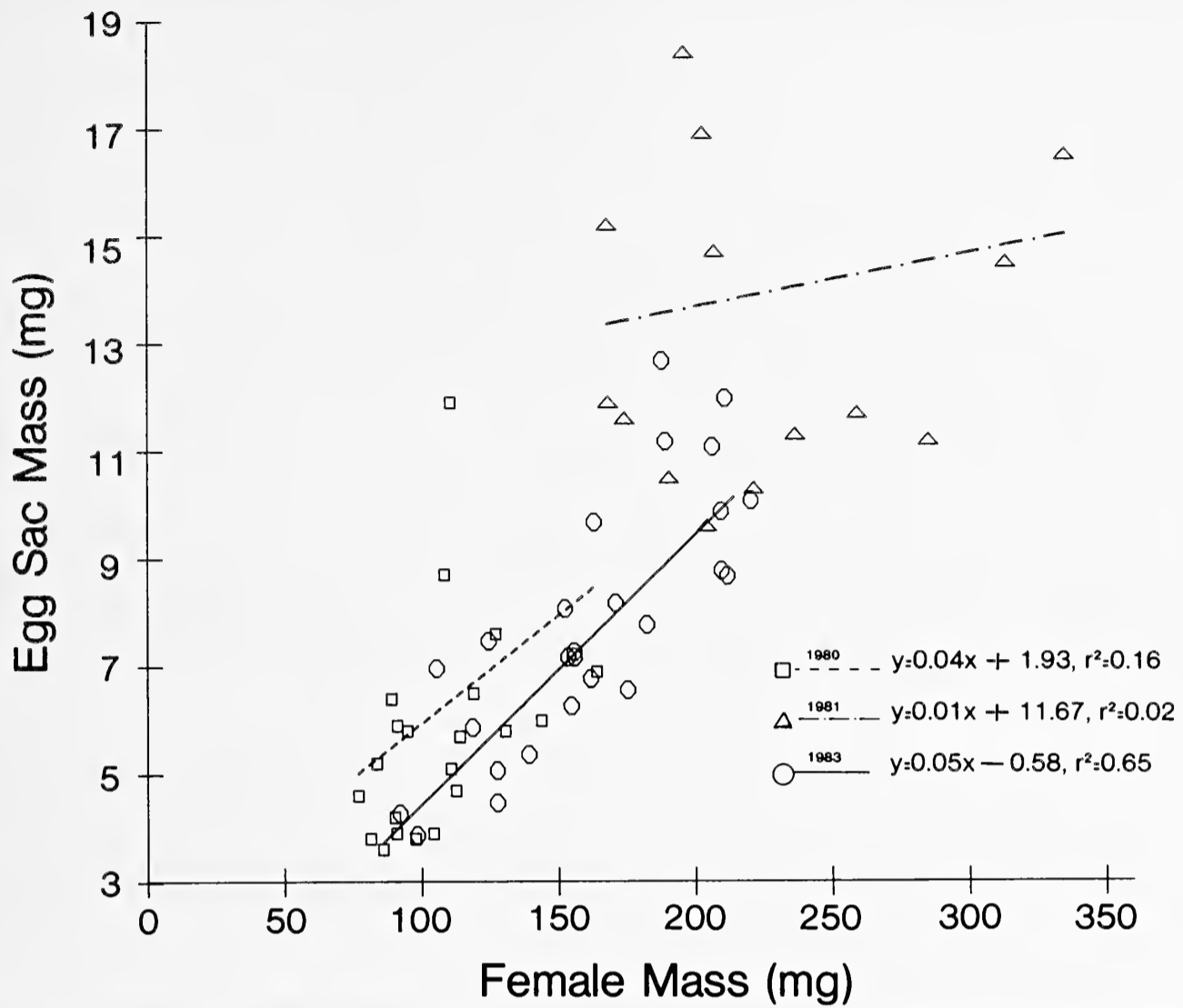
Fig. 3.—Regression of egg sac mass against female mass of *Peucetia viridans* for three years. r^2 is the coefficient of determination.

The larger the female the greater the mass of the egg sac. However, when egg sac mass per young is examined, it can be seen that this parameter has also been optimized by natural selection (Tables 1 and 2). It is obvious that large clutches require more silk for the same degree of protection, but the subtle point is that small females tend to allocate the same amount of energy to egg sac construction per offspring as do large females. Because the construction of an egg sac is a surface to volume related phenomenon, allometric theory predicts the allocation of less silk per young in larger clutches; since egg sac mass per young is constant, egg sacs around larger clutches are likely thicker.

We examine now the broader implications of these life history parameters in this species. Assume that a parameter is a constant from one year to the next if in two of the three years it is not significantly different from the other years. As seen in Table 1, clutch mass, clutch size, mean mass of young, relative clutch mass and egg sac mass per young would be constants. Female size and egg sac mass would therefore be the only variables by year. Under these conditions, it appears that populations of *P. viridans* tend to produce clutch sizes, clutch masses, MMY's, RCM's, and MEY's near optimal values. Female mass and the mass of an egg sac are the parameters left as response variables, able to fluctuate from year to year depending on environmental pressures. We propose the following hypothesis as an explanation for these observations.

Peucetia viridans females protect their offspring in two ways: by watching over the clutch and by covering the clutch with silk. the success of the former

protective mechanism depends on the females' endurance after oviposition; the latter mechanism depends on her prey capturing ability before oviposition. For a population to respond favorably to stochastic conditions in the environment (prey and predator presence, temperature, moisture, etc.) some natural history parameters may vary and others may remain constant, depending on the particular selection pressures unique to a species. In *P. viridans* maintenance of successful populations through time requires the tactic of adjusting female size and all the attributes contingent on size. Trade-offs between other parameters may be alternative reproductive tactics in other semelparous species, but in *P. viridans,* female mass and egg sac mass vary in response to environmental pressures to produce adequate numbers of optimal size offspring through optimal reproductive effort, protecting their clutches with optimal egg-sac silk per young.

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NESTS AND NEST-SITE SELECTION OF THE CRAB SPIDER *MISUMENA VATIA* (ARANEAE, THOMISIDAE) ON MILKWEED

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ABSTRACT

Adult female crab spiders *Misumena vatia* that had previously hunted in large milkweed clones built nests on non-flowering milkweeds more often than predicted and used smaller than average leaves for their nests. These results suggest that they actively select nest sites at both stem and leaf levels. In commencing a nest, spiders first pulled the distal third of a leaf under the rest of the leaf, secured it with silk, and then rested inside this space. A few days later they laid their eggs there, sealed the edges of the leaf around the egg mass with silk and then guarded the nest, typically resting on its lower side. Spiders always left the last stem upon which they hunted before nesting and usually selected milkweed leaves on a stem several meters away from their hunting site for their nest site.

INTRODUCTION

The choice of a nest site is one of the most important decisions made by animals that deposit eggs. Not only must these nests be placed where physical conditions permit the development of eggs, and of hatchlings if they remain, but the location must also be satisfactory for the adults, if they latter guard them. Further, if the site is not guarded by parents, it is essential that if offer protection from egg parasites or predators. A poor choice subjects the eggs to a wide range of unfavorable factors. The stakes are particularly high if an individual lays many or all of its eggs at a single site, for the probability of all-or-none success at this stage of the life cycle is high. Not surprisingly, many species of animals exhibit precise nest-site selection behavior (Hildén 1965, Partridge 1978, Morse 1980).

Although considerable general information exists on where spiders place their egg sacs, much of it concerns web-building species (e.g., Comstock 1940, Bristowe 1958), and few quantitative data exist on egg placement for sit-and-wait spiders such as crab spiders (see Enders 1977). Here I report on the characteristics of nests and of nest sites selected by solitary, leaf-nesting crab spiders [*Misumena vatia* (Clerck (Thomisidae)] that hunt in common milkweed (*Asclepias syriaca*) immediately prior to nesting.

METHODS

I gathered data on the nests of *Misumena* in a one-ha field in Bremen, Lincoln Co., Maine, U.S.A., during July and August of 1980-1984. Although the vegetation is composed primarily of grasses, a large clone of common milkweed consisting of about 1500 flowering and non-flowering stems grows in the middle, and three smaller clones occur elsewhere in the field. Almost all of the nests were placed on milkweed. Several species of small forbs also grow throughout the field.

I recorded the height of the nest, the height of the milkweed stem, and the length and width of the leaf selected for the nest. If possible I recorded the distances that spiders moved between their last hunting site and their nesting site. I also measured stem height and leaf dimensions from random samples of flowering and non-flowering stems in the study area. Data for most of the variables came from 72 free-ranging spiders; however, I supplemented data on leaf choice and nest height with information on 50 individuals confined at the time of egg-laying to large screen cages placed over milkweed stems. Sample sizes often differ because I did not gather data on all of the variables from each spider.

RESULTS

Distance between last feeding site and nest site.—Spiders typically placed their egg-sacs several meters from their last hunting site, and many of them moved toward the outside of the milkweed clone at this time. Individuals moving to the periphery traveled over twice as far (9.6 ± 9.1 m S.D., N = 14) as did those remaining within a clone (4.2 ± 3.2 m, N = 8) (P < 0.05 in a one-tailed t-test). However, as indicated by the large standard deviations, distances moved were extremely variable. Part of the difference in distances travelled could be a consequence of milkweed stems, or other satisfactory nest-sites, being much less dense around the periphery of the clone than in the center. If so, individuals reaching the periphery would have to travel farther to reach the next stem than would spiders in the center of the clone.

Characteristics of nest-sites.—Spiders laid their egg masses on the leaves of both flowering and non-flowering milkweed stems. They selected stems that were significantly shorter than those of the clone as a whole (Table 1), in large part

Table 1.—Stem choice of free-ranging *Misumena vatia* for nest sites on common milkweed.

Category	Height of sample of stems in clone		Height of stems used by spiders		P (Wilcoxon two-sample test)
	N	x̄ ± SD (cm)	N	x̄ ± SD (cm)	
Flowering and non-flowering	143[1]	68.0 ± 17.2	65	62.6 ± 19.1	<0.01
Flowering	103	76.8 ± 10.4	25	84.4 ± 11.2	<0.01
Non-flowering	101	49.2 ± 15.3	40	51.1 ± 10.5	>0.3

[1]Initially, I measured randomly-selected samples of 103 flowering and 101 non-flowering stems. However, because the clone averaged 72% flowering stems and 28% non-flowering stems over the study period, I produced the profile of flowering and non-flowering stems tested here by using the entire sample of 103 flowering stems (72% of the sample) and 40 non-flowering stems randomly chosen from the sample of 101 (the remaining 28% of the sample.)

the result of using significantly more non-flowering stems (40 of 65: Table 1) than predicted from the numbers of flowering and non-flowering stems during this study. Differences between the observed and predicted patterns of nest-site choice ranged from P < 0.02 to P < 0.001, G = 6.61 to 23.50, respectively.)

In spite of their apparent preference for non-flowering stems, spiders used a large number of flowering stems for nest sites. Because the clone is a rough rectangle of 20 x 30 m, and because most flowering stems are located in the center and non-flowering stems about the periphery (Fritz and Morse 1985), the relatively immobile, egg-laden spiders hunting in the middle of the clone may often not travel far enough to find a non-flowering stem. None of the spiders whose last hunting site was unambiguously known (N = 22) used that site for its nest.

Flowering stems used by spiders were significantly taller than the non-flowering stems that they used (Table 2). I then tested whether the spiders exhibited height preferences within these two categories of stems. They used flowering stems significantly taller than predicted by the heights of flowering stems within the clone, but the heights of non-flowering stems that they used did not differ significantly from the height predicted by the numbers of non-flowering stems within the clone (see Table 1). Thus, although spiders showed clear preferences for non-flowering stems, they also exhibited height preferences among flowering stems.

Spiders also placed their nests higher on flowering than non-flowering stems (Table 2). Egg masses were most frequently placed near the tops of milkweed stems (Table 2), often on the uppermost leaf wide enough to enclose them. Usually this leaf lay no more than 3-4 cm below the top of the terminal shoot of the stem. In few instances (8 of 93: 8.6%) did the spider build its nest more than 10 cm below the tip of the terminal shoot. In one such instance an egg sac was placed 45 cm up a 75 cm stem in a small axillary leaf that had developed subsequent to the loss of an original leaf.

On both flowering and non-flowering stems spiders used significantly shorter and narrower leaves than predicted by the mean sizes of leaves on these two stem types (Table 3). These results suggest that the spiders actively selected relatively small leaves, although they might also select leaves at the top of the stems, since most of the small leaves grow there. Further, they also used significantly longer

Table 2.—Characteristics of nest sites on common milkweed. N's not all equal because not all variables were measured each year.

Variable[1]	Flowering stems		Non-flowering stems		p[2]
	N	x̄ ± SD (cm)	N	x̄ ± SD (cm)	
Height of stem	25	83.4 ± 12.4	40	51.1 ± 10.5	<0.0001
Height of egg mass	25	76.6 ± 15.3	90[3]	47.8 ± 10.5	<0.0001
Length of opposite leaf	16	10.2 ± 1.9	65[3]	7.4 ± 1.5	<0.03
Width of opposite leaf	16	3.0 ± 0.8	65[3]	3.1 ± 1.8	>0.7

[1]No significant between-year differences occurred in any of these variables (P > 0.1 in each Kruskal-Wallis Test)

[2]Difference between flowering and non-flowering stems; one-tailed Wilcoxon two-sample tests

[3]Includes 50 nests on caged, non-flowering stems. These nests were included since they did not differ from those of free-ranging individuals in height of stem (P > 0.7). Neither did they differ in height of egg mass (P > 0.9), length of opposite leaf (P > 0.4), and width of opposite leaf (P > 0.4) (Wilcoxon two-sample tests).

Table 3.—Leaf choice of *Misumena vatia* for nest sites on common milkweed.

Category	Size of sample of leaves in clone[1]		Size of leaves used by spiders		P (Wilcoxon two-sample test)
	N	$\bar{x} \pm$ SD (cm)	N	$\bar{x} \pm$ SD (cm)	
Flowering stems, length	124	14.2 ± 2.2	16	10.2 ± 1.9	<0.0001
Flowering stems, width	124	5.3 ± 1.9	16	3.0 ± 0.8	<0.0001
Non-flowering stems, length	135	11.7 ± 4.1	65[2]	7.4 ± 1.5	<0.0001
Non-flowering stems, width	135	4.5 ± 1.9	65[2]	3.1 ± 1.8	<0.0001

[1]Mean length and width of leaves from 15 randomly-chosen flowering stems and 15 randomly-chosen non-flowering stems. Leaves are paired: only one leaf of a pair, randomly selected, was measured. Some of the lower leaves had fallen from flowering stems by the time spiders laid their eggs.

[2]Includes 50 nests on caged, non-flowering stems. These nests were included since they did not differ from those of free-ranging individuals in height of stem (P > 0.7). Neither did they differ in length of opposite leaf (P > 0.4) or width of opposite leaf (P > 0.4). (Wilcoxon two-sample tests).

leaves on flowering stems than on non-flowering stems; however, these leaves were not wider than those used on non-flowering stems (Table 2). This result suggests that leaf width is a more important factor than leaf length in determining leaf choice.

I observed three spiders unsuccessfully attempting to fashion a large leaf into a nest. Each one subsequently used a smaller leaf as a nest site. Although nests in this study were invariably placed on milkweed leaves, no other plants within the study site had leaves or leaflets nearly as large as those routinely used by the spiders. Common forbs and shrubs in the area included cow vetch (*Vicia cracca*), yellow-rattle (*Rhinanthus crista-galli*), goldenrod (*Solidago* spp.), red clover (*Trifolium pratense*), pasture rose (*Rosa carolina*), and meadow-sweet (*Spiraea latifolia*). All were periodically searched carefully for *Misumena* nests.

General description of nests.—On milkweed, *Misumena* initially bent under the distal tip of a leaf, securing it to the under side of this leaf with a few strands of silk. Typically they remained inside the resulting folded leaf for a day or more (2.1 ± 1.6 S.D. days, N = 56 nests censused each morning and evening) before laying their eggs there and completing the nest. However, a few individuals left this site and moved to another site (N = 9), where they subsequently laid their eggs.

Spiders turned under about one-third of a leaf in making a nest on milkweed. In seven nests that I measured, the turned-under tissue averaged 2.7 cm (± 0.3 cm S.D.) in length.

Spiders always laid their eggs at night (N = 122), and by morning had completed the majority of their nest construction. Although I did not observe them exhaustively at night, I saw two different individuals laying eggs, at 23:30 and 01:30, respectively. By the time I observed spiders the following morning (05:30 - 09:00), almost all of them had pulled the distal part of the leaf tightly to the under side of the rest of the leaf (fig. 1). However, in three of 122 instances (2.5%), spiders had not completed this process by morning, and the filmy silk surrounding the egg sac proper remained visible. Spiders that laid their eggs the preceding night had invariably positioned themselves on the under side of the nest by morning (Fig. 1). The three spiders that did not completely close their nests during the first night finished the task on the following night.

Within two to three days several spiders secured their nests with strands of silk to surrounding vegetation. With few exceptions they attached it to an adjacent leaf of the stem bearing the nest, especially the one immediately under the leaf in which the nest was placed. Fig. 1 illustrates a typical pattern. This extra silk increases the stability of the nest, and pulling it closer to the lower leaf may provide the attending female with a hiding place (Fig. 1). However, it also facilitates access to the nest from the flat surface of the leaf below.

Numerous additional lines of silk were often subsequently produced in the immediate vicinity of the nest (Fig. 1). They do not play a major role in stabilizing the nest, but are probably a mere consequence of the attending spider
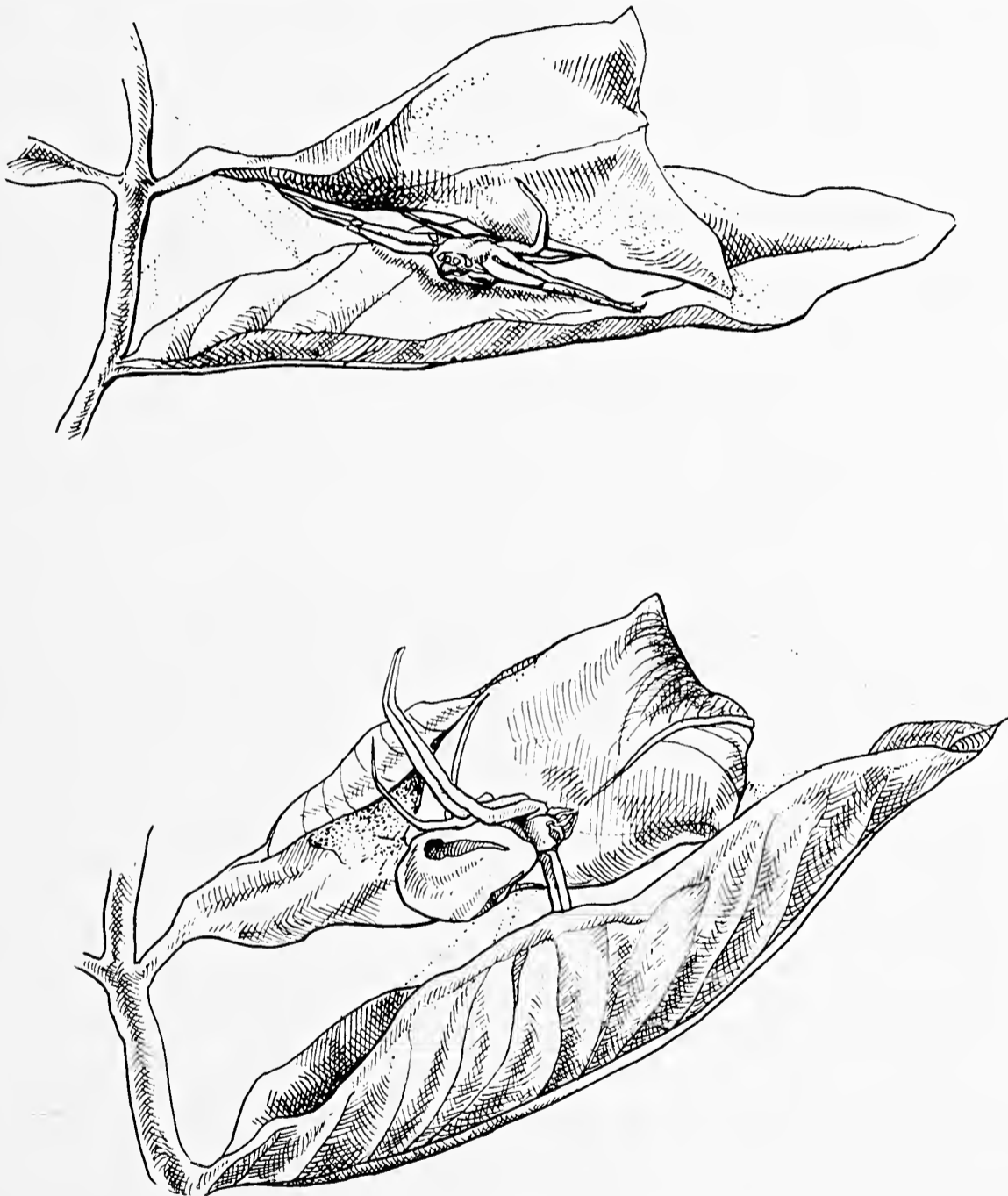
Fig. 1.—Nests of the crab spider *Misumena vatia* on common milkweed. **Upper:** A nest secured by strands of silk (immediately to left of spider's right forelimbs) to the leaf immediately under it, with the postreproductive female attending it in a position often assumed on nests drawn close to other leaves. However, many of the nests are made on leaves that do not grow closely to other leaves, and are therefore not attached to other structures. Strands of silk near the stem are intermittently laid down over the life of the nest and are unlikely to play a major role in stabilizing the nest. **Lower:** Nest rotated 90° to illustrate the position most frequently assumed by *Misumena* while attending nest. This extremely large postreproductive individual was 10 mm long (abdomen + cephalothorax) and weighed 110 mg. Illustrations by Elizabeth Farnsworth.

moving about near the nest. These post-reproductive individuals invariably left lines behind them wherever they moved.

I have occasionally found egg sacs of *Misumena* on other plants. Species used as nest-sites included pasture rose (*Rosa carolina*), spreading dogbane (*Apocynum androsaemifolium*), chokecherry (*Prunus virginiana*), and sensitive fern (*Onoclea sensibilis*).

DISCUSSION

Leaf choice.—Although crab spiders do not select milkweed leaves randomly, the mechanism governing this choice is not explicit. Spiders might either choose the highest leaves possible, or the leaves that provide ideal characteristics for a nest. However, a few data do suggest that leaf characteristics, rather than location, serve as the major basis for selection. Twice I have found spiders using small axillary leaves well down on the stem as nest sites. These leaves, which follow the loss of a main leaf, occur infrequently on milkweeds. They are also often the only medium-sized leaves below the tops of flowering plants. Additionally, individuals that used extremely large leaves experienced difficulty in manipulating them, probably because these leaves were thicker and larger than the ones usually used. All free-ranging individuals subsequently selected medium-sized leaves for nests. Only caged spiders confined to large leaves eventually fashioned nests out of them (Morse, unpubl.). In no instance did spiders using large leaves appose the two parts of the leaf closely, and, consequently, large areas of their nests were protected only by silk, probably making them extremely vulnerable to attack by parasitic insects (see Eason, Peck and Whitcomb (1967).

Problems of nest construction could also account for *Misumena*'s absolute choice of milkweed leaves as nest sites within the study area. Although the sample of free-ranging spiders I studied used milkweed leaves exclusively under natural circumstances, spiders that I confined to cages containing only pasture rose, spreading dogbane, or meadow-sweet fashioned nests of these leaves (Morse, unpubl.). None of these nests incorporated as much leaf material into the covering as did nests on medium-sized milkweed leaves; thus, larger areas were covered only by silk than in typical nests built on milkweed. It would be of interest to determine the spiders' relative preference for these different leaves as a function of the area of the resulting nests covered only by silk, and also as a function of the level of parasitism that such nests would experience. These nests, and nests on large milkweed leaves as well, could also be subject to greater desiccation than tightly-constructed nests. Hatching success of crab spider eggs in nests that I opened soon after laying was significantly lower than that of unmanipulated eggs (Morse, in prep.).

Movement to nest site.—The movement of spiders from their last hunting site, despite a mobility that was often inadequate to reach a different habitat, suggests a strong selective pressure for leaving the hunting site. Moving may minimize vulnerability to egg parasites. Egg parasitism by an ichneumonid wasp (*Trychosis cyperia*) and a phorid fly (*Megaselia* sp.) was relatively constant between 1980 and 1984, averaging about 15% per year (Morse and Fritz, in press). Simply moving away from the previously-used site might on average be advantageous. Moving is unlikely to bring a spider into a yet higher density of flowering stems

and other spiders, and possibly higher concentrations of parasites, and it could take the spider to an area of lower density.

However, because some individuals moved much greater distances than the mean distance between the last hunting site and the nest site, conflicting pressures, rather than absolute mobility, may constrain the length of their move. Dangers to the adults may be played off against those associated with egg parasitism and egg predation. I do not have quantitative data on spider mortality at this time, but because relatively long movements require descending into the grass year, spiders may become vulnerable to predators unlikely to disturb them on the milkweed stems. Two likely predators sometimes common in the study area are the meadow vole (*Microtus pennsylvanicus*) and the garter snake (*Thamnophis sirtalis*). Both species regularly prey on arthropods (Zimmerman 1965; Hamilton 1951). Further, during the one year of this study in which a *Microtus* outbreak occurred, twice as many spiders disappeared after leaving their last hunting site, not to be found again, than in any other year (Morse, unpubl.)

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RESEARCH NOTE

SUBMERGENT CAPTURE OF *DOLOMEDES TRITON* (ARANEAE, PISAURIDAE) BY *ANOPLIUS DEPRESSIPES* (HYMENOPTERA, POMPILIDAE)

Wasps of the family Pompilidae prey exclusively on spiders (Evans and Yoshimoto 1962). Female pompilids generally paralyze their prey and transport it to a nest before laying a single egg on the spider. One North American member of this family that is distinguished by its unusual mode of prey transport is *Anoplius depressipes* Banks. This species is the only non-parasitic, aquatic wasp in North America (Hagen 1978). Evans (1949) accumulated several fragmentary published and unpublished observations that he attributed to this species and concluded that *A. depressipes* transports its prey across the surface film of the water and is capable of crawling into the water and running on the bottom. The only known prey of *A. depressipes* are adult female fishing spiders of the genus *Dolomedes* (Evans 1949, Evans and Yoshimoto 1962, Kurczewski and Kurczewski 1968). These spiders are capable of diving into the water and remaining submerged for more than 30 min (Carico 1973). It has remained unknown whether *A. depressipes* ever stings *Dolomedes* spiders underwater before transporting them to its nest (Hagen 1978). Despite statements by McCafferty (1981) implying submergent prey capture by *A. depressipes,* there are no published accounts confirming this type of behavior.

The purpose of this note is to record an instance of submergent prey capture by *A. depressipes* that I observed at a small, artificial pond on Powdermill Nature Reserve, 3 km S of Rector, Westmoreland County, Pennsylvania. At approximately 1425 h on 1 August 1983, I noticed a large female *Dolomedes triton* on the water surface about 1 m from the shoreline. My attention was drawn to this spider initially because its behavior seemed peculiar. It dove below the surface and held onto a submerged plant stem for no apparent reason. In retrospect, I believe that the spider had detected the presence of a nearby *A. depressipes.* The spider resurfaced within a minute or two. During the following minute I observed a pompilid wasp (later identified as *A. depressipes*) fly toward the spider from farther out over the pond. The spider undoubtedly saw the wasp, because it ran rapidly away from the wasp along the water surface for about 25 cm before diving again. This time the spider stopped amongst denser vegetation (*Potamogeton* sp.) at a depth of 15-20 cm, near the bottom of the pond. The wasp followed the spider into the water 2-3 sec later and did not seem to slow down as it broke the surface (at the same point where the spider dove). The wasp swam down on an angle directly toward the spider and stung it within 5 sec. The spider attempted to evade the wasp a second time before being stung, but barely managed to start its legs in motion, and did not progress more than 2 cm. The

wasp and paralyzed spider reappeared at the surface within 2 sec of the attack. The wasp then proceeded to drag the spider across the surface film as it flew toward an inactive muskrat (*Ondatra zibethicus*) burrow in the bank. I interrupted this behavior on several occasions as the wasp approached the shoreline in an effort to capture it. The wasp flew away each time but returned to its victim within a few minutes, and eventually was allowed to resume its behavior without further disturbance. The wasp transported the spider across the water surface a total distance of about 2 m from where the attack occurred to a point along the shoreline even with the burrow entrance. The wasp then dragged the spider backwards (by biting a hind leg) another 20 cm across grassy vegetation, mud and an exposed root, up and into the burrow, where it disappeared from sight at 1436 h. I captured the wasp at the burrow on the following afternoon, but was unable to locate the spider despite a 15 min search of the emergent portion of the burrow's interior.

Subsequently, on both 16 and 19 August 1983, I observed several large, black pompilids (presumably *A. depressipes*) walking on floating water lily (*Nymphaea odorata*) leaves in two nearby ponds. These wasps seemed to be actively searching for *Dolomedes* spiders hiding inside curled-up water lily leaves, because they moved systematically from leaf to leaf, peering into those that were curled up. At 1851 h on 29 July 1985 I observed another *A. depressipes* dragging a paralyzed *D. triton* female across the water surface. Both specimens were collected as the wasp approached the opening of a partially submerged plastic drainage pipe.

I thank Howard E. Evans for verifying the identity of the initial wasp, and James E. Carico, William G. Eberhard, Howard E. Evans and C. J. McCoy for reviewing the manuscript. All specimens have been deposited in the entomological collection of Carnegie Museum of Natural History. These observations were made while I was engaged in research supported by the M. Graham Netting Research Fund of Carnegie Museum of Natural History.

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A HAWAIIAN WOLF SPIDER, *LYCOSA HAWAIIENSIS* SIMON FORAGING IN THE TOP OF A *METROSIDEROS POLYMORPHA* TREE

Of the lycosid spiders, most *Lycosa* species are ground dwellers (e.g., Dondale et al. 1971, Turnbull 1973, Bixler 1970). However, *Lycosa rabida* and *L. punctatum* have been found in vegetation (Kaston 1948, Barnes 1953, Whitcomb et al. 1963) and *L. rabida* has been noted on the lower branches of trees (Kuenzler 1958).

Several endemic Hawaiian species of *Lycosa* (see Simon 1900, Suman 1964, Gertsch 1973) are abundant in subalpine, alpine and aeolian zones of Hawai'i's highest mountains, and in aeolian habitats on fresh lava flows on the geologically active island of Hawai'i (Howarth 1979, Howarth and Montgomery 1980). Very little is known of their ecology and behavior. Their presence in barren lava regions is maintained by windborne prey transported onto the flows from adjacent vegetated areas. I have observed *Lycosa* on 'a'a lava flows at and above treeline on the island of Maui. Typically, the spiders forage at ground level, but may perch upon higher vantage points such as lava boulders and outcrops. I had never previously observed the spiders in low native shrubs nor collected them by sweeping vegetation.

On 1 September 1982, 14:54 h, at 1700 m elev. in the Ko'olau Gap of Haleakala on the island of Maui, a mature female *Lycosa hawaiiensis* Simon (c. 2.75 cm body length) was observed stationed upon the apical tips of a *Metrosideros polymorpha* tree (c. 2.4 m in ht.). The predominant vegetation was subalpine scrub near the upper limit of *Metrosideros* in the gap. The nearest neighboring tree was about 175 m away. Surrounding the tree were low, endemic, xerophytic plants (*Vaccinium, Coprosma, Deschampsia, Styphelia,* etc.), growing on largely unweathered 'a'a lava and cinder. The weather was mostly clear, with convectional winds moving up the gap from the northeast, 5-10 knots. The broken, rocky terrain provided habitat for an abundant *Lycosa* population. The spiders were commonly seen running upon crags and between clinker. The arboreal spider was collected after observations of her behavior and found to be the same species as those seen on the ground.

The atypical location of the adult female spider above the substrate and in the apical branches of a lone tree seemed unusual, so I stopped and observed her behavior for about 15 minutes. The spider was perched at the terminal growth of leaves, near several senescing inflorescences (about 35 cm from the nearest cluster). The spider's posterior three pairs of legs were clutched firmly upon the apical leaf buds of the tree, which swayed about occasionally in the wind. The front pair of legs were held free. The spider was motionless when first spotted, but soon after observations began, several large sarcophagid flies arrived and flew about the terminal branches of the tree in the vicinity of the inflorescences. When the flies passed close to the spider, she darted after them, but failed to capture any. I presented the knob-like end of a flowerstalk of the composite week, *Hypochaeris radicata,* to the spider, and waved the flower bud close to her face. The spider immediately lunged and grasped the bud in her chelicerae. Her grip was tenacious enough so that she retained hold on the stalk when I released it.

It was clear that the spider was foraging in the tree, and had not been on the terminal branchtips by chance. Vegetational perching is seen frequently among

the Thomisidae and Oxyopidae, and to a lesser extent, among the Salticidae. Thomisids and salticids were represented in the area, but perhaps due to the more open nature of the subalpine setting, lycosids were by far the most abundant arachnids in the vicinity. Since the majority of the lycosid spiders seen at the site were encountered on the ground, I initially suspected that the tree-inhabiting individual was senescing or showing aberrant behavior. However, its vigorous pursuit of flying insects and ready attack at a proferred object suggest otherwise.

Although previous surveys of canopy arthropods in Hawai'i have not encountered lycosid spiders (Gagne 1979), observation of a female lycosid on *Dubuatia menziesii* (a sturdy, compact-leaved alpine shrub) in Haleakala (Gagne pers. comm.) suggests that venturing upon vegetation during foraging activities may not be unusual among the subalpine *Lycosa* in Hawai'i. Further observations are needed to clarify this point.

I wish to acknowledge critical comments on the manuscript by Wayne Gagne and Francis Howarth of the Bernice Pauahi Bishop Museum, Department of Entomology, Willis J. Gertsch in Portal, Arizona, and Phil S. Ward of the University of California, Davis Entomology Department. Lawrence W. Pinter kindly made the species determination of the voucher specimen (in the Bernice Pauahi Bishop Museum).

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ADHESIVE TECHNIQUE FOR CAPTURE
OF BURROW-DWELLING SPIDERS

The suitability of *Geolycosa* spp. for field studies has been recognized and exploited in investigations of demography, wasp predation, activity patterns, metabolism and thermoregulation (Humphreys 1974, 1975a, 1975b, 1978; Gwynne 1979; McQueen 1978, 1979, 1980, 1983; McQueen and Culik 1981). Adult spiders of this group inhabit tubular burrows which extend straight down 20-40 cm, terminating in a slightly enlarged side chamber at the bottom. Humphreys (1974) employed traps to capture *G. godeffroyi* (L. Koch), but noted less than 100% success in all populations studied. McQueen (1978) experimented with numerous capture techniques for *G. domifex* (Hancock) ((= *G. missouriensis* (Wallace 1942)) and resorted to use of a medical otoscope for monitoring burrow occupants.

During an experimental field study of *Geolycosa rafaelana* (Ch.), I developed a technique for capture of adults without damage to the spider or its burrow. The capture device employed adhesive strips cut from the inner surface of Raid Roach Traps (© 1980, S. C. Johnson and Son, Inc.). The adhesive was wrapped around the end of a paper clip, which was suspended into the burrow with string. A termite or ant was placed on the adhesive as bait, stimulating the spider to grasp with its chelicerae, and thereby becoming firmly embedded in the adhesive. Following extraction from the burrow, the spider was released by brushing a drop of corn cooking oil against the adhesive surface.

This technique was used to capture more than 150 adult spiders for marking and release during a two year period. Capture success was 100% except during April-May, when females bearing egg cases were unreceptive to capture, and would actively extrude the device from their burrows. Commercial adhesive for trapping insects (Tangle-Trap) was found to be too thin for effectively embedding the spider's chelicerae. Passive traps employing adhesive strips placed within the burrow entrance succeeded in snaring some individuals by one or more legs, but leg loss (and resultant escape of spider) occurred when the strip was removed from the burrow.

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FUNCTIONAL WEBS BUILT BY ADULT MALE
BOWL AND DOILY SPIDERS

It is generally accepted in the arachnological literature that adult female web-building spiders build species-typical webs while adult males do no web-building other than that required for courtship and sperm induction (e.g. Savory 1928, Opell 1982), though there is at least one published report that adult male uloborid spiders sometimes construct webs (Eberhard 1977). Immature bowl and doily spiders (*Frontinella pyramitela,* Linyphiidae) of both sexes as well as adult females have long been known to build relatively complex sheet webs consisting of a bowl-shaped horizontal sheet, an underlying flat sheet (the doily), and a barrier meshwork of silk that is above the bowl and doily.

We observed web-building by adult males while we were investigating the behavioral effects of the chemical constituents of webs built by *F. pyramitela* (Suter and Hirscheimer in press). In the course of those studies, we collected spiders of all ages and both sexes from webs in Poughkeepsie and Millbrook, New York, during May and June 1984. In the laboratory, the spiders were placed on glass or wooden hexapods in 3.8 l plastic jars where each could build a web (for details of techniques, see Suter 1985). Usually within a day or two after a spider built a web, the spider was removed from the web and placed on a new hexapod, and the web was stored for subsequent testing. All spiders were maintained in the laboratory on a diet of fruit flies (*Drosophila melanogaster*).

We recorded the data of construction of all webs and the molt dates of every individual spider. These data allowed us to determine the last day on which male

spiders definitely could build webs. It did not enable us to determine what the first day was on which they could not build webs. These two measures might well have been different, since a spider may not have built a web on a given day though he still had the capability to do so. Our method of measurement, the last day on which males definitely could build webs, is actually the more conservative of the two, and indeed male spiders may have had the ability to build webs on several subsequent days.

Of the six immature males that reached maturity in the laboratory, two never built species-typical webs as adults. Instead they built rudimentary platforms that consisted of a diffuse and very small (1-3 cm diameter) horizontal sheet supported by a few strands of silk below. These structures resembled crude versions of the normal "doily." Each of the remaining four adult males built a fully functional and structurally complete species-typical web soon after the final molt. One male, brought into the laboratory as an adult, also built functional and species-typical webs. The last day on which we could ascertain that adult males built species-typical webs ranged from 2 to 7 days after the final molt (Table 1). The last web built by each male tended to be truncated (i.e. the bowl was relatively flat and the vertical dimension of the entire web was reduced relative to the heights of webs constructed by adult females and juveniles), but still had an identifiable "bowl" and "doily." These webs were as functional as those of other sex and age classes in that prey items could still be captured on them.

Because adult males of this species emerge in the spring at the same time as females (Suter 1985), adult males are not dependent upon their own web-building abilities to capture food. During most of their active adult lives, males make use of females' webs for predation. This is rare among spiders because in most species the males take no food during adulthood (Bristowe 1985). Male bowl and doily spiders feed frequently while cohabiting on females' webs and capture about 37% of the prey that hit the web despite competitive activities of the females (Süter 1985). Of what benefit then, might it be to adult males to expend energy and nutrients in building webs when they could expend the same resources in search of females?

When a male comes upon a female's web that already has a resident male on it, the two males engage in an an agonistic interaction which the larger (heavier) male wins most of the time (Austad 1983, Suter and Keiley 1984). And when a male comes upon a female's web with no resident male on it, the male's size will likewise determine the outcome of contests with subsequent intruder males. Thus male size is probably closely tied to male reproductive success and it will be advantageous to adult males to be as large as possible when leaving their own

Table 1.—Construction of functional webs by adult male spiders.

Spider	Date of final molt	Adult age (days) when last web was built
1	5/26	7
2	5/28	3
3	5/30	6
4	5/31	2
5	*	>5

*Captured as an adult on 5/14.

webs. Because the mass of a spider, one measure of size, is directly related to the amount of food that it consumes, a male may benefit by trying to capture as many prey as he can for as long as he can, before setting off to find females.

According to Austad (1982), first male sperm priority is operative in bowl and doily spiders; that is, the first male to inseminate a given female will fertilize about 90% of her eggs. Finding virgin females, then, is crucial to the reproductive success of a male, and any delay in beginning the search reduces the probability that the male will find a virgin female.

Thus males have to weigh the benefits of capturing more prey against the costs of delaying their search for unmated females. The optimum behavior for a male depends upon at least three variables: nutritional status, season, and size. The spider's nutritional status determines what his energy reserves are and therefore how long he can spend searching for females before starving. The time of year is an important variable because the intensity of intermale competition varies with male and virgin female densities which vary seasonally (Suter 1985). And size is important because it is the primary determinant of male success in intermale agonistic interactions. [Size can be measured both as lengths of body parts and as mass. The latter is a good predictor of the outcome of intermale interactions in bowl and doily spiders (Suter and Keiley 1984)].

Therefore, if a male were small at maturity, early encounters with females might prove futile because of competition with other males, and the addition of mass would be advantageous. In contrast, if the male were large, additional mass might be far less advantageous than early encounters with females. This putative relationship between mass at maturity and cessation of male web-building is easily tested. We plan to test the relationship during the 1985 season.

We thank William Eberhard and Steven Austad for their helpful reviews of this manuscript.

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ON THE CHILEAN SPIDERS OF THE FAMILY
PALPIMANIDAE (ARACHNIDA, ARANEAE)

Only two species of palpimanid spiders have previously been recorded from Chile. *Anisaedus pellucidas* Platnick is known only from Antofagasta and Atacama provinces in northern Chile, and (judging by the presence of a translucent embolar flange) seems most closely related to *Anisaedus rufus* (Tullgren) of northwestern Argentina (Platnick, N. I. 1975. Amer. Mus. Novit., 2562:1-32). Two localities can now be added to the only previous records of *A. pellucidas* from Atacama province (Platnick, N. I. 1977. J. Arachnol., 3:203-205): 40 km S Copiapó (700 m), 23-25 October 1983 (L. E. Peña G.), 1 male, and between El Tránsito and Pinte (1100-1600 m), 25-27 October 1980 (L. E. Peña G.), 1 male, 1 female, all in the American Museum of Natural History (AMNH).

The second species, *Otiothops lanus* Platnick, is known only from the Quebrada de la Plata in Santiago province. It differs from all other previously known *Otiothops* in having relatively small posterior median eyes separated by almost twice their diameter; this discrepancy was perhaps responsible for the original description of the species as a *Fernandezina* (Zapfe, H. 1961. Invest. Zool. Chilenas, 7:141-144). It was of particular interest, therefore, to discover (among material recently sent to the AMNH by Dr. Luis E. Peña G.) a male of a second Chilean species of *Otiothops* from Maule province. The new species resembles *O. lanus,* rather than other *Otiothops,* in eye pattern. Although
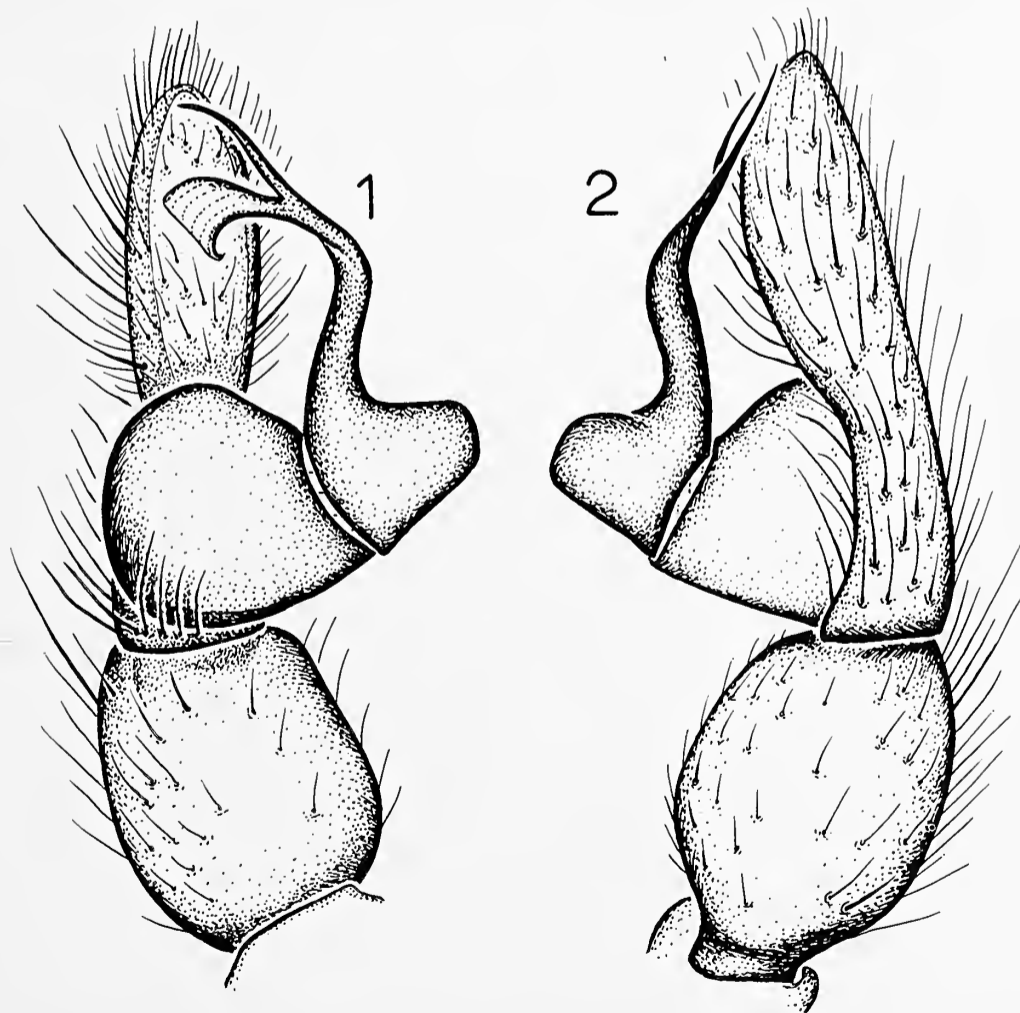
Figs. 1, 2.—Left male palp of *Otiothops maulensis:* 1, ventral view; 2, retrolateral view.

outgroup comparison with the Stenochilidae indicates that the separated posterior median eyes are plesiomorphic, the distolaterally originating and distally bifid embolus suggests that the new taxon is indeed the sister species of *O. lanus*.

Otiothops maulensis, new species
Figs. 1, 2

Type.—Male holotype from W of Cauquenes, Maule, Chile (May 1984, L. Irarrazaval), deposited in AMNH.

Etymology.—The specific name refers to the type locality.

Diagnosis.—Males can be distinguished from those of all other *Otiothops* except *O. lanus* by the widely separated posterior median eyes, and from those of *O. lanus* by the proximally bulging embolus (Figs. 1, 2).

Male.—Total length 3.28 mm. Carapace 1.55 mm long, 1.15 mm wide. Femur I 1.19 mm long, 0.54 mm wide. Cephalic area moderately elevated. Posterior median eyes separated by twice their diameter. Abdomen with scattered brownish purple patches on pale brown background. Claw tufts reduced to few setae surrounding onychium. Palp with globose tibia, long narrow cymbium, and retrolaterally prolonged bulb almost entirely occupied by reservoir. Embolus originating retrolaterally near tip of bulb, distally bifid, with proximal lobe translucent, distal lobe sharply pointed (Figs. 1, 2).

Female.—Unknown.

Material Examined.—Only the holotype.

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LABORATORY INFECTION OF *GARYPUS CALIFORNICUS* (PSEUDOSCORPIONIDA, GARYPIDAE) WITH NEOAPLECTANID AND HETERORHABDITID NEMATODES (RHABDITOIDEA)

Entomogenous nematodes of the genera *Neoaplectana* and *Heterorhabditis* are being commercially produced as biological control agents for use against a variety of insect pests (Poinar, Jr., G. O. 1983. Proc. Tenth Int. Congr. Plant Prot. 2:751-758). Tests are being conducted to examine the ability of these nematodes to infect non-insect representatives of the Arthropoda. The present study was conducted to determine if members of these nematode genera could infect representatives of the Pseudoscorpionida under laboratory conditions.

The nematodes used in this study were the 42 strain of *Neoaplectana carpocapsae* Weiser and the NC strain of *Heterorhabditis heliothidis* (Khan, Brooks, and Hirschmann) which had been reared on wax moth larvae in the laboratory.
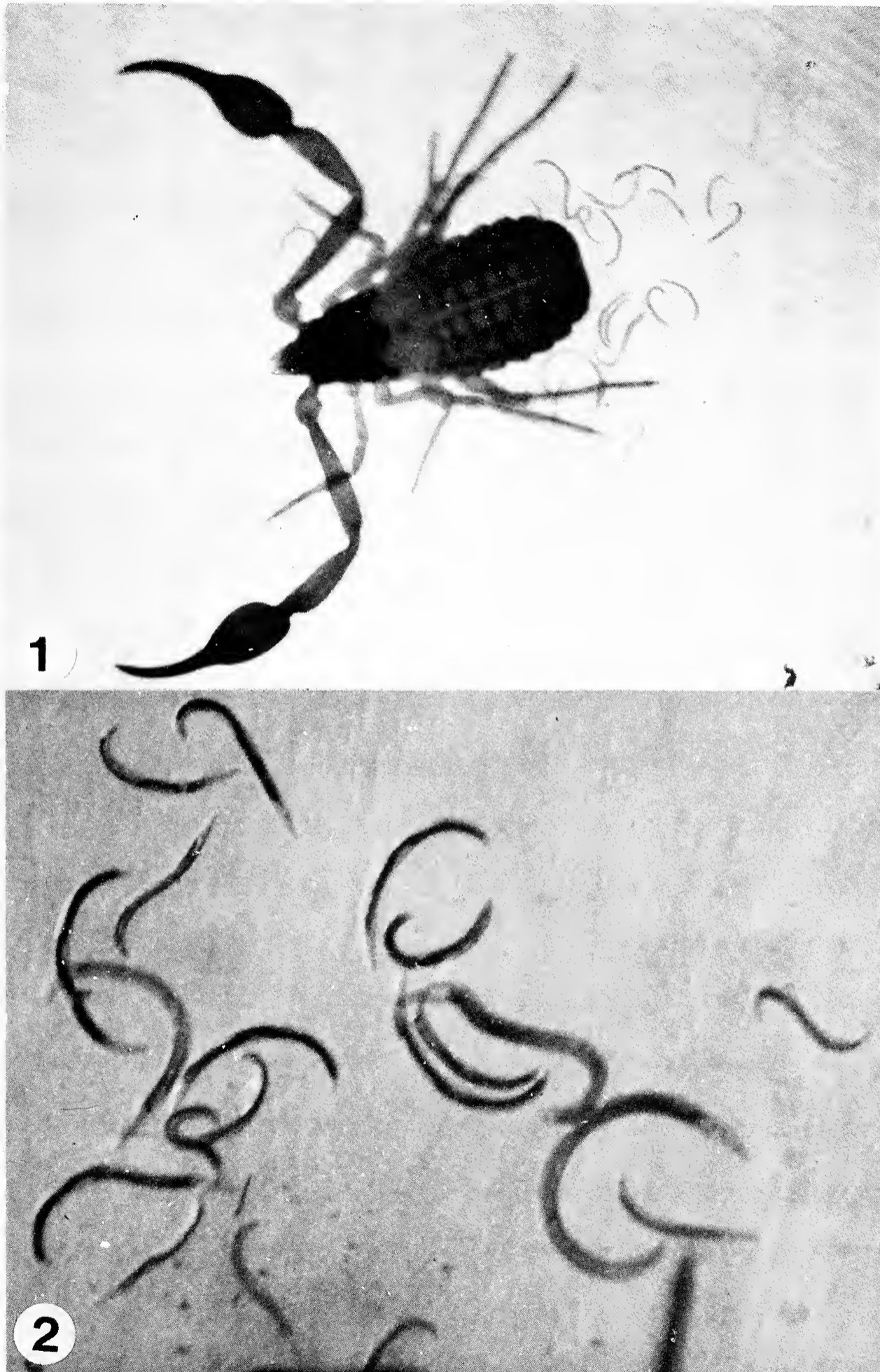

Fig. 1.—An adult *G. californicus* killed by *N. carpocapsae.* Mature nematodes removed form the pseudoscorpion surround the abdomen of the dead host.

Fig. 2.—Adults of *N. carpocapsae* removed from the abdomen of an infected *G. californicus.*

Specimens of the pseudoscorpion *Garypus californicus* Banks were collected at Bolinas Point, California, on September 23, 1984. They were brought to the laboratory and placed individually in 5 cm diameter petri dishes lined with a filter paper disc which had an area of 18.1 cm². One cc of infective stage nematodes in water was added to the filter paper in each dish. This resulted in 12 x 10⁴ nematodes/dish for *N. carpocapsae* and 11 x 10⁴ nematodes/dish for *H. heliothidis*. Ten *G. californicus* were placed in dishes containing *N. carpocapsae:* eight were challenged with *H. heliothidis* and four served as controls. Control dishes had 1 cc of water only added to the filter paper and were maintained similar to the treatments. A small piece of cotton gauze was placed in each dish as a refuge for the pseudoscorpion, and adult *Drosophila* were added as a source of food. The experiments were run at room temperature and extended for one week.

At the time of death, a drop of hemolymph was removed from the pseudoscorpion and plated out on a culture plate of Tergitol 7 agar plus TTC (triphenyltetrazolium chloride). The symbiotic bacteria (*Xenorhabdus* spp.) carried by the nematodes produce a characteristic color reaction on this medium. The presence of the bacterium in a host's hemolymph indicates that the nematodes were able to infect and enter the body cavity of the host. Dissections were performed at regular intervals after the pseudoscorpions died in order to follow nematode development.

By the end of the second day after initial contact, all treated hosts were dead. The control specimens remained alive for the duration of the experiment. Samples of hemolymph removed from the dead hosts revealed the presence of the nematodes' symbiotic bacteria (*Xenorhabdus* spp.).

The nematodes developed to the adult stage and produced progeny inside the dead pseudoscorpions (Figs. 1 and 2). However, foreign bacteria rapidly entered the host cadavers and greatly lessened the conditions for nematode development. As a result, few infective stages were produced.

This is the first report describing the ability of neoaplectanid and heterorhabditid nematodes to infect pseudoscorpions. It indicates that these nematodes are not as restricted in their parasitic habits as originally thought.

The present results show that *G. californicus* is highly susceptible to these nematodes under laboratory conditions with all deaths occurring 1-2 days after initial contact. However, this arachnid is a poor developmental host since bacteria associated with the host enter the cadaver and inhibit establishment of the nematode's symbiotic bacteria which are required for parasite multiplication.

In a program involving the placement of these nematodes on the soil surface of agricultural or horticultural land (Poinar, 1983, op. cit.), most pseudoscorpions would avoid contact with the parasites by the cryptic nature of their physical habitats (e.g. under bark of trees, in moss, under debris on the beach, etc.).

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AN UNUSUAL SPECIES OF *TYRANNOCHTHONIUS*
FROM FLORIDA (PSEUDOSCORPIONIDA, CHTHONIIDAE)

The genus *Tyrannochthonius* is tropicopolitan in distribution, including tropical America (Hoff 1959, Mahnert 1979, Muchmore 1973, 1977); and though it has long been known to occur in the United States (Chamberlin and Malcolm 1960), no U.S. species has ever been described. Now with our increasing interest in and knowledge of West Indian species (Muchmore 1984, 1986), it seems appropriate to describe a unique epigean form from Florida and Alabama.

Nearly 40 years ago J. C. Chamberlin recognized as new two individuals of *Tyrannochthonius* found in northwestern Florida. He began a description of the form but, unfortunately, never completed and published it; an illustration of the palp was published, without a name, by Chamberlin and Malcolm (1960: Fig. 1A). Later, as part of a broad survey of the American species of *Tyrannochthonius*, the senior author restudied Chamberlin's specimens and expanded the description. More recently the junior author has received and studied new material from Florida and Alabama and has brought the description to its final form.

Tyrannochthonius floridensis, new species
Figs. 1-4

Material.—Holotype male (WM1664.01004) and 20 paratypes (6 males, 8 females, 6 nymphs) from litter in a sinkhole 3 mi. NW Marianna, Jackson County, Florida, 8 September 1968, S. Peck; one paratype male from Florida Caverns State Park, Jackson County, Florida, 9 September 1968, S. Peck; 2 paratypes (1 male, 1 female) from Rock Bluff, Liberty County, Florida, 27 April 1927, [T. H.] Hubbell; one paratype male from Moundville State Park, Moundville, Hale County, Alabama, 7 July 1967, S. Peck and A. Fiske. All types are in the Florida State Collection of Arthropods, Gainesville, except those from Rock Bluff, which are in the Cornell University Insect Collection, Ithaca, NY.

Diagnosis.—A small, epigean species of *Tyrannochthonius* characterized by the presence (usually) of a small seta at the base of the apical projection of the coxa of leg I, and the absence (usually) of a preocular dwarf seta on the carapace; tergites 1-4 each with 4 setae and tergites 5-8 each with 6 setae.

Description (based mainly on 12 mounted specimens).—Male and female very similar, though female usually a little larger and with slightly more robust palps. Carapace subquadrate; epistome a low, rounded lobule, barely evident between the 2 median setae (Fig. 1); with 4 conspicuous, corneate eyes; chaetotaxy usually 4-4-4-2-2, though two paratypes have a single preocular dwarf seta on one side or the other. Coxa I with a broad, rounded apical projection, which usually bears a small seta (m) at its base mesially (Fig. 2); complete coxal chaetotaxy 2-2-1:m-3-0:2-1or2-CS:2-3:2-3; each coxa II with an oblique row of 6-10 terminally incised spines (CS).

Abdomen typical. Tergal chaetotaxy of holotype 4:4:4:4:6:6:6:6:7:4:T2T:0; others similar. Sternal chaetotaxy of holotype (male) 10:[4-4]:(3)13-12/6(3):(3)6(3):8:8:8:8:8:9:0:2; other males similar; female usually 10:(3)6(3):(3)6(3):-.
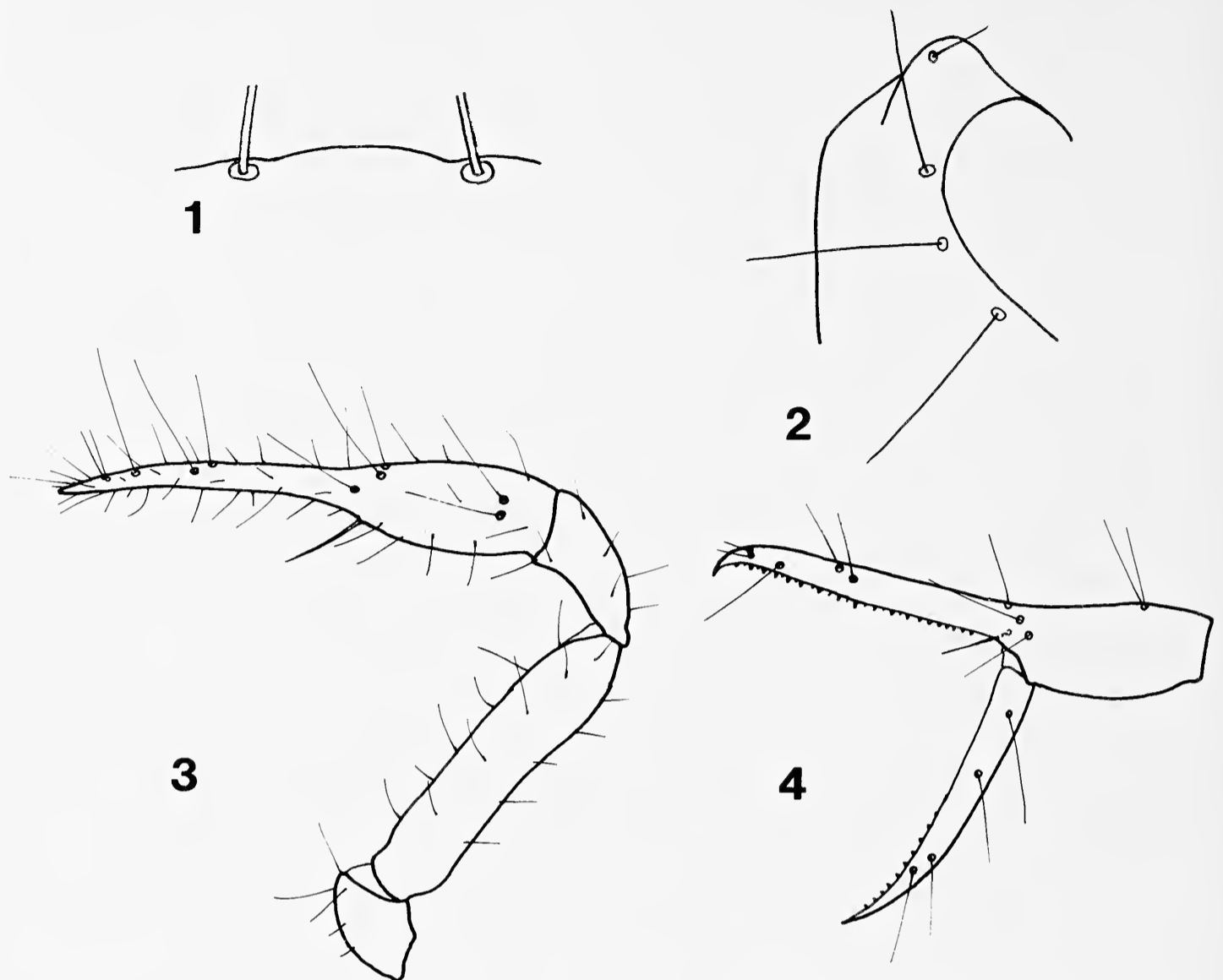
Figs. 1-4.—*Tyrannochthonius floridensis,* new species: 1, epistome and flanking setae on anterior margin of carapace; 2, anteromedial part of left coxa I, showing apical projection and setae; 3, dorsal view of right palp; 4, lateral view of left chela.

Chelicera about ¾ as long as carapace; hand with 5 setae; flagellum of 6-7 irregularly pinnate setae; fixed finger with one large distal tooth followed proximally by 7-9 much smaller teeth; movable finger with about 15 small teeth; galea a low elevation in both sexes.

Palp as shown in Fig. 3; femur 4.4-4.6, tibia 1.8-1.95, and chela 4.65-5.45 times as long as broad; hand 1.7-2.0 times as long as deep; movable finger 1.6-1.85 times as long as hand. Trichobothria as shown in Fig. 4; on movable finger *sb* distinctly nearer to *b* than to *st*. Hand with one heavy spinelike seta on medial side near base of fingers. Fixed finger with 16-20 widely spaced, prominent macrodenticles and 12-16 microdenticles interspersed distally; movable finger with 7-10 macrodenticles distally and 6-9 interspersed microdenticles, and 8-10 very low, rounded teeth basally. Sensillum at dental margin, usually nearer to trichobothrium *st* than to *sb*.

Legs typical: leg IV with entire femur 2.25-2.5 and tibia 4.1-4.55 times as long as deep; a prominent tactile seta on the proximal third of telotarsus IV.

Measurements (mm).—Figures given first for the holotype followed in parentheses by ranges of the 11 mounted paratypes. Body length 1.31 (1.00-1.40). Carapace length 0.39(0.335-0.445). Chelicera 0.29(0.26-0.325) long. Palpal femur 0.415(0.375-0.465) by 0.085(0.08-0.105); tibia 0.185(0.17-0.205) by 0.095(0.085-0.11); chela 0.60(0.53-0.69) by 0.11(0.11-0.14); hand 0.22(0.20-0.26) by

0.115(0.105-0.15); movable finger 0.375(0.355-0.43) long. Leg IV: entire femur 0.385(0.355-0.42) by 0.155(0.155-0.18); tibia 0.28(0.245-0.31) by 0.065(0.06-0.07); metatarsus 0.13(0.115-0.15) by 0.05(0.045-0.055); telotarsus 0.26(0.23-0.295) by 0.035(0.03-0.04).

Etymology.—The name originally selected by J. C. Chamberlin is retained, *floridensis* referring to Florida where the first specimens were found.

Remarks.—*T. floridensis* is apparently unique in the genus in having a small seta on the apical projection of coxa I. Such a seta (sometimes 2 or 3) is regularly present in many chthoniid genera, but not in *Tyrannochthonius* or the related *Lagynochthonius* and *Paraliochthonius* (cf. Muchmore 1984, 1986). It remains to be seen whether its occurrence is of any phylogenetic significance.

In addition, *T. floridensis* is unusual in having the epistome very low, broad, and rounded. The usual form of the epistome in epigean species of *Tyrannochthonius* is distinctly triangular, closely flanked by 2 setae (cf. Muchmore 1984). Some cavernicolous species of the genus have low, rounded epistomes (unpublished observations), but in few if any are they as insignificant as in *T. floridensis*.

We acknowledge the first recognition of the species by the late J. C. Chamberlin and are greatly indebted to S. B. Peck for providing the more recent material.

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EFFECTS OF METHOD AND TIME OF PRESERVATION ON VOLUMETRIC MASS ESTIMATES OF SPIDERS (ARANEAE)

Various techniques have been used to back-estimate the live masses (i.e. the masses prior to killing and preservation) of preserved spiders (see Hagstrum 1971, Rogers et al. 1977, and Greenstone et al. 1985a, for literature reviews). We have recently described a technique in which live masses were regressed on an estimate of volume derived by treating the specimen as a cylindrical solid of uniform density having height equal to total length and diameter equal to the mean of greatest widths of the carapace and abdomen. A regression containing such data for 101 animals of the families Lycosidae, Salticidae, Araneidae, Oxyopidae, and Thomisidae explained 95.7% of the variation in mass and was superior to traditional methods using total length or carapace width rather than volume as the estimator (Greenstone et al. 1985a).

Although the technique employed spiders which were preserved directly in 70% ethanol, it was intended for estimating live masses of spiders which had been sticky-trapped using the adhesive Tack Trap™(Animal Repellents Inc., Griffin, Georgia). Such specimens must be soaked for four days each in paint thinner and toluene before final preservation in 70% ethanol. This series of solvent changes could conceivably affect their shape and size and, hence, volume estimate. In order to determine whether the volume-mass regression would be different using animals trapped in this fashion, and also to determine whether the time since preservation affects the regression of mass on the volume estimate, we performed the following experiment.

On June 12, 1984, we collected spiders by sweeping in native tall grass prairie at the Tucker Prairie Preserve, 27 km east of Columbia in Callaway Co., Missouri. In order to minimize variability only araneids were used. The animals were returned alive to the laboratory and weighed on a Mettler AE 160 electronic balance. Following this they were ranked from lowest to highest mass and then assigned serially and alternately to either of two treatment groups to ensure that both groups covered approximately the same range in masses. The first group (hereinafter referred to as "direct-ethanol") was preserved directly in 70% ethanol. The second (hereinafter "sticky-trapped") was placed on a previously prepared 12.7 mm (½") mesh hardware cloth sticky trap (Greenstone 1985b) with the exact location of each animal on the trap recorded. The trap was then placed in the field for a week as per our normal protocol. Following this the animals were removed from the trap and placed for four days each in paint thinner and toluene before final preservation in 70% ethanol.

To determine the effect of preservation time on the volume estimate the animals in each set were measured five times at set intervals. We anticipated that the most rapid changes would happen in the early phases of preservation and therefore made our first two measurements at weekly intervals. To minimize the possible adverse effects of excessive handling of the specimens we made the remaining three measurements at bi-weekly intervals. Overall, then, the measurement period covered a total of eight weeks following preservation.

Sign tests (Siegel 1956) were performed on the volume estimates at the beginning and end of each interval to determine whether significant increases or
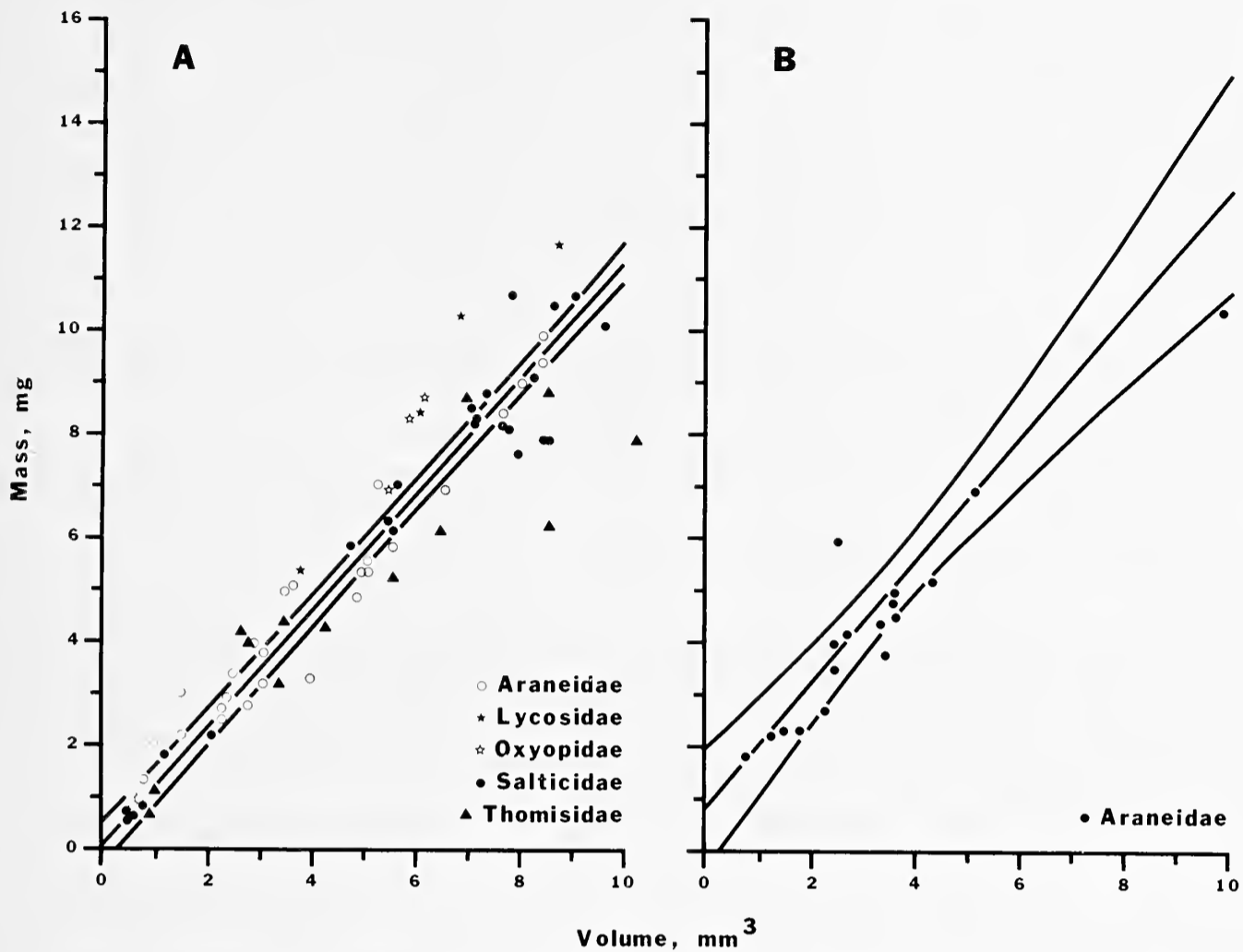
Fig. 1.—Regression lines, 95% confidence bands, and data for volume-mass regressions for original direct-ethanol data set (Greenstone et al. 1985a) (Fig. 1A) and for sticky-trapped set (Fig. 1B). Fig. 1A shows only that portion of the original data set covering the same volume range as the sticky-trapped set.

decreases had occurred during the interval. Sample sizes for each comparison were fifteen for the direct-ethanol set and eighteen for the sticky-trapped set. In the direct-ethanol there was a significant (P <0.025) decrease amounting to 19% (arcsin transformation of original data) in the volume estimate in the first week of preservation. None of the succeeding intervals showed significant change although there was an almost-significant (P <0.10) increase of 22% between the first and fourth week estimates. The sticky-trapped set showed a significant (P <0.02) increase of 9.5% during the first week interval and a significant (P <0.02) decrease of 6.0% during the second; all subsequent intervals were non-significant (P >0.60). In both samples, then, following one or two weeks of alternating increases or decreases in volume estimate there were no significant differences between the initial (one week) estimate and subsequent estimates following not more than six weeks preservation. This appears to be ample time to wait before making measurements to be sure that further changes will not occur.

To determine whether the regressions of live mass on that of direct-ethanol preserved and of previously sticky-trapped spiders differ, the sticky-trapped sample may be compared with either the simultaneously preserved direct-ethanol fifteen animal set of araneids or the original 101 animal direct-ethanol set (Greenstone et al. 1985a). Figure 1 shows the data for the sticky-trapped set (Fig. 1B) and that portion of the 101 animal set which covers the same range in volume (Fig. 1A), and the 95% confidence bands for the complete data sets. The

variances of these two samples are significantly different (P <0.01, Bartlett's Test for Homogeneity of Variances, Sokal and Rohlf 1969). Therefore t-tests on slopes and intercepts with unequal variance were performed (Snedecor and Cochran 1967). Both of these were non-significant (t = 0.690 and t = 2.880, respectively, P >0.50 in both cases). Failure to reject is not due to the added variance in the 101-animal set due to inclusion of non-araneids, because comparison of the sticky-trapped set with the simultaneously direct-ethanol preserved araneid set is not significant (t = 1.1223, P >0.20, t = 0.1002, P >0.50, slope and intercept, respectively).

There is therefore no evidence that prior sticky-trapping followed by passage through paint thinner and toluene alters the relationship between estimated volume and live mass for ethanol preserved spiders.

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THE JOURNAL OF ARACHNOLOGY

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(a). Do not use abbreviations to indicate that a new name or a new combination is being proposed in a primary heading (e. g., *A-us x-us,* new species, rather than *A-us x-us* n. sp. or comparable abbreviations).

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2. Type numbers flush to left margin, and start entry on fifth space. The second, and subsequent, lines of one entry must also be indented five spaces. . . . .*species*

(c). Synonymies must follow the abbreviated style shown below:

> *A-us x-us* Jones 1930:3, 1935:9; Russell 1945:453; Smith 1954a:16, 1954b:678; Cooper and Lim 1955:18 (in part).
> *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 *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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