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ON THE USE OF AMPULLATE GLAND SILKS BY WOLF SPIDERS (ARANEAE, LYCOSIDAE) FOR ATTACHING THE EGG SAC TO THE SPINNERETS AND A PROPOSAL FOR DEFINING NUBBINS AND TARTIPORES

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ABSTRACT. The means by which female wolf spiders attach an egg sac to their spinnerets was investigated using scanning electron microscopy. In four *Pardosa* species, we observed that silk fibers emerging from ampullate gland spigots had been affixed to the surface of the egg sac. More specifically, primary (1°) and secondary (2°) major ampullate (MaA) glands and 1° and 2° minor ampullate (MiA) glands all contributed fibers for this purpose. The diameters of the 2° MaA and 2° MiA fibers were greater than those of the 1° MaA and 1° MiA fibers and, correspondingly, the widths of the 2° ampullate spigots were clearly greater than those of the 1° ampullate spigots. Larger 2° ampullate spigots were also observed in adult females of species from three other lycosid genera. Thus, 2° ampullate glands, which in araneoids function only in juveniles during proecdysis, are not only functional in adult female lycosids (and adult females of several other families), but they appear to play a greater role than the 1° ampullate glands in egg sac attachment. Observations made on the 1° and 2° ampullate spigots of adult females from species belonging to several other families are also presented. Cuticular structures referred to as nubbins and tartipores are present in some spinning fields on spinnerets. A proposal is made for defining these terms by a criterion, namely their different origins, which differs from that applied previously.

Keywords: Ampullate silk gland, *Pardosa*, *Hogna*, *Trochosa*, Lycosoidea

With some exceptions, those spiders that typically carry their egg sacs using only their spinnerets belong to one of the following three lycosoid taxa: the family Lycosidae, the family Trechaleidae, or the subfamily Rhoicininae (with *Shinobius* considered a member of the latter taxon, Yaginuma 1991; Sierwald 1993). The familial placement of Rhoicininae is uncertain (Sierwald 1993; Carico 1993), but its members are currently listed in Trechaleidae (see Platnick 2002). The exceptions referred to include other lycosoids (sensu Griswold et al. 1999) (e.g., the ctenid *Cupiennius*, Barth et al. 1991; Silva Davila in press) as well as non-lycosoids (e.g., the nesticids *Nesticus*, *Eidmannella*, Nielsen 1932:201; Bristowe 1958:223; Pötzsch 1963:30; the zorids *Voraptus*, *Neoctenus*, Lawrence 1964:34; Silva Davila in press, though in the latter paper *Neoctenus* is transferred to Trechaleidae). The spinnerets are also involved in carrying the egg sac in at least some genera within the lycosoid family Pisauridae (see Discussion), but here the chelicerae play the principal role in securing the egg sac, which is positioned below the sternum. At times, lycosids hold the egg sac in a similar attitude; e.g., during the last phase of egg sac construction, when assisting in spiderling emergence, or sometimes when fleeing, after one has attempted to take the egg sac away from the mother (e.g., Montgomery 1903; Lécaillon 1905). And, conversely, some pisaurids occasionally ‘‘drag the sac from the spinnerets alone in the same manner as a lycosid’’ (Bishop 1924:28).

As described in Carico (1993), Sierwald (1990a, 1993), Scheffer (1905) and literature cited by the first two authors, differences exist among lycosids, trechaleids, rhoicinines, and pisaurids with regard to egg sac structure and the maternal care afforded post-emergent spiderlings. Typically, the egg sacs of lycosids and rhoicinines are spherical or lenticular, those of pisaurids are spherical, while those of trechaleids are hemispherical. A seam joining the upper and lower valves of the egg sac is apparent among lycosids, trechaleids, and some rhoicinines (*Shinobius*), but not in some other rhoicinines (*Rhoicinus*) or pisaurids, and only in trechaleids is a 'skirt' (Carico 1993) produced at the seam.

Lycosid, trechaleid, and rhoicinine females continue to carry their progeny for a number of days after they have emerged from the egg sac (lycosids about 2–14 days, e.g., McCook 1884; Montgomery 1903:72,76,82,90; Engelhardt 1964:303,387; *Trechalea* about 17–19 days, Carico et al. 1985; *Shinobius* about 4 days, Kaihotsu 1988). But while lycosid spiderlings climb onto the mother's abdomen during this period, trechaleid spiderlings and at least *Shinobius* spiderlings (among rhoicinines) climb onto the outside of the egg sac, which the female continues to carry. However, Yaginuma (1991), specifying two *Arctosa* and one *Hygrolycosa* species, reports that transport on the egg sac, rather than on the mother's abdomen, also occurs in some lycosids. In those instances in which trechaleid spiderlings have been observed on the mother's abdomen, this appears to be due to crowding on the egg sac with consequent spill-over (Carico 1993), just as lycosid spiderlings may spill over onto their mother's cephalothorax.

Among pisaurids (where known), the egg sac is carried by the female until shortly before the young emerge, or at latest when the first spiderlings begin to emerge (Gertsch 1979:197). Typically, the egg sac is then secured within a nursery web. The mother builds the network of silk fibers that constitute the nursery web before and/or after the end of the egg-sac-carrying period, often on vegetation, with the spiderlings adding fibers after their emergence. The post-emergent spiderlings remain within the nursery web, guarded by the mother (though see Montgomery 1909: 556; Forster 1967:84), for a period of time that again varies considerably, sometimes even within a species (e.g., *Dolomedes fimbriatus* (Clerck 1757) spiderlings may remain in the nursery web from 3 or 4 days (Bristowe 1958:191) to about 3 weeks (Nielsen 1932: 134)). After this period the spiderlings disperse. Kaihotsu (1988) reports that *Shinobius* females, after carrying their young on the outside of the egg sac for a few days, then hang the egg sac with spiderlings in a nursery web, where the spiderlings remain for about one day.

This study is concerned with the specific silk glands used by lycosids for attaching the egg sac to the spinnerets. The impetus for the study can be explained as follows. Observations made on spinnerets by a number of workers indicated that a certain category of ampullate silk glands, what we call secondary (2°) ampullate silk glands, are functional in juvenile spiders of most, if not all, entelegyne taxa. However, in only some entelegynes are 2° ampullate glands also functional in adults (sometimes only in the females, as in lycosids). The only role assigned to these silk glands that we were aware of when we began this study is to produce silk fibers during one specific period in the molt-intermolt cycle of juveniles (detailed below). The question thus arose, what are 2° ampullate silk glands used for when they are retained in adults? It occurred to us that if these silk glands are involved in egg sac attachment in lycosoids, it might be a situation in which we could, in effect, catch spiders in the act of drawing fibers from these glands and, thus, demonstrate their use in at least one specific application in certain adult spiders. At that time we were not aware that Carico (1993) had already observed certain 2° ampullate gland fibers being used for egg sac attachment to the spinnerets in trechaleids. As we describe below, trechaleids and the lycosids that we have examined (primarily *Pardosa*) show similarities and differences with respect to egg sac attachment, including in their use of 2° ampullate silks. In partial answer to the above question, all we know at this time is that adult females of at least some lycosid and trechaleid (Carico 1993) genera use silk from 2° ampullate glands to help secure the egg sac to the spinnerets.

To provide a better overall perspective on 2° ampullate silk glands and their roles, the following section reviews different categories of ampullate silk glands. It is followed by four sections dealing with nubbins and tartipores, protuberances present in some spinning fields. These sections are included because our interpretations of spinneret micrographs obtained during this study rely on and make reference to these protuberances. And because our basis for distinguishing nubbins from tartipores differs from that of earlier authors, and also differs from our own earlier views, the first of these four sections explains how we arrived at our current definitions for nubbins and tartipores. The last three sections review some aspects of the occurrence of these protuberances. We hope this overview will be useful in light of the growing importance of these structures in phylogenetic studies. In addition to presenting observations made on the spinnerets and egg sacs of some female lycosids, this paper contains comparative observations made on the spinnerets of male lycosids and the spinnerets of spiders from several other families in which adult females retain apparently functional 2° ampullate glands.

Categories of ampullate silk glands and their roles.—The ampullate silk glands of spiders within the Orbiculariae and some other taxa (e.g., Hersiliidae, Kovoor 1984; Segestriidae, Clubionidae, Gnaphosidae, Thomisidae, Kovoor 1987; Oxyopidae, Kovoor & Muñoz-Cuevas 1998) can be divided, on the basis of histochemical differences, into major ampullate silk (MaA) glands and minor ampullate silk (MiA) glands (reviewed in Kovoor 1977, 1987; also Kovoor & Peters 1988). The ducts of the MaA glands connect to spigots located on the anterior lateral spinnerets (ALS) while MiA gland ducts connect to spigots on the posterior median spinnerets (PMS). In some other spiders, however, including the Lycosidae, histochemical differences are not readily apparent between those ampullate glands with ducts that empty on the ALS versus those with ducts emptying on the PMS (Kovoor 1976, 1987). One may therefore question the validity of recognizing two different types of ampullate glands in such taxa. Nevertheless, for clarity and in keeping with precedents (e.g., Platnick et al. 1991:2), any ampullate glands with ducts attached to the ALS will be called MaA glands and any with ducts attached to the PMS will be called MiA glands (Table 1).

In more basal araneoids, including those in the families Araneidae and Tetragnathidae (Griswold et al. 1998), both the MaA and MiA glands can be further subdivided into a single pair of primary (1°) MaA/MiA glands and two pairs of 2° MaA/MiA glands (Table 1) (Townley et al. 1993; Tillinghast & Townley 1994). Observations made on spinnerets (Coddington 1989; Forster et al. 1990; Peters & Kovoor 1991; Hormiga 1994a,b, 2000; Griswold et al. 1998) suggest a tendency for the more derived araneoids to lack 2° MiA glands. The 1° MaA and 1° MiA glands function in each juvenile stadium from immediately after ecdysis (even as the spider is hanging by its ‘molting threads’) until about the beginning of the following proecdysis (the few days preceding ecdysis during which internal changes take place in preparation for ecdysis), as well as throughout adulthood (Townley et al. 1993). During proecdysis these glands are remodeled, rendering them temporarily nonfunctional (Townley et al. 1991). The task of producing ampullate silk during each proecdysis is taken over by one of the two pairs of 2° MaA glands and one of the two pairs of 2° MiA glands. Each pair of 2° ampullate glands cycles through growth and regression phases, reaching maximum size and accumulation of luminal contents at proecdyses in every other juvenile stadium, with one pair of 2° MaA/2° MiA glands producing silk during proecdysis in even-numbered stadia and the other pair functioning in odd-numbered stadia (Townley et al. 1993). Because only one of the two pairs of 2° MaA/2° MiA glands produces silk in a given juvenile stadium (i.e., is ‘open’, see Table 1), there is only one 2° MaA spigot on each ALS and one 2° MiA spigot on each PMS of juveniles (in addition to the single 1° MaA spigot and single 1° MiA spigot on each ALS and PMS, respectively). After the final molt, with no additional proecdyses to pass through, both pairs of 2° MaA/2° MiA glands degenerate (Sekiguchi 1955b; Townley et al. 1991). Thus, 2° ampullate glands do not function in adults and only nonfunctional vestiges, termed nubbins (Coddington 1989; Yu & Coddington 1990), of 2° ampullate spigots are present on adult ALS and PMS (Sekiguchi 1955b; Peters 1955; Mikulska 1966; Wilson 1969). This situation exists in both sexes. External examinations of spinnerets indicate that this description, outlined in Table 1, applies not only to basal araneoids, but to some non-araneoids (e.g., oxyopids, Kovoor & Muñoz-Cuevas 1998), and, whatever their superfamilial placement, to some mimetids (see data for *Mimetus* in Table 3; see also mimetid spinneret micrographs in Platnick & Shadab 1993). Interestingly, it may be that the above description applies to some species within the mimetid genus *Ero*, but not others (cf. figs. 29, 30 with figs. 41, 42 in Platnick & Shadab 1993, noting especially the presence of a MiA nubbin and MiA tartipore (tartipore defined below) in fig. 42 and the

Table 1.—The division of ampullate silk glands into different categories on the basis of which spinnerets receive their ducts (major vs. minor), whether glands are functional in both juveniles and adults or just in juveniles during proecdysis (primary (1°) vs. secondary (2°)), and whether 2° ampullate glands have an outlet to the extracorporeal environment in a given stadium or not (open vs. blocked). This scheme is based on observations made primarily on *Araneus* (Townley et al. 1993; Townley 1993; Tillinghast & Townley 1994) and applies to both sexes. Lycosids and the species from the other families in Table 2 deviate from this table only in that 2° MaA and 2° MiA glands of females apparently function not only in juveniles during proecdysis, but one pair of each is functional in adults as well. The double-headed arrows between open and blocked 2° ampullate glands indicate that a given pair of glands is alternately open and blocked; open throughout one stadium (i.e., from one ecdysis to the next), blocked throughout the following stadium, open again in the stadium after that, and so on.

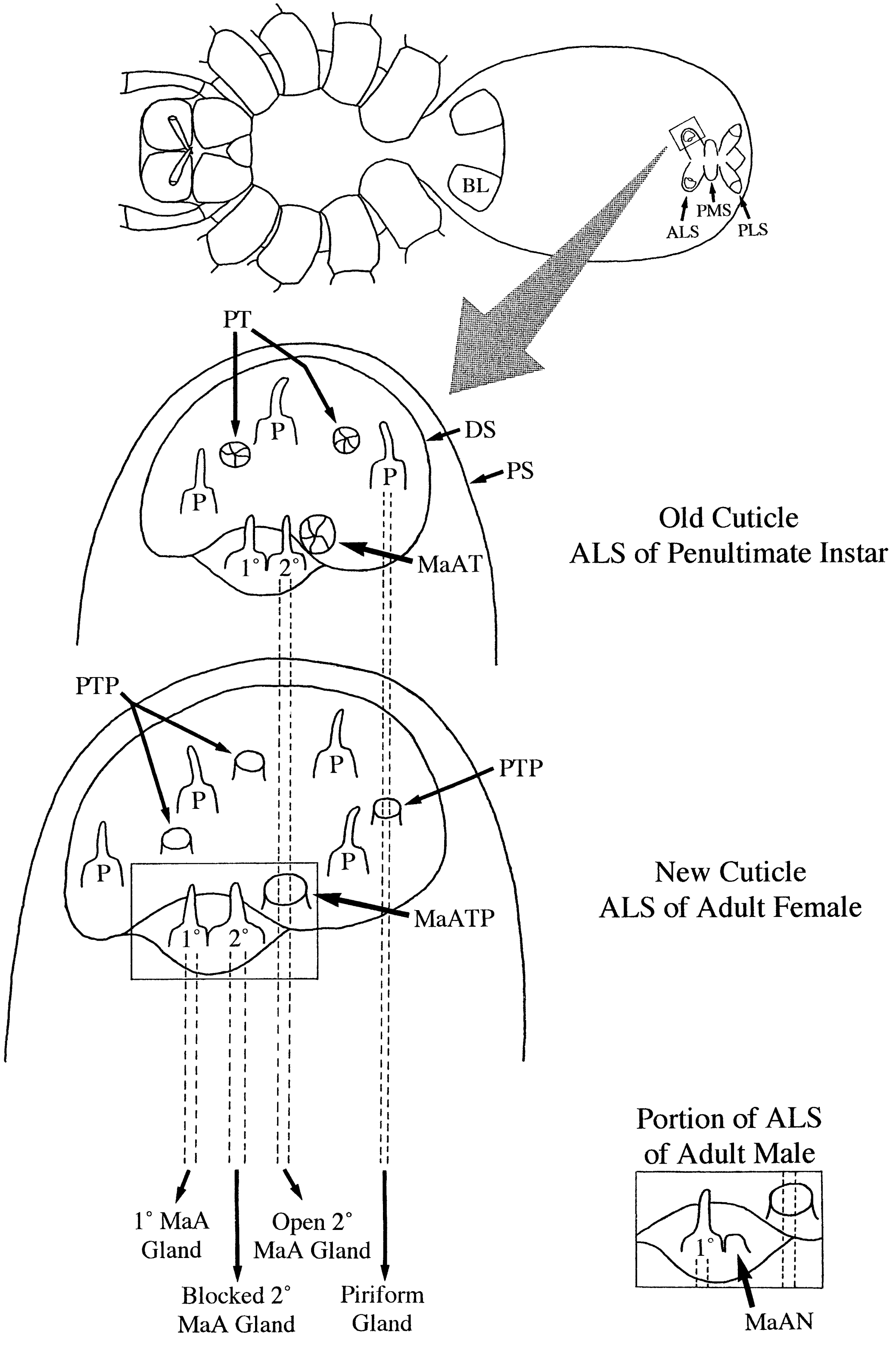
Ampullate Silk Glands 6 pairs produce silk fibers used in a variety of applications including draglines and non-sticky structural elements of webs							
Major Ampullate Silk (MaA) Glands 3 pairs ducts lead to anterior lateral spinnerets (ALS)				**Minor Ampullate Silk (MiA) Glands** 3 pairs ducts lead to posterior median spinnerets (PMS)			
1° MaA Glands 1 pair functional in juveniles (from ecdysis to start of next proecdysis) and adults	**2° MaA Glands** 2 pairs functional in juveniles only (during proecdysis only)			**1° MiA Glands** 1 pair functional in juveniles (from ecdysis to start of next proecdysis) and adults	**2° MiA Glands** 2 pairs functional in juveniles only (during proecdysis only)		
	Open 2° MaA Glands 1 pair ducts connect to spigots that open to the outside environment	⟷	**Blocked 2° MaA Glands** 1 pair ducts do not connect to spigots that open to the outside environment		**Open 2° MiA Glands** 1 pair ducts connect to spigots that open to the outside environment	⟷	**Blocked 2° MiA Glands** 1 pair ducts do not connect to spigots that open to the outside environment

absence of these protuberances in fig. 30; see also Schütt 2000:145).

In contrast to the situation just described for basal araneoid taxa, examinations of spinnerets from spiders in certain amaurobioid (sensu Griswold et al. 1999) and dionychan (sensu Coddington & Levi 1991) families, including the Lycosidae (Table 2), reveal a sexual dimorphism wherein males appear to conform to the above description, but females do not (Fig. 1). Instead, adult females retain apparently functional 2° MaA and 2° MiA spigots, one pair of each, indicating that they use 2°, as well as 1°, ampullate glands as adults. In trechaleids, Carico (1993) has observed the use of 1° and 2° MiA silks by adult females for securing the egg sac to the spinnerets. Here we report that adult female *Pardosa* use 1° and 2° MaA and 1° and 2° MiA silks to attach their egg sacs to their spinnerets. The 2° ampullate fibers have greater diameters than the 1° ampullate fibers, indicating a greater contribution from the 2° ampullate glands to the support of the egg sac.

Terminology.—*Nubbins and tartipores:* As mentioned, the term 'nubbin' has been applied to cuticular protuberances on adult ALS and PMS that appear to be nonfunctional vestiges of 2° MaA and 2° MiA spigots, respectively. Other cuticular protuberances, scattered within piriform and aciniform spinning fields (Kovoor 1986; Platnick 1990; Yu & Coddington 1990), as well as on the PMS and posterior lateral spinnerets (PLS) of at least some mygalomorphs (Glatz 1973; Palmer 1990), have been called 'tartipores' (Shear et al. 1989; Yu & Coddington 1990). Originally, the distinction between a nubbin and a tartipore was based on whether the protuberance is a morphological singular and can, therefore, be uniquely designated (nubbin) or if it is one of several, or many, such structures on a single spinneret that are designated collectively (tartipore) (Yu & Coddington 1990; see also Coddington 1989:81). Both nubbins and tartipores were tentatively interpreted to be vestigial spigots. Additional observations, however, revealed that the protuberances identified as tartipores are not vestigial spigots. Instead, they are the remains of collared openings that formed in the cuticle when it was first being laid down during proecdysis beneath the old cuticle (Townley et al. 1993). The openings allowed silk gland ducts to maintain their attachments to spigots on the old cuticle during proecdysis, despite the formation of the intervening new cuticle (Fig. 1). Thus, while some protuberances do seem to be vestigial spigots, others have a very different origin, being remnants of these openings.

After realizing that we were actually dealing with two different categories of cuticular protuberances, we made an ill-devised attempt to both retain the original distinction between nubbins and tartipores (singulars versus multiples) and distinguish vestigial spigots from remnants of openings by use of the adjectives 'vestigial-type' and 'non-vestigial-type', respectively (Townley et al. 1993). We soon abandoned this approach in favor of another, not previously published, that is concerned only with the two different origins of the protuberances under consideration (for further explanation see Townley 1993:7, 8). The latter approach, which we will follow in this paper, retains the terms nubbin and tartipore, but defined as follows: *Nubbin:* a nonfunctional, only partially formed, i.e. vestigial, spigot, either morphologically singular or multiple. *Tartipore:* a cuticular scar, morphologically singular or multiple, that results, after ecdysis, from a collared opening forming in the developing exoskeleton during proecdysis; the opening accommodates a silk gland duct, allowing the duct to remain attached to a spigot on the old exoskeleton during proecdysis. By these definitions the protuberances that were initially called tartipores (those among piriform and aciniform spigots) are still called tartipores (Fig. 1). However, only some of the structures previously referred to as nubbins are still called nubbins by our definition. For example, as in earlier reports, we identify as nubbins those nonfunctional protuberances in some adults that occur where functional 2° MaA/2° MiA spigots would have formed if the spider had instead molted to yet another juvenile instar (see Figs. 1, 13, 15). But there are other protuberances near ampullate spigots in many adult and juvenile araneomorphs, previously called nubbins (e.g., Yu & Coddington 1990; Townley et al. 1991, 1993; Tillinghast & Townley 1994), that we now identify as ampullate tartipores, including the ''second nubbin'' on the PMS of adult anapids and some synotaxids (Griswold et al. 1998:41) and the ''second remnant'' on the PMS of adult oxyopids (Kovoor & Muñoz-Cuevas 1998:


BL
PMS
ALS
PLS
PT
P
DS
PS
MaAT
1°
2°
Old Cuticle
ALS of Penultimate Instar
PTP
PTP
MaATP
New Cuticle
ALS of Adult Female
Portion of ALS
of Adult Male
MaAN
1° MaA
Gland
Open 2°
MaA Gland
Blocked 2°
MaA Gland
Piriform
Gland

136). This is not the first time such protuberances have been referred to as tartipores (Platnick & Forster 1993:7, 9; Griswold et al. 1998:11), but in these earlier instances the distinction made between tartipores and nubbins was not stated. The term tartipore was perhaps applied solely because of the resemblance between ampullate tartipores and the more well known tartipores in piriform and aciniform spinning fields, rather than because of recognition of what tartipores, as here defined, represent. As indicated above, ampullate tartipores mark the sites where 2° ampullate gland ducts passed through the cuticle during the most recent proecdysis, enabling 2° ampullate glands to function throughout proecdysis (Fig. 1). Note that Fig. 1 depicts only the ALS from a lycosid and so only spigots, tartipores, and ducts of MaA and piriform glands are shown. Bear in mind that a comparable situation exists on the PMS with the spinning apparatus of MiA and aciniform glands, respectively.

Ampullate gland nubbins versus ampullate gland tartipores.—When examining spinnerets, care must be taken if one wishes to determine whether ampullate nubbins and tartipores are present or not, as well as distinguish the former category from the latter. Viewing the spinnerets at various angles and from different directions is sometimes required. In some adult araneoids, for example, the MiA nubbin and MiA tartipore on a PMS often occur side by side (e.g., Coddington 1989:fig 16; Platnick et al. 1991:fig. 271, lower black arrow, tartipore on left, nubbin right; Townley et al. 1991:fig. 24; lower arrow to tartipore, upper to nubbin; Hormiga et al. 1995:fig. 16C, nubbin left, tartipore right) and can be interpreted as a single structure if viewed at too low a magnification or from an

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Figure 1.—Schematic diagram of the left anterior lateral spinneret (ALS) of a female lycosid during proecdysis, shortly before the ecdysis that yields an adult. The upper ALS diagram represents the cuticle of the penultimate instar which will be cast off at ecdysis. The ALS diagram below this represents the underlying, newly-formed cuticle which will be part of the exoskeleton of the adult. Shown is the entire distal segment (DS) of the ALS, to which the major ampullate (MaA) spigots (labeled as '1°' and '2°') and piriform spigots (P) are restricted, atop the more distal portion of the ALS proximal segment (PS).To aid orientation, a much less magnified depiction of the same part of the left ALS is enclosed by a box in the ventral view of the spider, shown at top, in which the spinnerets are presented as if artificially spread. By late proecdysis, the duct of the primary (1°) MaA gland, previously connected to a spigot on the old cuticle (that labeled '1°'), has just been re-modeled (Townley et al. 1991, 1993) and is now connected to a spigot on the new cuticle (again labeled '1°') (silk gland ducts are indicated by dashed lines). Thus, the 1° MaA gland, nonfunctional during proecdysis, will again be functional immediately after ecdysis. Collared openings (tartipore progenitors) form in the new cuticle to accommodate the ducts of any silk glands that are to remain functional throughout proecdysis. The ducts of two such silk glands are shown connected to spigots on the old cuticle. After ecdysis the collapsed forms of these openings (tartipores) will remain evident in the new cuticle. A single MaA tartipore progenitor (MaATP) forms on each ALS of the new cuticle to accommodate the duct of a secondary (2°) MaA gland. Multiple piriform tartipore progenitors (PTP) also form on each ALS, one per piriform gland duct. (For clarity only a few piriform spigots are shown, and of those on the old cuticle, the duct connected to only one is shown. In reality, more piriform spigots are present and it appears that each piriform spigot on the old cuticle remains connected to a functioning duct, thus requiring the formation of one PTP on the new cuticle for each piriform spigot on the old cuticle.) The 2° MaA gland identified as 'open' will become 'blocked' at ecdysis (because its outlet, the spigot, will be lost along with the rest of the old cuticle), and, conversely, that identified as 'blocked' will become 'open' (since the 2° MaA spigot it is connected to will be open to the outside environment after ecdysis). The portion of the female new cuticle shown within a box differs from the situation in males (depicted at lower right) because 2° ampullate spigots do not form in adult males. Only ampullate nubbins (MaA nubbin (MaAN) on ALS, MiA nubbin on PMS) form in the positions occupied by 2° ampullate spigots in adult females and, thus, all 2° ampullate glands are 'blocked' and nonfunctional in adult males. Structures not drawn precisely to scale. BL, book lung; ALS, anterior lateral spinneret; PMS, posterior median spinneret; PLS, posterior lateral spinneret; DS, distal segment of anterior lateral spinneret; PS, proximal segment of anterior lateral spinneret; P, piriform gland spigot; PT, piriform tartipore; PTP, piriform tartipore progenitor; 1°, primary major ampullate gland spigot; 2°, secondary major ampullate gland spigot; MaAT, major ampullate tartipore; MaATP, major ampullate tartipore progenitor; MaAN, major ampullate nubbin.

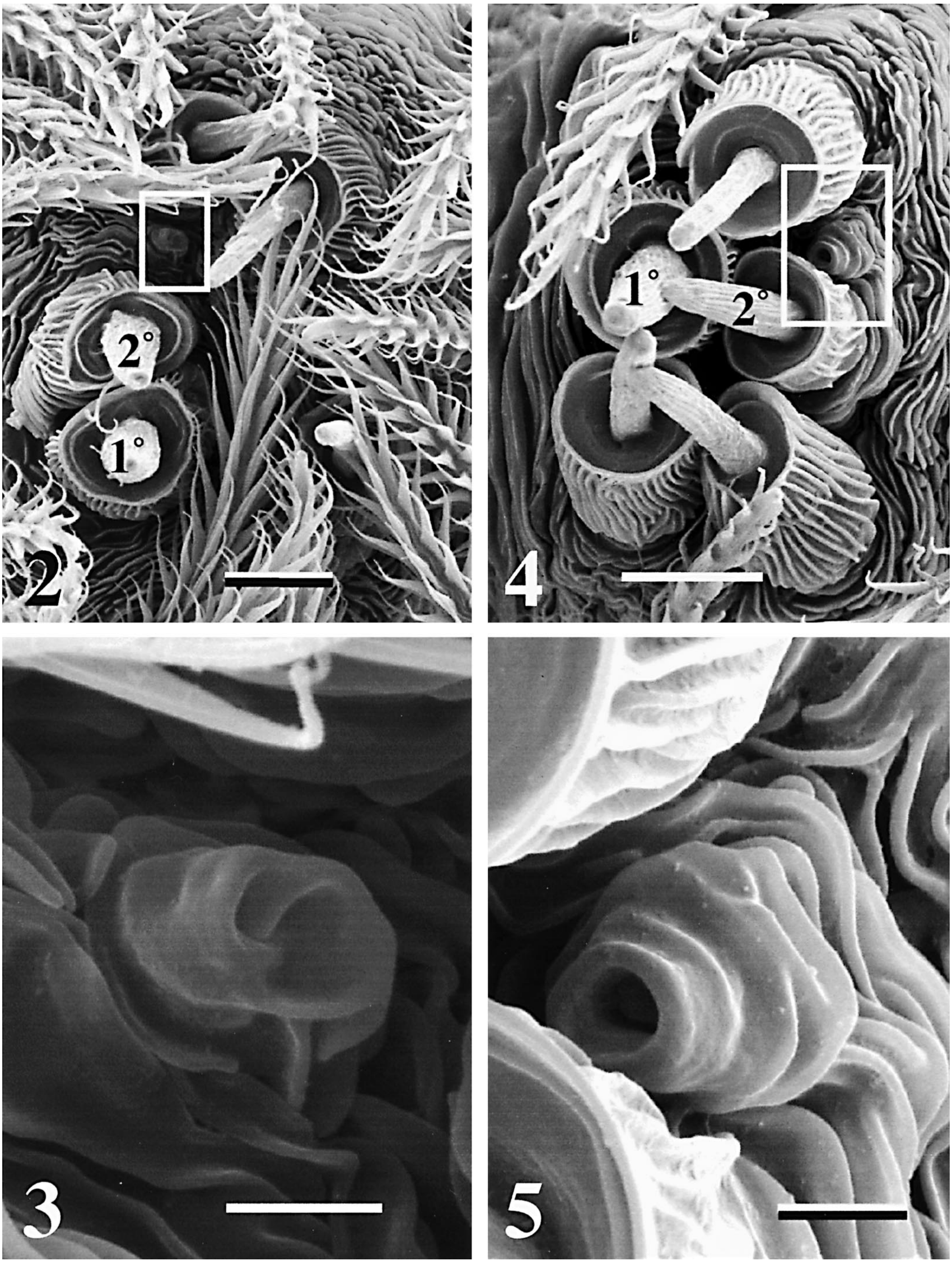
inopportune angle, or if the MiA nubbin is especially small. In describing the PMS of adult males of two anapid species, Platnick et al. (1991:60) noted the presence of ‘‘a large posterior minor ampullate gland spigot accompanied by a vestigial remnant bearing a short lobe on its medial side’’. The ‘‘vestigial remnant’’ is a MiA tartipore, the ‘‘short lobe’’ is a MiA nubbin. Even with careful observation it can sometimes be difficult, especially with certain species, to discern a given tartipore or nubbin. We were puzzled for a time by our inability to spot a MaA tartipore on the ALS of juvenile and adult *Araneus cavaticus* (Keyserling 1882) until it became clear that this tartipore occurs at a site where, in this species, the cuticle is typically compressed or overhung by the piriform spinning field and the tartipore is obscured (Townley et al. 1993). In contrast, single or multiple MaA tartipores are often clearly visible in many other araneomorphs as a number of published micrographs attest (several were cited in Townley et al. 1993:36 as ‘‘non-vestigial-type MaA nubbins’’; other examples include Platnick et al. 1991: fig. 16, multiples in *Gradungula*, fig. 39, a single in *Thaida*, fig. 277, a round single in *Pachygnatha* next to smaller oblong MaA nubbin; Harvey 1995: fig. 11, a single in *Ambicodamus* posterolateral to the 2° MaA spigot; Davies 1998a:fig. 68, a single in *Jalkaburra* lateral to the 2° MaA spigot; Platnick 1999: fig. 3, a single in *Liocranoides* between and lateral to 1° and 2° MaA spigots; Hormiga 2000:plate 42B, a single in *Laminacauda* posterolateral to MaA nubbin, larger than the multiple piriform tartipores). In this paper, single MaA tartipores can be seen in Figs. 1, 8, 9, 12, 13, 16, 18, 22, 24, 26, 28, 30, 32, 34, 36, 40 & 41 and single MiA tartipores can be seen in Figs. 10, 11, 14, 15, 19–21, 23, 25, 27, 29, 31, 33, 35, 37–39 & 42.

Given that the occurrence and number of ampullate ‘‘nubbins’’ (i.e., ampullate nubbins and/or tartipores) are being used as characters in cladistic analyses (Coddington 1990; Hormiga et al. 1995; Scharff & Coddington 1997; Griswold et al. 1998, 1999; Hormiga 2000), accurately determining the presence/absence of ampullate tartipores and nubbins, and making a clear distinction between the two, can only aid phylogenetic studies.

Occurrence of tartipores.—Tartipores can occur in the exoskeletons of adults and juveniles, at least as early as second instars (see Methods for the definition of the first instar used in this paper). We have not seen and are not aware of any reports of tartipores in first instars. However, given the occurrence of functioning silk glands and spigots in postembryos of at least some mygalomorph taxa (Bond 1994), the possibility of tartipores in first instars of such taxa cannot be dismissed. But at least for those araneomorphs in which functional silk glands and spigots first appear in first instars, tartipores do not need to form until deposition of the second instar cuticle begins. Consequently, for such spiders, tartipores would first be seen in second instars. (The presence of one, presumably 1°, MaA spigot base per ALS in *Nephila* (Tetragnathidae) postembryos has been described by Bleher (2000), but their ability to produce silk is uncertain and only the ducts of 2° ampullate glands are known to be accommodated by ampullate tartipores.)

It is of interest, therefore, that protuberances, reminiscent of but recognizably different from tartipores, are sometimes evident on the ALS and PMS of first instars, in positions consistent with those of ampullate tartipores in later instars. We have seen them near 2° ampullate spigots on the ALS and PMS of first instar *Pardosa xerampelina* (Keyserling 1877) (Figs. 2–5) and *Octonoba sinensis* (Simon 1880) (Uloboridae), and on the PMS of first instar *Argiope aurantia* Lucas 1833 (Araneidae) and *Herpyllus ecclesiasticus* Hentz 1832 (Gnaphosidae). We tentatively refer to them as ‘pre-tartipores’ (not to be confused with the tartipore progenitors referred to in Fig. 1). If they truly are precursors of the tartipores in later instars, their occurrence suggests that the epithelial cells that are capable of forming tartipores, at least ampullate tartipores, are already determined by the postembryo stage.

Occurrence of nubbins.—In general, nubbins as here defined occur in adults, being more abundant in males (largely since silk glands used solely or primarily in prey capture tend to regress in adult males), and are ontogenetically vestigial. That is, they are located in adults in positions where functional spigots would have formed if the spider had remained a juvenile after its most recent molt. In addition to the MaA and MiA nubbins present in a variety of adult male and female araneocla-



Figures 2–5.—ALS and PMS from a first instar *Pardosa xerampelina* (removed from dorsum of its mother's abdomen) showing protuberances, tentatively termed 'pre-tartipores', in positions that are held by ampullate tartipores in later instars: 2. Right ALS, entire spinning field shown (two MaA and three piriform spigots), pre-tartipore in box; 3. Higher magnification of pre-tartipore from Fig. 2; 4. Right PMS, entire spinning field shown (two MiA and three aciniform spigots), pre-tartipore in box; 5. Higher magnification of pre-tartipore from Fig. 4. Posterior at top, lateral at right in all four figures. Scale bars (2, 4) = 5 μm; (3, 5) = 1 μm.

Table 2.—Spider species in which adult females are known to have two MaA spigots (1° and 2°) on each ALS and two MiA spigots (1° and 2°) on each PMS while adult males have one MaA spigot (1°) on each ALS and one MiA spigot (1°) on each PMS. The families listed here are almost certainly not the only ones that contain species fitting this description. Note that *Neoramia* (Agelenidae) apparently do not fit this description (Griswold et al. 1999); nor do some salticid genera (see 'Ampullate gland spigot, nubbin, tartipore complements' in Results) or several amaurobiid genera, including *Amaurobius* (see 'Comparative ampullate gland spigot morphology' in Discussion). Also, this description may not extend to all *Coras* species (see 'Ampullate gland spigot, nubbin, tartipore complements' in Results).

Family	Species	References
Lycosidae	*Gladicosa gulosa* (Walckenaer 1837)	this study
	Pardosa amentata (Clerck 1757)	Richter 1970
	Pardosa lapidicina Emerton 1885	this study
	Pardosa lugubris (Walckenaer 1802)	Wąsowska 1977
	Pardosa modica (Blackwall 1846)	this study
	Pardosa moesta Banks 1892	this study
	Pardosa saxatilis (Hentz 1844)	this study
Pisauridae	*Dolomedes scriptus* Hentz 1845	this study
	Pisaurina mira (Walckenaer 1837)	this study
Agelenidae	*Agelena labyrinthica* (Clerck 1757)	Kokociński 1968
	Agelenopsis naevia (Walckenaer 1842)	this study
	Agelenopsis potteri (Blackwall 1846)	this study
Amaurobiidae	*Coras aerialis* Muma 1946	this study
Thomisidae	*Misumenops asperatus* (Hentz 1847)	this study
	Xysticus cristatus (Clerck 1757)	Wąsowska 1977
Philodromidae	*Tibellus oblongus* (Walckenaer 1802)	Wąsowska 1967, 1977; this study
Clubionidae	*Clubiona phragmitis* C.L. Koch 1843	Mikulska 1969; Wąsowska 1969; Wiśniewski 1986a,b
Miturgidae	*Cheiracanthium mildei* L. Koch 1864	this study
Salticidae	*Salticus scenicus* (Clerck 1757)	this study

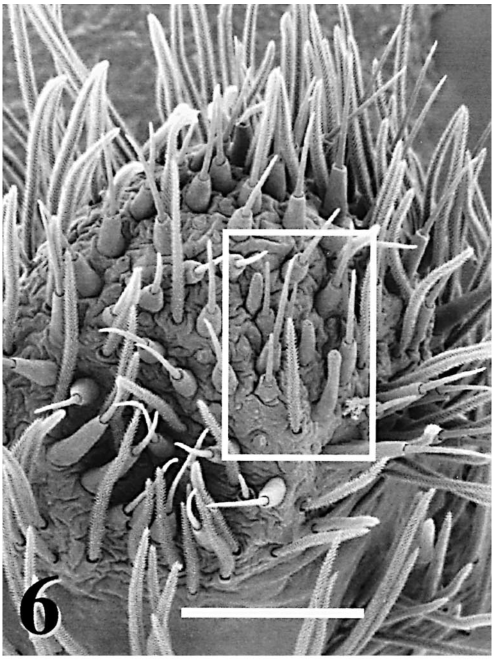
dans, flagelliform and aggregate nubbins form on the PLS of many adult male araneoids (Sekiguchi 1955a; Peters & Kovoor 1991:fig. 3b; Platnick et al. 1991:fig. 275; Townley et al. 1991:fig. 16; Townley 1993:fig. 16; Griswold et al. 1998:figs. 25D, 39D, 43D), though a number of males within the 'reduced piriform clade' of Griswold et al. (1998) (see also Hormiga 2000) and the Micropholcommatidae (Schütt 2000) retain the aggregate/flagelliform spigot triad. Other examples include aciniform nubbins on the PMS (Müller & Westheide 1993) and PLS (pers. obs.) of adult male *Argiope* and on the PMS of some adult male uloborids (Kovoor & Peters 1988:53), pseudoflagelliform nubbins on the PLS and paracribellar nubbins on the PMS of some adult male deinopoids (Kovoor & Peters 1988; Peters 1992), paracribellar nubbins on the PMS of adult male austrochilids (Peters 1983; Platnick et al. 1991:fig. 33), and nubbins of uncertain gland type on the ALS of adult male *Hypochilus*, next to the single, large ampullate spigot (Platnick et al. 1991:fig. 4; Townley 1993:figs. 17D,E). By the interpretation of Platnick et al. (1991:51) the latter would be MaA nubbins.

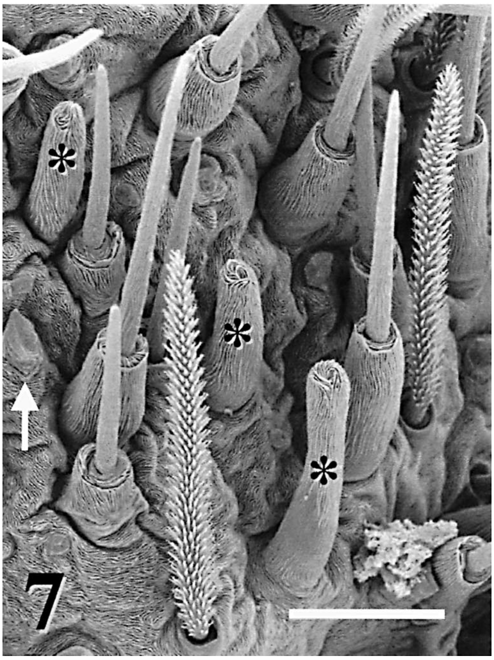
Among the examples of exceptions to the general rule are nubbins occasionally seen in early instar *Cyrtophora* (Araneidae) that suggest phylogenetic vestiges of either aggregate or flagelliform spigots. In an examination of six first instar *Cyrtophora citricola* (Forskål 1775), on one PLS Peters (1993:figs. 11b, c) observed a single ''shaft-like structure'' on the vestigial plate of the aggregate-flagelliform triad. (On nine PLS one or two ''knobs with pores'' were seen on these vestigial plates, but we do not interpret these as nubbins.) Nubbins that are also apparently phylogenetic vestiges of aggregate spigots are often retained right up to maturity in female *Drapetisca socialis* (Sundevall 1833) (Linyphiidae); functional aggregate spigots are absent throughout the ontogeny of these spiders (Schütt 1995). The occurrence of a MaA nubbin on the ALS of penultimate instar female *Malala lubinae* Davies 1993 (tentatively Amaurobiidae, Platnick 2002) (Davies 1993) is also atypical.

In the course of the present study we observed a few consistently-located aciniform nubbins on the PMS (Figs. 19–21) and PLS (Figs. 6, 7) of some juvenile and adult lycosids, the details of which are given in the Results. The reason these nubbins form with as much regularity as we have seen, particularly in *Hogna*, remains to be explained. Certainly, it is not unusual in an aciniform or piriform spinning field to encounter occasional incompletely formed spigots (i.e., nubbins). But such nubbins are presumably teratological, given their random and, typically, asymmetrical occurrence (present on one spinneret but not its pair). The occurrence of aciniform nubbins in *Hogna*, on the other hand, is neither random nor asymmetrical. Because they are present in juvenile females, they are another example of atypical nubbins.

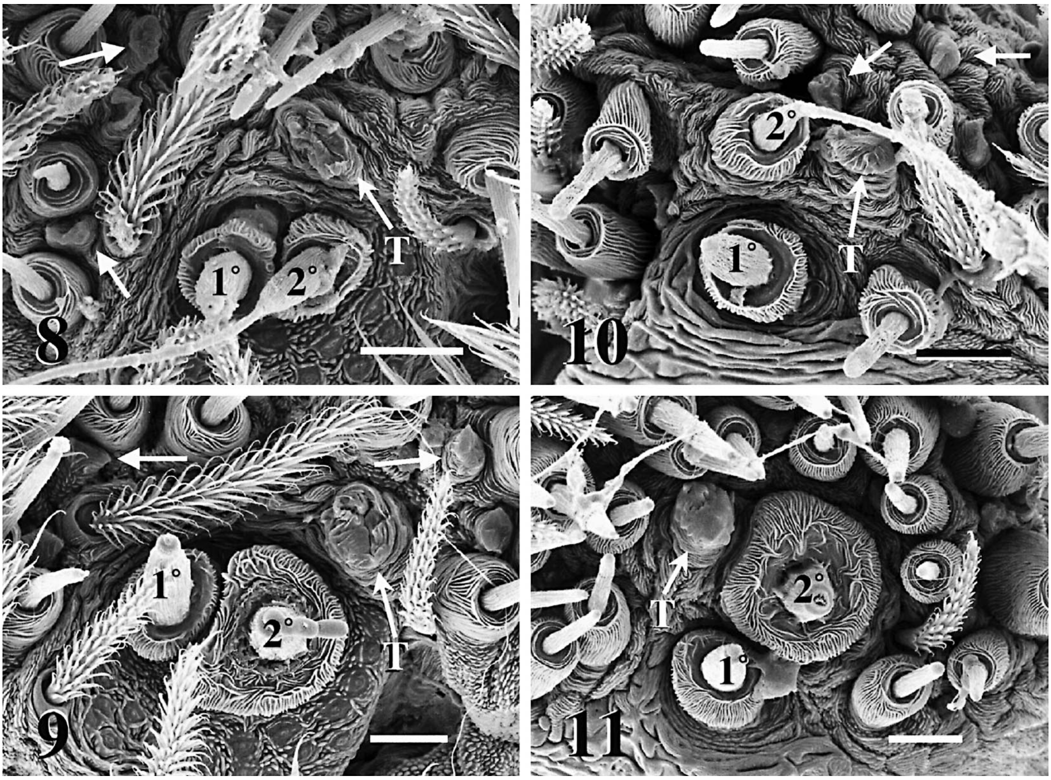
Nubbins resulting from different gland types and, in some cases, nubbins of the same gland type in different taxa vary considerably in the extent to which their development proceeds before it is aborted. Thus, nubbins may range from being small mounds or small spherical or oblong protuberances, e.g., in the case of some MaA and MiA nubbins, to being essentially normal spigot bases on which shafts never develop, e.g., in the case of many aciniform and paracribellar nubbins of adult males, as well as the aforementioned nubbins of adult male *Hypochilus*. It may even be with these more developed nubbins that a shaft does sometimes form on the spigot base, but the junction of the base and shaft appears malformed, suggesting that the spigot and/or the silk gland it serves actually are not functional.

At the opposite extreme, we have indications that in some taxa (the three examples seen thus far are dionychans) it is common for certain nubbins not to form at all. In an adult male *Salticus scenicus* (Clerck 1757) (Salticidae), we observed single 2° ampullate nubbins on both ALS and the left PMS, but not on the right PMS (Table 3). That this individual had 2° MiA spigots when it was a penultimate instar, on the right PMS as well as the left PMS, is indicated by the MiA nubbin on the left PMS and the MiA tartipores on both PMS. The same situation was seen in an adult male *Tibellus oblongus* (Walckenaer 1802) (Philodromidae) and an adult male *Misumen-*





Figures 6–7.—Right PLS on the last exuvium shed by a female *Hogna* sp. killed while a penultimate instar (i.e. the cuticle of the antepenultimate instar is shown): 6. Three aciniform nubbins, among aciniform (and cylindrical?) spigots, can be seen within the box; 7. Higher magnification of the three aciniform nubbins (*) from Fig. 6, arrow to example of an aciniform tartipore. Posterior at left, lateral at top in both figures. Scale bars (6) = 100 μm; (7) = 25 μm.



Figures 8–11.—Portions of the ALS and PMS containing the ampullate spigots, from an adult female *Pardosa saxatilis* and the last exuvium shed by this individual (i.e. the cuticle of the penultimate instar): 8, 10. Penultimate instar; 9, 11. Adult; 8, 9. Left ALS (posterior at right, lateral at top); 10, 11. Right PMS (posterior at left, lateral at top). Note the relative increase in diameter of the bases of the 2° MaA and 2° MiA spigots in the adult cuticle and that the MiA tartipore and 2° MiA spigot switch positions from one instar to the next. Unlabeled arrows point to examples of piriform (Figs. 8–9) or aciniform (Fig. 10) tartipores. Scale bars = 10 μm.

ops asperatus (Hentz 1847) (Thomisidae), except that for the latter it was on the left PMS that a MiA nubbin was lacking (Table 3). The one MiA nubbin that was present on the *S. scenicus* and *M. asperatus* individuals was very small, as was the right MiA nubbin on a second adult male *M. asperatus*. But the left MiA nubbin on the latter spider was much larger (likewise in the *T. oblongus* individual), clearly showing cuticular sculpturing in the form of longitudinal ridges like those on the bases of the 1° MiA spigots.

Finally, in adult males it is sometimes the case with multiple nubbins that not all of the spigots of a given gland type are represented by nubbins; some appear to develop into functional spigots (at least they have shafts and the base-shaft junctions do not look malformed).

METHODS

Spiders examined.—Spinnerets with attached egg sacs were examined by scanning electron microscopy (SEM) in *Pardosa moesta* Banks 1892 (6 specimens), *Pardosa lapidicina* Emerton 1885 (2 specimens), *Pardosa modica* (Blackwall 1846) (1 specimen), *Pardosa littoralis* Banks 1896 (1 specimen), and *Trochosa ruricola* (De Geer 1778) (1 specimen). The numbers of specimens given include only those that yielded useful information. The *P. littoralis* was collected in central South Carolina. The others were collected in southeastern (se) New Hampshire (NH).

Other spinnerets were also examined, both from several lycosid species (without attached egg sacs) and from species belonging to other families (mostly those in which adult females retain functional 2° MaA/2° MiA glands) (see Table 3). These were also collected in se NH with the following exceptions: *P. xerampelina* (se NH and southwestern Maine), *Pardosa hortensis* (Thorell 1872) (Luxembourg), *Pardosa lugubris* (Walckenaer 1802) (Luxembourg), *Gladicosa gulosa* (Walckenaer 1837) (southern NH and central Virginia), *Hogna helluo* (Walckenaer 1837) (se NH and central Virginia), *Agelenopsis naevia* (Walckenaer 1842) (central Virginia and western North Carolina), *Coras aerialis* Muma 1946 (se NH and southwestern Maine), *Coras lamellosus* (Keyserling 1887) (southwestern Maine), *Coras montanus* (Emerton 1890) (southwestern NH), *Misumenops oblongus* (Keyserling 1880) (southwestern NH), *Thanatus rubicellus* Mello-Leitão 1929 (central Virginia), and *Phidippus audax* (Hentz 1845) (western Pennsylvania and se NH). Some spiders were collected as juveniles and several antepenultimate or penultimate instar lycosids were prepared for SEM immediately. The others were raised to the adult stage with shed exuvia saved for later examination. Spinnerets on exuvia from a few of the lycosids were prepared for SEM, as described below, in order to compare juvenile and adult spinning fields within the same individual. There were two reasons for examining spinnerets other than lycosid spinnerets to which egg sacs were attached: first, to gain a more complete view of spinning field morphology in lycosids, since attached egg sacs usually make clear viewing of spinning fields difficult or impossible; and, second, to compare spinning fields, especially ampullate spigots, between males and females, between juveniles and adults, and among different lycosid and non-lycosid species.

Spiders were identified using keys and descriptions given, primarily, in Chamberlin & Ivie (1941), Carico (1972, 1973), Dondale & Redner (1978, 1982, 1990), Brady (1979, 1986), Kaston (1981), Roberts (1985), Heimer & Nentwig (1991), Roth (1993), and Prentice (2001). Family assignments and taxonomic citations follow Platnick (2002). Voucher specimens for this study are deposited in the Museum of Comparative Zoology, Harvard University. Most consist only of cephalothoraxes and isolated epigyna since the spinnerets of nearly all collected specimens were processed for SEM.

SEM.—Spinnerets without attached egg sacs were artificially spread in preparation for SEM using the forceps squeeze technique of Coddington (1989), which is a modified version of a technique suggested to that author by J. Kovoor. Carbon dioxide anesthetized spiders were severed at the pedicel, the tines of fine forceps were placed on either side of the spinnerets, one dorsad and one ventrad, and the forceps were squeezed. Any fecal material ejected from the stercoral sac through the anal tubercle was either absorbed with a tissue or rinsed off with distilled water. Inspired by Coddington's (1989) recommendation that live spiders be killed by immersion in boiling water or fixative to spread spinnerets, the spread spinnerets were immersed in boiling water (about 2–5 sec depending on the size of the abdomen) as a kind of first fixation.

The forceps were then held closed using a snug-fitting rubber O-ring (Fine Science Tools, Inc.) and their tips with the held abdomen were inserted through a hole, just large enough to accommodate the forceps, made in the cap of a 20 ml scintillation vial filled with a modified version of Karnovsky's (1965) fixative containing only 1% glutaraldehyde / 1% formaldehyde in 0.1 M cacodylate buffer, pH 7.2. Abdomens were kept refrigerated in the fixative from overnight to several days, allowed to come to room temperature, transferred to distilled water for about 20 min, and then taken through an ethanol series (30%, 50%, 70%, 85%, 95%, 100% used once, 100% fresh; 1–2 hr in each $< 70\%$, 2 hr-overnight in each $\geq 70\%$). Finally, the samples were immersed in hexamethyldisilazane (HMDS) (Nation 1983) overnight and then allowed to air dry. All solutions/solvents were also in scintillation vials so transfers were made by moving cap, forceps, and abdomen as a unit from one vial to the next. Abdomens were mounted on pin-type SEM specimen mounts (stubs) with carbon adhesive tabs (Electron Microscopy Sciences) and carbon paste (Structure Probe, Inc.), sputter-coated with gold/palladium (about 20 nm), and examined on an AMR Model 3300 FE field-emission SEM operated with a 7 kV accelerating voltage.

Some lycosid spinnerets with an attached egg sac were prepared for SEM using the same protocol just described, except that the specimen was not immersed in boiling water and the spinnerets were only partially spread

Table 3.—Ampullate spigot (spig), nubbin (nub), and tartipore (tart) complements in examined spiders belonging to the families listed in Table 2, as well as in examined *Mimetus* (see 'Categories of ampullate silk glands etc.' in the introductory section). Where these complements differed between the left and right spinnerets of an individual, both numbers are shown, with the left spinneret value placed on the left. With the exception of spinnerets from *P. mira* juveniles (identified by P. Sierwald), the spinnerets from those juveniles that are identified to species were obtained either from exuvia shed by spiders raised to adults or from the progeny of identified females. *n* = number of individuals examined. Ad = adult, ALS = anterior lateral spinneret, An = antepenultimate, F = female, M = male, MaA = major ampullate, MiA = minor ampullate, P = penultimate, PMS = posterior median spinneret, U = unknown.

Family Species	Instar	Sex	*n*	Number of MaA spig per ALS	Number of MaA nub per ALS	Number of MaA tart per ALS	Number of MiA spig per PMS	Number of MiA nub per PMS	Number of MiA tart per PMS
Lycosidae									
Gladicosa gulosa (Walckenaer 1837)	Ad	F	4	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Hogna sp.	An	F	1	2	0	1	2	0	1
	P	F	1	2	0	1	2	0	1
Hogna aspersa (Hentz 1844)	Ad	F	1	2	0	1	2	0	1
Hogna helluo (Walckenaer 1837)	P	F	1	2	0	1	2	0	1
	Ad	F	2	2	0	1	2	0	1
Pardosa sp.	An or P	F	6	2	0	1	2	0	1
	P	M	3	2	0	1	2	0	1
Pardosa hortensis (Thorell 1872)	P	F	1	2	0	1	2	0	1
	Ad	F	1	2	0	1	2	0	1
Pardosa lapidicina Emerton 1885	Ad	F	2	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Pardosa littoralis Banks 1896	Ad	F	1	2	0	1	2	0	1
Pardosa lugubris (Walckenaer 1802)	P	M	1	2	0	1	2	0	1
Pardosa modica (Blackwall 1846)	Ad	F	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Pardosa moesta Banks 1892	Ad	F	8	2	0	1	2	0	1
	Ad	M	1	1	1	1	1,2	1,0	1
	Ad	M	1	1	1	1	1	1	1
Pardosa saxatilis (Hentz 1844)	P	F	1	2	0	1	2	0	1
	Ad	F	2	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Pardosa xerampelina (Keyserling 1877)	1st	U	4	2	0	0	2	0	0
	2nd	U	1	2	0	1	2	0	1
	4th	U	1	2	0	1	2	0	1
	Ad	F	1	2	0	1	2	0	1
Trochosa ruricola (De Geer 1778)	3rd	U	1	2	0	1	2	0	1
	Ad	F	1	2	0	1	2	0	1
Trochosa terricola Thorell 1856	Ad	M	1	1	1	1	1	1	1

Table 3.—Continued.

Family Species	Instar	Sex	*n*	Number of MaA spig per ALS	Number of MaA nub per ALS	Number of MaA tart per ALS	Number of MiA spig per PMS	Number of MiA nub per PMS	Number of MiA tart per PMS
Pisauridae									
Dolomedes scriptus Hentz 1845	Ad	F	3	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Dolomedes tenebrosus Hentz 1844	Ad	F	1	2	0	1	2	0	1
Pisaurina mira (Walckenaer 1837)	An or P	F	1	2	0	1	2	0	1
	Ad	F	2	2	0	1	2	0	1
	An	M	1	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Agelenidae									
Agelenopsis naevia (Walckenaer 1842)	Ad	F	2	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Agelenopsis potteri (Blackwall 1846)	Ad	F	6	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Amaurobiidae									
Coras aerialis Muma 1946	Ad	F	1	2	0	1	2	0	1
	Ad	M	2	1	1	1	1	1	1
Coras lamellosus (Keyserling 1887)	Ad	F	1	2,1	0,1	1	2	0	1
Coras montanus (Emerton 1890)	Ad	M	1	1	1	1	2	0	1
Thomisidae									
Misumena vatia (Clerck 1757)	Ad	F	1	2	0	1	2	0	1
Misumenops asperatus (Hentz 1847)	Ad	F	2	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
	Ad	M	1	1	1	1	1	0,1	1
Misumenops oblongus (Keyserling 1880)	Ad	F	1	2	0	1	2	0	1
Xysticus emertoni Keyserling 1880	3rd	U	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1	1
Xysticus ferox (Hentz 1847)	Ad	M	2	1	1	1	1	1	1
Xysticus punctatus Keyserling 1880	4th	U	1	2	0	1	2	0	1
	5th	U	2	2	0	1	2	0	1

Table 3.—Continued.

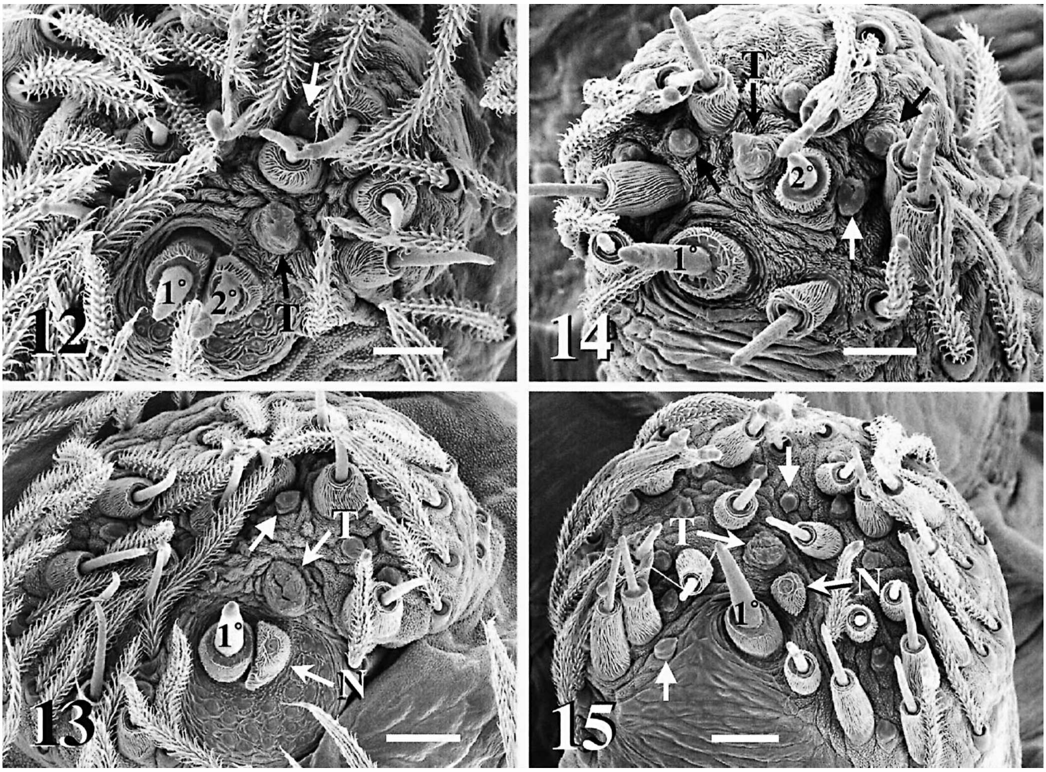
Family Species	Instar	Sex	*n*	Number of MaA spig per ALS	Number of MaA nub per ALS	Number of MaA tart per ALS	Number of MiA spig per PMS	Number of MiA nub per PMS	Number of MiA tart per PMS
Philodromidae									
Philodromus vulgaris (Hentz 1847)	Ad	M	1	1	1	1	1	1	1
Thanatus rubicellus Mello-Leitão 1929	Ad	M	1	1	1	1	1	1	1
Tibellus oblongus (Walckenaer 1802)	Ad	F	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1,0	1
Miturgidae									
Cheiracanthium mildei L. Koch 1864	Ad	F	2	2	0	1	2	0	1
	Ad	M	3	1	1	1	1	1	1
Salticidae									
Phidippus audax (Hentz 1845)	Ad	F	2	2	0	1	2	0	1
	Ad	M	3	2	0	1	2	0	1
Salticus scenicus (Clerck 1757)	Ad	F	1	2	0	1	2	0	1
	Ad	M	1	1	1	1	1	1,0	1
Sitticus pubescens (Fabricius 1775)	Ad	M	1	?	?	?	1	1	1
Mimetidae									
Mimetus notius Chamberlin 1923	Ad	M	2	1	1	1	1	1	1
Mimetus puritanus Chamberlin 1923	Ad	F	2	1	1	1	1	1	1
	Ad	M	2	1	1	1	1	1	1

by placing the forceps more anteriorly on the abdomen with the tines extending only partway across the width of the abdomen. While some spiders were severed at the pedicel, others were left intact. With other specimens, Peters' (1982) paraffin technique was applied after anesthetization, with or without squeezing the abdomen. Hot paraffin was added either dorsally or ventrally to the spinnerets and the adjacent part of the egg sac, fusing the egg sac to the spinnerets. The abdomen with attached egg sac was then immersed directly in 70% ethanol, taken to 100% ethanol as above, then transferred to benzene, which was changed twice over the course of at least a few weeks. The specimen was then air dried, mounted, sputter-coated, and examined. We never settled on a uniform protocol since no one of the variants emerged as clearly superior to the others with all specimens or species, though squeezing the abdomen is most often warranted.

As mentioned, spinnerets on exuvia shed by a few lycosids were also examined by SEM. These were prepared by isolating the spinneret group and sticking it to a carbon adhesive tab on a SEM stub. A small volume of an aqueous solution containing a detergent (to reduce surface tension and increase wettability) was then applied to the spinnerets prior to attempting to uncrumple the spinnerets. We used Laemmli's (1970) sodium dodecyl sulfate electrophoresis sample buffer, diluted to about half strength, for this purpose, though other compositions would no doubt serve at least as well. While immersed in this solution, an insect pin or a tine on a pair of fine forceps was inserted into each spinneret in order to re-expand it and allow its spinning field to be viewed. The spinneret group was then fixed (though this is probably not necessary), dehydrated, treated with HMDS, air dried, mounted, sputter-coated, and examined as described above.

Distinguishing 1° ampullate spigots from 2° ampullate spigots.—In the results presented below, differences between 1° and 2° ampullate fibers and spigots of adult female lycosids are noted. Our interpretation of the relative contributions made by 1° and 2° ampullate glands to egg sac attachment relies on having identified 1° and 2° ampullate spigots correctly. We considered four lines of evidence in making these identifications and, in the manner of Coddington (1989), the same kind of reasoning can be applied to many other spider families. (1) Since 2° ampullate spigots are represented only by ampullate nubbins in adult male lycosids (Figs. 13, 15), their positions relative to the 1° ampullate spigots can be used as a key to distinguishing 1° from 2° ampullate spigots in adult females and juveniles. (2) Because only 2° ampullate glands are functional during proecdysis (right up until the old cuticle is shed from the spinnerets), the only ampullate fibers emerging from spigots on the old cuticle during proecdysis are 2° ampullate fibers (Townley et al. 1993). Consequently, the only ampullate fibers on the exuvium after ecdysis pass through 2° ampullate spigots (Townley et al. 1991:figs. 14–15; Townley et al. 1993:fig. 4). While 2° ampullate fibers do not invariably remain attached to exuvia, they do so with enough regularity that examinations of exuvia can be used to determine which ampullate spigots are 1° and which are 2°. Thus, in our scans of lycosid exuvia, we have only observed ampullate fibers emerging from those spigots that we have identified as 2° ampullate spigots, never from those identified as 1° ampullate spigots (Figs. 8, 10, 19, 20). (3) In general, ampullate tartipores, resulting from openings made to accommodate 2° ampullate gland ducts (see Terminology section above), occur closer to 2° ampullate spigots than 1° ampullate spigots. The ampullate tartipores on lycosid ALS and PMS likewise occur closer to the spigots identified as 2° ampullate spigots (e.g., Figs. 18, 21). (4) The arrangement of MaA and piriform spigots on the ALS of lycosids is essentially the same as in *A. cavaticus* (the same cannot be said of the arrangement of spigots on the PMS where the MiA spigots are located). In this araneid we have observed by dissection that the 2° MaA ducts lead to the more posteriorly placed ampullate spigot on each ALS (Townley et al. 1991, 1993). The spigot identified as the 2° MaA spigot in lycosids likewise occurs posterior to that identified as the 1° MaA spigot.

Definition of first instar.—Downes' (1987) definition for the first instar is followed in this report with subsequent instars numbered accordingly. A spider becomes a first instar as a result of the first ecdysis that produces an exuvium that both has legs and does not remain attached to the spider. In the period



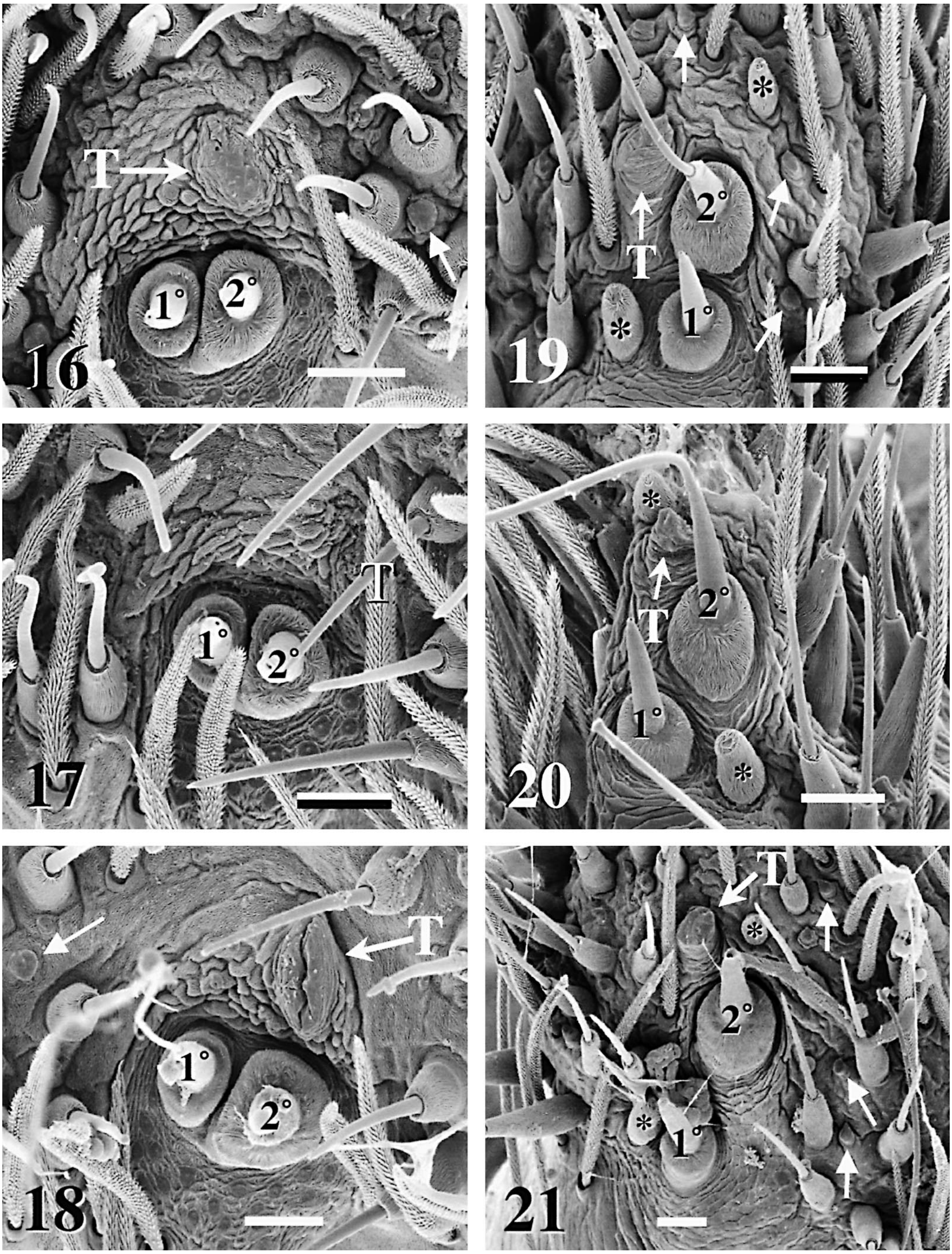
Figures 12–15.—Entire spinning fields on ALS and PMS from a penultimate instar male *Pardosa* sp. and an adult male *Pardosa modica*: 12, 14. Penultimate instar; 13, 15. Adult; 12, 13. Left ALS (posterior at right, lateral at top); 14, 15. Right PMS (posterior at left, lateral at top). Note that 2° MaA and 2° MiA spigots are represented in the adult male only by MaA and MiA nubbins, respectively. Unlabeled arrows point to examples of piriform (Figs. 12–13) or aciniform (Figs. 14–15) tartipores. Scale bars (12, 14) = 10 μm; (13, 15) = 20 μm.

between hatching and the ecdysis that yields a first instar, the spider is a postembryo (Downes 1987).

RESULTS

Abbreviations on micrographs.—AC = attachment cone; C = cylindrical gland spigot; ES = egg sac; N = MaA nubbin (if the spinneret is an ALS) or MiA nubbin (if the spinneret is a PMS); 1° = 1° MaA spigot (on ALS) or 1° MiA spigot (on PMS); 2° = 2° MaA spigot (on ALS) or 2° MiA spigot (on PMS); T = MaA tartipore (on ALS) or MiA tartipore (on PMS); l = left; r = right.

Ampullate gland spigot, nubbin, tartipore complements.—Spinnerets from male and female representatives of three lycosid genera (*Pardosa*, *Gladicosa*, *Trochosa*) were examined, as were those from females only of the genus *Hogna* (Table 3). With one clearly anomalous exception (see Table 3), no variation was seen with regard to the number of ampullate gland spigots/nubbins/tartipores for a given sex at a given stage of development. Assuming these genera present the typical, if not invariable, lycosid condition, adult females and juveniles of both sexes that are at least second instars have two MaA spigots and one MaA tartipore on each ALS (Figs. 8, 9, 12, 16–18, 22, 40, 41) and two MiA spigots and one MiA tartipore on each PMS (Figs. 10, 11, 14, 19–21, 23, 38, 39, 42) (first instars lack tartipores, Figs. 2–5), while adult males have one MaA spigot, one MaA nubbin, and one MaA tartipore on each ALS (Fig. 13) and one MiA spigot, one MiA nubbin, and one MiA tartipore on each PMS (Fig. 15). The 2° MaA and 2° MiA spigots of juvenile males are vestigial in adult males, being represented only by 2° MaA/2° MiA nubbins.



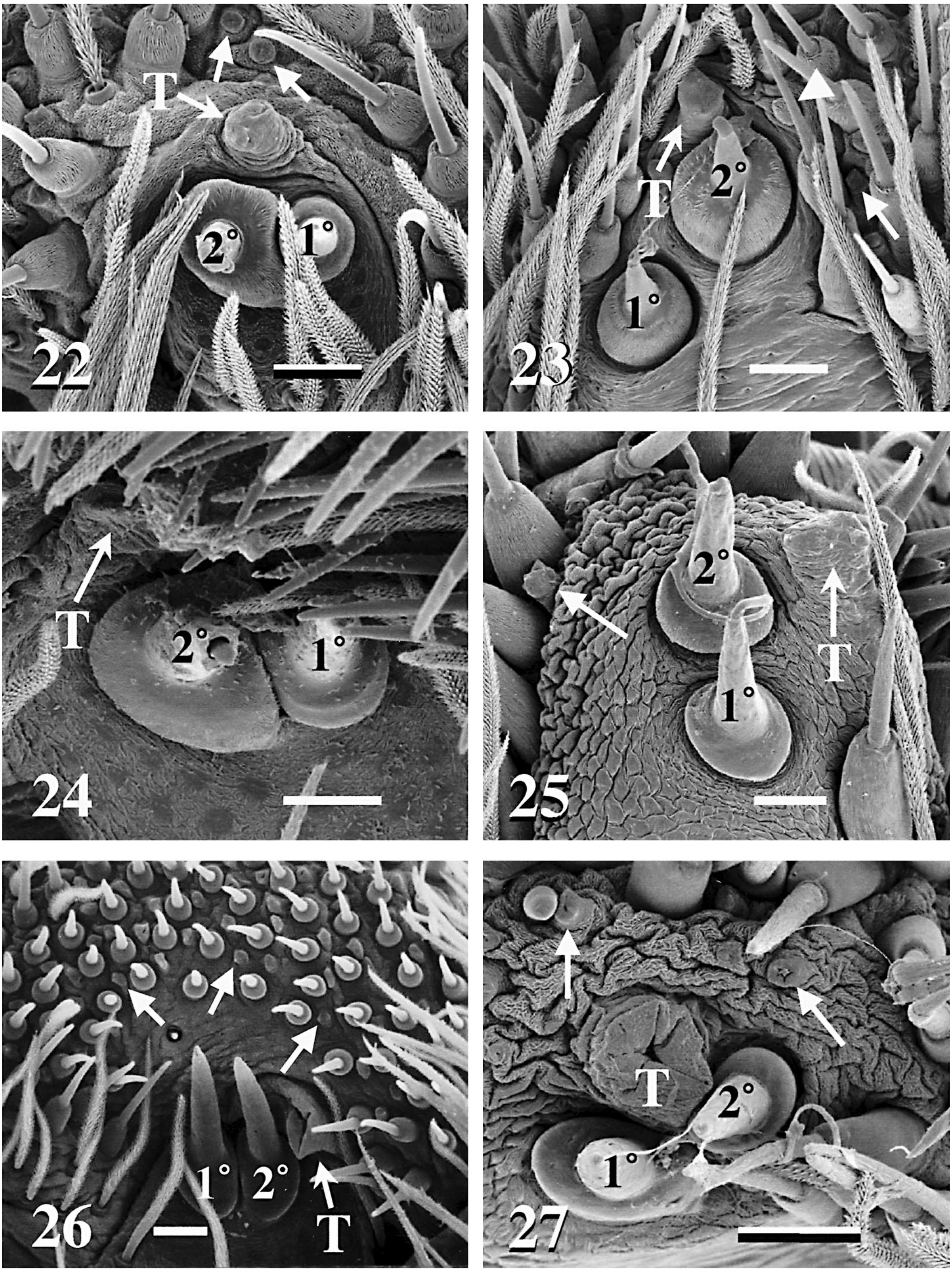
Figures 16–21.—Portions of the ALS and PMS containing the ampullate spigots, from an adult female *Hogna helluo* and the last exuvium shed by this individual (i.e. the cuticle of the penultimate instar), as well as from the last exuvium shed by a female *Hogna* sp. killed while a penultimate instar (i.e. the cuticle of the antepenultimate instar; the same exuvium from which the PLS in Figs. 6–7 was taken): 16, 19. Antepenultimate instar; 17, 20. Penultimate instar; 18, 21. Adult; 16, 17, 18. Left ALS (posterior at right, lateral at top); 19, 21. Left PMS (posterior at right, lateral at top); 20. Right PMS (posterior at left, lateral at top). The MaA tartipore is largely obscured in Fig. 17. Unlabeled arrows point to examples of piriform (Figs. 16, 18) or aciniform (Figs. 19, 21) tartipores. Asterisks (*) identify the two aciniform nubbins on each PMS. Scale bars = 25 μm.

With regard to ampullate spigot/nubbin/tartipore complements, apart from the absence of a MiA nubbin on one PMS in single adult male specimens of *M. asperatus* and *T. oblongus,* no departures from the lycosid condition were observed when viewing spinnerets from the pisaurid (Figs. 24–27), agelenid (Figs. 28, 29), thomisid (Figs. 32, 33), philodromid (Figs. 30, 31), and miturgid (Figs. 34, 35) species listed in Table 3. The same is true of the *C. aerialis* examined. But in an adult female *C. lamellosus*, the number of MaA spigots/nubbins differed between the right and left ALS (Table 3). The formation of a MaA nubbin rather than a 2° MaA spigot on one ALS in this individual again seems to be an example of an anomaly. More significant was the presence of 2° MiA spigots on both PMS (and the absence of 2° MaA spigots on both ALS) of an adult male *C. montanus* (Table 3). This indicates that, in *Coras*, complements differ either interspecifically or intraspecifically. In *P. audax*, adult males, as well as adult females (Figs. 36, 37), retain 2° MaA and MiA spigots (Table 3). This is also the case in the salticid *Philaeus chrysops* (Poda 1761) (Millot 1935) and is consistent with Millot's (1935:509) statement that sexual dimorphism in the spinning apparatus of salticids is negligible. It is, therefore, worth noting that adult male specimens of *S. scenicus* and *Sitticus pubescens* (Fabricius 1775) (one of each species) lacked 2° ampullate spigots (Table 3), though for the latter we have only PMS data. These spigots were represented by nubbins and, in the case of one PMS on the *S. scenicus* individual, it appears that even the nubbin did not form (see 'Occurrence of nubbins' in the introductory section). As an adult female *S. scenicus* did have 2° ampullate spigots (Table 3), it appears that some salticids match the lycosid condition (Table 2) while others do not.

Relative sizes of 1° and 2° ampullate gland spigots.—In early instar lycosids (first and second instar *P. xerampelina*, third instar *T. ruricola*), 1° and 2° MaA spigots are roughly comparable in size, with the bases and shafts of the 1° MaA spigots a little greater in diameter than those of the 2° MaA spigots (Fig. 2). Typically, MiA spigots more clearly differ in size, again with the shafts and bases of 1° MiA spigots wider than those of 2° MiA spigots (Fig. 4). In *Pardosa* of both sexes, the 1° ampullate spigots, especially the 1° MiA spigots (Fig. 14), may retain marginally to moderately greater size through the penultimate instar, or 1° and 2° ampullate spigots may have about the same diameter (Figs. 8, 12). In contrast, in female *Hogna,* it is the 2° ampullate spigots that tend to be larger in the antepenultimate (Figs. 16, 19) and penultimate (Figs. 17, 20) instars. The difference is more pronounced on the ALS, with the bases of the 2° MaA spigots clearly larger than those of the 1° MaA spigots. Also, the difference in size between ampullate spigots and nearby aciniform or piriform spigots is greater in these *Hogna* juveniles than in juvenile *Pardosa*, due, seemingly, to disproportionately larger ampullate spigots (rather than smaller aciniform and piriform spigots) (cf. Figs. 8, 10, 12, 14 with Figs. 16, 17, 19, 20).

With the final molt in female *Pardosa*, the bases of the 2° ampullate spigots become decisively wider than those of the 1° ampullate spigots (cf. Fig. 8 with Fig. 9, and Fig. 10 with Fig. 11, all taken from the same individual). The degree to which this occurs varies noticeably within a species. Nevertheless, it has been apparent in all adult female *Pardosa* that we have examined (Table 3). The relative disparity between 1° and 2° ampullate spigots may also increase after the last molt in female *H. helluo* so that it is perhaps more obvious in adults than in penultimate instars that the bases of the 2° ampullate spigots have greater diameters than those of the 1° ampullate spigots (cf. Fig. 17 with Fig. 18, and Fig. 20 with Fig. 21). However, the changes seen following the last molt in *Hogna* females are certainly not as dramatic as those observed in *Pardosa*. In adult female *G. gulosa* (Figs. 22, 23) and *T. ruricola* (Fig. 43), the bases of the 2° ampullate spigots, especially the 2° MaA spigots, are likewise of greater diameter than the 1° ampullate spigot bases.

Among the adult female pisaurids examined (Table 3), noticeably (but not greatly) wider 2° ampullate spigot bases were observed on the ALS and/or PMS of all three *Dolomedes scriptus* Hentz 1845 (Figs. 24, 25), though one of these had 1° and 2° MaA spigots of essentially the same size while a second spider had 1° and 2° MiA spigots of similar size. There was also little difference in size between 1° and 2° ampullate spigots on the one *D. tenebrosus* Hentz 1844 examined, with 2° spigots



Figures 22–27.—Portions of the ALS and PMS containing the ampullate spigots, from adult females: 22, 23. *Gladicosa gulosa* (Lycosidae); 24, 25. *Dolomedes scriptus* (Pisauridae); 26, 27. *Pisaurina mira* (Pisauridae); 22, 24. Right ALS (posterior at left, lateral at top); 26. Left ALS (posterior at right, lateral at top); 25, 27. Right PMS (posterior at left, lateral at top); 23. Left PMS (posterior at right, lateral at top). Unlabeled arrows point to examples of piriform (Figs. 22, 26) or aciniform (Figs. 23, 25, 27) tartipores. An arrowhead in Fig. 23 points to an aciniform nubbin. Scale bars = 25 μm.

only marginally larger. In *Pisaurina*, 1° and 2° MaA spigots were of about the same size (Fig. 26) and 1° MiA spigots were larger than 2° MiA spigots (Fig. 27).

Among the non-lycosoid adult females examined (Table 3, Figs. 28–37), larger-diameter 2° ampullate spigot bases were observed only on the ALS (and not the PMS) of two thomisids, *M. oblongus* (Figs. 32, 33) and *Misumena vatia* (Clerck 1757). The difference was small and, moreover, in two *M. asperatus* females the 1° MaA spigots were larger than or about the same size as the 2° MaA spigots (not shown). Likewise, in *Agelenopsis* (Figs. 28, 29), *Coras* (not shown), *Tibellus oblongus* (Walckenaer 1802) (Figs. 30, 31), *Cheiracanthium mildei* L. Koch 1864 (Figs. 34, 35), *P. audax* (Figs. 36, 37), and *S. scenicus* (not shown), 2° ampullate spigots were either about the same size as the 1° ampullate spigots or smaller (though in adult *P. audax*, male and female, the 2° ampullate spigots were longer and in the one examined *S. scenicus* adult female, 2° MiA spigots were longer than 1° MiA spigots while 1° and 2° MaA spigots were of about equal length).

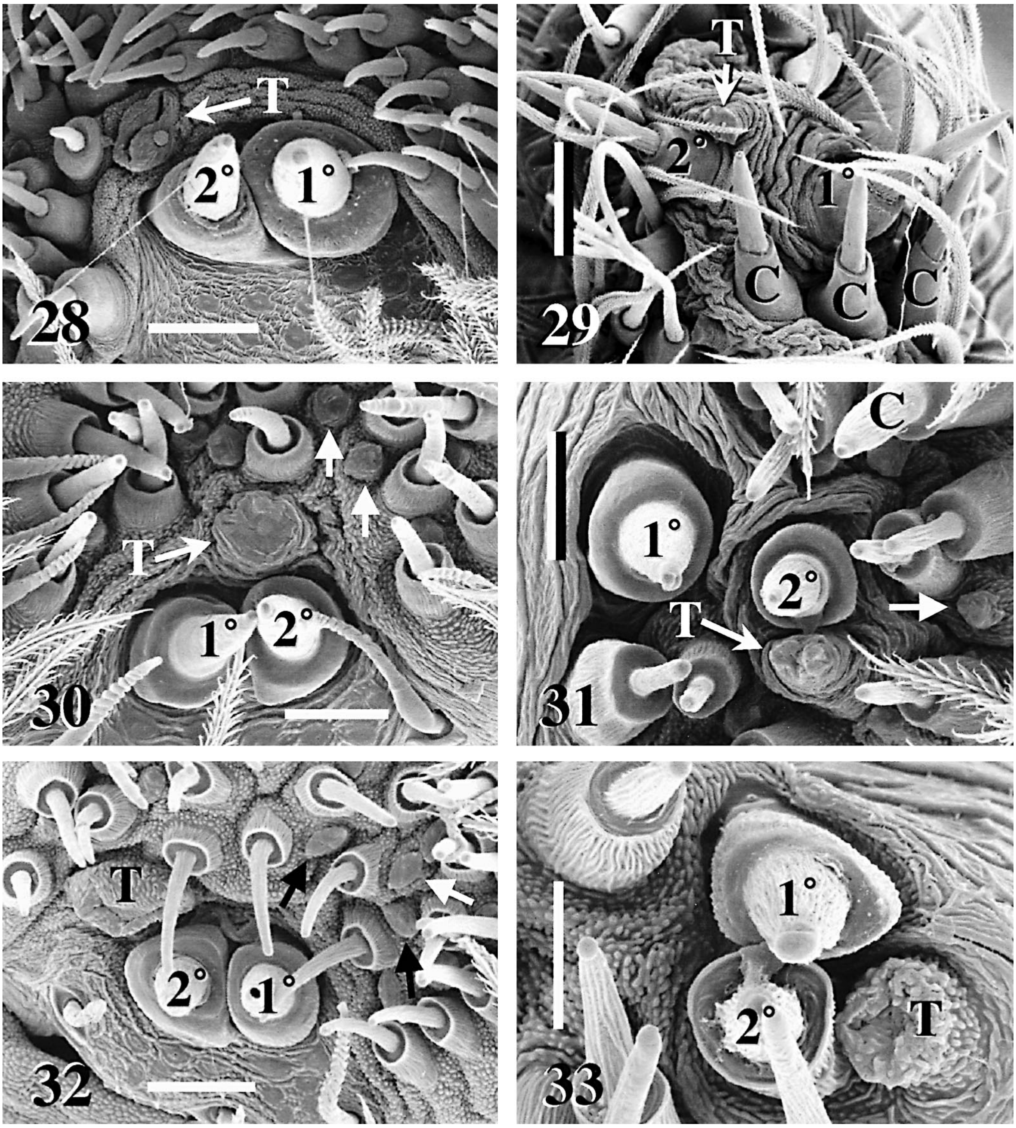
Egg sac attachment.—In the four *Pardosa* species examined with attached egg sacs, eight silk fibers emanating from the 1° and 2° MaA spigots and the 1° and 2° MiA spigots were attached to the egg sac (Figs. 38–42). Likewise, in a single specimen of *T. ruricola*, 1° and 2° MaA fibers at least were used to secure the egg sac to the spinnerets (Fig. 43). We were unable, however, to determine if this individual was also using MiA fibers. In some preparations, single to several piriform fibers accompanied MaA fibers, but in no instances were fibers observed coming from aciniform or cylindrical (= tubuliform) gland spigots, including those on the PLS.

In all five species, 2° ampullate fibers had greater diameters than 1° ampullate fibers (Figs. 38–43, 49). Measurements obtained on some of these fibers from four of these species are presented in Table 4 and, though the data are few, provide an indication of the disparity between 1° and 2° ampullate fibers. In contrast, on the left ALS of one of the examined adult female *D. scriptus*, the 1° MaA spigot was only slightly smaller than the 2° MaA spigot and silk fibers emerging from these spigots had diameters of 2.40 μm and 2.50 μm, respectively. On the left ALS of an adult female *M. asperatus*, the 1° and 2° MaA spigots were about the same size and fibers emerging from them had diameters of 2.47 μm and 2.00 μm, respectively.

Ampullate fibers from the spinnerets are typically attached to the surface of the egg sac by groups of fibers that often take the form of a cone (Figs. 38, 40, 44, 46, 48). The fibers in these ''attachment cones'' have smaller diameters than the 1° ampullate fibers (Fig. 47 and many of them appear to be fused to one another (Figs. 45, 47). They extend beyond the cone for a short distance on the surface of the egg sac. A single attachment cone secures one or more ampullate fibers to the egg sac. Thus, one (Fig. 44) to several (Figs. 38, 48) cones in close proximity affix the eight ampullate fibers. There appears to be a generic difference with regard to the number of cones that are typically produced (one or two in *Gladicosa* and *Trochosa*, several in *Pardosa*), but more observations are needed to verify this.

Aciniform nubbins.—Though not an objective of this study, a small number of aciniform nubbins were noticed on several lycosid specimens and we think their seemingly non-random occurrence warrants mention. In four female *Hogna* individuals (two adult *H. helluo*, one adult *H. aspersa* (Hentz 1844), one penultimate instar *Hogna* sp.), two aciniform nubbins were observed on each PMS in the vicinity of the MiA spigots. (No male *Hogna* have been examined.) They were also present on the most recent exuvium shed by the penultimate instar (i.e., the cuticle of the antepenultimate instar) and on the last exuvium shed by one of the adult *H. helluo*. One of these nubbins occurs anterior to the 1° MiA spigot, the other lateral or posterolateral to the 2° MiA spigot (Figs. 19–21). In addition, three aciniform nubbins were observed on each PLS, roughly in the middle of the spinning field, in the penultimate instar and its most recent exuvium (Figs. 6, 7), as well as in one adult *H. helluo*. On the other examined *Hogna* cuticles, either one or two aciniform nubbins were found per PLS, though this could be because these PLS preparations were not fully expanded and additional nubbins were obscured.

We have not seen these aciniform nubbins in *Pardosa* or *Trochosa*. In an adult male *G. gulosa*, two aciniform nubbins were on the left PMS in the same positions as in *Hogna*, but only the more lateral of the two was present



Figures 28–33.—Portions of the ALS and PMS containing the ampullate spigots, from adult females: 28, 29. *Agelenopsis naevia* (Agelenidae); 30, 31. *Tibellus oblongus* (Philodromidae); 32, 33. *Misumenops oblongus* (Thomisidae); 28, 32. Right ALS (posterior at left, lateral at top); 30. Left ALS (posterior at right, lateral at top); 29, 31, 33. Right PMS; 29, 33 Posterior at right, lateral at bottom; 31 Posterior at top, lateral at right. Unlabeled arrows point to examples of piriform (Figs. 30, 32) or aciniform (Fig. 31) tartipores. Scale bars (28) = 25 μm; (29) = 50 μm; (30–32) = 15 μm; (33) = 10 μm.

on the right PMS, and none were found on the PLS. Of four adult female *G. gulosa*, one had a single lateral aciniform nubbin on one PMS (Fig. 23) but none on the other PMS or either PLS, while on a second female we could find only one nubbin on one of the PLS. No aciniform nubbins were seen on the spinnerets of the other two females (though on one of these our views of the PMS and PLS were limited as the spinnerets were not well spread).

DISCUSSION

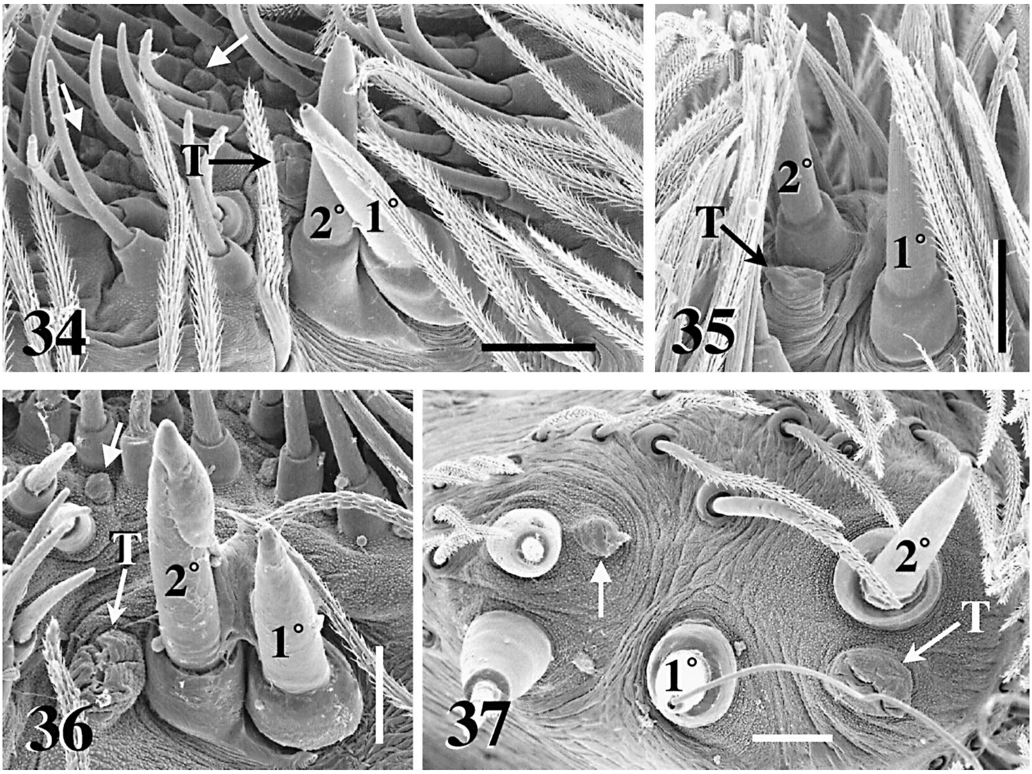
The observations presented in this paper demonstrate that adult females of at least some species of lycosids use 1° and 2° MaA/MiA gland fibers to connect the egg sac to the

Table 4.—Diameters (in μm) of ampullate fibers produced by adult female lycosids for attaching the egg sac to the spinnerets. Measurements were made by SEM at magnifications $> 10{,}000\times$. n = number of individuals from which fibers were measured. For each spider, corresponding fibers from both ALS/PMS were measured and averaged. For *P. moesta* and *P. lapidicina*, the means so obtained for each individual were then used to calculate the overall means ± their standard errors.

Species	*n*	1° MaA fibers	2° MaA fibers	1° MiA fibers	2° MiA fibers
Pardosa moesta Banks 1892	5	0.83 ± 0.038	2.56 ± 0.120	0.76 ± 0.020	2.57 ± 0.171
Pardosa lapidicina Emerton 1885	2	0.99 ± 0.026	3.93 ± 0.319	0.93 ± 0.090	3.86 ± 0.181
Pardosa littoralis Banks 1896	1	0.90	2.86	0.50	2.53
Trochosa ruricola (De Geer 1778)	1	1.31	3.06		

spinnerets. Given the greater diameter of the 2° ampullate fibers (Table 4), they presumably constitute the more indispensable part of this tether.

Egg sac attachment in lycosids versus trechaleids and rhoicinines.—In contrast to *Pardosa* females that use both MaA and MiA fibers (1° and 2°) for attaching the egg sac, for a total of eight ampullate fibers, Carico (1993) reports that trechaleid females use only MiA fibers (but, again, both 1° and 2°; see his fig. 4) for this purpose, for a total of four ampullate fibers. And while 2° ampullate fibers are considerably wider than 1° ampullate fibers in



Figures 34–37.—ALS and PMS from adult females: 34, 35. *Cheiracanthium mildei* (Miturgidae); 36, 37. *Phidippus audax* (Salticidae); 34, 36. Portion of right ALS containing the MaA spigots (posterior at left, lateral at top); 35. Portion of left PMS containing the MiA spigots (posterior at right, lateral at top); 37. Left PMS, entire spinning field shown (two MiA and two aciniform spigots) (posterior at right, lateral at top). Unlabeled arrows point to examples of piriform (Figs. 34, 36) or aciniform (Fig. 37, the only one) tartipores. Scale bars = 25 μm.

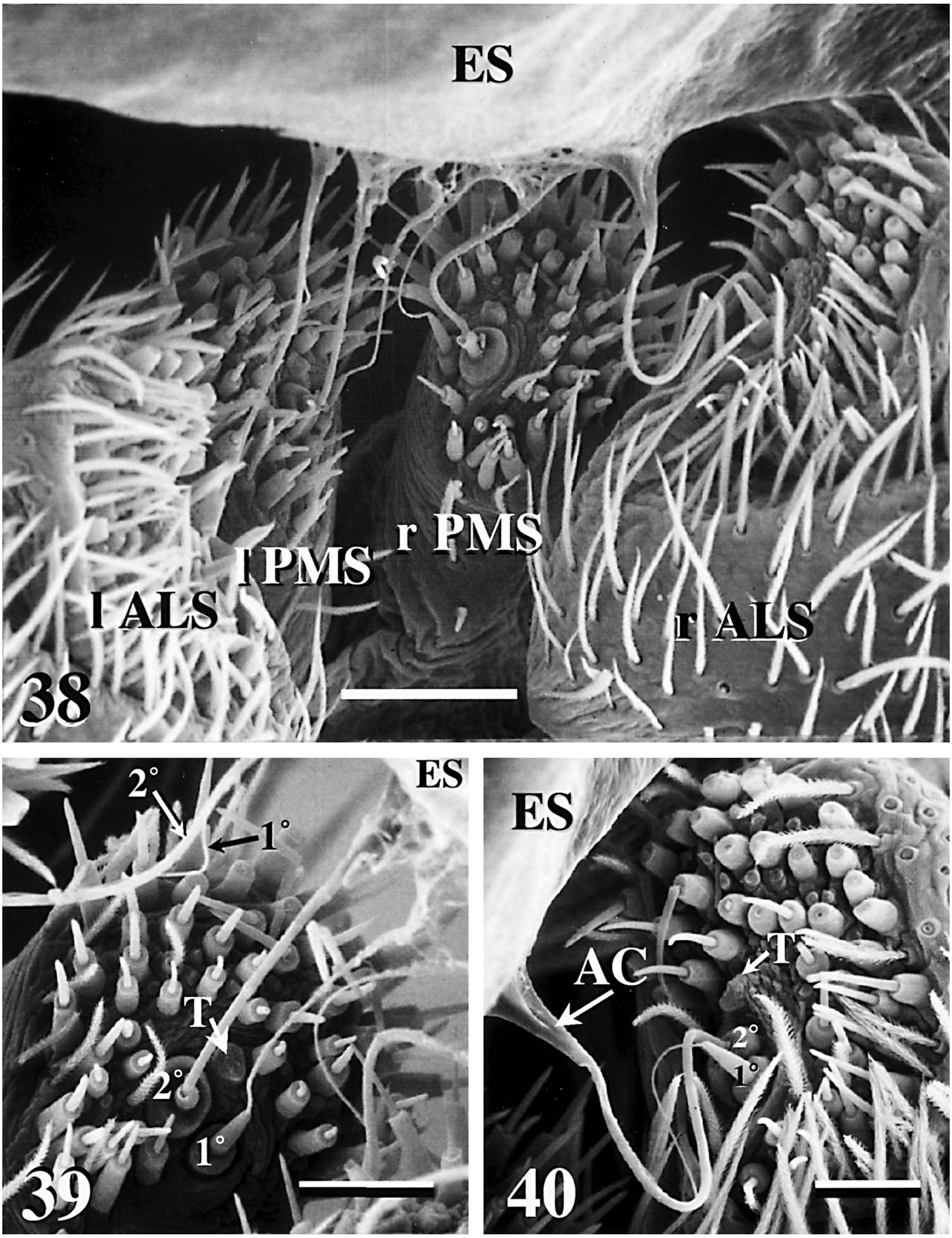
Pardosa and *Trochosa* (at least on the ALS of the latter, Table 4), the 1° and 2° MiA fibers of *Hesydrus,* shown in fig. 4 of Carico (1993), do not appear to differ substantially in diameter. Carico (1993:230) describes these trechaleid MiA fibers as 'strong' and this seems apt considering that our measurements of 2° ampullate fiber diameters in *Pardosa, Trochosa,* and *Dolomedes* were in the range of about 2.3–4.4 μm, whereas the MiA fibers in Carico's fig. 4 have diameters of about 9–12 μm. Thus, what the trechaleid tether lacks in number of fibers is perhaps more than made up for in strength per fiber. Additional comparisons between these two families are made in the appropriate sections below.

In contrast to lycosids and trechaleids, it has been reported that *Rhoicinus* and *Rhoicinaria* (the latter currently placed in Amaurobiidae, see Platnick 2002) carry their egg sacs attached to the posterior spinnerets; i.e., the PLS (see Exline 1950, 1960). If true, attachment is presumably accomplished using fibers from aciniform and/or cylindrical glands, rather than ampullate gland fibers.

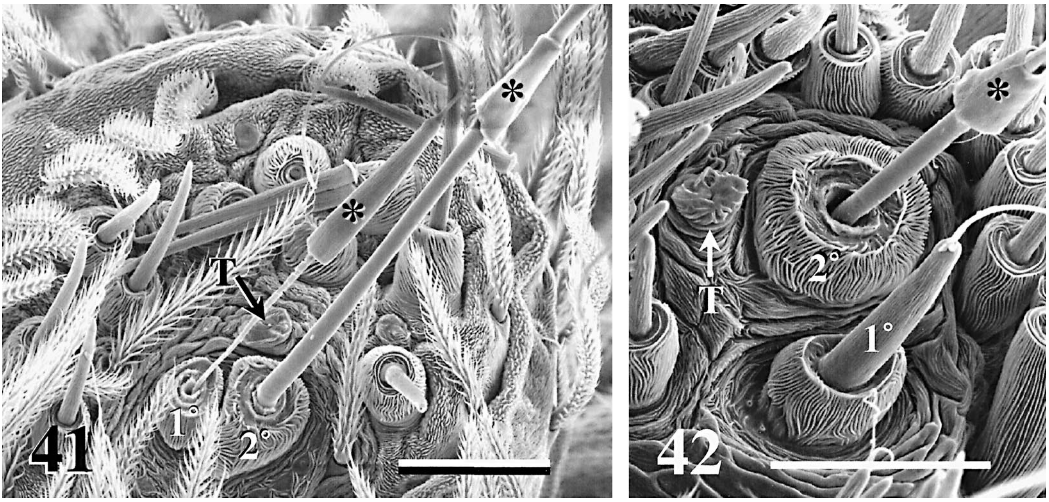
Ampullate glands in lycosids versus araneoids.—To us, the female lycosid's (or trechaleid's) use of 2° ampullate silk is most interesting when compared with the araneoid condition. The evidence to date indicates that 2° ampullate glands produce silk in araneoids only during proecdyses (Townley et al. 1993) and, therefore, these glands are not needed and not functional in adults of either sex. What occurs in adult female lycosids (and adult females from some other families, Tables 2, 3) appears to be a variation on this scheme. As in araneoids, the 2° ampullate glands of juvenile lycosids apparently produce silk during proecdyses. This is indicated by the presence of ampullate tartipores in second instar through adult lycosids and is consistent with the replacement of 2° ampullate spigots by 2° ampullate nubbins in adult males (Table 3; Figs. 1, 12–15). In araneoids, the final molt differs from the preceding molts, with regard to the ampullate glands, in that the blocked 2° ampullate glands present in the last juvenile instar (see Table 1) remain blocked and do not re-develop in the adult. And because the open 2° ampullate glands present in the last juvenile instar become blocked and regress in the adult, as they do after each molt, the adult contains two sets of blocked 2° ampullate glands, rather than one blocked set and one open set (as in juveniles). From our observations on spinnerets, we infer that this difference between the final molt and all preceding molts does not exist in female lycosids (among others). That is, the blocked 2° ampullate glands present in a penultimate instar female lycosid do become open 2° ampullate glands in the adult and re-develop accordingly (Fig. 1). Presumably, they are not functional immediately after the last ecdysis, requiring at least a day or two to re-develop and accumulate luminal contents, but would thereafter be able to produce silk fibers concurrently with the 1° ampullate glands.

On the other hand, it would seem that the 2° ampullate glands of female lycosids (*Pardosa* at least) are not completely unresponsive to the hormonal changes that culminate in an adult being produced, as evidenced by the enlarged 2° ampullate spigots of adults (e.g., Figs. 9, 11). And given the greater diameters of 2° ampullate fibers in adult females (relative to the 1° ampullate fibers), there may also be internal changes to the 2° ampullate glands, such as substantial increases in the calibers of their ducts, that occur at the same time.

Other functions of 2° ampullate gland fibers.—Though we have only observed 2° ampullate fibers being used for egg sac attachment, we are not suggesting that this is the only role the 2° ampullate glands play in the adult female. Instead, it may be that when these spiders are not carrying egg sacs, fibers from these glands are used for other purposes. One possibility is that they contribute to the dragline. Such an application of 2° ampullate silk may be especially significant for species in which adult female draglines stimulate courtship behaviors in adult males (reviewed in Tietjen & Rovner 1982; also, e.g., Stratton & Uetz 1983; Lizotte & Rovner 1989; Hebets et al. 1996; Fernández-Montraveta & Ruano-Bellido 2000). As in egg sac attachment, the greater diameter of these fibers might also make them better suited to this role than the 1° ampullate fibers. Mechanically, the 2° ampullate fibers would present a more substantial trail that might be more easily discerned by males and, from a chemosensory perspective, the greater surface area of a 2° ampullate fiber has greater potential for presenting pheromones to males. Considering that 2° ampullate spigots (implying functional 2° ampullate



Figures 38–40.—Spinnerets with attached egg sac in adult female *Pardosa modica*: 38. 1° and 2° MaA fibers from both ALS and 1° and 2° MiA fibers from both PMS are attached to the egg sac; 39. Left PMS from the same preparation, showing more clearly the emergence of fibers from the MiA spigots, as well as 1° and 2° MaA fibers from the left ALS in the upper left corner; 40. Right ALS from the same preparation, showing the emergence of fibers from the MaA spigots. The MaA fibers from this ALS are attached to the egg sac by a well-defined (and undamaged) attachment cone. Note that the 2° ampullate fibers have considerably greater diameters than the 1° ampullate fibers. The PLS are out of the field of view in Fig. 38 (no fibers were observed coming from the PLS). Scale bars (38) = 100 μm; (39, 40) = 50 μm.



Figures 41–42.—Ampullate fibers used for egg sac attachment in *Pardosa littoralis* (posterior at right, lateral at top): 41. Portion of left ALS showing 1° and 2° MaA fibers; 42. Portion of left PMS showing 1° and 2° MiA fibers. Both micrographs were taken after the egg sac was removed from the spinnerets. In preparing the spider for SEM (before the egg sac was removed), the shafts (*) of both MaA spigots and the 2° MiA spigot became detached from the bases. Scale bars = 25 μm.

glands) are present in adult females belonging to several other families in which egg sacs are not carried on the spinnerets (Tables 2, 3), and assuming fibers from these spigots play a useful role(s) in such females, it would seem likely that adult female lycosids use 2° ampullate fibers for purposes in addition to egg sac transport. On the other hand, the greater material and energetic cost of producing the larger-diameter 2° ampullate silk may limit its use in other applications.

Comparative ampullate gland spigot morphology.—After observing the relatively large 2° ampullate spigots of adult female lycosids, we were curious to know if this feature is unique to lycosids, or perhaps to lycosids, trechaleids, and rhoicinines. Such a limited occurrence would more strongly suggest that the mode of egg sac transport used by these spiders may have been made possible by or facilitated by selection for enlarged 2° ampullate spigots from which relatively large-diameter 2° ampullate fibers are drawn. And in this context, might this feature extend to pisaurids as well? Several authors have noted that adult female pisaurids transport their egg sacs, held under the sternum, using not only their chelicerae and palps, but also silk from the spinnerets (e.g., Lécaillon 1905:137; Bishop 1924:27–28; Nielsen 1932:133, 135; Bristowe 1958:187, 190; Dondale & Redner 1990: 322; Carico 1976:63, 1993:235–236), and Carico (1993) has suggested that egg sac transport using the spinnerets is plesiomorphic for lycosids, trechaleids, and pisaurids. This raises the possibility that ampullate silk may also play a role, albeit a less crucial one, in egg sac transport in the Pisauridae. On the other hand, Roberts (1995:236) has ‘‘. . . never seen any threads running between the sac and the spinners . . . ’’ in pisaurids, which points up the desirability of investigating the extent and nature of silk use in egg sac transport within this family. Or are relatively large 2° ampullate spigots unrelated to egg sac transport, with such spigots routinely encountered among those entelegynes that retain 2° ampullate spigots as adults, yet do not use ampullate silk for egg sac transport? Questions such as these prompted us to begin examining, as opportunities have arisen, spinnerets of such non-lycosid entelegynes.

At present, our survey is very limited (Table 3) and needs to be expanded, including examining more lycosids and other lycosoids. Thus, we lack satisfactory answers to the above questions. As detailed below, from what data we have and from observations reported in the literature, it seems that 2° ampullate spigots are generally not larger than 1°

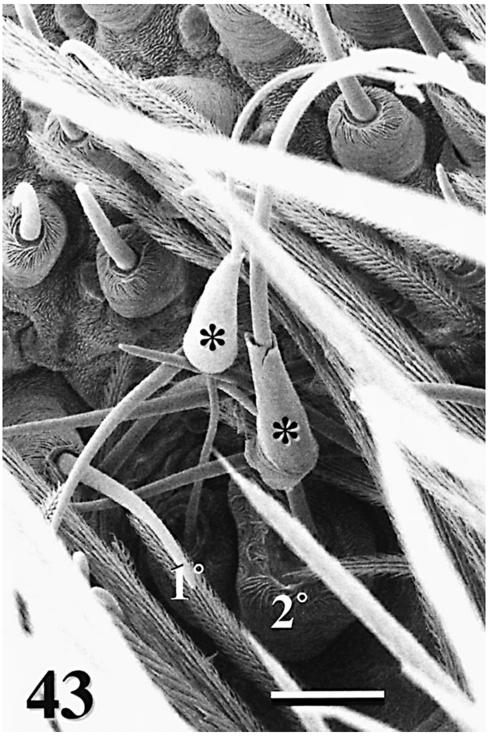


Figure 43.—Portion of left ALS containing the MaA spigots (posterior at right, lateral at top), showing MaA fibers that were being used for egg sac attachment in *Trochosa ruricola*. The micrograph was taken after the egg sac was removed from the spinnerets. As in Fig. 41, the shafts (*) of both MaA spigots became detached from the bases while processing the specimen for SEM. Scale bar = 20 μm.

ampullate spigots among entelegynes. But on the other hand, larger 2° ampullate spigots are neither restricted to lycosoids, nor are they present in all lycosoids that use spinnerets, solely or in part, to carry the egg sac. Among the examined non-lycosoids in this study (Figs. 28–37, Table 3), 2° ampullate spigots tended to be smaller or about the same size as 1° ampullate spigots.

This description also applies to the MaA spigots of several amaurobioids (sensu Griswold et al. 1999). Davies (1998b:74) has noted that in *Tasmarubrius* (Amaurobiidae) the ALS of an adult female has two MaA spigots, with the anterior one, i.e. the 1° MaA spigot, larger. Wang (2000) provides micrographs of ALS from several adult female amaurobiids, including *Rubrius* and *Callobius* in which the two MaA spigots appear similar in size. A micrograph of a *Coelotes* right ALS in the same paper (Wang 2000:fig. 4) indicates that the 2° MaA spigot is larger than the 1° MaA spigot, but because the position of the MaA tartipore in the *Callobius* figure indicates the right ALS, rather than the left ALS as stated in the caption, it may be that the figured *Coelotes* spinneret is actually the left ALS, in which case the 1° MaA spigot is larger. In a description of the amaurobioid subfamily Kababininae, Davies & Lambkin (2000a) state that the two MaA spigots on the female ALS are of unequal size. From their fig. 5C of a right ALS in *Malarina*, it appears that the 1° MaA spigot is again larger. And in several amphinectids, 1° MaA spigots are larger than 2° MaA spigots in adult females. Davies (1998a), in describing a *Quemusia* species, states that the anterior MaA spigot (i.e., the 1°) is ‘‘much larger’’ than the posterior MaA spigot (2°), and, in both a *Magua* species and a *Buyina* species, reports that the anterior MaA spigot is larger than the posterior one. 1° and 2° MaA spigots of similar size can be seen on an ALS of an adult female *Liocranoides* (Tengellidae) in fig. 3 of Platnick (1999).

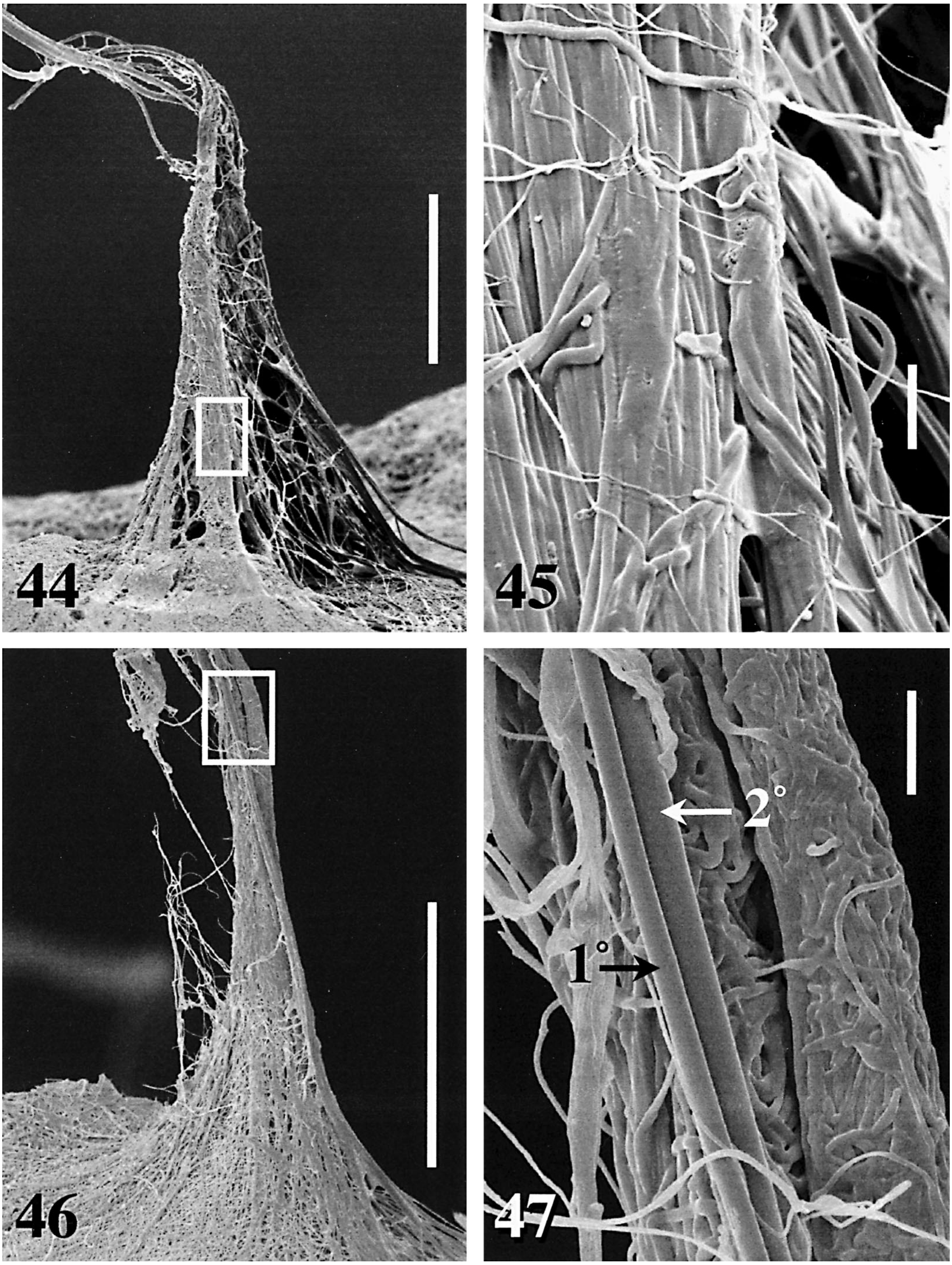
In contrast, several published micrographs demonstrate that larger 2° ampullate spigots, even if not prevalent, are not unique to lycosoids. In fig. 11 of Harvey (1995), an ALS from the nicodamid *Ambicodamus* is shown on which the 2° MaA spigot is conspicuously wider than the 1° MaA spigot. Larger 2° ampullate spigots also occur in some lamponids (Platnick 2000: *Lamponina* ALS, figs. 287 & 288; *Lamponella* ALS, figs. 354 & 355; female *Centrothele* PMS, figs. 408 & 409).

Among the pisaurids examined we saw examples of 2° ampullate spigots that were smaller than, or about equal in size to, 1° ampullate spigots (*Pisaurina*, Figs. 26, 27), as well as examples of 2° ampullate spigots that were noticeably larger than their 1° counterparts (some, though not all, *Dolomedes*, Figs. 24, 25). If enlarged 2° ampullate spigots in lycosids are part of an adaptation facilitating egg sac transport using the spinnerets, then these mixed observations may be a reflection of the supplemental role, at most, that ampullate silk plays in pisaurid egg sac transport. If ampullate silk is not used by pisaurids for egg sac transport, then examples of larger 2° ampullate spigots in pisaurids might simply reflect phylogenetic relatedness between lycosids and pisaurids (e.g., Dondale 1986; Griswold 1993; Silva Davila in press).

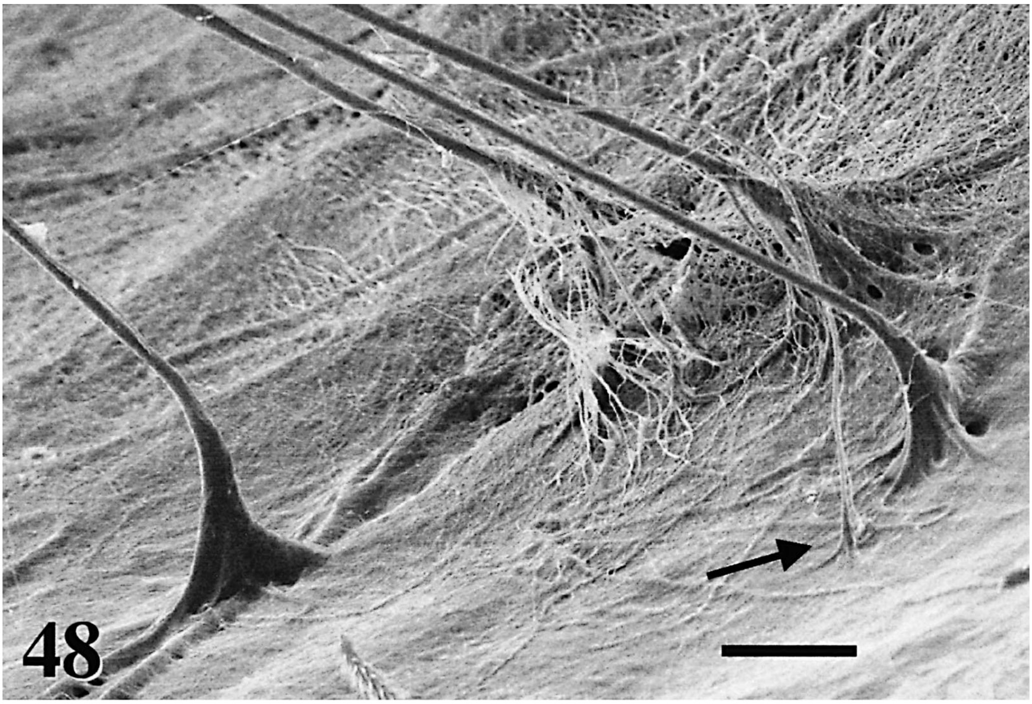
Given our observations on spinnerets from lycosids and pisaurids, and considering that data obtained thus far suggest the Trechaleidae as sister group to the Lycosidae (Sierwald 1990b, 1993; Griswold 1993) or to Lycosidae + Pisauridae (Silva Davila in press), we would have expected 2° ampullate spigots to be larger than 1° ampullate spigots in trechaleids (at least with the MiA spigots since these are used for egg sac attachment (Carico 1993)). But in Carico's (1993) fig. 4 of a *Hesydrus* PMS the 2° MiA spigot (to the right of the 1° MiA spigot in this figure, above the MiA tartipore) does not appear to be larger than the 1° MiA spigot. It may, in fact, be smaller. As mentioned above, the fibers emerging from these spigots also do not differ conspicuously in diameter. But both fibers are very wide, relative to those that we have measured in *Pardosa*, *Trochosa*, and *Dolomedes*, and both spigots are large relative to the aciniform and cylindrical spigots that surround them. There is the possibility, therefore, that trechaleids (*Hesydrus* at least) do have enlarged 2° MiA spigots, but that it is not immediately obvious because the 1° MiA spigots are also enlarged. Since only MiA fibers are used by trechaleids for egg sac attachment (Carico 1993), it would be of value to examine the MaA spigots to see if they and the silk fibers they produce are noticeably smaller than their MiA counterparts. The larger diameters of trechaleid MiA fibers, compared with lycosid and pisaurid ampullate fibers, lead us to speculate that this difference may be related to a behavioral difference among the three families. If an egg sac becomes detached, lycosid and pisaurid females will reattach it, while trechaleid females will not (Carico et al. 1985; Carico 1993). Nor, incidentally, do *Shinobius* (Rhoicininae) females reattach a detached egg sac (Kaihotsu 1988: 17). Do the larger-diameter trechaleid fibers make detachment and, thus, the need for reattachment less likely than among lycosids and pisaurids? The possibility was raised above that the greater cost to a spider of producing larger-diameter fibers may result in more restricted use of such fibers. Thus, do adult female trechaleids use MiA silk exclusively or primarily for egg sac attachment? Again, additional observations are clearly needed.

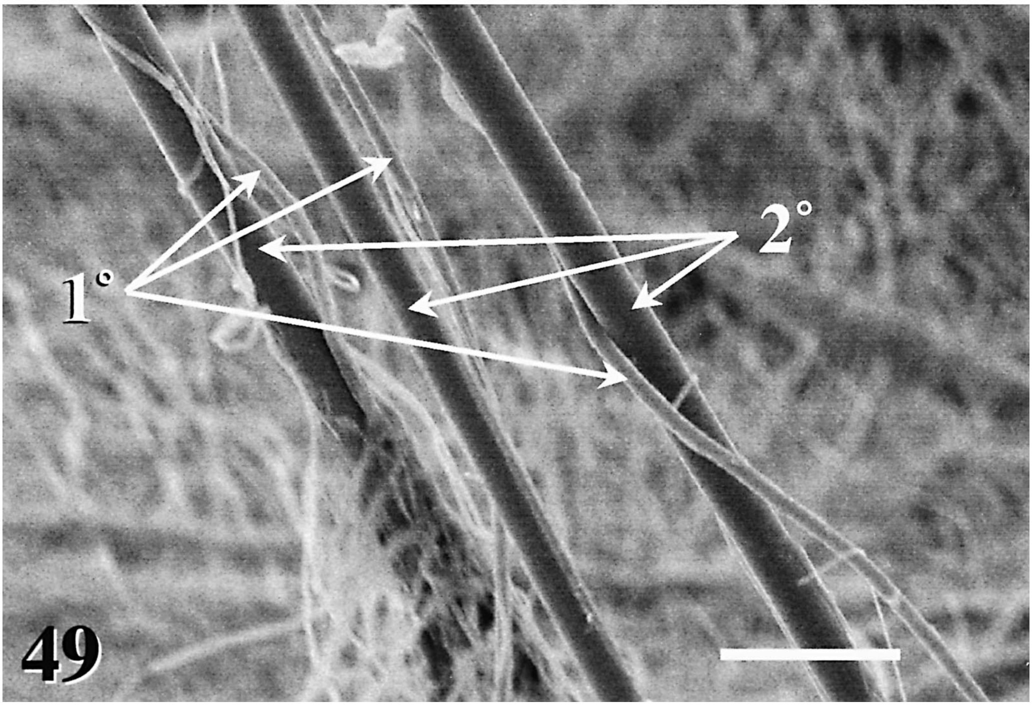
The only scans of rhoicinine spinnerets we have seen are those presented in the description of *Heidrunea* (Brescovit & Höfer 1994). In fig. 6c of Brescovit & Höfer (1994), both PMS of an adult female are shown. We tentatively identify the tartipore, present on each PMS and located just posterior to the three most anterior spigots, as a MiA tartipore. The two spigots immediately posterior to this tartipore are presumably the MiA spigots, with the 2° MiA spigot and MiA tartipore juxtaposed. If these identifications are correct, then the bases of the 1° MiA spigots are wider than those of the 2° MiA spigots. The significance of this observation to any correspondence between the size of 2° ampullate spigots and the use of ampullate silk in egg sac transport, is unknown at present since we do not know if *Heidrunea* attach their egg sacs to their spinnerets and, if they do, if ampullate gland fibers are used. Recall that *Rhoicinus* have been reported to attach egg sacs to the PLS (Exline 1950, 1960), indicating that ampullate gland silks are not involved.

As an aside, we note that amaurobiids of the genera *Amaurobius* and *Callobius* are not included in Table 2 even though Hajer's (1990) observations indicate that they conform to the description given in the table legend. This is because others have reported only a single MiA spigot on each PMS in adult females of these two genera (Platnick et al. 1991:62, 64; Griswold et al. 1999; Wang 2000; the latter contains SEM scans of their PMS), and our own observations on a single specimen of an adult female *Callobius bennetti* (Blackwall 1846) coincide with these latter reports. Thus, the 2° ampullate spigot sexual dimorphism considered in Table 2 seems to apply to the 2° MaA spigots only. Such is the situation observed in the amaurobiid genus *Tasmarubrius* (Davies 1998b) and in the amaurobioid subfamily Kababininae (Davies 1999; Davies & Lambkin 2000a, b). Even this more limited sexual dimorphism is absent in some genera currently included (some very tentatively) in the Amaurobiidae (Platnick 2002) given that adult females of *Storenosoma*, *Otira*, *Midgee*, *Manjala*, *Malala* (Davies 1999; Davies & Lambkin 2001), and *Retiro* (Griswold et al. 1999) have only a single MaA



Figures 44–47.—Attachment cones that affix ampullate fibers to the surface of the egg sac: 44, 45. From a *Gladicosa gulosa* egg sac, with the boxed area in Fig. 44 shown at higher magnification in Fig. 45; 46, 47. From a *Trochosa ruricola* egg sac, with the boxed area in Fig. 46 shown at higher magnification in Fig. 47. On the *G. gulosa* egg sac, it appeared that all the ampullate fibers were attached by this one cone, while on the *T. ruricola* egg sac, one 1°/2° pair of ampullate fibers was attached by a separate, more poorly formed or damaged cone. In Figs. 45, 47 note the fusion among many of the fibers that constitute the cones. Scale bars (44, 46) = 100 μm; (45, 47) = 5 μm.





Figures 48–49.—Surface of a *Pardosa moesta* egg sac, at the site where the eight ampullate fibers coming from the ALS and PMS are attached. 48. Each 2° ampullate fiber (the four thickest, most obvious fibers in the micrograph) is attached by a separate attachment cone, one of which is not well-defined or is damaged. Only two of the 1° ampullate fibers are affixed in the same cone as their 2° counterpart. An arrow points to the site where one 1° ampullate fiber is affixed by its own very small cone. 49. The six more closely spaced ampullate fibers from Fig. 48 are shown at higher magnification so that the 1° fiber accompanying each 2° fiber can be seen more clearly. Scale bars (48) = 25 μm; (49) = 10 μm.

spigot on each ALS, accompanied by a MaA nubbin.

Ampullate fiber attachment to the egg sac.—We have not made a specific attempt to determine the glandular origin of the principal fibers that form the cone-like structures by which ampullate fibers are affixed to the surface of the egg sac. Casual observations from SEM micrographs suggest the piriform glands as the most likely candidates. Among females with egg sacs, the only fibers we have observed emerging from spigots are ampullate and piriform fibers. Also, fusion among fibers seen on cones is reminiscent of the fusion that has been described among piriform fibers from webs of *C. citricola* (Peters 1993). It must be acknowledged, however, that fusion has also been observed among other fiber types, including aciniform-A fibers from at least some uloborids (Peters & Kovoor 1989) and cylindrical fibers from *A. aurantia* (Stubbs 1991; Stubbs et al. 1992; Foradori et al. 2002). A role in attaching ampullate fibers to the egg sac surface is consistent with the piriform glands' well known function of producing attachment discs that secure ampullate fibers to various substrates (e.g., Apstein 1889; Warburton 1890; Richter et al. 1971).

From descriptions of trechaleid egg sacs in Sierwald (1990a:8–9; 1993:62), Brescovit et al. (2000:14), and especially Carico (1993: 230, 236), and from figs. 5–6 in the latter paper, it appears that a single attachment cone secures the four MiA fibers to the surface of the egg sac in at least several genera within this family. A single cone may also affix the eight ampullate fibers to the egg sac in some lycosids (e.g., *Gladicosa*), but others (*Pardosa*) typically produce several closely spaced cones that serve to attach these ampullate fibers.

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