Morphology and Ontogeny of Female Copulatory Organs in American Pisauridae, with Special Reference to Homologous Features (Arachnida: Araneae)

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ABSTRACT

Sierwald, Petra. Morphology and Ontogeny of Female Copulatory Organs in American Pisauridae, with Special Reference to Homologous Features (Arachnida: Araneae). *Smithsonian Contributions to Zoology*, number 484, 24 pages, 62 figures, 1989.—The morphology and ontogeny of the female copulatory organs in American Pisauridae were analyzed in order to formulate a groundplan of the female copulatory organs and to define homologous features. Decisions on homology were based on criteria of relative position, morphological similarity, and ontogenetic evidence. The existing literature on the ontogeny of female copulatory organs in spiders is reviewed. Based on data obtained through the present study, the evolution of the female copulatory organs in entelegyne spiders is discussed.

Contents

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Petra Sierwald

Introduction

In most newer taxonomic studies in spiders, the female copulatory organs are well illustrated. However, the descriptions, drawings, and the labelling of drawings often lack details, such as the exact trajectories of ducts, the position of the copulatory opening, and detailed studies on the structure of spermathecae. Gering (1953:36) stated that a study on the female copulatory system of spiders is urgently needed, "with at least an effort at standardization of terminology."

Gering's statement is still valid. There are only a very few studies available that combine detailed morphological data of the female copulatory organs with discussions on homologous features. A small number of studies were done early this century by Järvi (1905, 1912), Engelhardt (1910), Osterloh (1922), Petrunkevitch (1925), and Blauvelt (1936) on selected groups of spiders. More recent examples include Gering's study on some Agelenidae (1953), Wiehle's work (1967) on *Meta segmentata* (Clerck, 1758) and Baum's publication on Oecobiidae (1972).

The lack of knowledge about the homologous status of characters hampers the use of these organs for reconstructing phylogeny, since the distinction between primitive and derived character states can be applied to homologous structures only (for a recent discussion see Patterson, 1982). The present study is an attempt to collect morphological data on the female copulatory organs, allowing a comparative analysis in order to homologize structures of these organs between genera. The American pisaurid genera are used here as an example. The study is restricted to those genera that build a nursery-web as parental care. The nursery-web is prosposed to define a monophyletic unit. Therefore, a number of South American genera, usually assigned to the Pisauridae are excluded (see Carico, 1986).

The following criteria were applied to reach decisions on the homologous status of features: (a) criterion of position, and (b) criterion of special similarity (Remane, 1956; Wiley, 1981: 130–138). This study is the first to use the ontogeny of the female copulatory organs in several pisaurid species in order to recognize parts of the mature copulatory organ as being either homologous or nonhomologous by comparing their ontogenetic development, since "the mode of development itself is the most important criterion of homology" (Nelson, 1978:335). Furthermore, ontogenetic evidence can facilitate the polarization of characters.

In many groups of spiders, subadult females possess immature stages of their copulatory organs. These primordial stages appear in the body wall of the opisthosoma directly above the epigastric furrow. They are visible as small sclerotized spots of various shapes. Despite their common occurence they have never been studied in detail nor have they been described in taxonomic monographs.

As a result of the present study, certain terms formerly applied to parts of the female copulatory organs are newly defined according to homologies proposed herein. The data obtained herein are used to discuss Järvi's (1908) hypotheses on homology of certain parts in the female copulatory organs. Recently, Forster (1980) and Forster and Platnick (1985) suggested possible evolutionary pathways leading to the formation of receptaculate genitalia in female entelegyne spiders. Their proposed theories are also discussed on the basis of the results of the present study.

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1

sonian Institution, Washington, D.C., USA, in 1985. The insect zoo supplied crickets and fruitflies as spider food. Ms. S. Braden, Ms. H. Wolf, and Mr. S. Larcher helped to take the SEM-photographs; Mr. V. Krantz did the darkroom work. Their support is gratefully acknowledged. I wish to thank Dr. J. Carico (Lynchburg College, Lynchburg, Virginia) for his tremendous help in collecting specimens and fruitful discussions of the project. Ms. K. Smith helped with the collection of specimens in the Washington, D.C. area. Dr. J. Coddington acted as principle advisor during the fellowship. His encouragement, many favors, and constructive criticism throughout the study are thankfully acknowledged. I wish to thank Dr. J. Coddington, Ms. P. Mikkelsen, Dr. N. Platnick, and Dr. W. Shear for critically reading the manuscript.

For this study, specimens were borrowed from the following collections: American Museum of Natural History (AMNH, New York), Academy of Natural Sciences (Philadelphia), National Museum of Natural History (USNM, Washington, D.C.), Museum of Comparative Zoology (MCZ, Cambridge, USA), and Muséum National d'Histoire Naturelle (MNHN, Paris).

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Material and Methods

MATERIAL.—For the present study, the structure of the mature female organs of the following taxa were analyzed: *Dolomedes scriptus* Hentz, 1845, (Lynchburg, Virginia; USNM); *D. tenebrosus* Hentz, 1843, (Washington, D.C; USNM); *Pisaurina mira* (Walckenaer, 1837), (Lynchburg, Virginia; USNM); *Tinus peregrinus* (Bishop, 1924), (Mexico, Nuevo Leon, Linares, July 1956; AMNH); *Thaumasia* cf. *velox* Simon, 1898 (Brazil, Mato Grosso; MNHN Boc. 2047b No. 11775; use of the name *T. velox* has to be regarded as provisional); *Architis tenuis* Simon, 1898 (Colombia, Meta, Puerto Lopez; MCZ); *A. nitidopilosa* Simon, 1898 (Peru, Tingo Maria; AMNH; det. *A. tenuis* by Carico), and *Staberius spinipes* (Taczanowski, 1873) (Peru, Pucallpa, Nov. 1946; AMNH).

The results were compared with the literature on the morphology of these organs in other species of the same genera. Data on the ontogeny of the female copulatory organs of the following species were obtained in the course of this study: *Dolomedes scriptus, D. triton* (Walckenaer, 1837), *D. vittatus* Walckenaer, 1837, *D. okefinokensis* Bishop, 1924, *D. tenebrosus, Pisaurina mira, Tinus peregrinus,* and *Thaumasia* cf. *velox*. Data on the anlagen of the female copulatory organs in *Thalassius rubromaculatus* Thorell, 1899, and *Thal. spinossisimus* (Karsch, 1879) are included in the study (see Sierwald, 1987).

Juvenile specimens of *Dolomedes scriptus, D. triton, D. tenebrosus,* and *Pisaurina mira* were collected in Washington,

D.C., and Lynchburg, Virginia. The animals were reared in the laboratory and fed daily with small crickets and fruit flies. Their exuviae were collected in order to obtain complete series of all primordial stages, thus allowing the study of the course of development. The exuviae were preserved in 75% ethanol. In addition, late primordial stages in other *Dolomedes* species mentioned above, and in *Thalassius* Simon, 1885, in *Tinus peregrinus* (Mexico, Nuevo Leon, Linares; AMNH) and in *Thaumasia* cf. *velox* (Panama, Barro Colorado Island; USNM) are included in the study.

METHODS.—Parts of the body wall containing the anlagen were mounted temporarily in Hoyer's mounting medium to prepare camera lucida drawings of the pre-epigyna. The anlagen were then mounted on stubs to study the pre-vulvae in the scanning electron microscope (Cambridge Stereoscan 100, Hitachi 570). No cleaning of the anlagen obtained from exuviae was necessary. To mount the delicate early stages on the stubs, the following method proved to be successful: A round glass cover slip of appropriate site was glued on the stub with conductive carbon paint. After drying, the glass cover slip was covered with an adhesive film ("sticky tabs"; Ernest Fulham, Inc., Latham, New York 12110). A small drop of water was placed on the stub. The specimens were floated onto the water surface ventral side down, where they spread out. After evaporation of the water the specimens adhered to the stub. Specimens of later stages and mature organs were glued onto the stub using water soluble household glue. The specimens were then air dried for 24 hours.

To scan mature organs some animals were fixed as they molted to adulthood. At this stage various parts of the vulvae are often not yet heavily sclerotized (as observed in *Thalassius spinosissimus*; see Sierwald, 1987). The tissue was removed from dissected genitalia by soaking in a Trypsin solution (pinch of Trypsin in 10 ml water). The use of potassium hydroxide (KOH) is not recommended for this purpose, because it was found to damage the surface of spermathecae and other chitinous parts. However, KOH, as well as clove oil, were used to clear darkly sclerotized structures. To trace the trajectories of the ducts in the vulvae, the specimens were dried in air for a few minutes. After subsequent submersion in Hoyer's, the air in the ducts reflects light, thus allowing their course to be traced (recommended by Carico, pers. comm.).

DEFINITIONS, ABBREVIATIONS, AND TEXT CONVENTIONS

DEFINITION OF TERMS.—In the following, the term epigynum refers to the external parts, and the term vulva to the internal parts of the female copulatory organ. The German term "anlage" (plural anlagen) is used to refer to actual structures of the primordial stages, e.g., anlage of spermatheca. Anlagen of the epigynum and of the vulva are called pre-epigynum and pre-vulva, respectively (regardless of stadium). Atrium refers to a widened cavity that leads into the copulatory ducts or directly into the spermathecae. Copulatory duct describes that

part of the duct that connects the copulatory opening with the spermatheca. Fertilization duct defines that part of the duct that connects the spermatheca with the uterus externus. In the description of the groundplan of the female copulatory organs in Pisauridae new terms to name different parts of the spermatheca will be introduced herein. For further discussion and evaluation of terms used to describe female copulatory organs in spiders see Gering (1953) and Bhatnagar and Rempel (1962).

ABBREVIATIONS.—With examples of equivalent terms used by other authors, whose papers are cited in this study:

ab	accessory bulb (used by Carico and Holt, 1964)
at	atrium (used by Carico and Holt, 1964)
bs	base of spermatheca
cd	copulatory duct (Carico and Holt, 1964: bursa copulatrix; Engelhardt, 1910, Wiehle, 1967: Einführungsgang; Osterloh, 1922: Begattungsgang, Begattungskanal; Bertkau, 1875: Einführungskanal)
co	copulatory opening (Engelhardt, 1910, Wiehle, 1967: Einführungsöffnung; Osterloh, 1922: Eingangsöffnung; Järvi, 1905: Paarungsöffnung)
epf	epigynal fold (used by Järvi, 1905: epigyneale Furche (epigynal furrow))
fd	fertilization duct (Strand, 1906: Samenkanal; Engelhardt, 1910, Osterloh, 1922, Wiehle, 1967: Befruchtungsgang, Befruchtungskanal)
h	hood
hs	head of spermatheca
ilm	external, inner lateral margin of the epigynal fold
ll	lateral lobes, area lateral to the outer, lateral margins of the epigynal folds, often vaulted
mf	middle field between the lateral lobes (Järvi, 1905: Septum)
olm	external, outer lateral margin of the epigynal fold
s	spermatheca (Engelhardt, 1910: Receptaculum seminis, Samenbehälter; Strand, 1906, Bertkau, 1875: Samentasche; Osterloh, 1922: Receptaculum)
ss	stalk of spermatheca

All references to figures presented in this paper are made using "Figure/Figures"; references to figures in other papers are abbreviated with "fig." Terms used by other authors to describe parts of the female copulatory organs are added in parentheses and quotation marks to facilitate use of the cited text.

Review of Previous Studies on the Ontogeny of Female Copulatory Organs

So far, primordial stages of the female copulatory organs have been mentioned and partly described for single species in Agelenidae (Strand, 1906), Theridiidae (Bhatnagar and Rempel, 1962), Lycosidae (Sadana, 1972), Psechridae (Levi, 1982), and Ctenidae (Lachmuth et al., 1985). A more detailed description of the primordial stages of female copulatory organs is available only for several species of the pisaurid genus *Thalassius* (Sierwald, 1984, 1987).

The ontogenetic development of the female copulatory organs has been described for three species only, *Agelena labyrinthica* (Clerck, 1758), *Latrodectus curacaviensis* (Müller,

1776), and *Lycosa chaperi* Simon, 1885. The three studies were done by Strand, Bhatnagar and Rempel, and Sadana, respectively. They used reared material of different stages and employed mainly histological sections to observe the development. These three species belong to three different and not closely related families. To date, the available data are fragmentary and sporadic, and do not allow conclusions on phylogeny.

Strand (1906) gave the first account of the existence of primordial stages of the female copulatory organ in the funnel-web spider (Agelenidae) *Agelena labyrinthica*. He studied primarily the development of ovaries and testes and their ducts in spiderlings shortly before hatching from the eggs until the second post-embryonic stage using histological methods. Additionally, he studied antepenultimate and penultimate instars. He (1906:527, pl. 8: fig. 15) found ectodermal primordial stages of the copulatory organs ("das Scheidensystem, die Samentaschen und die Epigyne (Vulva)") in sections of antepenultimate and penultimate instars. In the antepenultimate instar, the spermathecae and their lumina were already developed; the fertilization duct was not yet formed. According to his studies there were no major developmental changes in the following instar.

Bhatnagar and Rempel (1962:489, figs. 56–62) studied the development in the cobweb spider (Theridiidae) *Latrodectus curacaviensis*. They found four primordial stages starting from the fourth instar. The first stage consists of a pair of invaginations formed by the hypodermal cells. This first anlage is situated internally in the anterior uterine wall, immediately in front of the opening of the uterus externus. In later development, the two invaginations deepen and each of them develops a ventral and dorsal lobe. The ventral lobes will form the "bursae copulatrices" (= copulatory ducts), the dorsal lobes will become the spermathecae. The fertilization ducts appear in the fifth (preantepenultimate) instar. From the sixth (antepenultimate) instar onward, the anlage shifts gradually to its mature ventral external position. Maturity is achieved in the eighth instar.

Sadana (1972) conducted a similar histological study on the post-embryonic development of the epigynum and vulva of the wolf spider (Lycosidae) *Lycosa chaperi*, but he included illustrations of the complete anlage in different stages in ventral and dorsal views. The first primordial stage, visible externally, appears in the seventh instar just above the epigastric furrow. The author described the anlage as a pair of horseshoe-shaped sclerotized thickenings of the body wall. In the posterior part of those sclerotized thickenings, two invaginations occur. Each sclerotized thickening enlarges and encloses a weakly sclerotized central area. The epigynal folds originate from these weakly sclerotized areas encircled by the sclerotized thickenings in the eighth (preantepenultimate) instar. In later development, through the adult 11th instar, the invaginations will form the different sections of the spermathecae (called "spermatheca sp 1–sp 4"). Sadana observed that the fertiliza-

tion ducts develop in the ninth (antepenultimate) instar: Two simultaneous invaginations, one from the wall of the uterus externus and the other from the wall of the spermatheca 1, will fuse, thus forming the fertilization duct. It is possible that the posterior part of the epignal fold was slightly curved in the penultimate stage. In this case the fertilization duct would have appeared twice in sagittal sections, thus Sadana's observation would be an artifact.

Levi (1982:115, figs. 29, 36, 83) and Lachmuth et al. (1985:338, fig. 5) illustrated the pre-epigyna of Psechridae and Ctenidae respectively, based on museum material. Lachmuth et al. distinguished seven different stages in *Cupiennius salei* (Keyserling, 1877).

For several species in the genus *Thalassius*, two different primordial stages of the female copulatory organs were found in museum material (Sierwald, 1984, 1987). The anlagen were cut out and the tissue was removed. The anlagen were studied mainly with light microscopy, and some with SEM. Illustrations of the anlagen in dorsal and ventral views were presented. The anlagen of the spermathecae were identified in antepenultimate and penultimate instars. In the *rubromaculatus* species-group, the anlage of a saccate process of the fertilization duct was identified in penultimate instars. Females of *Thalassius spinosisimus* preserved during or immediately after their final molt do not possess a fully-developed fertilization duct (Sierwald, 1987, figs. 21–24).

Bhatnagar and Rempel, and also Sadana detected developmental changes within each instar for *Latrodectus curacaviensis* and *Lycosa chaperi*. The present study observes only the changes from one instar to the other, because the exuviae were used. The advantage of this method is that the entire, intact anlage can be viewed and studied. Furthermore, use of the scanning electron microscope allowed the identification of certain areas by their surface texture. Additionally, complete series of all primordial stages of single individuals could be studied, thus allowing the comparison of development among different individuals and the detection of variablity in the developmental pattern.

Groundplan of the Female Copulatory Organs in Pisauridae

This study resulted in a groundplan (basic arrangement of elements) of pisaurid female copulatory organs that can be applied to all genera studied in the family so far. Therefore, terms used herein refer to organs or parts of organs that are here proposed to be homologous.

The female copulatory organs in Pisauridae originate from two longitudinal epigynal folds (Figures 1, 3). The two external margins (ilm, olm) of these folds, the body wall between them (the middle field, mf), and parts of the surrounding body wall form the epigynum. The margins of the folds may run straight from anterior to posterior (as in *Dolomedes scriptus*, Figure 3) or transversely (as in *D. tenebrosus*, Figure 5); they may

be a distance apart as in *Dolomedes* or close together as in *Tinus* (Figure 11). The outer lateral margin of each epigynal fold (olm) may extend to overlap (partly or totally) the middle field (Figure 1; as in *Thalassius* and *Staberius*). The margins of the epigynal folds may be curved as in *Thaumasia* (Figure 13) and *Pisaura*.

The surrounding body wall contributes to elements of the epigynum. It is often more strongly sclerotized; it may be vaulted and produce a knob as in *Tinus nigrinus* F.O. Pickard-Cambridge, 1901 (see Carico, 1976, fig. 18). In other pisaurid genera it may form deep depressions (as in *Thalassius spinosissimus*, see Sierwald, 1987, fig. 17) or hood-like structures (as in *Thaumasia*, Figure 13).

The internal parts of the folds extend inside the body like pockets and form the different elements of the vulva (Figure 1). Basically, the vulva consists of a pair of ducts that connect the copulatory openings of the epigynum with the uterus externus. In various positions along each duct lies an organ, often refered to as "spermatheca," which serves as a container for sperm. Most Pisauridae (Figures 2, 16–18) possess complex spermathecae, consisting of three distinct parts. The blind ending of the apical portion is often rounded and dilated and its wall bears conspicuous pores (head of spermatheca, hs). The adjacent part is mostly narrow and contains a duct (stalk of spermatheca, ss) that leads to the base of the spermatheca (bs). The base of the spermatheca may be dilated as well. It often contains a large lumen. (In the past, spermathecae in the genus *Dolomedes* were described as simple ball-shaped structures (Carico and Holt, 1964; Carico, 1973, figs. 51, 52). It will be shown in this paper that the "accessory bulb" (Carico and Holt, 1964) in the vulva of *Dolomedes* is homologous to the head of the spermatheca in other pisaurid genera.)

The copulatory duct and fertilization duct are usually connected either with the base or the stalk of the spermatheca (Figure 2), but never with the head of the spermatheca.

Structure of the Mature Female Copulatory Organs in American Pisauridae

Carico gave good illustrations of the female copulatory organs in *Dolomedes* (see Carico, 1973; Carico and Holt, 1964), *Pisaurina* (see Carico, 1972), *Tinus* (see Carico, 1976), and *Architis* and *Staberius* (see Carico, 1981). The results obtained through the present study suggest a new and different interpretation of certain parts of the organs.

GENERIC COMPARISONS

Dolomedes Latreille, 1804

In the epigynum of *Dolomedes scriptus*, the epigynal folds run rather straight from anterior to posterior (Figure 3). There is a distinct space between them, forming a middle field. The external margins of the folds are heavily sclerotized. The
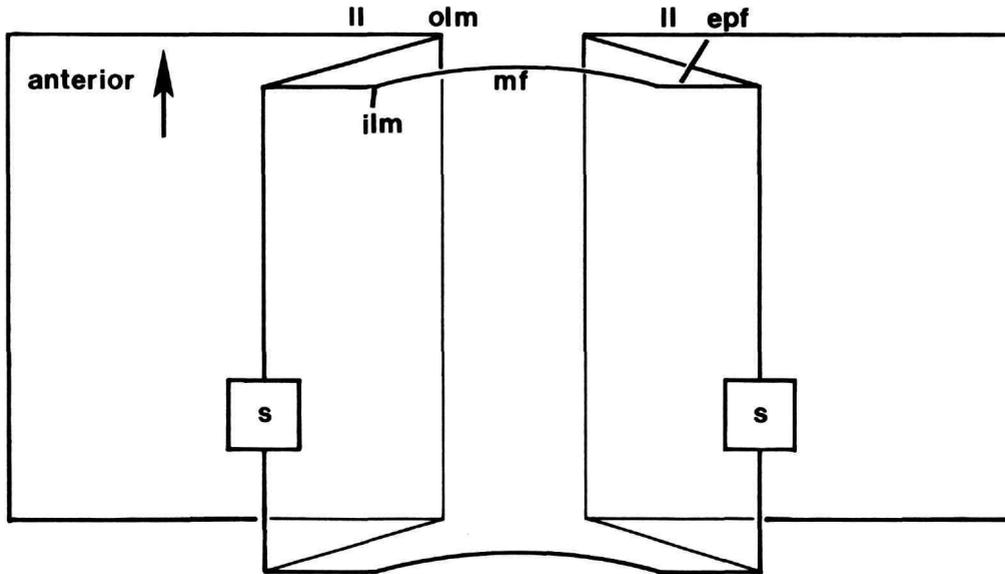
FIGURE 1.—Schematic drawing of the groundplan of female copulatory organs in Pisauridae, seen from the dorsal side, internal view.
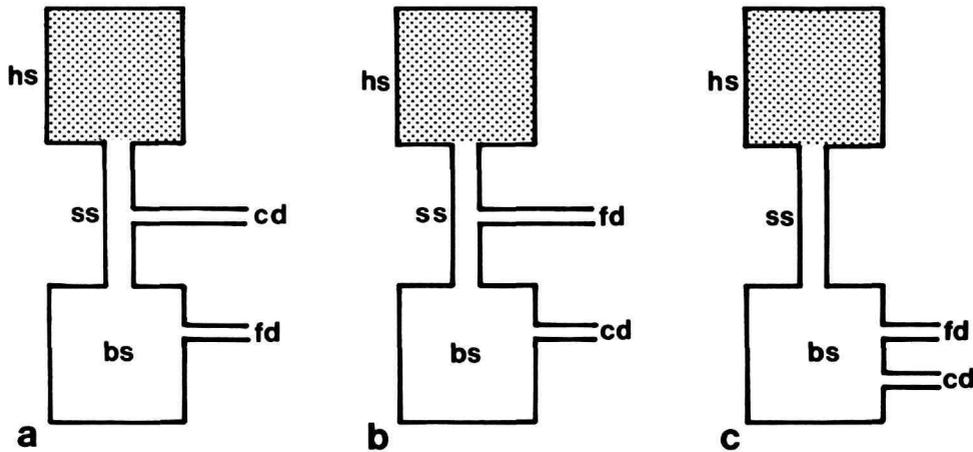

FIGURE 2.—Schematic drawing of spermathecae in Pisauridae, showing the different types of connection of the copulatory and fertilization ducts. *a, Tinus, Pisaura; b, Architis, Pisaurina, Thalassius; c, Dolomedes, Thaumasia, Staberius.*

internal parts of the folds form the atria (Figure 4; at). The copulatory openings (co) lie at the posterior base of each fold. They lead into a coiled tube.

Four morphologically different parts of the tube can be distinguished. (1) The part adjacent to the copulatory opening, containing the copulatory duct (cd), is broad and flattened (=

"bursa copulatrix" sensu Carico and Holt, 1964). (2) The following part is often dilated (= "spermatheca" sensu Carico and Holt). The dilation is not clearly visible in Figure 4. (3) Attached to the dilated part is a small knob (= "accessory bulb" sensu Carico and Holt). Its apical portion is covered with pores (Figure 7; ab). (4) The remaining part of the tube contains the
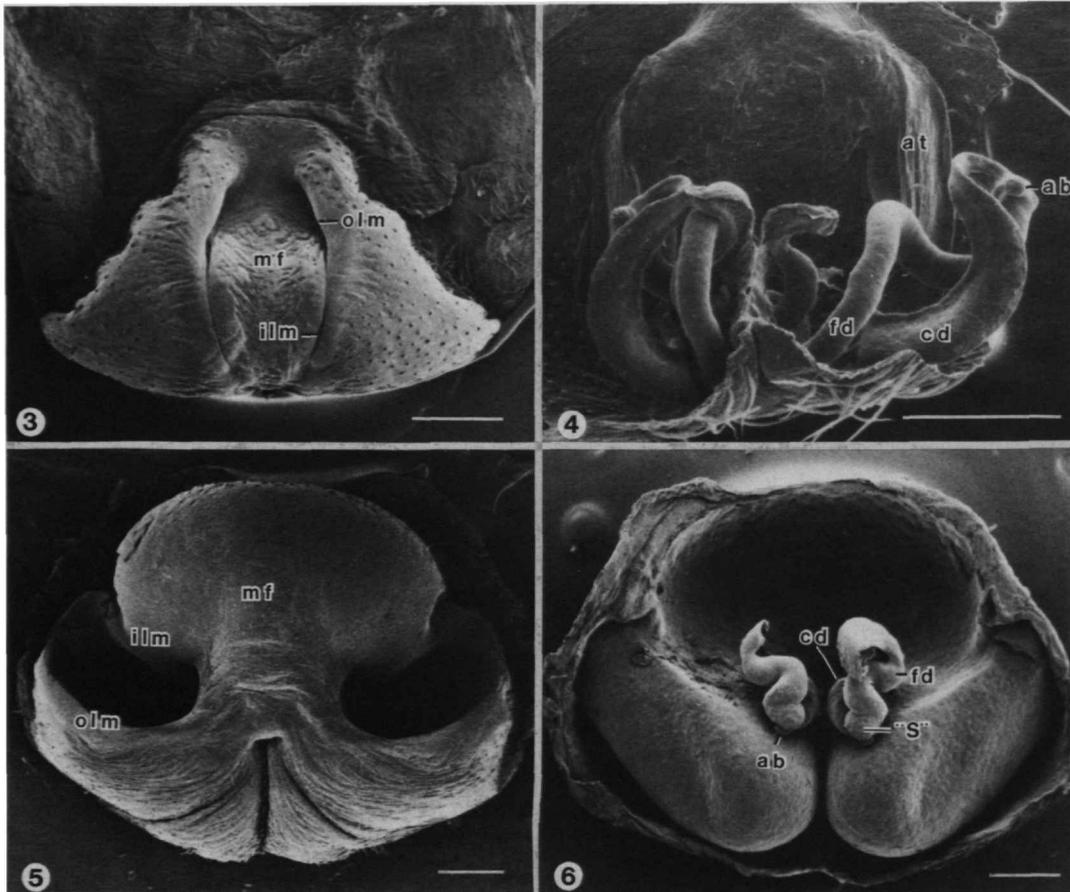
FIGURES 3, 4.—*Dolomedes scriptus:* 3, epigynum; 4, vulva, tubes on the right side artificially stretched.
FIGURES 5, 6.—*D. tenebrosus:* 5, epigynum; 6, vulva, left "seminal valve" broken off; "S" = spermatheca sensu Carico and Holt. Scale lines = 0.4 mm.
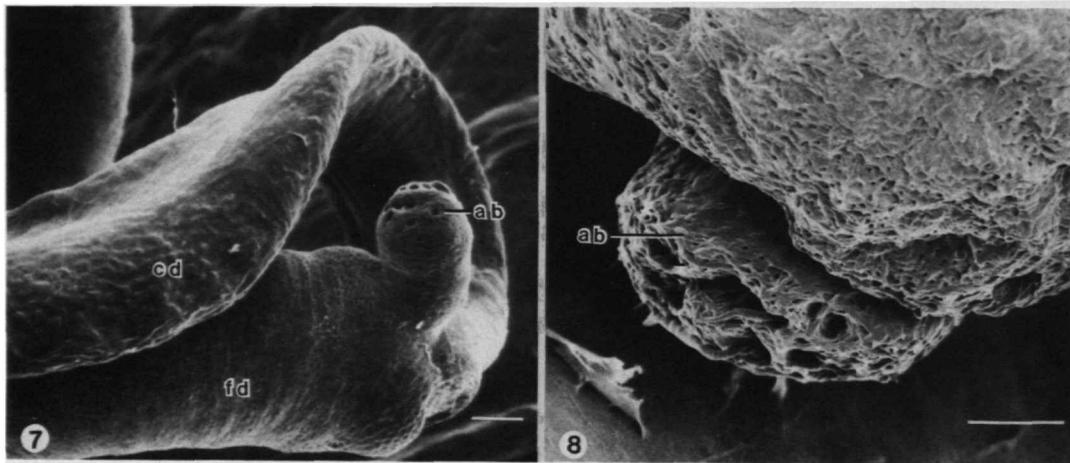
FIGURES 7, 8.—"Accessory bulb": 7, *D. scriptus;* 8, *D. tenebrosus.* Scale lines = 25 μm.
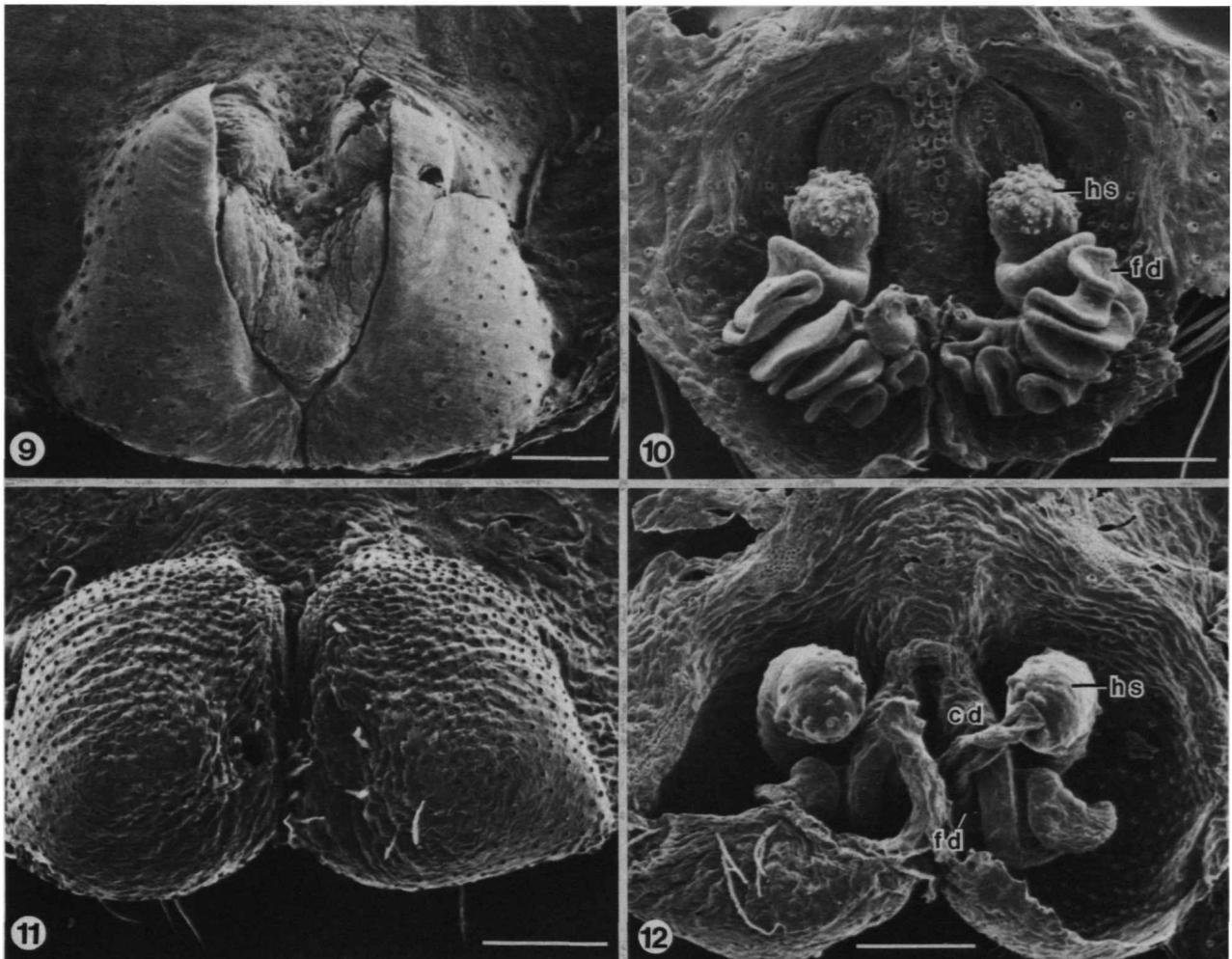
FIGURES 9, 10.—*Pisaurina mira:* 9, epigynum; 10, vulva.
FIGURES 11, 12.—*Tinus peregrinus:* 11, epigynum; 12, vulva. Scale lines = 0.2 mm.

fertilization duct. It is tubular and ends with a flattened structure (called "seminal valve" by Carico and Holt). The latter is attached to the uterus externus. The female copulatory organs in other species of the *Dolomedes fimbriatus*-group (see Carico and Holt) possess an identical basic structure. Species-specific characters are found in the shape of the sclerotized field surrounding the epigynum and in the number and form of loops of the copulatory and fertilization ducts (Carico, 1973).

In *D. tenebrosus* (Figure 5) and *D. okefinokensis,* the epigynal folds run transversely. An area of the body wall anterior to the epigynal folds is heavily sclerotized and elevated (= "median elevation" sensu Carico and Holt, 1964). The copulatory openings are situated at the median corners of the epigynal folds. The short copulatory duct (Figure 6; cd) runs

dorsoventrally. The dilated part of the tube (Figure 6; "S") is clearly visible and it bears a perforated knob (Figure 8) as in other *Dolomedes* species. The adjacent twisted tube, containing the fertilization duct, runs from posterior to anterior, ending in a flattened sclerotized structure.

Pisaurina Simon, 1898

In *Pisaurina mira,* as well as in other species of the genus, the epigynal folds run in form of the letter V (Figure 9). The copulatory opening is situated halfway along the fold. It empties directly into the base of the spermatheca (Figures 10, 17; co, hs). The head of the spermatheca is dilated and bears conspicuous pores. The long fertilization duct arises from the spermathecal stalk (ss) on the ventral side. It loops back and

forth towards the middle of the vulva. The number of loops in the fertilization duct is species-typical (see Carico, 1972).

Tinus F.O. Pickard-Cambridge, 1901

In *Tinus peregrinus*, the two epigynal folds are close together for their entire length (Figure 11). Lateral to the outer margins of the folds the body wall is vaulted. In the anterior part of the epigynum the surrounding body wall is modified in some species (e.g., forming a knob anterior to the lateral lobes in *T. nigrinus* and *T. palictlus* Carico, 1976). The copulatory openings are situated (in all species but *T. prusius* Carico, 1976) at the anterior end of the folds (Figures 12, 18; co). The adjacent copulatory duct undergoes a species-specific number of loops (numerous in *T. nigrinus*), until it joins with the stalk of the spermatheca (Figures 12, 18). The head of the spermatheca is dilated and bears numerous pores. The fertilization duct is very short and arises from the base of the spermatheca.

Thaumasia Perty, 1833

The genus *Thaumasia* is known only from the original descriptions of its 16 species. The spiders of the genus are distributed in Central and South America. The copulatory organs of *Thaumasia* have never been studied in sufficient detail; a taxonomic revision of the genus is needed (Carico, in prep.; pers. comm).

In *Th.* cf. *velox*, the epigynal folds merge posteriorly to form a V (Figure 13). The anterior part of each epigynal fold is covered by a hood, forming a pocket-like entrance to the copulatory openings (Figure 13; h). Each pocket of the epigynum leads into the copulatory duct. The vulva is very complex (Figures 14–16). The first part of the copulatory duct is a wide, membranous saccate tube. This tube is twisted, coiled, and forms several large loops (Figure 16; cd_1). The end of the copulatory duct is narrower, tubular, and sclerotized (Figure 16; cd_2). The sclerotized part of the copulatory duct empties into the large, oval, sclerotized base of the spermatheca. The stalk of the spermatheca runs laterally. The head of the spermatheca is rather small. The short fertilization duct arises at the base of the spermatheca.

Architis Simon, 1898

Adult females of *Architis nitidopilosa* and *A. tenuis* were studied. In *A. tenuis*, the external margins of the epigynal folds are inconspicuous and form an anterior curve (Figure 22). The middle field and the surrounding body wall are slightly sclerotized, but lack special features. The copulatory opening leads directly into the base of the spermatheca. The spermatheca is elongated with indistinct head, stalk, and basal region. The pores in the wall of the head of the spermatheca are restricted to its tip (Figure 23). The short fertilization duct leads from the base of the spermathecae to the posterior end
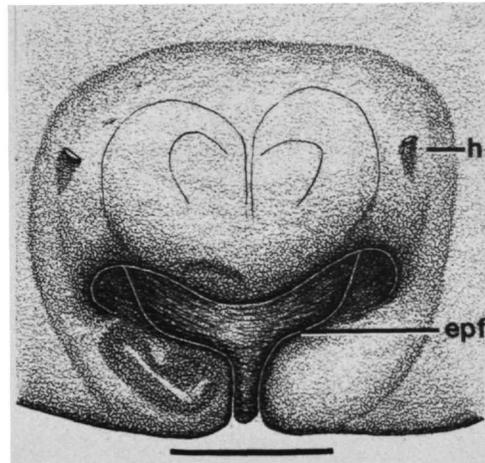

FIGURE 13.—*Thaumasia velox:* epigynum. Scale line = 0.5 mm

of the epigynal fold.

In *A. nitidopilosa*, the copulatory opening leads into a looped copulatory duct that is enclosed in a large, sclerotized, sausage-shaped structure (Figures 19, 25). This feature is present in all other *Architis* species except *tenuis*. The copulatory duct empties into the base of the spermatheca. The pores in the wall of the spermathecae are restricted to two regions, one at the tip of the spermathecae (Figures 20, 21), the other laterally on a small elevation. *Architis cymatilis* Carico, 1981, and *A. ikuruwa* Carico, 1981 have similar knobs (see Carico, 1981:149, figs. 29, 31). In these species, the copulatory duct is also enclosed in a sclerotized structure.

Carico's description of the vulva of *A. nitidopilosa* fits the drawing labelled as *A. tenuis* (Carico, 1981:149, fig. 27), and vice versa. In the series from Colombia (MCZ), males of *A. tenuis* were together with a female, whose copulatory organs agree with Carico's description of these organs for *tenuis*, but with his drawing labelled as *nitidopilosa* (Carico, 1981:149. figs. 27 and 33).

Staberius Simon, 1898

In *Staberius spinipes* (Figure 26), the epigynal folds are moderately separated (Carico, 1981:151, figs. 36, 37). Their outer lateral margins on each side overlap the middle field and are fused along the midline. The anterior edges of the lateral lobes are not attached to the body wall, but provide access to the copulatory openings located in the resulting cavity. The copulatory openings lead into the looped copulatory ducts that are each enclosed in an oval sclerotized bulb. These sclerotized bulbs are fused with each other, whereas they are separate in all *Architis* species. The copulatory duct empties into the base of the spermatheca. The spermatheca possesses a conspicuous head, a stalk, and a base with an enlarged lumen. Due to limited material, this species was not studied with the SEM. Therefore,
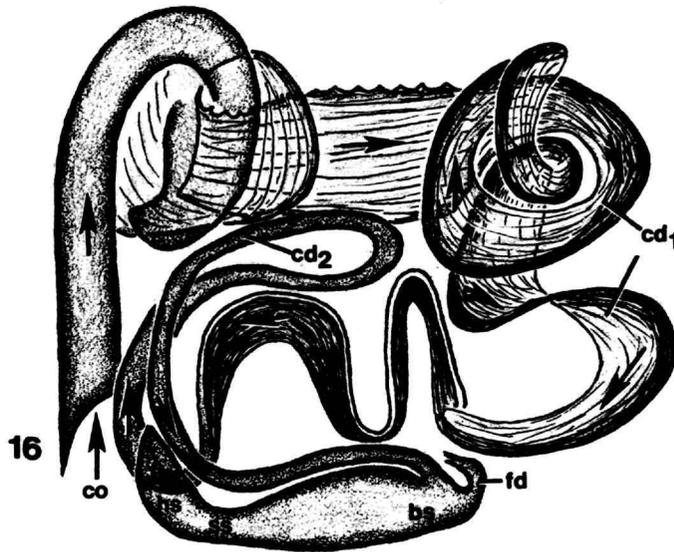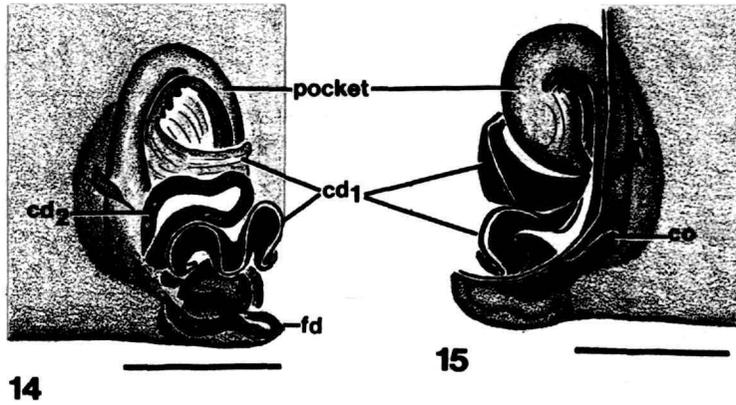
FIGURES 14–16.—*Thaumasia velox:* 14, vulva, ventral view, left side only; cd_1 = saccate anterior portion of copulatory duct, cd_2 = sclerotized posterior portion of copulatory duct; 15, vulva, dorsal view, outer body wall of epigynum removed, left side only; 16, trajectory of ducts, schematic; drawn from ventral. (Arrows indicate direction of copulatory duct from copulatory opening to spermatheca; scale lines = 0.5 mm).
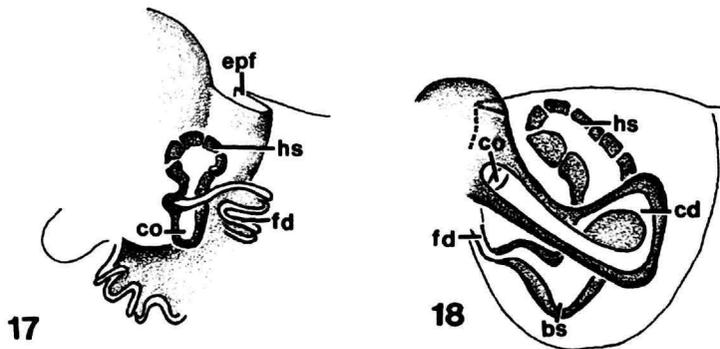
FIGURES 17, 18.—Trajectory of ducts in vulvae, schematic: 17, *P. mira;* 18, *T. peregrinus.*
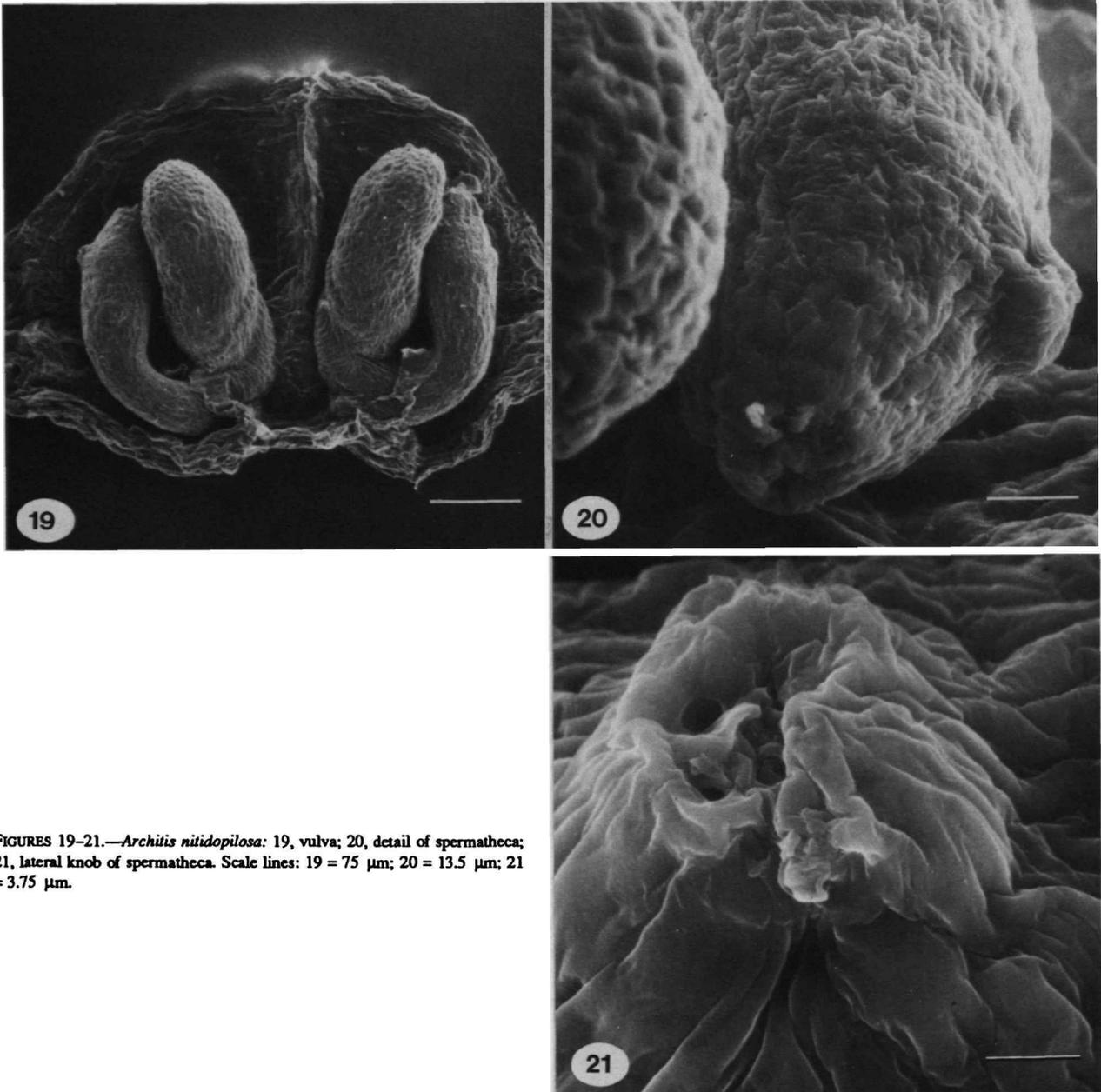
FIGURES 19–21.—*Architis nitidopilosa*: 19, vulva; 20, detail of spermatheca; 21, lateral knob of spermatheca. Scale lines: 19 = 75 μm; 20 = 13.5 μm; 21 = 3.75 μm.

the distribution of the pores in the wall of the spermathecae could not be determined. The fertilization duct leads from the stalk of the spermatheca to the posterior end of the epigynal fold and appears to run ventrally to the spermatheca (Figure 26).

DESCRIPTION OF ANLAGEN

The anlagen of the female copulatory organs in *Dolomedes*

scriptus, *D. tenebrosus*, and *Pisaurina mira* commence as a pair of shallow, longitudinal pockets. Figure 27 shows a ventral (external) view of the first anlage. The external margins of the folds and the internal base of the fold are sclerotized. The internal bases are sometimes visible through the body wall. With each molt, the epigynal folds become larger and more darkly sclerotized. The external margins of the epigynal folds will form the epigynum, while the inner parts will develop into the vulva. The thin wall of the uterus externus is shed together
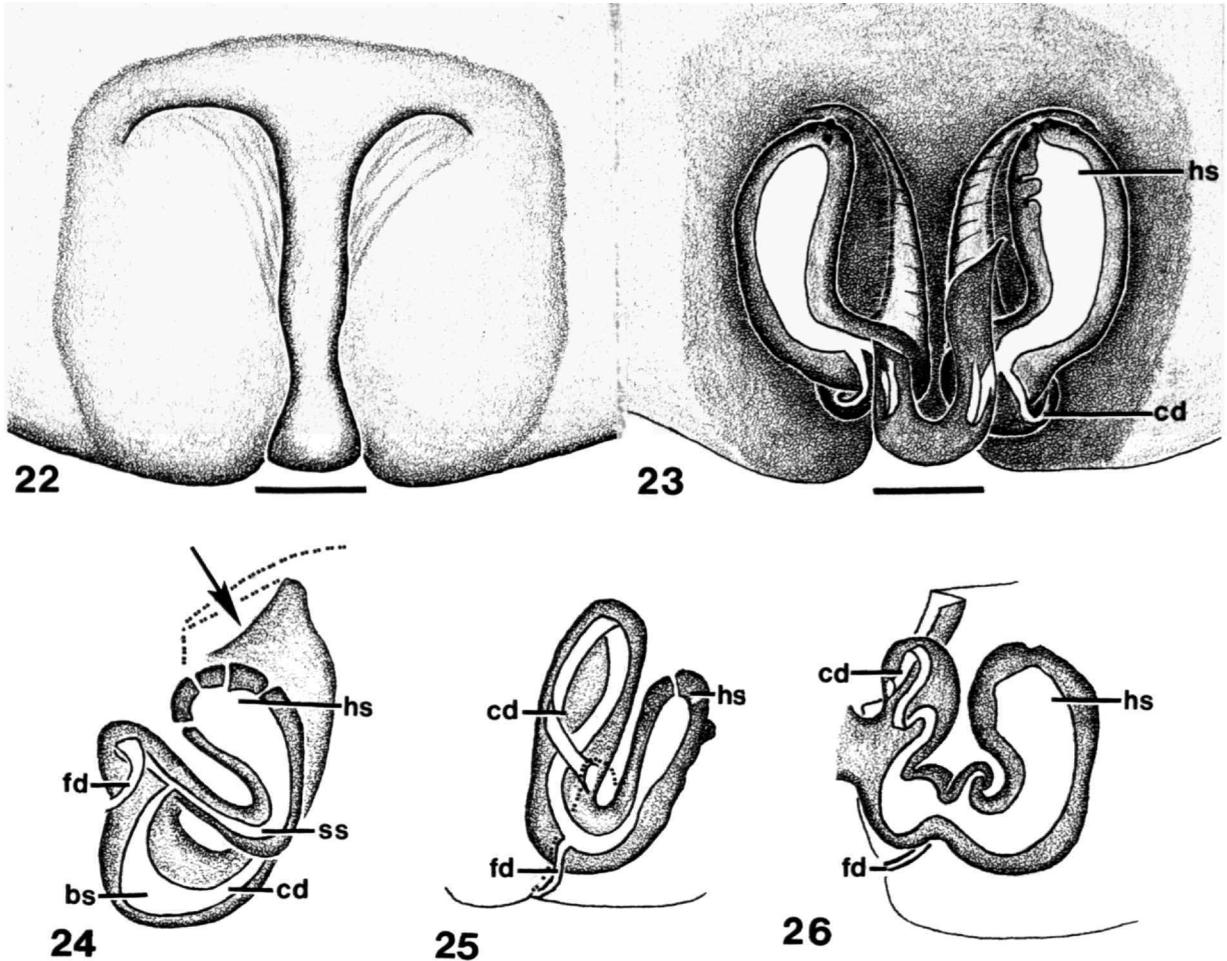
FIGURES 22, 23.—*Architis tenuis:* 22, epigynum; 23, vulva.
FIGURES 24–26.—Trajectory of ducts in the vulva, schematic: 24, *Thalassius spinosissimus,* arrows indicate trajectory of copulatory fold; 25, *Architis nitidopilosa;* 26, *Staberius spinipes.* Scale lines = 0.2 mm.

with the body wall of the opisthosoma. It remains attached to the anterior edge of the epigastric furrow. Using light microscope and SEM, no special structures were found in the walls of the uterus externus.

PRE-EPIGYNA (Figure 27).—Early stages of the anlagen are very similar in all three species. The epigynal folds run rather straight from anterior to posterior. In later stages (Figures 28–32, 62) the external margins of the epigynal folds become more heavily sclerotized. Their shape changes gradually, resembling more and more the adult epigynum. Figures 28 and 29 show the pre-epigyna in the last two instars prior to the final molt (= antepenultimate and penultimate instars) of *Pisaurina mira*. The penultimate pre-epigyna of *Dolomedes vittatus* (Figure 30), of *D. triton* (Figure 31), and of *Tinus peregrinus* (Figure 32) are already quite similar to the adult form.

PRE-VULVAE.—The internal parts of the epigynal folds will form the ducts and the spermathecae. The first two to three
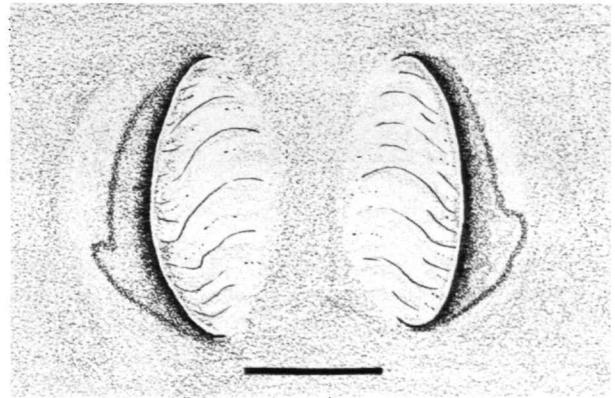

FIGURE 27.—*Dolomedes scriptus:* first anlage of female copulatory organ, ventral view, pre-epigynum. Scale line = 0.05 mm.
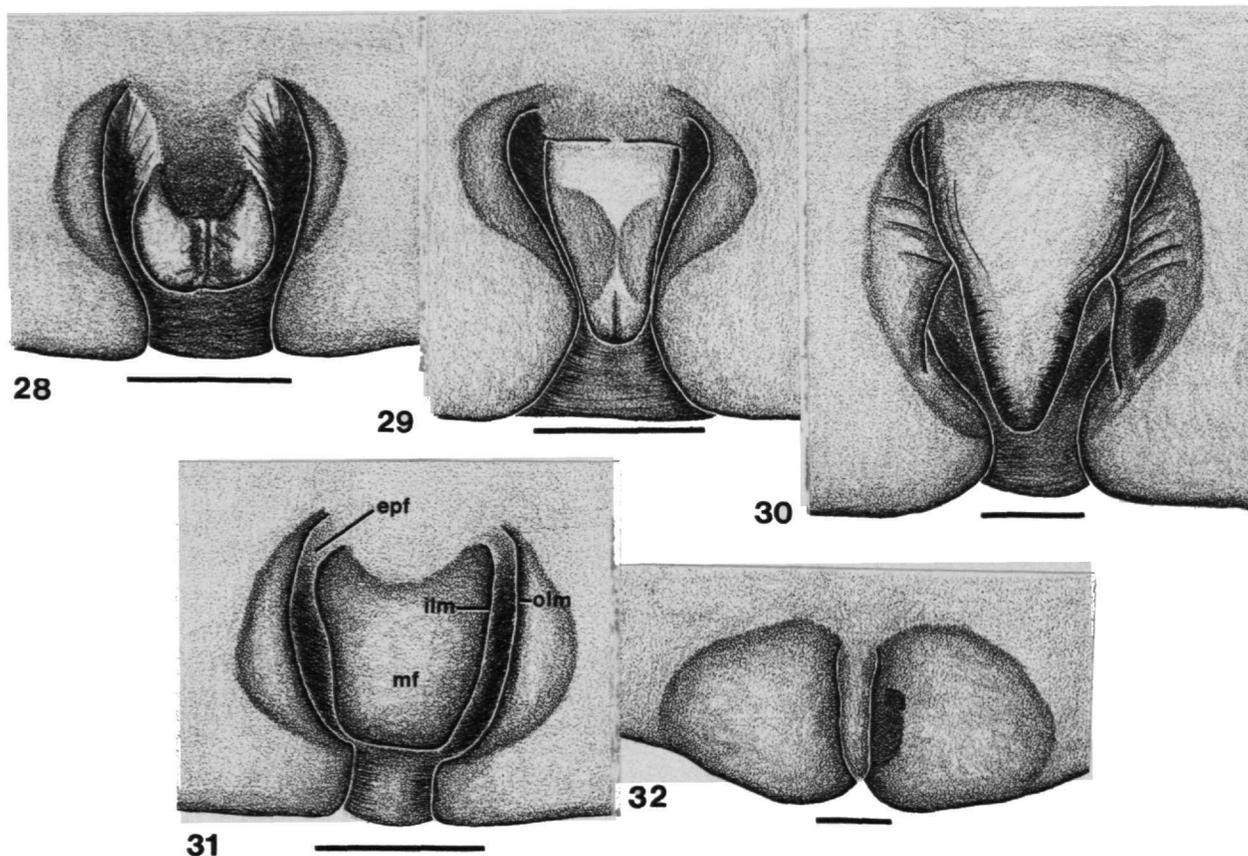
FIGURES 28, 29.—*Pisaurina mira*, pre-epigyna: 28, antepenultimate instar; 29, penultimate instar.
FIGURES 30–32.—Pre-epigyna, penultimate instars: 30, *Dolomedes vittatus;* 31, *D. triton;* 32, *Tinus peregrinus.*
Scale lines = 0.2 mm.

stages are rather similar in all three species (compare Figures 27, 33, 40, 41, 52, 53). Already in the first stage a small dilated and pointed area occurs about midway along the inner epigynal fold. The surface of this area is rough (Figures 41, 44, *Dolomedes tenebrosus*, II. primordial stage). The internal epigynal pockets are therefore divided by this differently structured area into anterior and posterior sections. The anterior part of the fold is often not as deep (Figures 40, 41, *D. tenebrosus*; Figures 52, 53, *Pisaurina mira*) as the posterior part and may also be sclerotized to a lesser extend.

DESCRIPTION OF DEVELOPMENT

In *Dolomedes scriptus* (Figures 33–35, 39; series of anlagen produced by a single specimen), the two epigynal folds run straight from anterior to posterior throughout the course of development. The pointed area in the pre-vulva already bears pores (Figure 33). In the course of development, it increases in size and the pores become more conspicuous. In late stages,

this area has developed into a rounded knob (Figures 35, 39). The posterior section of the epigynal fold is thicker and more heavily sclerotized in the late stages (Figure 34). Penultimate stages in other *Dolomedes* species show comparable features. In *D. triton*, the knob is clearly visible (Figure 36); in *D. vittatus*, it is small and hardly vaulted (Figures 37, 38).

In the adult stage, the accessory bulb is the only part that bears conspicuous pores in the wall (Figures 7, 8). The elevated knob of the early stages is therefore identified as the anlage of the accessory bulb. The position of the anlage, dividing the fold into two morphologically different sections, supports this hypothesis.

In *D. tenebrosus* (Figures 40–49; series of anlagen produced by a single specimen), the position of the epigynal folds changes from an anterior-posterior course to the transverse course of the mature organ. During development, the anlage of the accessory bulb is distinctive (Figures 44, 45, 49). The sequence of *D. tenebrosus* shows that only the epigynal folds develop in the early stages, whereas in the later stages, the
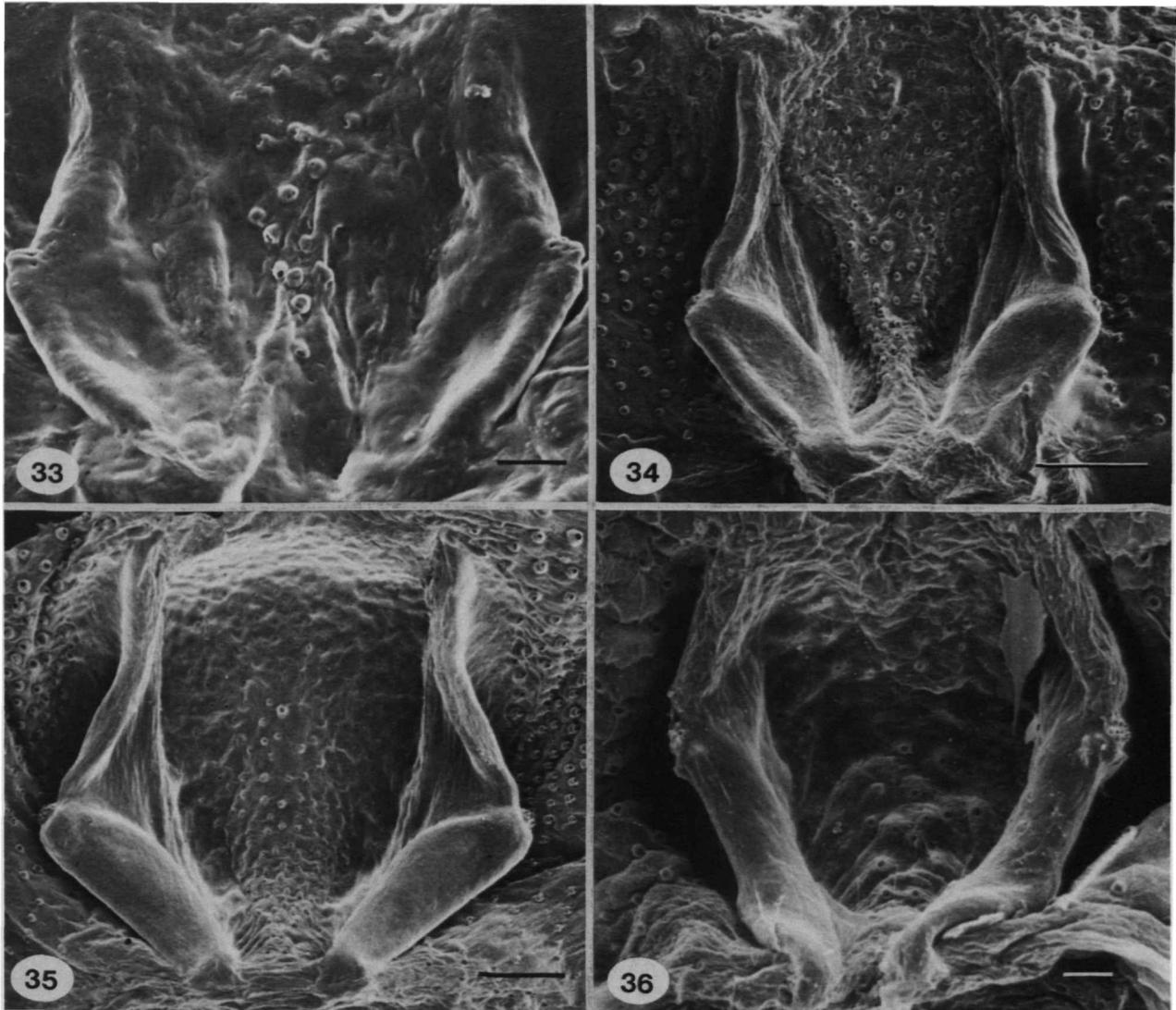
FIGURES 33–35.—*Dolomedes scriptus,* pre-vulvae: 33, III, primordial stage; 34, V, primordial stage, antepenultimate instar; 35, VI, primordial stage, penultimate instar.
FIGURE 36.—*Dolomedes triton* : Pre-vulvae, penultimate instars. Scale lines: 33, 36 = 25 μm; 34, 35 = 100 μm.

middle field and the surrounding body wall differentiate as well to form certain elements of the epigynum (Figures 43–48). The anlage of the penultimate instar of *D. okefinokensis* (Figure 50) is very similar to the penultimate stage in *D. tenebrosus* (Figure 48).

In *Pisaurina mira* (Figures 52–58; series of anlagen produced by a single specimen), the first stage (Figure 52) is very similar to the first stage in *D. tenebrosus* (Figure 40). Further development in *P. mira* is characterized by the enlargement of the posterior section of the epigynal fold. In earlier stages, the central areas of the epigynal folds show the

same rough surface (Figure 54) as seen in *Dolomedes tenebrosus* (Figure 44). In the last stage in *P. mira,* this area has developed into a ball-shaped structure bearing conspicuous pores (Figure 57). The head of the spermatheca (Figure 10) is the only part of the mature organ of *P. mira* that bears pores. Therefore, the central area of the epigynal folds of the anlagen is herein identified as the anlage of the head of the spermatheca.

For *Tinus peregrinus* (Figure 51), the last instar was observed. The epigynal folds already show a considerable degree of differentiation. The anlage of the head of the spermatheca, which is very similar to that of *Pisaurina* (Figure

57), already lies anterior to the future copulatory duct. The anlage of the copulatory duct runs first from anterior to posterior, then toward the anterior again, forming a loop (Figure 51; arrows).

In *Thaumasia* (Figures 59, 60), one penultimate instar was available. The specimen was preserved shortly before its final molt and the mature organ was already developed beneath the anlage. This level of development allows the immature specimen to be identified as belonging to *velox*.

The anterior part of the epigynal fold is membranous, while the posterior part is bulging and strongly sclerotized. The anlage of the head of the spermatheca (Figure 60) is ball-shaped and quite similar to the anlagen in *Pisaurina* and *Tinus*. Compared to the mature organ of *Thaumasia* cf. *velox*, with its coiled and twisted copulatory duct (Figures 14–16), the penultimate anlage is rather simple.

The shape of any parts of the anlagen varies between individuals. This was observed in *Pisaurina mira*, where two penultimate instars from different individuals were compared (Figures 55, 58). Likewise, the course of development is not strictly stereotyped. The degree of differentiation varies slightly in different individuals of the same instar.

NUMBER OF PRIMORDIAL STAGES

In *Dolomedes scriptus* (three complete series of anlagen from single individuals), six primordial stages were found, in *D. tenebrosus* (two complete series of anlagen) seven stages were observed. The number of *Dolomedes* specimens reared

FIGURE 37.—*Dolomedes vittatus*: pre-vulvae, penultimate instars; arrow indicates position of anlage of "accessory bulb". Scale line = 100 μm.
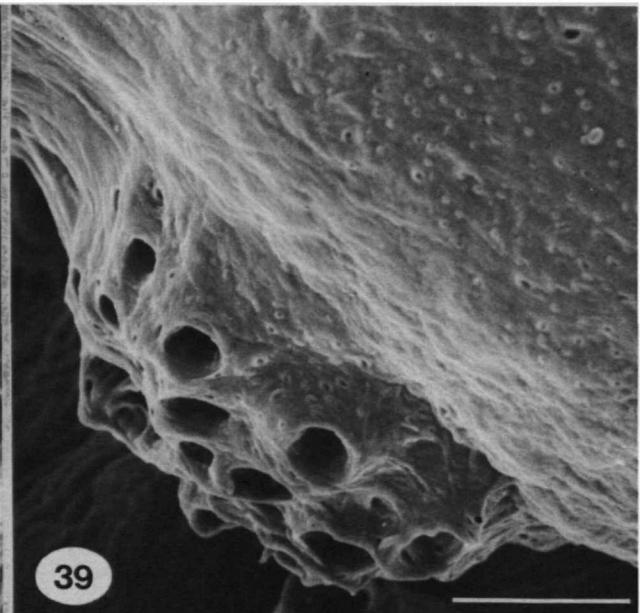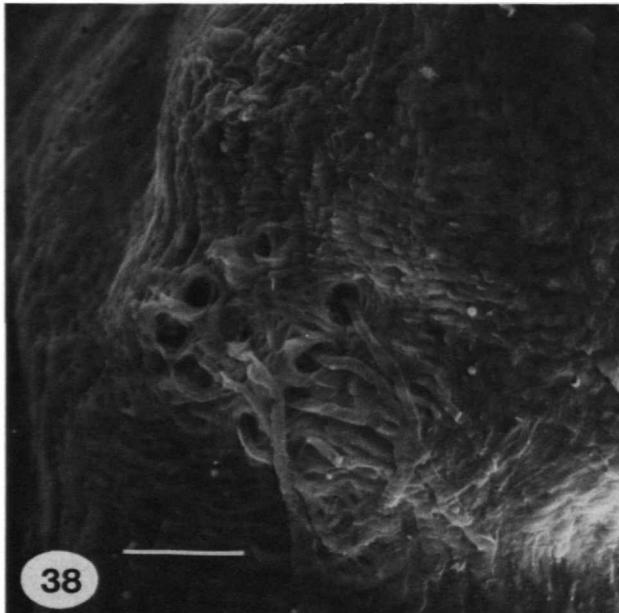
FIGURES 38, 39.—Anlage of "accessory bulb": 38, *D. vittatus*; 39, *D. scriptus*. Scale lines = 10 μm.
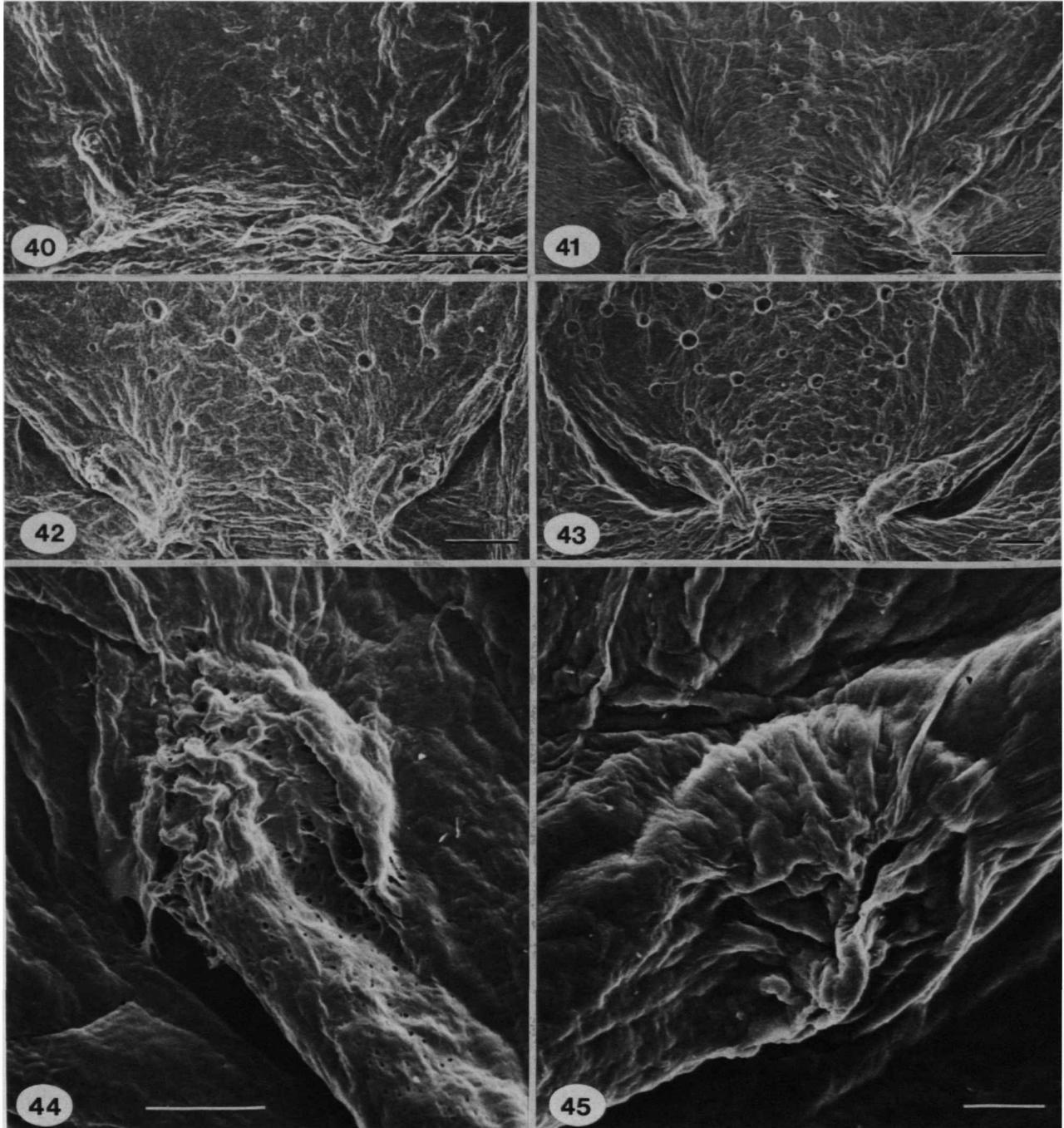
FIGURES 40–45.—*Dolomedes tenebrosus*, pre-vulva: 40, I. primordial stage; 41, II. primordial stage; 42, III. primordial stage; 43, IV. primordial stage; 44, II. primordial stage, anlage of "accessory bulb"; 45, IV. primordial stage, anlage of "accessory bulb". Scale lines = 40–43 = 50 μm; 44, 45 = 10 μm.
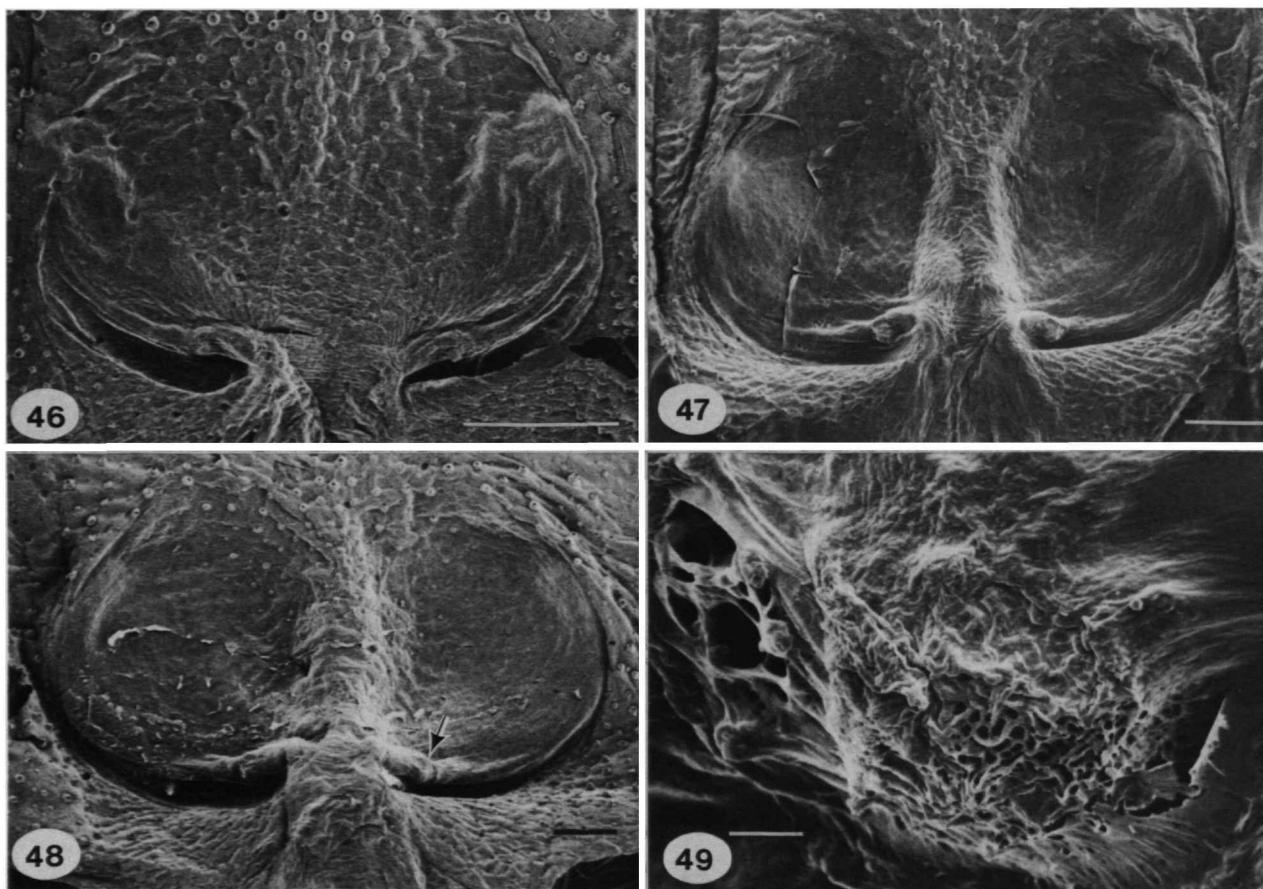
FIGURES 46–49.—*Dolomedes tenebrosus*, pre-vulva: 46, V. primordial stage; 47, VI. primordial stage, antepenultimate instar; 48, VII. primordial stage, penultimate instar; arrow indicates anlage of "accessory bulb"; 49, VII. primordial stage, anlage of "accessory bulb". Scale lines: 46–48 = 0.2 mm; 49 = 10 μm.
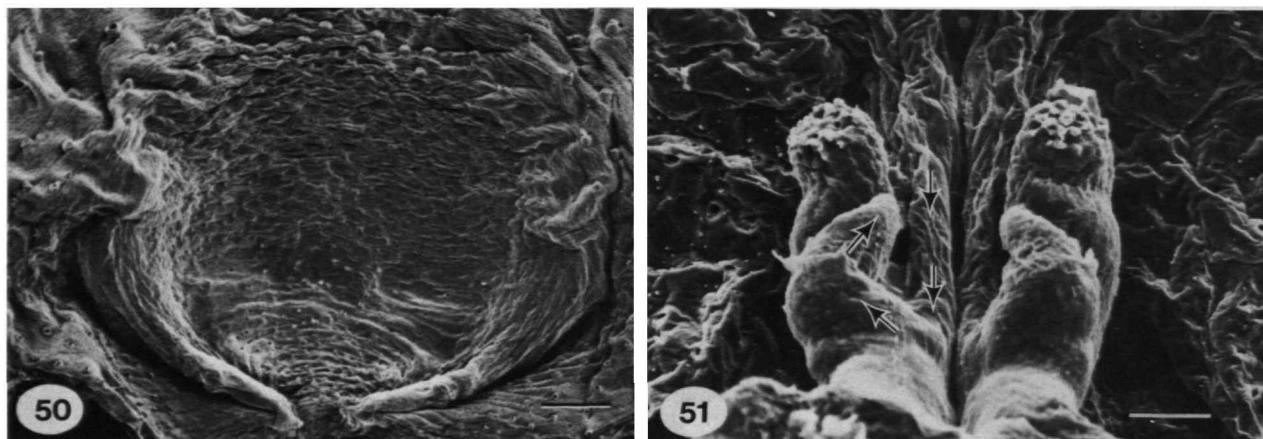
FIGURES 50, 51.—Pre-vulvae, penultimate instars: 50, *D. okefinokensis;* 51, *Tinus peregrinus*, arrows indicate trajectory of anlage of copulatory duct. Scale lines: 50 = 10 μm; 51 = 20 μm.
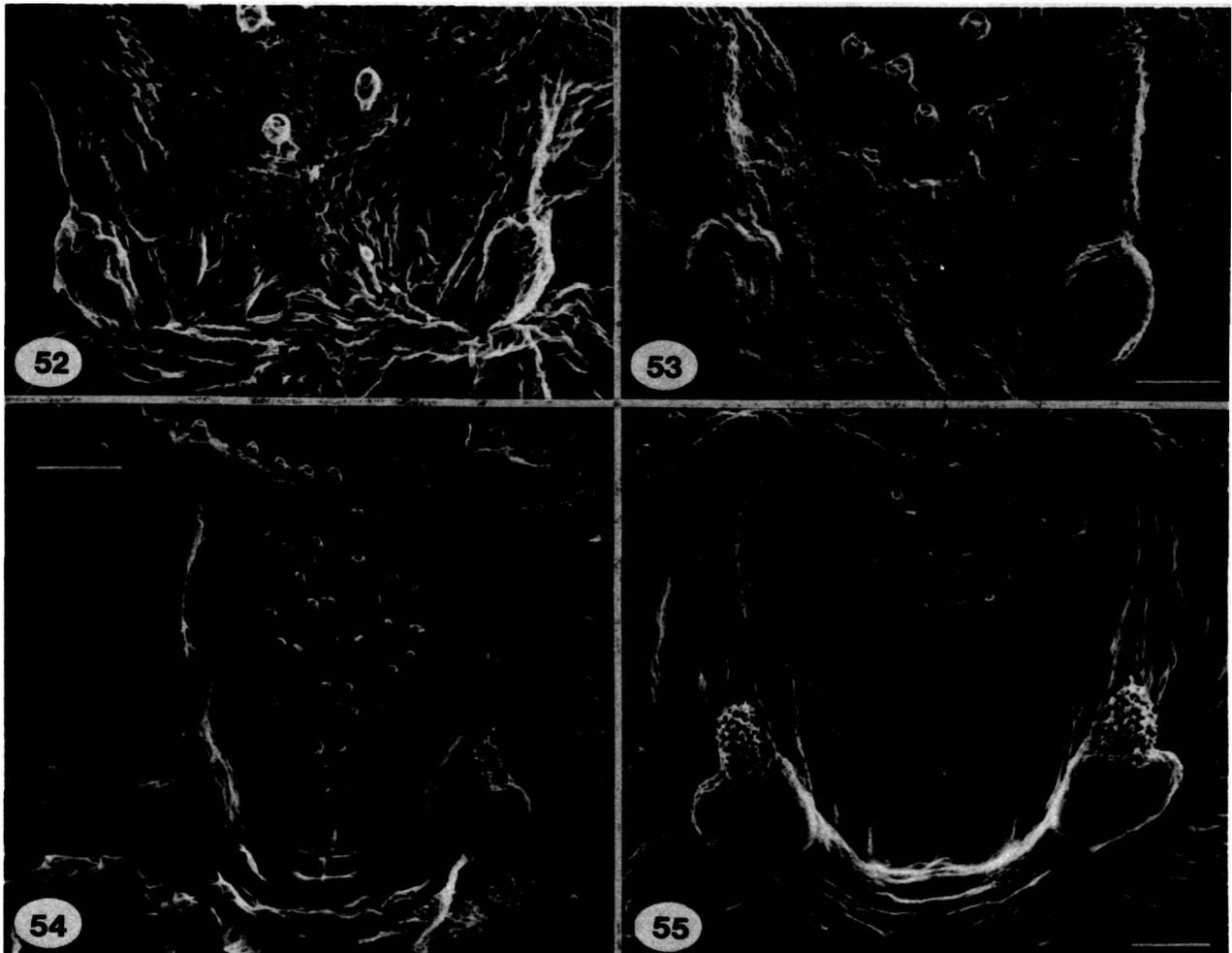
FIGURES 52–55.—*Pisaurina mira*, pre-vulva: 52, I. primordial stage; 53, II. primordial stage; 54, IV. primordial stage, antepenultimate instar; 55, V. primordial stage, penultimate instar. Scale lines: 52, 53 = 25 μm; 54, 55 = 50 μm.

was too small to furnish data on the variability of primordial stages.

In *Pisaurina mira* (five complete series of anlagen) the number of primordial stages varied between three and five. In specimens with only three primordial stages, the anlagen of the antepenultimate and penultimate instars were less fully differentiated, resembling the early anlagen of specimens (Figures 52, 53) that produced five primordial stages. Specimens with only three or four primordial stages molted following their third or fourth anlage to apparently "normal," mature females.

Summary of Results

The female copulatory organs of American Pisauridae are formed by differentiation of two longitudinal folds (epigynal folds); the external margins of the folds, the middle field between them and the surrounding body wall eventually form the epigynum. The internal base of the folds will form the vulva with a copulatory duct, a tripartite spermatheca, and a fertilization duct.

The female copulatory organs develop over the course of several juvenile instars. Their anlagen appear in the ventral body wall directly above the epigastric furrow, corresponding to the location of the future mature organ. In all species studied, the early premature folds are short and weakly sclerotized. They run straight from anterior to posterior. Internally, a pointed area can be distinguished, often showing pores or rough surface texture. The anterior and posterior parts of the internal folds are distinctly different in structure.
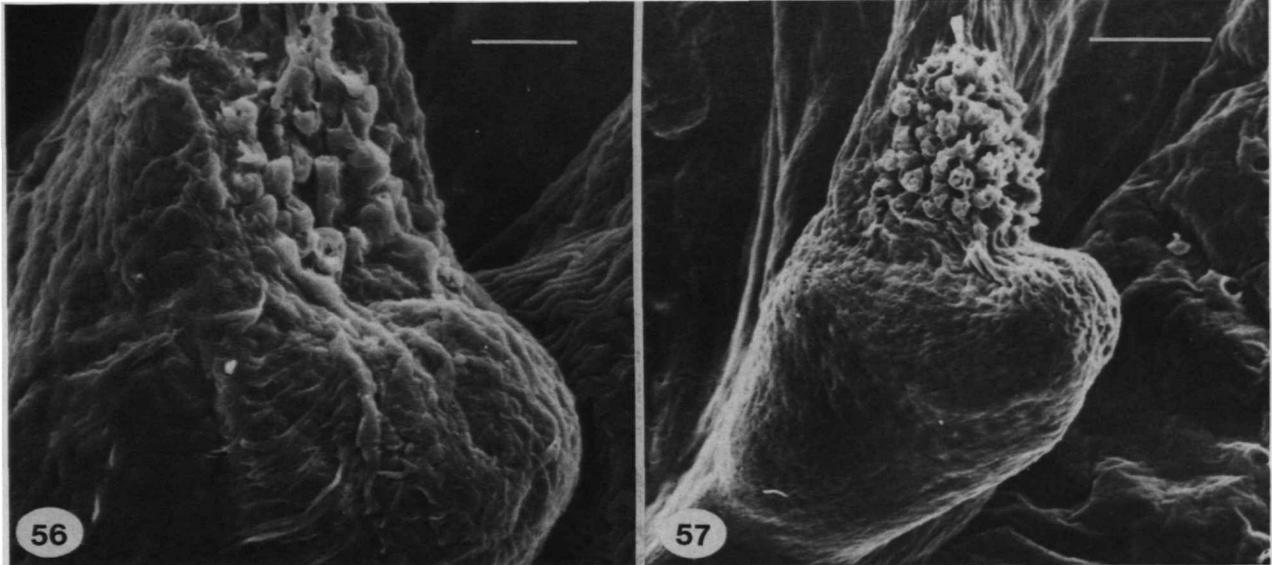
FIGURES 56, 57.—*Pisaurina mira*, anlage of head of spermatheca: 56, IV. primordial stage; 57, V. primodial stage. Scale lines: 56 = 10 μm; 57 = 25 μm.

In later development, the pre-epigyna change and resemble more closely the adult epigynum. In the pre-vulva, the pointed area becomes ball-shaped and perforated.

Certain developmental features appear to be common for all pisaurids observed in this study. The pace of development is slow in the early stages; major changes occur with the final molt. The anlage of the head of the spermatheca (homologous with the "accessory bulb" in *Dolomedes*, see "Conclusions") develops early in ontogeny and is very similar in all species studied. The copulatory and fertilization ducts are formed late in ontogeny. The anlage of the penultimate instar of *Tinus peregrinus* possesses the highest degree of differentiation of the observed anlagen.

The development of the female copulatory organs in *Thalassius* agrees with the observations made in *Dolomedes* and *Pisaurina*. The anlage of the head of the spermatheca is large and ball-shaped (Figure 61), bearing conspicuous pores. The posterior part of the epigynal fold is more heavily sclerotized than the anterior part. (Because museum material was used for the study in *Thalassius*, only two stages were observed. For a detailed description of the female copulatory organs in *Thalassius*, see Sierwald, 1987.)

Conclusions

POSITION OF EPIGYNAL FOLDS.—From ontogenetic evidence, a straight anterior-posterior course of the epigynal folds in the mature organ, as in *Dolomedes scriptus* and *Tinus*, has to be regarded as primitive. Derived character states are present in *Dolomedes tenebrosus* and *D. okefinokensis* (transverse
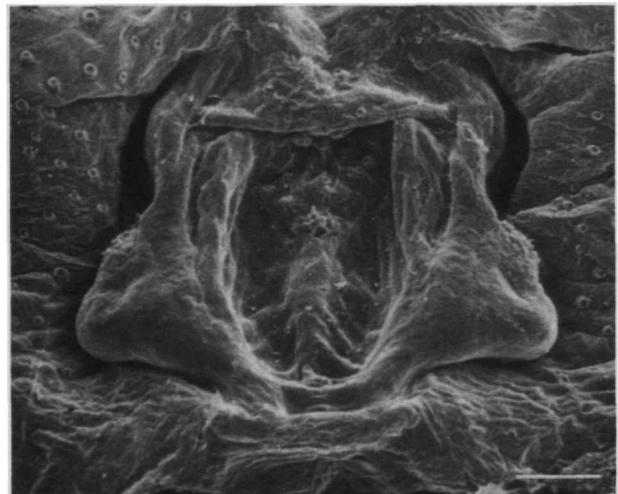
FIGURE 58.—*Pisaurina mira:* penultimate instar, pre-vulva. Scale line = 50 μm.

course of epigynal folds), and in *Thaumasia* and *Pisaura* (curved epigynal folds).

THE SPERMATHECAE.—The spermatheca consists of a perforated head, a narrow stalk, and a dilated base containing an enlarged lumen. In the present study, the head of the spermatheca and the "accessory bulb" in *Dolomedes* are the prominent features observed through the entire course of development. From the similarity in development and morphology, the accessory bulb in *Dolomedes* and the head of the
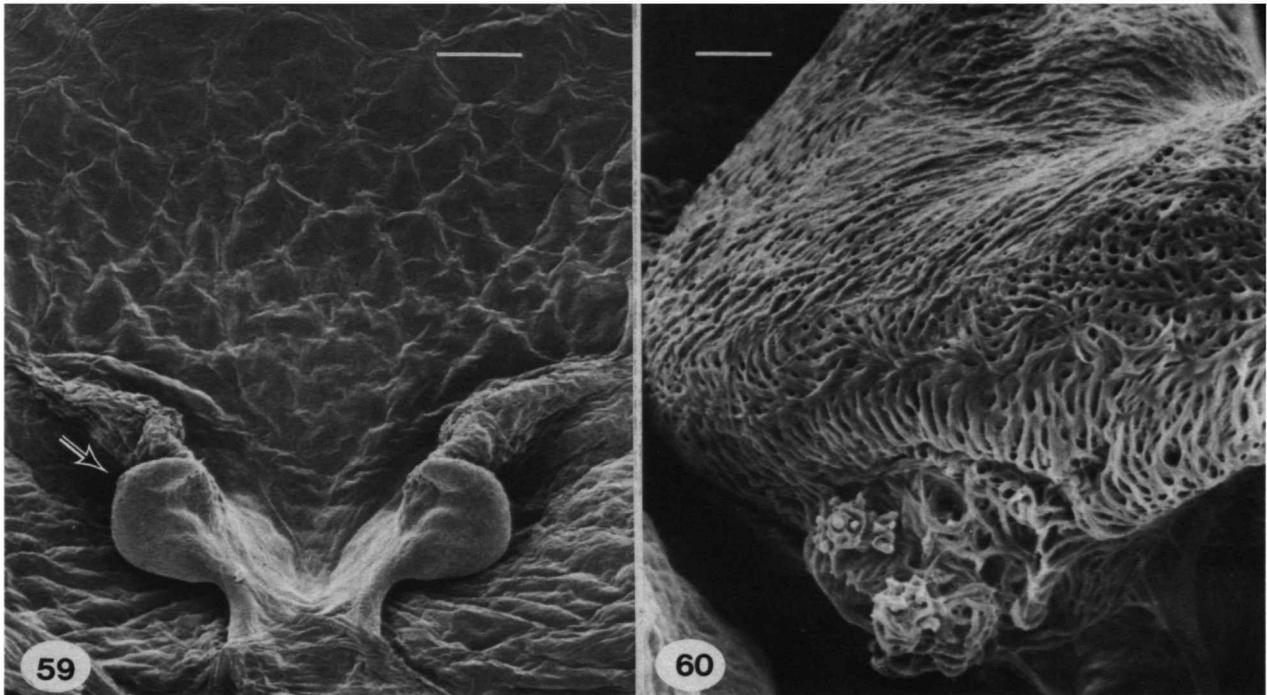
FIGURES 59, 60.—*Thaumasia* cf. *velox*, penultimate instar: 59, pre-vulva, arrow indicates position of anlage of head of spermatheca; 60, anlage of head of spermatheca. Scale lines: 59 = 50 μm; 60 = 5 μm.
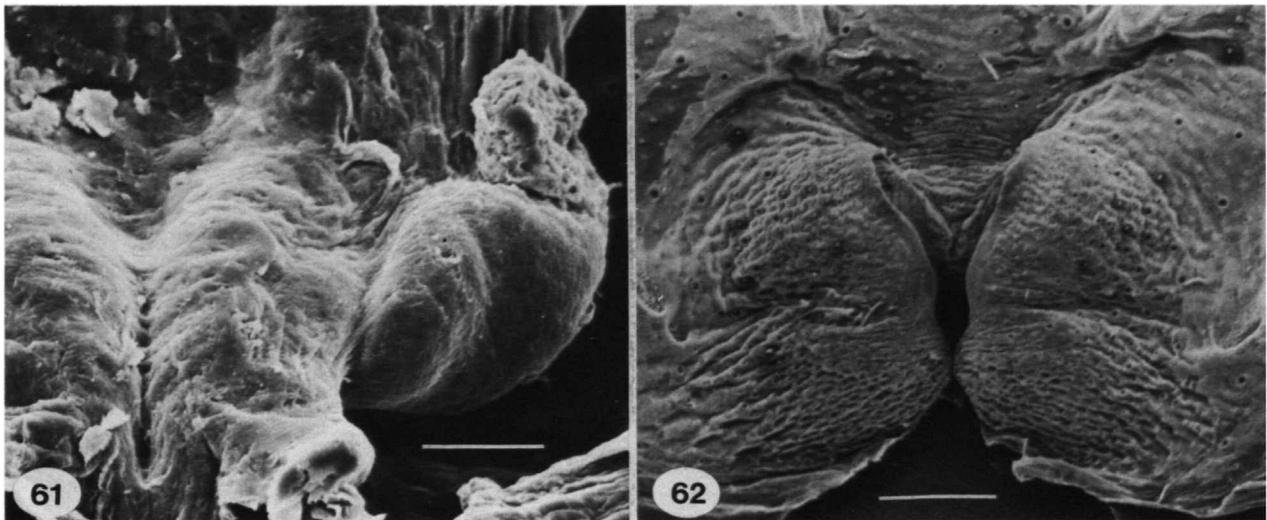
FIGURES 61, 62.—*Thalassius*, penultimate instar: 61, *Thal. rubromaculatus*, pre-vulva, right side of anlage; 62, *Thalassius spinosissimus*, pre-epigynum. Scale lines: 61 = 50 μm; 62 = 200 μm.

spermatheca in other American Pisauridae are shown to be homologous. In penultimate instars of *Dolomedes scriptus* (Figure 35), the anlage of the accessory bulb already resembles the head of a spermatheca and is very similar to the anlagen of the head of the spermatheca in other species such as *Pisaurina mira* (Figure 57), *Thaumasia velox* (Figure 60) and *Thalassius* (Figure 61). The occurence of pores in both the anlagen and the mature organ is an important feature to identify

the accessory bulb and the head of the spermatheca as being homologous. Based on its position, the functional "spermatheca" (Figure 6; "S") in *Dolomedes* can therefore be interpreted as an enormously enlarged base of the spermatheca.

Järvi (1905:29), in his excellent analysis on the female copulatory organ of *Dolomedes limbatus* Hahn, 1831 (= *Dolomedes fimbriatus* Clerck, 1758), identified the accessory bulbs as the primary spermathecae ("primäre Receptacula (pr. r.)" = "Anhänge der sekundären Receptacula"; pl. 5: fig. 6). He considered the "spermathecae" (sensu Carico and Holt, 1964) as secondary structures. He compared the female copulatory organs of *Dolomedes*, *Pisaura*, and *Lycosa* and based his conclusions on similarities in position and structure of the spermathecae in these genera.

Järvi used the term "primary" in the sense of primitive. Note that Engelhardt (1910:38) and Osterloh (1922:379) defined the primary spermatheca as the one that communicates with the copulatory duct, the secondary spermatheca as the one that communicates with the primary spermatheca, etc.

The pores in the wall of the head of the spermathecae occur very early in ontogeny and are apparently wide spread among entelegyne spiders. They may therefore be a plesiomorphic character. Apparently, the head region of the spermathecae may show a high degree of diversity, e.g., reduction in size as in *Dolomedes*, disjunct distribution of the pores over the head region as in *Architis*. Based on ontogenetic evidence, these character states are derived and may be useful in reconstructing phylogeny as they identify monophyletic groups. Further studies in the Pisauridae will furnish more data in different genera and allow the use of these characters.

Thus far, it is not possible to identify the stalk or the base of the spermatheca in anlagen of the copulatory organs. In some groups, the different sections of the spermatheca may be inconspicuous in the mature organ, e.g., very small (as in *Pisaurina*) or modified (as in *Dolomedes*). Such conditions can hamper the identification of homologies.

THE COPULATORY DUCT.—Based on ontogenetic evidence, the most primitive condition of the copulatory duct may be represented by *Thalassius spinosissimus* (Figure 24). The copulatory duct consists of a fold (copulatory fold, see Sierwald, 1984, 1987) that joins the base of the spermatheca. Since the copulatory duct develops with the final molt, no further ontogenetic evidence is available to polarize other occurring character states concerning the copulatory duct.

In *Dolomedes* and *Tinus*, the copulatory duct is a solid, sclerotized tube that performs a number of loops. This may be regarded as a derived condition. The copulatory duct in *Thaumasia* seems to represent another state. It is differentiated into an anterior saccate section and a posterior sclerotized section.

Carico (1981:144) interpreted the sausage-shaped structures in the vulva of *Architis nitidopilosa* as a second pair of spermathecae ("...median spermathecae with coiled lumens"). This opinion may be refuted. Following the formation of the

spermathecae in Pisauridae proposed herein, this structure is not homologous with any part of the spermatheca, but rather with the copulatory duct. An enclosed copulatory duct occurs in *Staberius* and in all but one *Architis* species (the copulatory duct is reduced in *A. tenuis*). This character state seems to be a synapomorphy for both genera.

In *Pisaurina*, the copulatory duct is missing, the copulatory opening empties directly into the base of the spermatheca.

THE FERTILIZATION DUCT.—Like the copulatory duct, the fertilization duct develops with the final molt. Therefore, no ontogenetic evidence is available to ordinate polarities of different character states. In *Architis*, *Staberius*, *Tinus*, and *Thaumasia*, the fertilization ducts are short and possess no further features. (The "fertilization duct" sensu Carico (1976) in *Tinus nigrinus* is part of the copulatory duct.) In *Dolomedes*, the fertilization duct is a solid sclerotized tube, undergoing a number of loops. In *Pisaurina*, the fertilization duct is very long and coiled. Since the morphologies of the female copulatory organs in other pisaurid genera are virtually unknown, it is not possible to polarize the observed character states.

COMMUNICATION OF THE DUCTS WITH THE SPERMATHECA.— As mentioned earlier, the copulatory and fertilization ducts always communicate either with the stalk or the base of the spermatheca, but never with the head. Figure 2 shows the different types of structures that have been observed in Pisauridae so far. The formation of the spermathecae, the types of connections with fertilization and copulatory ducts, and the length, loops, and curves of both ducts are potentially valuable character systems that may provide apomorphies to define monophyletic groups within the genera commonly assigned to the family Pisauridae as more morphological data become available.

PHYLOGENETIC CONCLUSIONS.—The groundplan of the female copulatory organs proposed herein is based upon those American Pisauridae known to build a nursery-web (excluding *Trechalea* and other South American genera, see Carico, 1986). With the inclusion of further nursery-web Pisauridae, variation and diversity within this groundplan may become evident. No predictions can be made regarding whether this groundplan is valid for other spider families. In the majority of entelegyne spiders, the female copulatory organs are paired structures. Therefore, the groundplan proposed here may be plesiomorphic at a high categoric level.

Thus far, neither a set of synapomorphic characters to substantiate the monophyly of the Pisauridae, nor a sister group to Pisauridae, is known. The lack of an appropriate outgroup hampers the systematic analysis of Pisauridae. Several families have been proposed as relatives of Pisauridae: Dondale (1986:328) used Pisauridae as sister group to Lycosidae; Brady (1964:436) suggested a close relationship between Oxyopidae and Pisauridae; Homann (1971:263) included Pisauridae, Ctenidae, and Rhoiciinae as additional subfamilies in the Lycosidae; and Lehtinen (1967) assigned the pisaurid genera

to two different families, the Pisauridae and Dolomedidae. Lehtinen did not define synapomorphies for the Dolomedidae and Pisauridae sensu strictu. Further study of the structure of female copulatory organs with attention to homologous features may help solve the question of relationships among the spider families mentioned above. In addition, complementary studies on the male copulatory organs are needed to corroborate evidence for phylogenetic relationships based on female copulatory organs.

Due to the lack of data for other pisaurid genera, the results presented here do not allow reconstruction of the phylogeny of the American nursery-web Pisauridae. According to the data gathered so far, the American Pisauridae do not represent a monophyletic group, since the proposed groundplan of the female copulatory organs apparently contains only plesiomorphic traits. *Architis* and *Staberius* are probably sister taxa (but note that *Staberius* is monotypic). The morphology of the male copulatory organs (Carico, 1981, figs. 12–23, 34) supports this hypothesis. A close relationship between *Tinus* and *Thaumasia* (Comstock, 1980:631) is not supported by the results of this study, since no shared apomorphy can be defined at this point. The placement of *Pisaurina* is uncertain; the female, as well as the male, copulatory organs (Carico, 1972, figs. 13–22) appear to be derived. The relationship of *Dolomedes* to any other American nursery-web pisaurid is uncertain as well. Whereas the other genera are restricted to the Americas, *Dolomedes* is distributed worldwide; its closest relative may not be among the American Pisauridae.

Discussion

As mentioned in the introduction, detailed morphological studies that include analyses of the homologous status of characters are scarce. How do the data obtained in this study relate to findings in other entelegyne spiders? Can the data obtained contribute to the discussion of the evolution of receptaculate genitalia in female entelegyne spiders?

FORMATION OF THE SPERMATHECAE.—In general, the spermathecae appear to be diverse in structure and formation among entelegyne spiders. This fact is rarely acknowledged in taxonomic papers. In schematic drawings, the spermathecae of entelegyne spiders (as in Wiehle, 1967, fig. 29; Foelix, 1987, fig. 135a; Comstock, 1980, fig. 165) are often shown as round ball-like structures. Bertkau (1875:251) mentioned ball-shaped spermathecae ("Samentaschen") in epeirids, theridiids, thomisids and salticids. He noted that *Tegenaria* Latreille, 1804, and some other genera possess bottle-shaped spermathecae. Wiehle (1967:185) pointed out that in many spiders the spermathecae are composed of several distinct cavities. Järvi (1905:9–10) described the spermatheca of *Lycosa amentata* (Clerck, 1758) as consisting of a rounded head, a narrow stalk, and an often dilated basal part (1905:13). The diverse and complex morphology of the spermathecae in entelegyne spiders ought to provide evidence for phylogenetic relation-

ships among genera and families, once homologous parts can be identified.

HEAD OF SPERMATHECA.—Pores in the walls of spermathecae have been mentioned by several authors (Schimkewitsch, 1884:79; Engelhardt, 1910:38), and have always been associated with glands that surround the spermathecae. Wiehle (1967:185) made the general statement that in most entelegyne spiders, the walls of the spermathecae bear numerous pores and are embedded in glandular tissue. Comstock (1980:160) described a "gland of the spermathecae" as a distinct part in the female copulatory organs in "Aranea" (presumably *Araneus*). The function of the secretion of the spermathecal glands is not yet clear. It has been suggested that it may help to maintain the sperm for longer periods of time (Engelhardt, 1910:38; Forster, 1980:277).

Although most arachnologists know that pores in the walls of spermathecae are common, their occurrence and distribution are hardly ever considered in taxonomic monographs. This lack of data proves now to hamper the comparative morphology of the female copulatory organs in entelegyne spiders. Based on the fact that these pores occur widely throughout mygalomorph and araneomorph spiders, the question arises whether they are homologous. To answer this, it would be necessary to collect data concerning their abundance and distribution on the spermathecal heads of various genera. It would also be very useful to study the glands and the function of their secretion.

EVOLUTION OF THE FEMALE ENTELEGYNE COPULATORY ORGANS.—Forster (1980:277–288), based on his study of the organization of female copulatory organs in haplogyne spiders, concluded that the spermathecae in entelegyne spiders evolved from a particular region in the anterior wall of the uterus externus. The region was furnished with a gland to maintain the sperm after deposition in the uterus externus. Through subsequent invagination of this region, a receptaculate storage system evolved. Forster's hypothesis would imply that the spermathecae of all entelegyne spiders are homologous. Testing his hypothesis would need to include comparative studies on the morphology of spermathecae in entelegyne spiders and further ontogenetic studies in other spider groups. The results of this study lend support to his hypothesis inasmuch as the perforated head region of the spermatheca is shown to appear very early in ontogeny, and is presumably plesiomorphic. Additionally, pierced spermathecae or equivalent structures appear in many entelegyne families.

For the evolution of entelegyne spiders, Forster (1980:278) proposed a migration of the opening of the early spermatheca "beyond the gonopore onto the external surface of the abdomen and a new duct—the fertilization duct—develops to direct the sperm from the receptacula [= spermatheca] into the bursal cavity [= uterus externus]." Bhatnagar and Rempel (1962) found in *Latrodectus* that the anlage of the female copulatory organ originates internally as an ectodermal structure in the anterior wall of the uterus externus and migrates in the course

of development to the ventral external surface. The internal origin of the female copulatory organ in *Latrodectus* may be unique. However, if it occurs in other genera of theridiids or even other families, this would be important in interpretation of the evolution of entelegyne spiders. If it is shown to represent a primitive condition, it would furthermore support Forster's hypothesis of an internal origin of the female copulatory organs.

In Lycosidae (Sadana, 1972) and Pisauridae the female copulatory organs develop externally at the ventral surface of the opisthosoma and not in the uterus externus. This could be regarded as a derived mode of development of the female copulatory organs. Because Strand (1906) sectioned only antepenultimate and penultimate instars, his study does not include the very early stages of the anlagen.

Järvi (1905; 1908:755) presented a speculative model, based on comparative morphology of female copulatory organs in Lycosidae and Pisauridae. He postulated that the spermathecae are derivates of the anterior wall of the uterus externus ("Scheide"). According to his hypothesis, the spermathecae were originally located deeper inside the body, with their openings inside the uterus externus. The openings of the spermathecae later migrated to the outer ventral surface of the opisthosoma. Once located in the ventral body wall above the epigastric furrow, the shape of the openings changed to become slit-like, thus forming the epigynal folds. Osterloh (1922:377, 381) agreed with Järvi and argued that the fertilization groove ("Befruchtungsrinne") in *Meta segmentata* can be regarded as the aboral part of the epigynal fold sensu Järvi. Furthermore, he concluded (1922:386) that the fertilization ducts ("Befruchtungskanäle") evolved from fertilization grooves. This hypothesis would not require the fertilization duct of entelegyne spiders to break through secondarily as Forster suggested, but would allow for simultaneous evolution of the copulatory and fertilization ducts. In this very speculative model, all intermediate forms of receptaculate female genitalia would be functional. This hypothesis could be tested by studying the morphology and ontogeny of female copulatory organs in haplogyne spiders. Should such a study provide data on the homology of parts between haplogyne and entelegyne

spiders, the ontogenetic evidence could be important for the interpretation of primitive and derived character states.

Summary

(1) The female copulatory organs in American Pisauridae consist of two epigynal folds. The internal bases of the epigynal folds form the copulatory duct, a tripartite spermatheca, and the fertilization duct.

(2) In ontogeny, the female copulatory organs are built by two lateral, longitudinal folds above the epigastric furrow in the ventral body wall of the opisthosoma.

(3) Based on ontogenetic evidence, the spermathecae of all Pisauridae are homologous. The spermathecae possess a base with an enlarged lumen and a stalk that leads to the head of the spermatheca. The latter is covered with pores. The copulatory and fertilization ducts are never connected to the head of the spermatheca.

(4) In *Dolomedes*, the head of the spermatheca is reduced in size, and its enlarged base functions as a spermatheca proper. In *Architis*, the pores are restricted to one or two small regions on the head of their spermatheca. A straight anterior-posterior course of the epigynal folds (as in *Dolomedes scriptus*) is the primitive condition.

(5) The anlage of the head of the spermatheca with its pierced walls appears very early in ontogeny, thus supporting Forster's (1980) hypothesis on the evolution of female copulatory organs in entelegyne spiders.

(6) The diversity of the groundplan of the female copulatory organs in Pisauridae is not yet known. Neither are the Pisauridae sensu lato (Simon, 1898) nor sensu stricto (Lehtinen, 1967) defined by apomorphies. Several spider families were discussed as being close relatives, but no suitable outgroup has been established.

(7) As further data become available for other pisaurid genera, the character systems discussed in the present study will allow definitions of monophyletic groups within the Pisauridae, and selection of an appropriate outgroup in order to analyze the systematics of the family Pisauridae.

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