MORPHOLOGY AND EVOLUTION OF COBWEB SPIDER MALE GENITALIA (ARANEAE, THERIDIIDAE)

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ABSTRACT.   This study elucidates the homology of elements of the male palps in the spider family Theridiidae. We survey and illustrate 60 species from 29 out of the 86 currently recognized genera representing all subfamilies. The study is buttressed by a phylogenetic framework, and uses a new method to evaluate critically competing homology hypotheses based on various criteria. Among the classic criteria for homology, topology performed better than special similarity, and much better than function. Guided by those results, we propose names for and correspondences among the broad diversity of theridiid palpal tegular sclerites. We discuss the phylogenetic utility and distribution of key palpal characteristics, and evaluate existing evolutionary hypotheses of the theridiid palp and its components.

Keywords: Character homology, congruence, phylogeny, tests of homology, primary homology

Systematists in recent years broadly agree on the distinction between primary and secondary homology (e.g., de Pinna 1991). Primary homologies are almost Baconian observations—a, b, and c correspond or are similar in some way, and therefore may be the same structure modified during descent from a common ancestor. Such conjectures are what systematists call ''characters,'' and they constitute the columns in a standard phylogenetic data matrix; features of characters, x, y, and z then being ''character states.'' Phylogenetic analysis uses the fit of the distribution of states within characters and across characters as independent observations to choose a phylogenetic tree. Character states that provide support for nodes of the tree are termed secondary homologies (i.e., synapomorphies) because they have withstood the test of congruence under parsimony, or maximum likelihood, or whatever criterion guided tree choice. Secondary homologies, then, are primary homologies that have been tested phylogenetically (Farris 1983). Primary homologies, whether characters or character states, are background knowledge, untested postulates, assumed prior to analysis. However,

congruence only tests character states—the possibility that the characters themselves may be erroneous, or that a more parsimonious sorting of states into characters may be possible, is never formally tested (e.g., Patterson 1982; Rieppel & Kearney 2002). This represents a serious problem when taxa present several similar, but independent, features. For a well known example, birds have only three digits but which of the five present is in most other vertebrates is still controversial (Wagner 2005). Spiders present their own problems in character homology, particularly the sclerites of the complex entelegyne male palpus (e.g., Griswold et al. 1998). Male spider genitalia evolve fast enough to denote species (Eberhard 1985; Huber 2003, and a wealth of revisionary work), yet are a main source of data used to define major clades (Griswold et al., 2005). Unsurprisingly then, the nomenclature—which is to say the homology hypotheses—of the parts of the male bulb are contentious (Coddington 1990).

Although Comstock (1910) was not the first to study palps, his excellent, carefully labeled illustrations of major spider clades is the seminal work in comparative studies of the parts

of the male bulb. His proposed homologies and names are still used today to describe palpal diversity. Other early work includes Menge (1866, 1868, 1869), Osterloh (1922), and Gerhardt (1921, 1923). More recent reviews include Levi (1961), Shear (1967), Saaristo (1978, 2006), Heimer (1982), Coddington (1990), and Sierwald (1990). The morphology and nomenclature of araneid palps was discussed in detail by Grasshoff (1968, 1973), that of linyphiid palps by Merrett (1963), and of pholcid palps by Huber (1994, 1995, 1996), and Uhl et al. (1995). In addition, recent taxonomic revisions and cladistic analyses have discussed palpal homologies in theridiids and many related spider families (e.g., Hormiga 1994a, b, 2000; Scharff and Coddington 1997; Griswold et al. 1998, 1999, 2005; Agnarsson 2003, 2004, 2005, 2006a, b, c; Agnarsson & Kuntner 2005; Agnarsson et al. 2006, 2007; Agnarsson & Zhang 2006; Kuntner 2005, 2006, 2007; Miller 2007).

Despite this work, theridiid palpal sclerite names (homologies) are unstable. Levi (1953–1972) and Levi & Levi (1962) used a mostly consistent nomenclature for sclerites, but disavowed more general homologies despite using names broadly applied in other families (Levi 1961). Heimer (1982) homologized theridiid sclerites to those in other spider families. Heimer & Nentwig (1982) and Heimer (1986) proposed a detailed theory on the evolution of the theridiid "paracymbium" and Heimer (1986) also discussed the homology of the median apophysis. Saaristo (1978) discussed theridiid palpal morphology in detail suggesting several novel hypotheses, and Bhatnagar & Rempel (1962) described the ontogeny of the *Latrodectus* palp (probably *hesperus*, although identified as "*curacaviensis*"). All these authors disagreed among themselves about homology of palpal sclerites in theridiids in particular and araneoids in general. Most recently, Saaristo (2006) proposed yet another novel scheme of palpal homologies (one proposed without reference to a phylogeny), based on retraction of some, but not all, of his earlier views (see Saaristo 1978) and some apparent misinterpretations of both Coddington (1990) and Agnarsson (2004).

The diversity of views has hindered understanding the phylogenetic relationships among theridiids (see Agnarsson 2004) and other spiders (Coddington 1990; Griswold et al. 1998),

and perhaps because of this instability, authors of recent taxonomic papers on theridiids avoid classic palpal sclerite names. For example, Knoflach (1991–2002), Knoflach & Thaler (2000), Knoflach & van Harten (2000, 2001), and Knoflach & Pfaller (2004) label theridiid tegular sclerites consistently and imply homologies within theridiids, but use names like tegular apophysis I, II and III to avoid interfamilial homologies.

Many theridiids have relatively complex palps and diverse palpal conformations (Agnarsson 2004). The worst problems are the sclerites borne on the distal segment of the bulb (tegulum); of which Orbiculariae commonly have three, or sometimes four or more. The plesiomorphic theridiid condition is four sclerites (Agnarsson 2004), but some taxa have five, and many others three, two, or only one. Three names (embolus, conductor, median apophysis) are applied to sclerites in most spider families, while a multitude of other names are variously applied. Of these, only the embolus is not problematic; it contains the ejaculatory duct and conveys sperm to the female. Others, such as the radix, conductor, theridiid tegular apophysis, median apophysis, paramedian apophysis, suprategulum, conductor II, etc., are contentious.

Despite the bleak history of theridiid palpal nomenclature, we nevertheless present yet one more attempt at a durable system of names and homologies. We illustrate 60 theridiid species, belonging to 29 out of the 87 currently recognized genera (Platnick 2006; Agnarsson 2000, 2006a), representing all theridiid subfamilies and the known range of palpal morphologies. We use a new method (Agnarsson & Coddington unpublished ms.) to evaluate quantitatively primary homology hypotheses implied by different criteria of homology in order to propose a less arbitrary and more parsimonious explanation of palpal elements than have previous studies. We use the same method to compare our results to four previous hypotheses of theridiid homologies (Levi 1953–1972; Saaristo 1978; Coddington 1990; Agnarsson 2004) and we discuss the evolution of theridiid palps in a phylogenetic framework.

METHODS

Test of character homology.—Classical criteria for homology include topology, func-

tion, special similarity (similarity in fine detail), and ontogeny (e.g., de Beer 1971; Rieppel 1994, 2001; Hall 1995; Brigandt 2003). Although one of the most detailed studies of spider palpal ontogeny concerned *Latrodectus* (Bhatnagar & Rempel 1962), their study was not comparative, so that ontogeny cannot be compared across Theridiidae.

This study, therefore, is limited to topology, special similarity, and function. We use a new method (Agnarsson & Coddington unpublished ms.) that derives primary homology hypotheses under each criterion in turn but which then assesses them under those criteria not used in their formation. Obviously, primary homologies suggested by topological similarity may differ from those suggested by function or special similarity. The preferred set of homologies is that least contradicted by, or most congruent with, all criteria. Each criterion either supports, contradicts, or is neutral about any homology hypothesis. The method is quantitative in that support or agreement is scored as ''1,'' contradiction as ''0,'' and inapplicability as ''–,'' and these values are summed (or averaged) to reach a conclusion.

Figure 1 presents a didactic example in which two taxa each have three sclerites, provisionally named *r1–3* and *a1–3*, with differing functions (F1–F3), shapes (round or hexagon), and colors (white or black). Taking topology first, it implies that $r1 = a1$, $r2 = a2$, and $r3 = a3$. Sclerite *r1* differs from *a1* in color, *r2* from *a2* in function, and *r3* from *a3* in function and color, for a total of 4 differences. Taking function next, it implies $r1 = a1$, $r2 = a3$, and $r3 = a2$. Sclerite *r1* differs from *a1* in color, *r2* from *a3* in topology, shape, and color, and *r3* from *a2* in topology and shape, for a total of 6 differences. Taking similarity last, it implies $r1 = a3$ (the only black, round sclerite), $r2 = a2$, and $r3 = a1$. Sclerite *r1* differs from *a3* in topology and function, *r2* from *a2* in function, and *r3* from *a1* in topology and function, for a total of 5 differences. In this case, topology is preferred because it requires fewer hypothesized changes. Note that special similarity here offers two points of comparison, shape and color, whereas topology and function offer only one each. Similarity, therefore, counts ''more'' than topology or function, and one might wish to
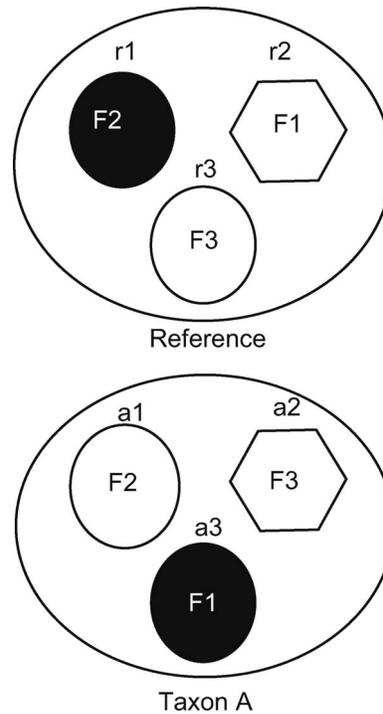

Figure 1.—Two taxa each have three sclerites, but their homologies are ambiguous. They perform three different functions, indicated as F1–F3; occur in various relative positions (topology), and differ in color and shape (black or white, round or hexagon; special similarity). Depending on which criterion is primary, different primary homology hypotheses result. Under topology, $r1 = a1$, $r2 = a2$, and $r3 = a3$; under function, $r1 = a1$, $r2 = a3$, and $r3 = a2$; under special similarity, $r1 = a3$, $r2 = a2$, and $r3 = a1$. See text and Agnarsson and Coddington (in press) for explanation.

give each criterion equal weight by averaging the points of comparison for special similarity prior to comparison with the other criteria (the equal weights approach). On the other hand, one could argue that complex homologies have more points of comparison and therefore deserve greater weight, so that all conflicts should simply be summed (the parsimony approach). The results of both points of view are presented here. In this didactic example, topology is preferable under both approaches (Agnarsson & Coddington unpublished ms.).

Another complication is unrestrained hypotheses of loss of one sclerite and gain of

another. Strictly speaking, an author might argue that *any* difference between two structures justifies the supposition that the one has been lost and the other gained, even in the face of many "similarities." Under the "gain/loss" approach such similarities are interpreted as convergences. Although not illustrated in Fig. 1, we attempt to constrain such an approach by counting the loss and gain each as one step, and each "convergence" between the lost and gained sclerites as an additional step. If transformation were preferred to loss/gain, such similarities would have required no explanation, and therefore count against the loss/gain hypothesis. For example, Saaristo (1978), Coddington (1990), and Agnarsson (2004) regarded the "third" tegular apophysis in Theridiidae as at least one novel sclerite, but Levi (1953–1972) called it a "radix," presumptively homologous to the araneid radix. The former authors therefore incur costs for hypothesizing a new sclerite, whereas Levi incurs costs only when topological, functional, or detailed attributes of the araneid and theridiid radices differ. We also freely admit that it is often impossible to know exactly what prior authors were thinking when they used classical sclerite names in Theridiidae. Our inferences in Table 1, although our best guess as to what those authors intended, are primarily to show how these logical procedures may resolve the problem of palpal sclerite homologies in Theridiidae (Tables 1, 2).

Abbreviations and conventions.—References to figures published elsewhere are listed in lowercase type (fig.); references to figures in this paper are capitalized (Fig.). Anatomical abbreviations appear in Appendix A.

Taxon choice.—Agnarsson (2004) analyzed theridiid phylogeny at the generic level using a matrix of 61 terminals (8 outgroup genera, 31 theridiid genera) and 242 characters, of which 88 (36%) pertained to the palpal organ. Based on these results (Fig. 2, see also Arnedo et al. 2004), we chose exemplars of 29 genera (16 represented by their type species) from across (and beyond) the cladogram, to represent theridiid palpal diversity for the purposes of this paper (see Appendix B, Table 1, and Figures 4–200). For simplicity, a portion of those were selected for analysis using the new method (Table 1); the inclusion of the remainder does not alter the results (Agnarsson & Coddington unpublished ms.). To the

best of our knowledge, omitted genera do not present dramatically different palpal configurations but seem to fit in the schema proposed here. Nevertheless, rare genera not covered by Agnarsson (2004) or, indeed, still undiscovered theridiids could change these results in the future. For the complete list of material examined in this study, see Agnarsson (2004), and Appendix B.

Figure 3 is a schematic "groundplan" of theridiid palps, representing the sclerites most commonly found in these spiders (Agnarsson 2004; Knoflach 2004). This groundplan facilitates discussion of phylogenetically important elements of the theridiid palp, and also serves as a reference against which primary homology hypotheses are compared (see "reference" in Fig. 1).

Specimen examination.—Specimens were examined under a Wild M-5A dissecting microscope. Male palps were immersed in concentrated KOH ($\sim$1 g/ml) for about one minute and then transferred to distilled water where rapid expansion of hematodochae took place in less than one minute (see Coddington 1990, modified from Shear 1967). In theridiids full expansion often requires unlocking the MA from the cymbium, and occasionally re-immersion in KOH. Artificial expansion of palps greatly facilitates understanding of palpal morphology (Coddington 1990), although it is a poor technique to understand how palps function (Huber 1993). In many cases, palps must be dissected to understand their anatomy. After examining the expanded palp, removal of the embolus (and sometimes other sclerites) facilitated examination of the tegulum and tegular sclerites residing behind or beneath the embolus. Sketches were made of preparations mounted as described in Coddington (1983) using both dissecting and compound microscopes equipped with camera lucida. For SEM examination, specimens were cleaned ultrasonically for one minute and then transferred to 100% ethanol overnight. The specimens were then dissected, and either critical point or air-dried. Specimens were glued to round-headed rivets using an acetone solution of polyvinyl resin, and sputter coated. All drawings were rendered in Adobe Photoshop, and plates were composed with Adobe Illustrator.

Table 1.—Results of the method outlined in Fig. 1 and the text, as applied to three problematic theridiid palpal sclerites: median apophysis (MA), theridioid tegular apophysis (TTA), and conductor (C) with topology as the primary criterion. Similar tables were compiled for function and special similarity and are summarized under the SS and FNC columns in Table 2. Scores are given for topology (TOP), special similarity (SS) and function (FNC) as secondary criteria. Dashes are inapplicables; question marks are unknowns. Special similarity includes three points of comparison: flexible or fused tegular connection (Cxn), sperm duct presence or absence (Dct), and membranous or sclerotized texture (Tex), which three scores are averaged under SS for each sclerite under the equal weights point of view (see text). The strict gain/loss point of view (see text) is tabulated in the G/L column. As the primary criterion, topology naturally does not conflict with itself as a secondary criterion (all scores = 1, or agreement) but it conflicts with function for the TTA and C, and with special similarity for MA and C. Subtotals by taxon (averages for TOP, SS, FNC, and G/L) and counts of conflict for parsimony (PAR) appear at right; grand totals are counts or averages of raw scores under each sclerite and are carried forward to Table 2.

	MA							TTA						
Taxon	TOP	Cxn	Dct	Tex	SS	Fnc	G/L	TOP	Cxn	Dct	Tex	SS	Fnc	G/L
Achaearanea tabulata	—	—	—	—	—	—	0	—	—	—	—	—	—	0
Achaearanea tepidariorum	—	—	—	—	—	—	0	—	—	—	—	—	—	0
Achaearanea trapezoidalis	—	—	—	—	—	—	0	—	—	—	—	—	—	0
Ameridion sp.1	1	1	0	1	0.67	1	1	1	1	1	1	1.00	0	0
Ameridion sp.2	1	1	0	1	0.67	1	1	1	1	1	1	1.00	1	0
Anelosimus eximius	1	1	0	1	0.67	1	1	1	1	1	1	1.00	?	0
Anelosimus vittatus	1	1	0	1	0.67	1	1	1	1	1	1	1.00	0	0
Argyrodes argyrodes	1	1	1	1	1.00	1	1	1	1	1	1	1.00	1	0
Argyrodes elevatus	1	1	1	1	1.00	1	1	1	1	1	1	1.00	1	0
Carniella schwendingeri	1	1	1	1	1.00	1	1	—	—	—	—	—	—	0
Coleosoma floridanum	1	1	0	1	0.67	1	1	1	1	1	1	1.00	1	0
Enoplognatha ovata	1	1	1	1	1.00	1	1	1	1	1	1	1.00	0	0
Enoplognatha sp.	1	1	1	1	1.00	1	1	1	1	1	1	1.00	0	0
Episinus angulatus	1	1	1	1	1.00	1	1	1	1	1	1	1.00	1	0
Episinus maculipes	1	1	1	1	1.00	1	1	1	1	1	1	1.00	1	0
Euryopis flavomaculata	1	1	1	1	1.00	1	1	1	1	1	1	1.00	0	0
Latrodectus geometricus	1	1	1	1	1.00	1	1	1	1	1	1	1.00	?	0
Neospintharus trigonum	1	1	1	1	1.00	1	1	1	1	1	1	1.00	1	0
Phoroncidia americana	1	1	1	1	1.00	1	1	1	1	1	1	1.00	0	0
Selkirkiella sp.	1	1	1	1	1.00	1	1	1	1	1	1	1.00	?	0
Steatoda americana	1	1	1	1	1.00	1	1	1	1	1	1	1.00	1	0
Styposis selis	1	1	1	1	1.00	1	1	1	1	1	1	1.00	0	0
Theridion cochise	1	1	0	1	0.67	1	1	—	—	—	—	—	—	0
Theridion frondeum	1	1	0	1	0.67	1	1	1	1	1	1	1.00	1	0
Theridion varians	1	1	0	1	0.67	1	1	1	1	1	1	1.00	1	0
Theridula emertoni	—	—	—	—	—	—	0	—	—	—	—	—	—	0
Theridula opulenta	—	—	—	—	—	—	0	—	—	—	—	—	—	0
Thymoites nr. *prolatus*	1	1	0	1	0.67	1	1	1	1	1	1	1.00	1	0
Grand Totals														

RESULTS AND DISCUSSION

Test of character homology.—Table 2 shows that topology outperforms similarity and function (columns TOP, SS, FNC) in accounting for theridiid palpal diversity whether assessed under the equal weights or parsimony approach; hypotheses based on topology are globally most congruent. Topology is fully congruent with some other criterion for each sclerite in all taxa. For example, median

apophysis topology agrees with function (locking the palp in the cymbium) and two similarities (texture and membranous attachment to the tegulum), but a second similarity (presence of a duct) is highly incongruent. If duct presence is used as a primary criterion, two sclerites would be recognized (corresponding to locking apophyses A and B of Saaristo (1978)). The two would be topologically and functionally identical, and phylo-

Table 1.—Extended.

C							Subtotals by Taxon						
TOP	Cxn	Dct	Tex	SS	FNC	G/L	TOP	SS	FNC	G/L	PAR	G/L	PAR
1	1	1	0	0.67	1	1	1.00	0.67	1.00	0.33	3	0.83	1
1	1	1	0	0.67	1	1	1.00	0.67	1.00	0.33	3	0.83	1
1	1	1	0	0.67	1	1	1.00	0.67	1.00	0.33	3	0.83	1
1	1	1	1	1.00	0	1	1.00	0.89	0.33	0.67	4	0.96	3
1	1	1	1	1.00	1	1	1.00	0.89	1.00	0.67	2	0.96	1
1	1	1	1	1.00	?	1	1.00	0.89	1.00	0.67	2	0.96	1
1	1	1	1	1.00	0	1	1.00	0.89	0.33	0.67	4	0.96	3
1	1	1	1	1.00	1	1	1.00	1.00	1.00	0.67	1	1.00	0
1	1	1	1	1.00	1	1	1.00	1.00	1.00	0.67	1	1.00	0
—	—	—	—	—	—	0	1.00	1.00	1.00	0.33	2	1.00	0
1	1	1	1	1.00	1	1	1.00	0.89	1.00	0.67	2	0.96	1
1	1	1	?	1.00	0	1	1.00	1.00	0.33	0.67	3	1.00	2
1	1	1	1	1.00	0	1	1.00	1.00	0.33	0.67	3	1.00	2
1	1	1	1	1.00	1	1	1.00	1.00	1.00	0.67	1	1.00	0
1	1	1	1	1.00	1	1	1.00	1.00	1.00	0.67	1	1.00	0
—	—	—	—	—	—	0	1.00	1.00	0.50	0.33	3	1.00	1
1	1	1	1	1.00	?	1	1.00	1.00	1.00	0.67	1	1.00	0
1	1	1	1	1.00	1	1	1.00	1.00	1.00	0.67	1	1.00	0
1	1	1	1	1.00	0	1	1.00	1.00	0.33	0.67	3	1.00	2
1	1	1	0	0.67	?	1	1.00	0.89	1.00	0.67	2	0.96	1
1	1	1	?	1.00	1	1	1.00	1.00	1.00	0.67	1	1.00	0
1	1	1	0	0.67	0	1	1.00	0.89	0.33	0.67	4	0.96	3
1	1	1	1	1.00	1	1	1.00	0.83	1.00	0.67	2	0.92	1
1	1	1	1	1.00	1	1	1.00	0.89	1.00	0.67	2	0.96	1
1	1	1	1	1.00	1	1	1.00	0.89	1.00	0.67	2	0.96	1
1	0	1	1	0.67	0	1	1.00	0.67	0.00	0.33	4	0.33	2
1	0	1	1	0.67	0	1	1.00	0.67	0.00	0.33	4	0.33	2
1	1	1	1	1.00	1	1	1.00	0.89	1.00	0.67	2	0.96	1
							1.00	0.92	0.77	0.58	66	0.92	31

genetically the loss of one would take place at the same instance as the origin of the other (Fig. 201). Similarly, function would make both topology, connection to the tegulum, and texture quite variable for the conductor and theridiid tegular apophysis. Under the topology rule, the conductor is consistently membranous.

We think this proposed homology scheme (Fig. 3, see also Figs. 4–200) is clearly more logical for theridiids than others hitherto proposed. While we have used classical names and hence implied testable interfamily homology hypotheses, we have not yet extended our test to other araneoid families. To effectively homologize sclerites (e.g., across Orbiculariae), a similarly detailed study is needed for each family. One difficulty in comparing theridiids with related families is that the theridiid bulb connects differently in

Table 2.—Results of the logic of Table 1 as applied to four prior analyses of theridiid palpal homologies (A04 = Agnarsson 2004; C90 = Coddington 1990; L62 = Levi 1953–1973; S78 = Saaristo 1978) and for all three primary criteria (TOP, FCN, SS). The column TOP carries forward the grand totals of Table 1. Either as mean performance under all criteria and accounting for gain/loss hypotheses (Grand mean) or simple step counting (parsimony) topology (TOP) as applied by Agnarsson (2004) outperforms other criteria and previous homology hypotheses.

Secondary criterion	Study or primary criterion						
	A04	C90	L62	S78	TOP	SS	FCN
Topology	1.00	0.61	0.68	0.67	1.00	0.93	0.77
Similarity	0.92	0.86	0.72	0.70	0.92	0.94	0.79
Function	0.77	0.48	0.61	0.41	0.77	0.75	1.00
Gain/Loss	0.58	0.58	0.86	0.31	0.58	0.52	0.59
Grand mean	0.82	0.63	0.72	0.52	0.82	0.78	0.79
Parsimony	66	129	121	181	66	74	87

the alveolus. In theridiids the subtegulum attaches mesobasally to the cymbium, but in the outgroups it attaches centrally. Therefore the orientation of the palpal bulb differs (e.g., the embolus appears to be proximal in the outgroups), but ventral-apical in theridiids. Nevertheless, the origin of the embolus is roughly opposite the fundus in all taxa considered here. Outgroup ''theridiid tegular apophyses'' and conductors are topologically and functionally similar to the theridiid condition as well.

The araneoid ''median apophysis'' is problematic. None of the primary homology criterion applied here to Theridiidae clearly corroborates any prior nomenclature of the median apophysis. As defined by other workers, the median apophysis topology varies across families, although theridiids are similar to araneids, which formed the basis for Comstock's (1910) nomenclature. Special similarity and function also differ. Difference in function is not surprising because our results suggest that it is the median apophysis homolog that forms part of the uniquely theridiid bulb-cymbium lock mechanism. These results show, yet again, that median apophysis nomenclature across spiders is inconsistent, and it remains to be seen if the sort of logic used here can improve the situation.

Composition and evolution of the male theridiid palp.—This study examined representatives of 29 theridiid genera, about 33% of the 87 currently recognized theridiid genera (Platnick 2006; Agnarsson 2000, 2006a). Palpal organs of 14 further genera are illustrated in Agnarsson (2004) and Knoflach (2002) (see

also Agnarsson 2003, 2005, 2006a, b; Agnarsson & Kuntner 2005; Miller & Agnarsson 2005). These 43 genera include all common, species-rich theridiid genera and thus represent the vast majority of theridiid diversity, while the majority of the omitted genera are small (20 monotypic, 13 with 2–3 species, and 8 with 4–8 species). We therefore feel that our results, summarized below, apply broadly to theridiids.

The male palp consists of six segments: the coxa, trochanter, femur, patella, tibia, and the tarsus modified for sperm transmission. Most of these segments may bear modifications that are phylogenetically informative (Figs. 4–200). The palpal femur, for example, is elongated in some theridiid genera (Figs. 111, 112) and the patella also is rarely elongated (Fig. 112). However, we focus our discussion on the tibia and especially the tarsus, forming the cymbium and the palpal bulb. The reader should refer to Coddington (1990) for further discussion on ontogeny and homology of palpal elements. An overview of the theridiid palp and its landmarks is given in Figure 3.

Tibia: The male palpal tibia is typically a simple, quasi-cylindrical, segment broadening somewhat towards the tip. In theridiid relatives such as linyphioids, nesticids, and synotaxids, the tibial rim (the long edge of the tibial tip) that faces the dorsum of the cymbium is inconspicuous (Figs. 189, 190, 195–198; see also Griswold 2001, fig. 140A) and irregularly hirsute. Theridiid tibiae are characteristically modified into a cup-like segment, with a broadened distal tip (Figs. 3, 4, 12, 16, 17, 29, 50, 57, 66–69, 71, 72, 75, 76,
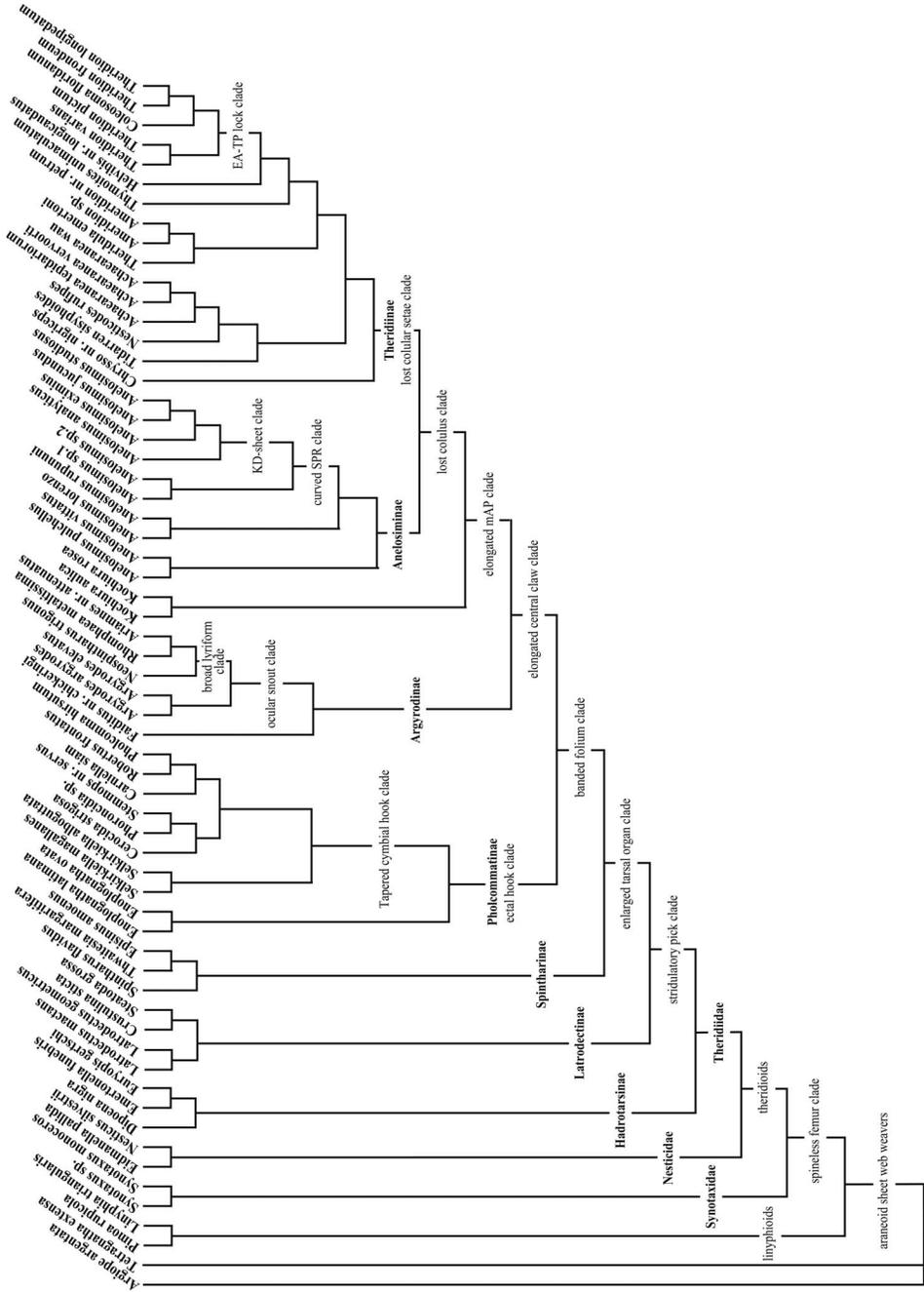
Figure 2.—Cladogram of Theridiidae (reproduced from Agnarsson 2004) labeled with subfamily and informal clade names, some of which refer to characters of the male palp. This cladogram forms the basis for the taxon choice in this study and is used to evaluate evolutionary hypotheses of palpal elements.
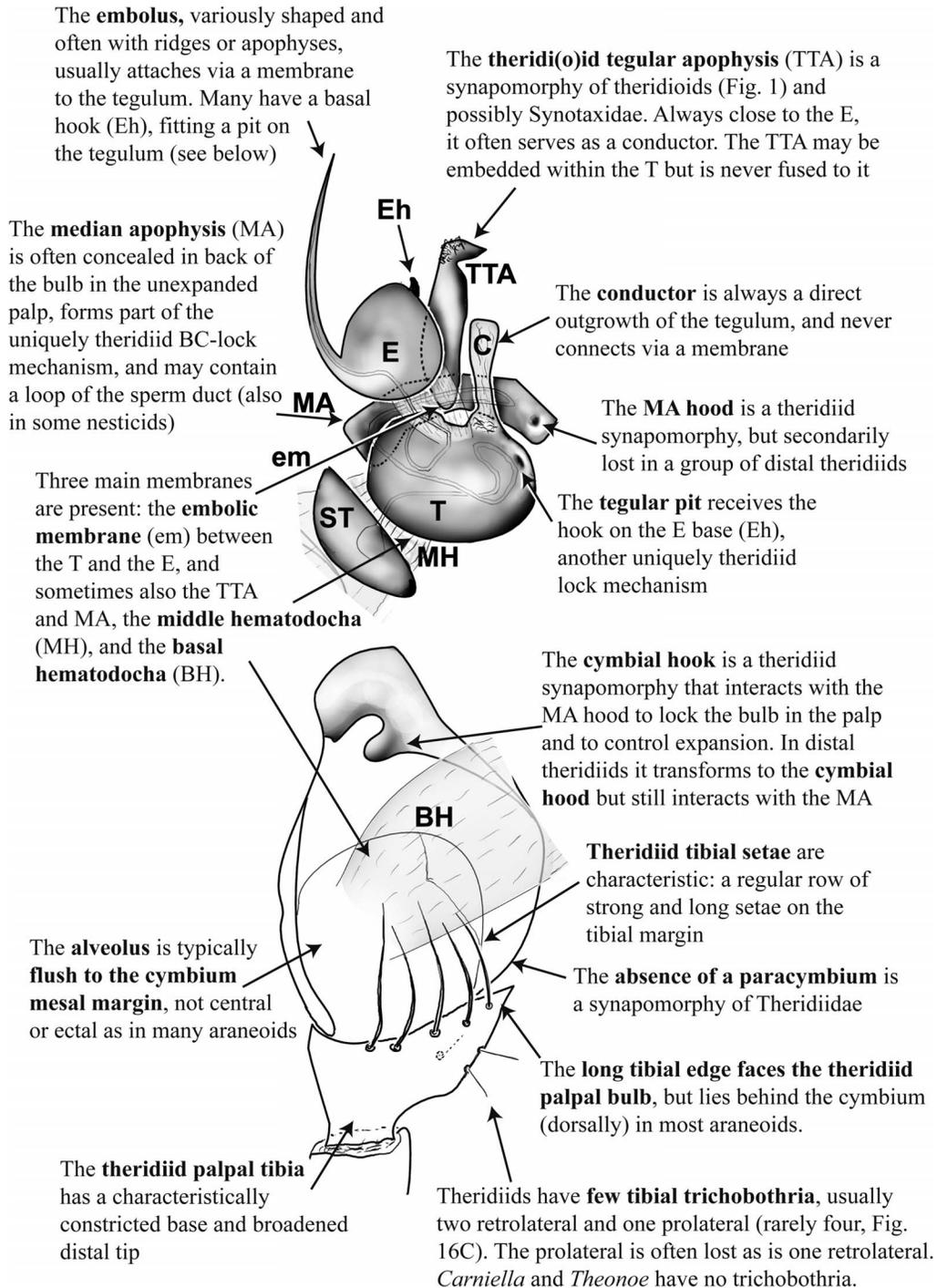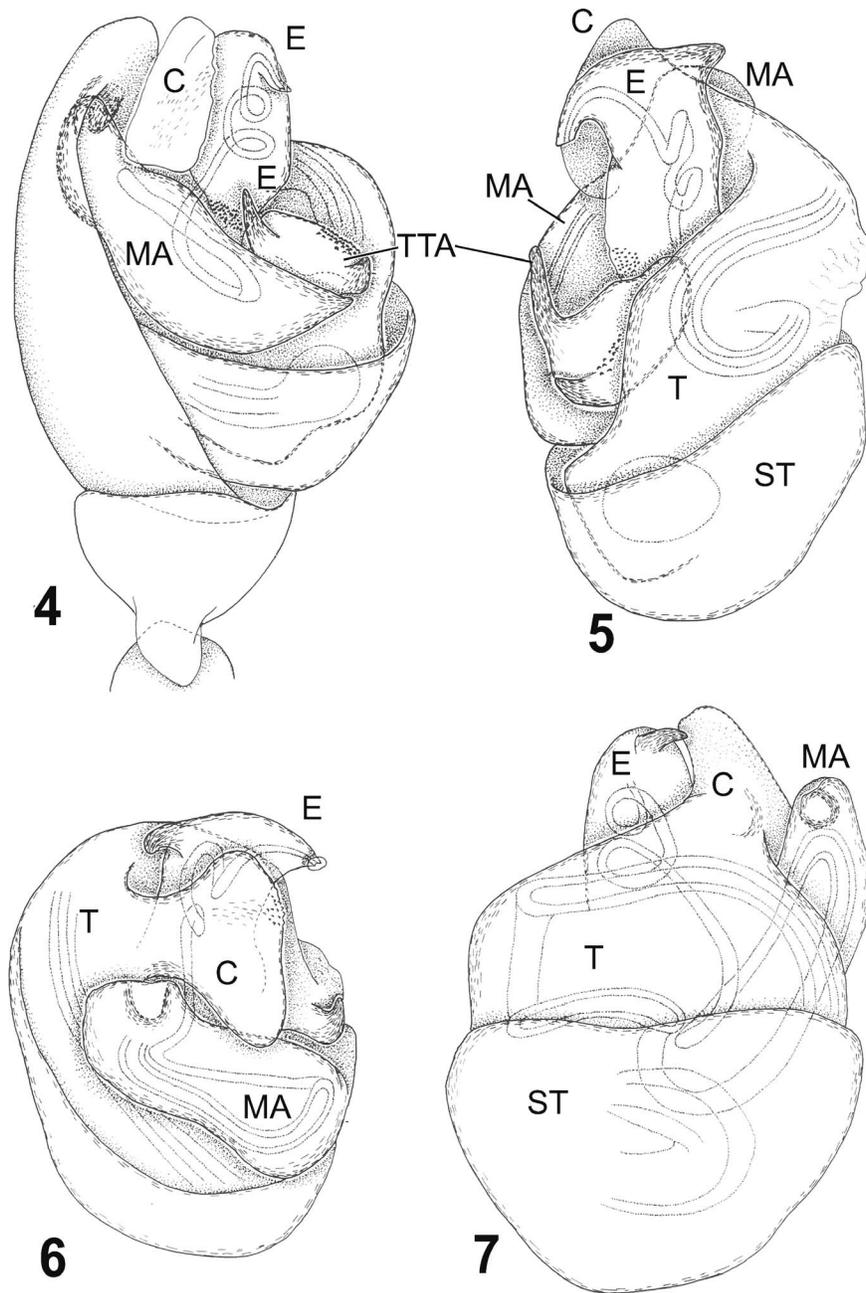
The **embolus,** variously shaped and often with ridges or apophyses, usually attaches via a membrane to the tegulum. Many have a basal hook (Eh), fitting a pit on the tegulum (see below)

The **theridi(o)id tegular apophysis** (TTA) is a synapomorphy of theridioids (Fig. 1) and possibly Synotaxidae. Always close to the E, it often serves as a conductor. The TTA may be embedded within the T but is never fused to it

The **median apophysis** (MA) is often concealed in back of the bulb in the unexpanded palp, forms part of the uniquely theridiid BC-lock mechanism, and may contain a loop of the sperm duct (also in some nesticids)

The **conductor** is always a direct outgrowth of the tegulum, and never connects via a membrane

The **MA hood** is a theridiid synapomorphy, but secondarily lost in a group of distal theridiids

Three main membranes are present: the **embolic membrane** (em) between the T and the E, and sometimes also the TTA and MA, the **middle hematodocha** (MH), and the **basal hematodocha** (BH).

The **tegular pit** receives the hook on the E base (Eh), another uniquely theridiid lock mechanism

The **cymbial hook** is a theridiid synapomorphy that interacts with the MA hood to lock the bulb in the palp and to control expansion. In distal theridiids it transforms to the **cymbial hood** but still interacts with the MA

Theridiid tibial setae are characteristic: a regular row of strong and long setae on the tibial margin

The **alveolus** is typically **flush to the cymbium mesal margin**, not central or ectal as in many araneoids

The **absence of a paracymbium** is a synapomorphy of Theridiidae

The **long tibial edge faces the theridiid palpal bulb**, but lies behind the cymbium (dorsally) in most araneoids.

The **theridiid palpal tibia** has a characteristically constricted base and broadened distal tip

Theridiids have **few tibial trichobothria**, usually two retrolateral and one prolateral (rarely four, Fig. 16C). The prolateral is often lost as is one retrolateral. *Carniella* and *Theonoe* have no trichobothria.

Figure 3.—Landmarks and descriptions of the major features and sclerites of the theridiid palp.

Figures 4–7.—*Dipoena melanogaster*. 4, male palp mesal; 5, bulb removed from cymbium, ectal; 6, apical; 7, dorsal; note loops of sperm duct within T, MA and E.

80, 87, 88, 92, 96, 97, 100, 104, 105, 107–109, 111–113, 131, 140, 146, 150, 157, 161, 162, 166, 170) (see also Agnarsson, 2004). The distinct tibial rim thus formed always faces the palpal bulb in the cymbium. The rim, furthermore, carries a highly regular row of

strong and long, usually serrated setae (Figs. 3, 12, 14, 100, 104, 105, 107–109).

The number and distribution of tibial trichobothria is also phylogenetically informative. Agnarsson (2004) found that the reduction to two retrolateral trichobothria (versus
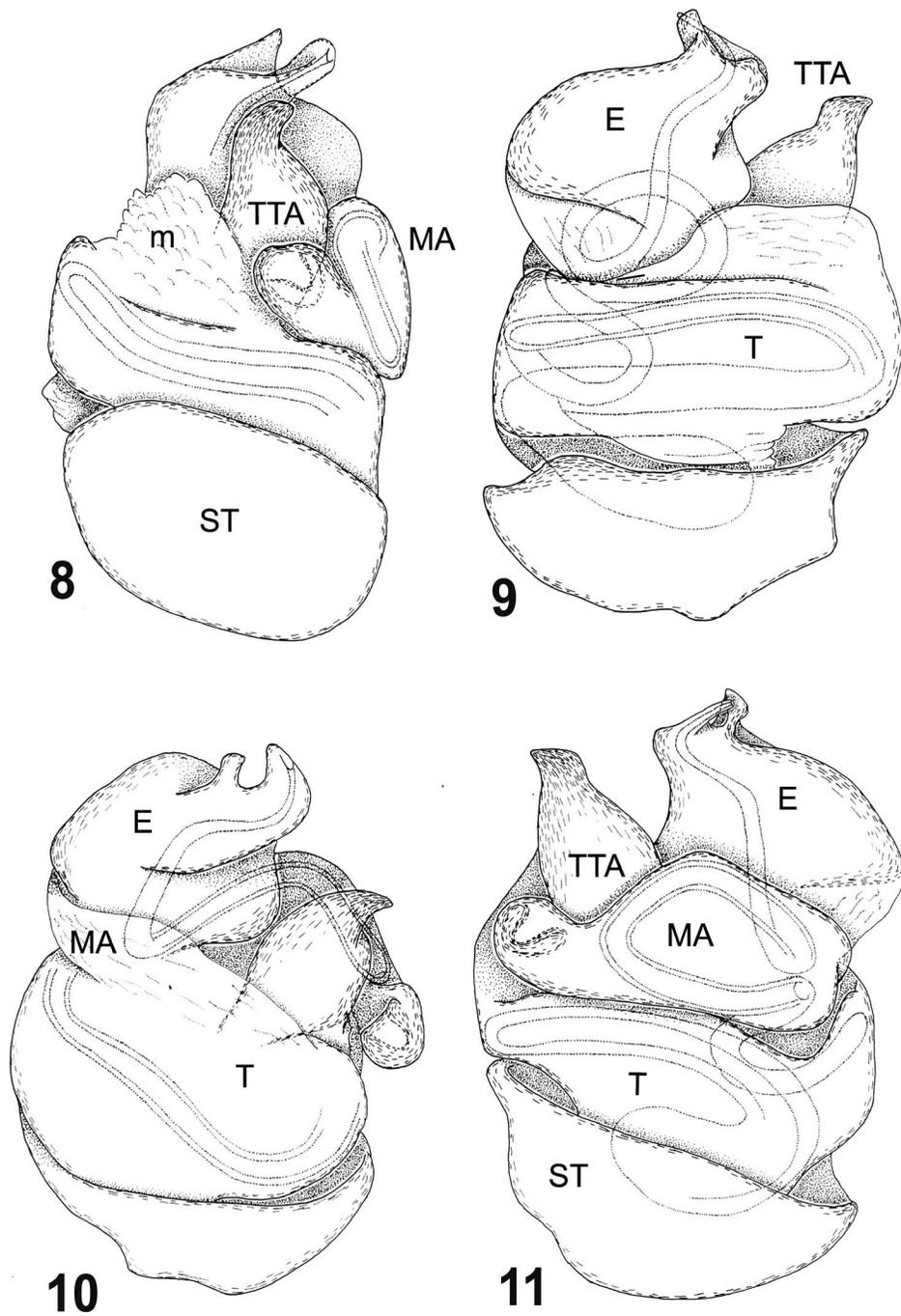
Figures 8–11.—*Euryopis flavomaculata*. 8, bulb removed from cymbium, mesal-dorsal; 9, ectal; 10, apical-dorsal; 11, ventral; conductor absent, note loop of sperm duct within MA.
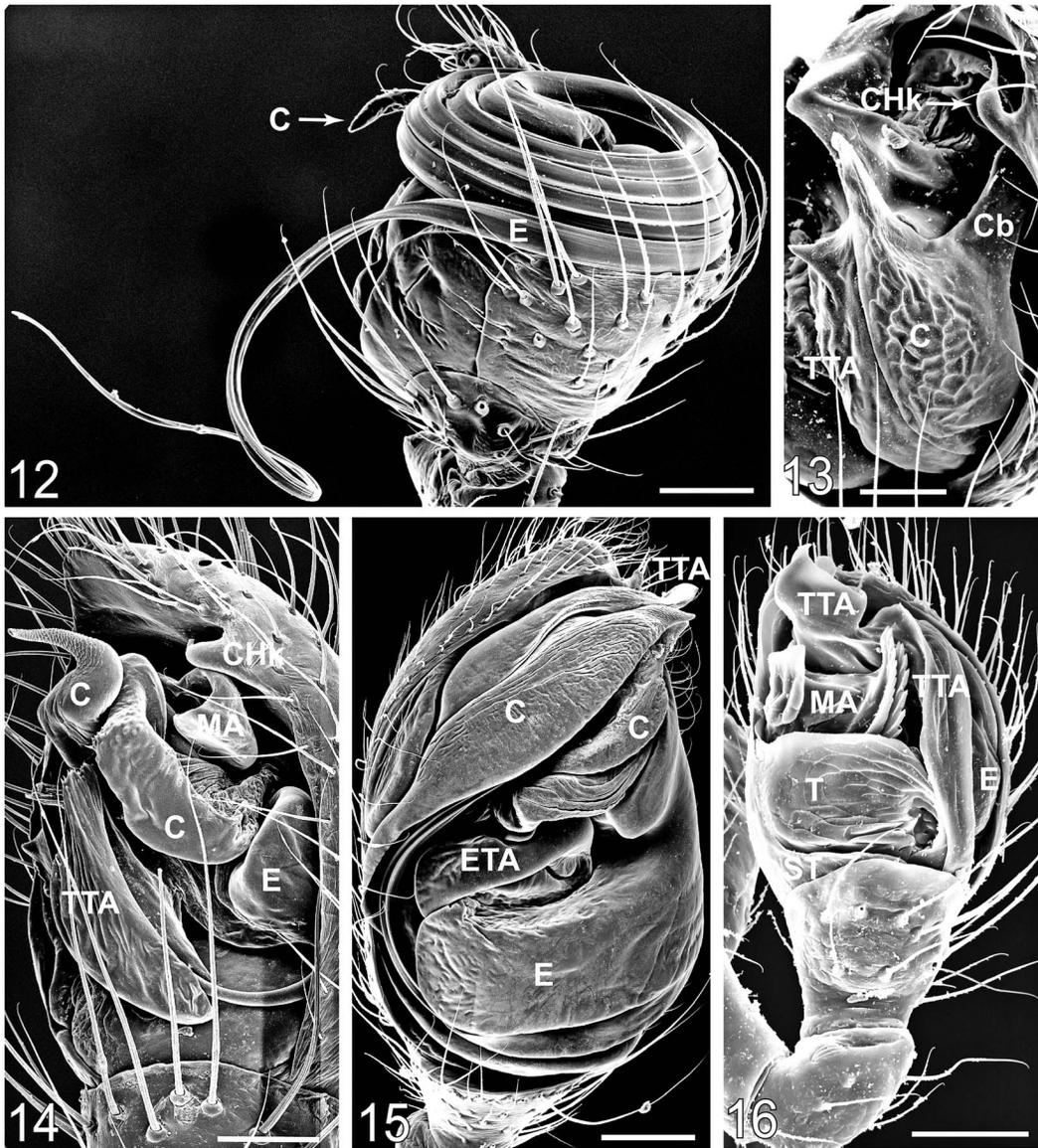
Figures 12–16.—12, *Latrodectus geometricus* C.L. Koch 1841; 13, *Selkirkiella* sp. note the bent and sharp tipped cymbial hook, a synapomorphic condition for Pholcommatinae, the tight juxtaposition of C and TTA is a synapomorphy of *Selkirkiella*; 14, *Enoplognatha ovata*; 15, *Episinus maculipes* Cavanna 1876, the huge and complexly folded C is a synapomorphy of Spintharinae; 16, *Styposis selis* Levi 1964, the ectal E with tip inside a TTA groove suggests affinities with Pholcommatinae. Scale bars: 12, 14, 15 = 100 μm; 13, 16 = 50 μm.

three or more in outgroups, Fig. 195) characterizes the spineless femur clade (*Synotaxus* plus the theridioid lineage, also reduced in cyatholipids, see Griswold 2001). Typically theridiids have two retrolateral and one prolateral trichobothria (Figs. 3, 19, 71). Independent reductions to one retrolateral trichobothrium are synapomorphies for Theridiinae and a clade within Pholcommatinae (Fig. 104). Absence of tibial trichobothria unites the pholcommatines *Carniella* (Fig. 50) and *Theonoe* (Figs. 96, 97). The loss of the prolateral trichobothrium is an unambiguous theridiine synapomorphy.
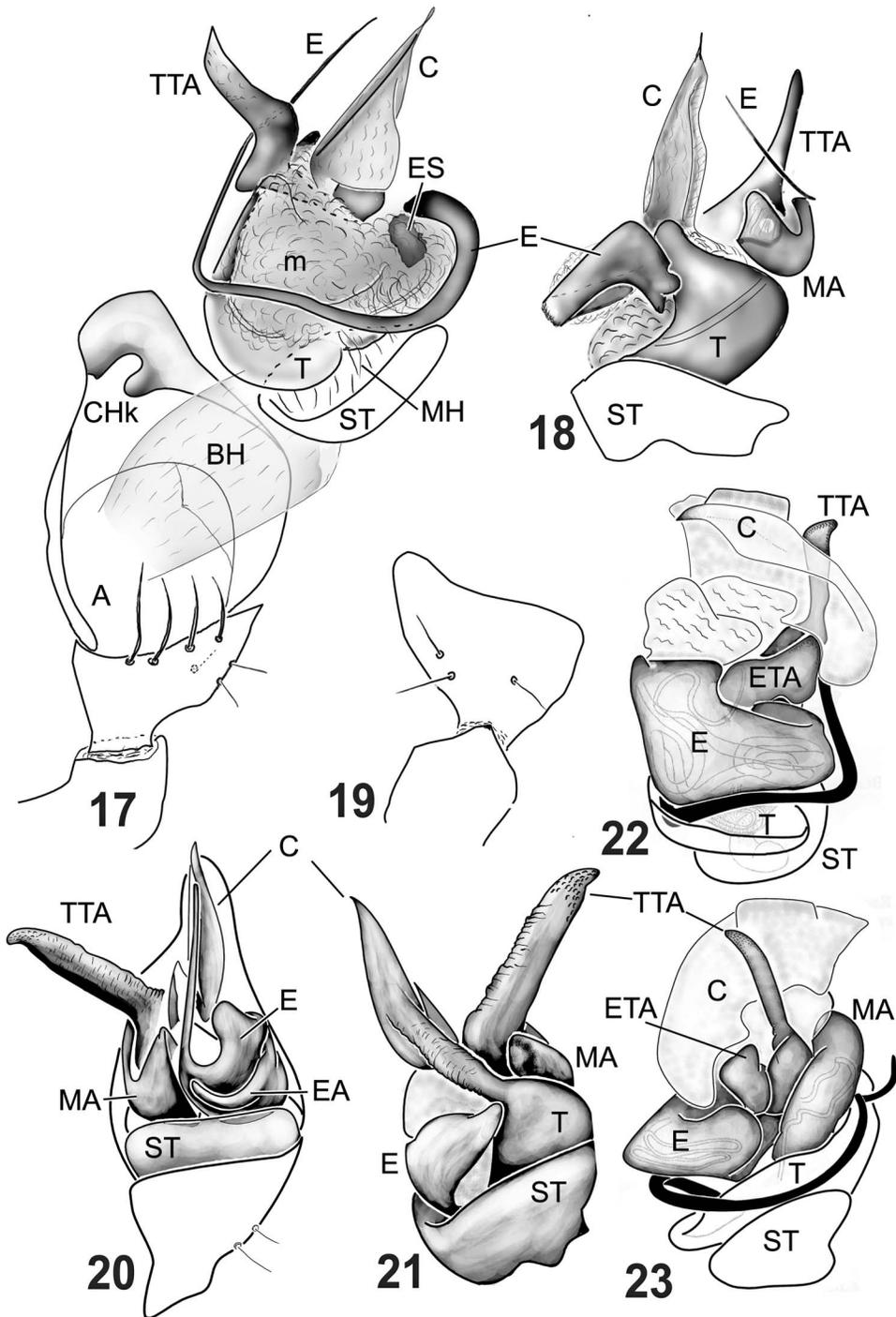
Figures 17–23.—17–19, *Steatoda americana* (Emerton 1882). 17, male palp ventral expanded; 18, bulb dorsal, removed from cymbium; 19, tibia dorsal view; 20, 21, *Steatoda albomaculata* (De Geer 1778), 20, palp ventral; 21, bulb removed from cymbium, dorsal view (redrawn from Knoflach 1996a); 22, *Episinus angulatus*, bulb removed from cymbium, ventral (redrawn from Knoflach 1993b), 23, mesal. 22, 23 reproduced from Agnarsson (2004) with permission from Blackwell Publishing.
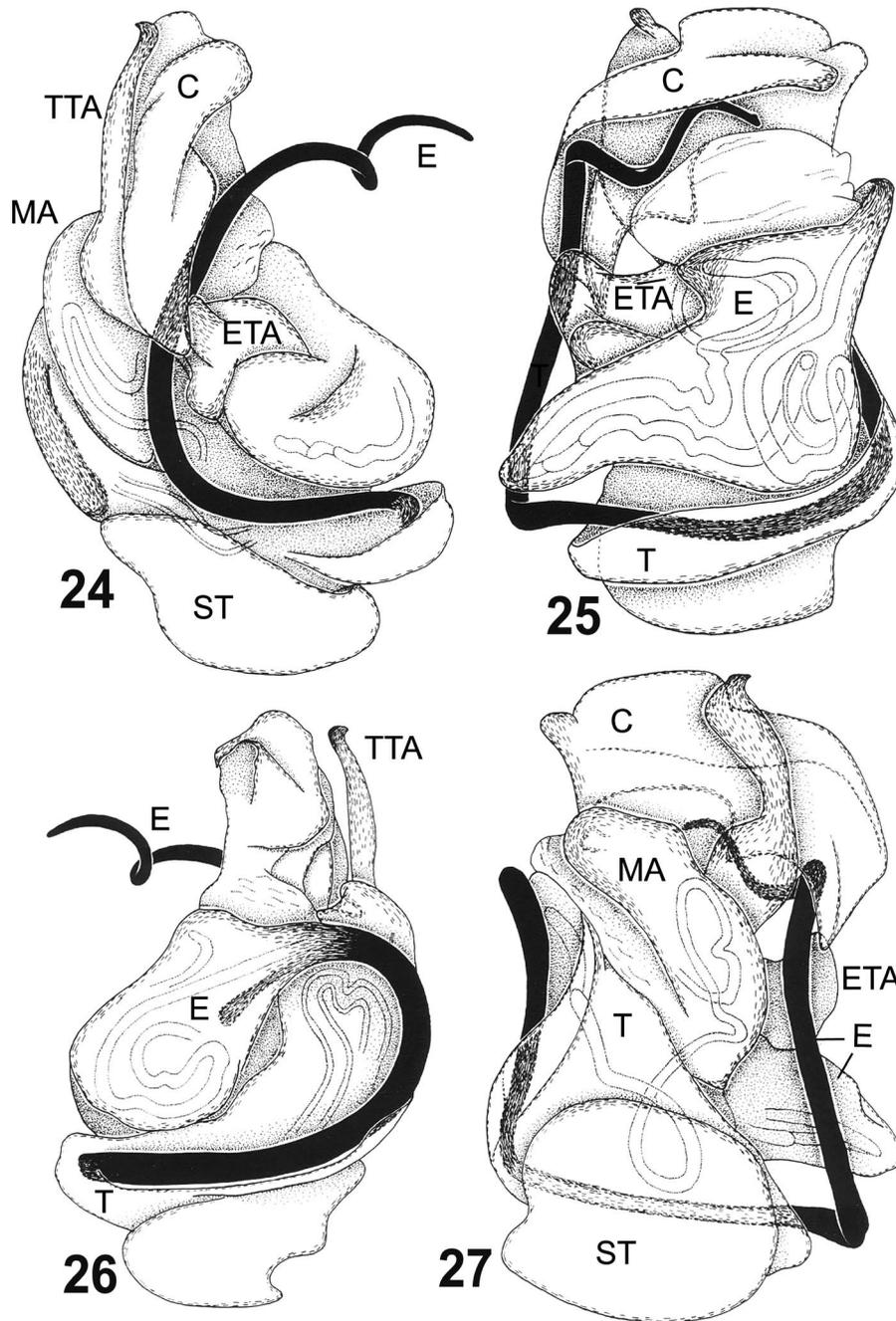
Figures 24–27.—*Episinus truncatus*. 24, bulb removed from cymbium, mesal; 25, ventral; 26, ectal; 27, dorsal; a third tegular sclerite ETS is present; note convoluted sperm duct within E and loop within MA; ventral tegulum conducts a part of the distal E.
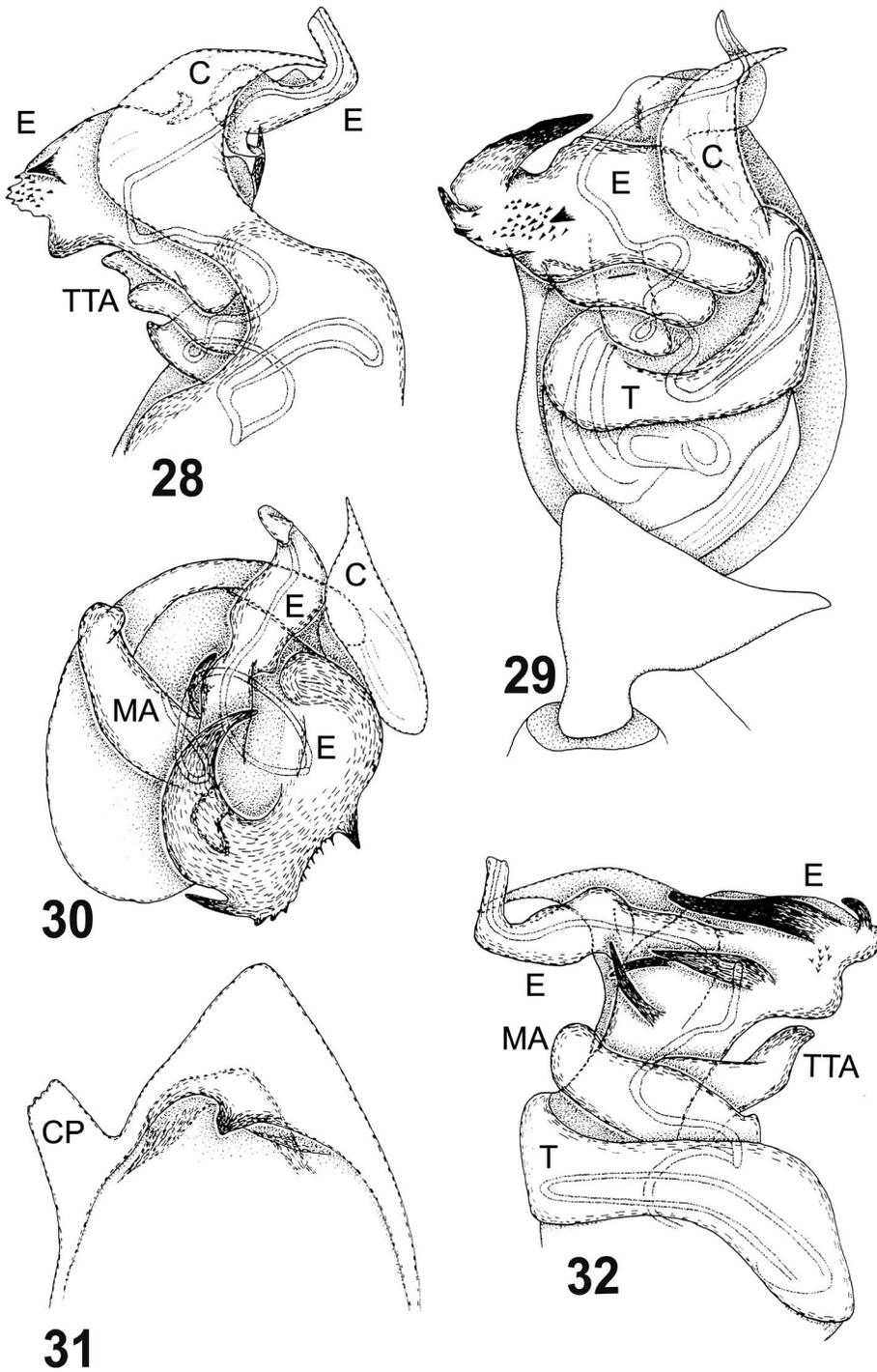
Figures 28–32.—*Crustulina guttata*. 28, distal bulb, ectal; 29, palp expanded, ventral; 30, bulb removed from cymbium, apical; 31, cymbium, ventral; note large, mesal cymbial process; 32, bulb removed from cymbium, mesal-dorsal; embolus bears numerous processes.
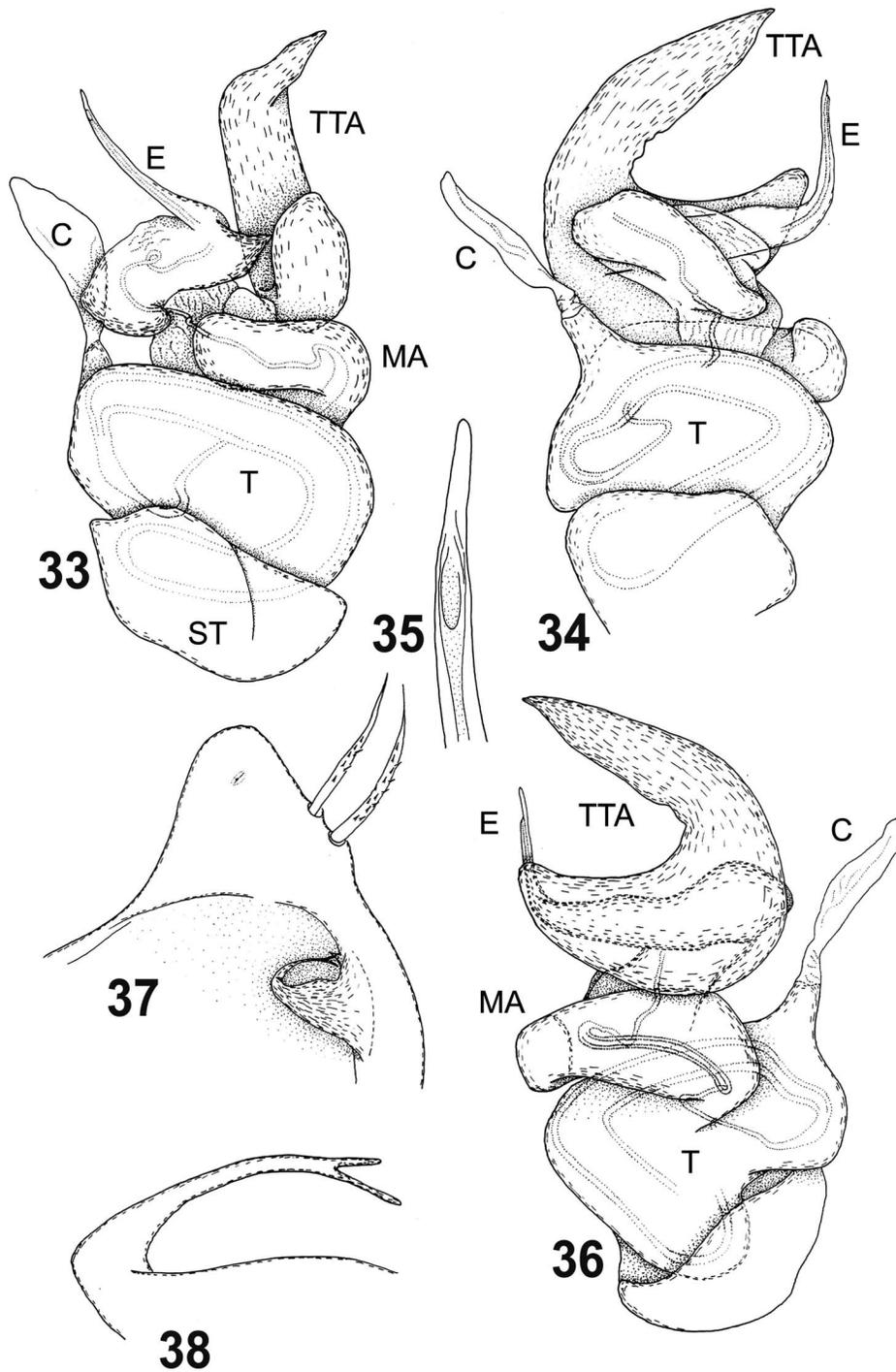
Figures 33–38.—*Steatoda bipunctata*. 33, bulb slightly expanded and removed from cymbium, ectal; 34, dorsal; 35, ventral; sperm duct narrows when leaving T, then widens within MA and again becomes constricted when passing to E; 36, tip of embolus; 37, tip of cymbium, ventral; 38, tip of cymbial hook.
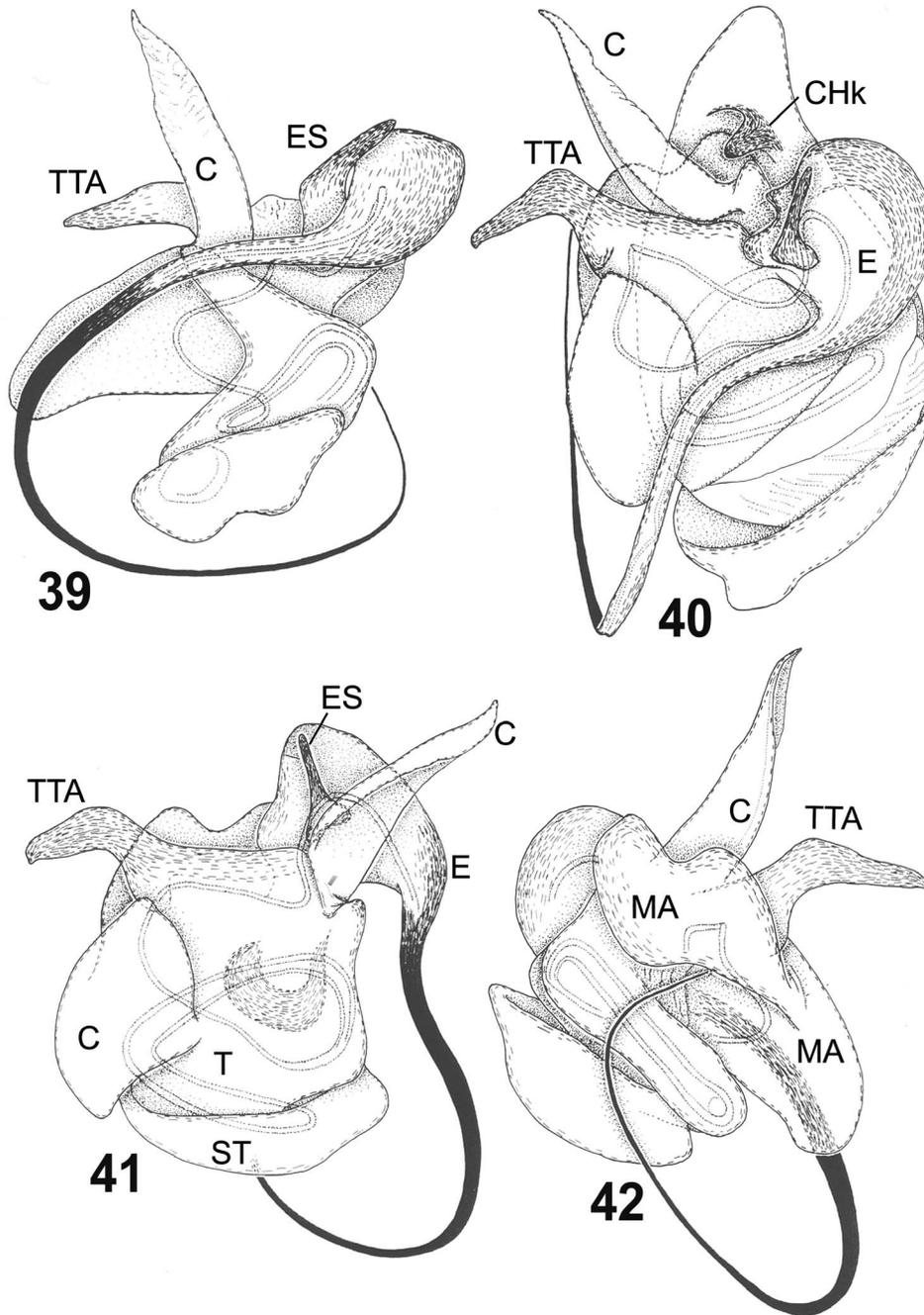
Figures 39–42.—*Steatoda phalerata* (Panzer 1801). 39, bulb removed from cymbium, ectal; 40, apical-ventral; 41, mesal; 42, ventral.

Cymbium: Comstock (1910) defined the cymbium as the basal portion of the tarsus expanded to protect and partially surround the genital bulb. In more recent use, the cymbium refers to the entire entelegyne palpal tarsus (e.g., see Grasshoff 1968, p. 38, 39, fig. 33; Ledoux & Canard 1981, p. 12), which we follow here. Theridiid cymbial shape varies and
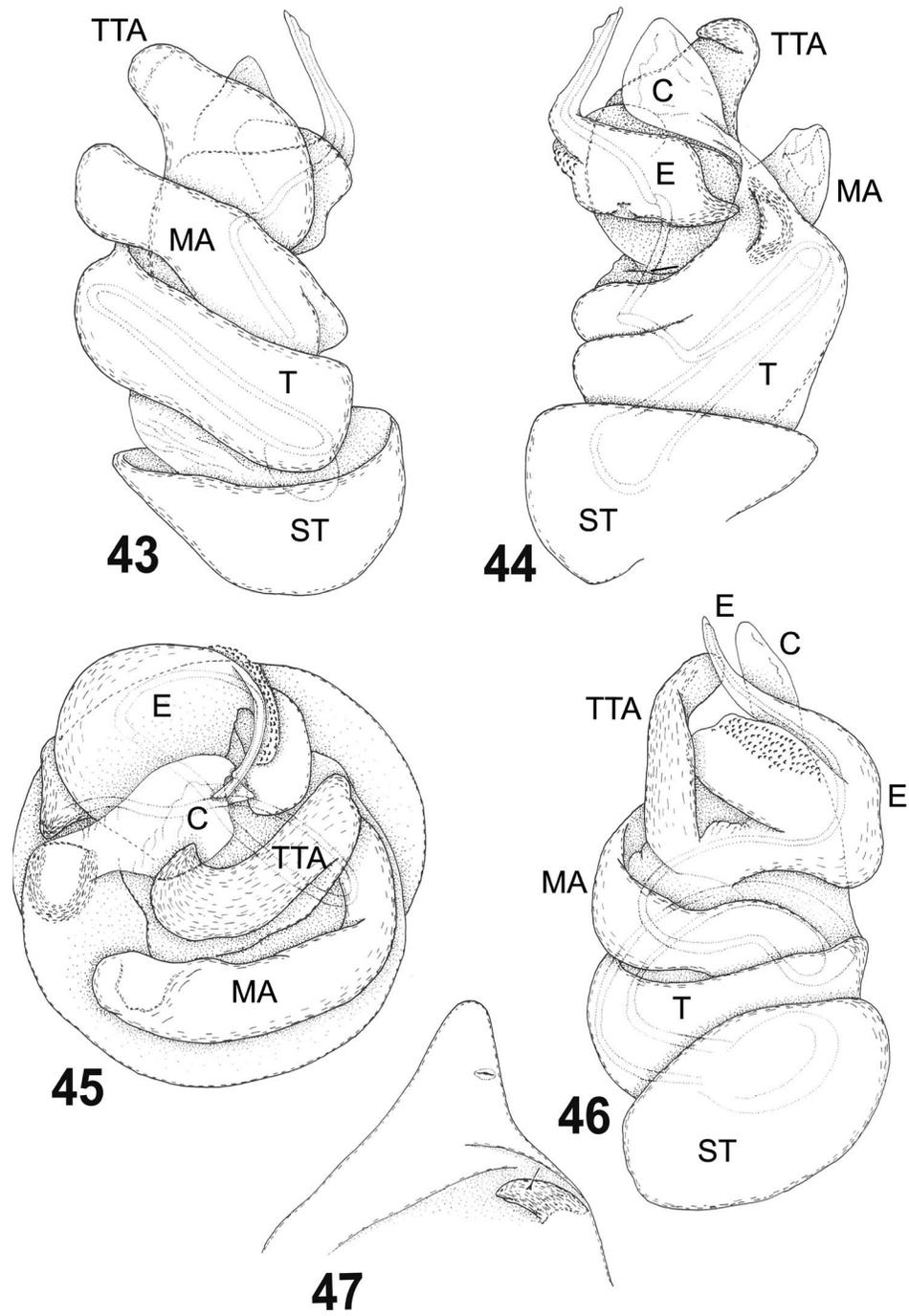
Figures 43–47.—*Steatoda triangulosa*. 43, bulb removed from cymbium, mesal; 44, ectal-dorsal; 45, apical; 46, ventral; 47, tip of cymbium, ventral; note tegular pit in 44 close to conductor, into which an embolar process articulates.

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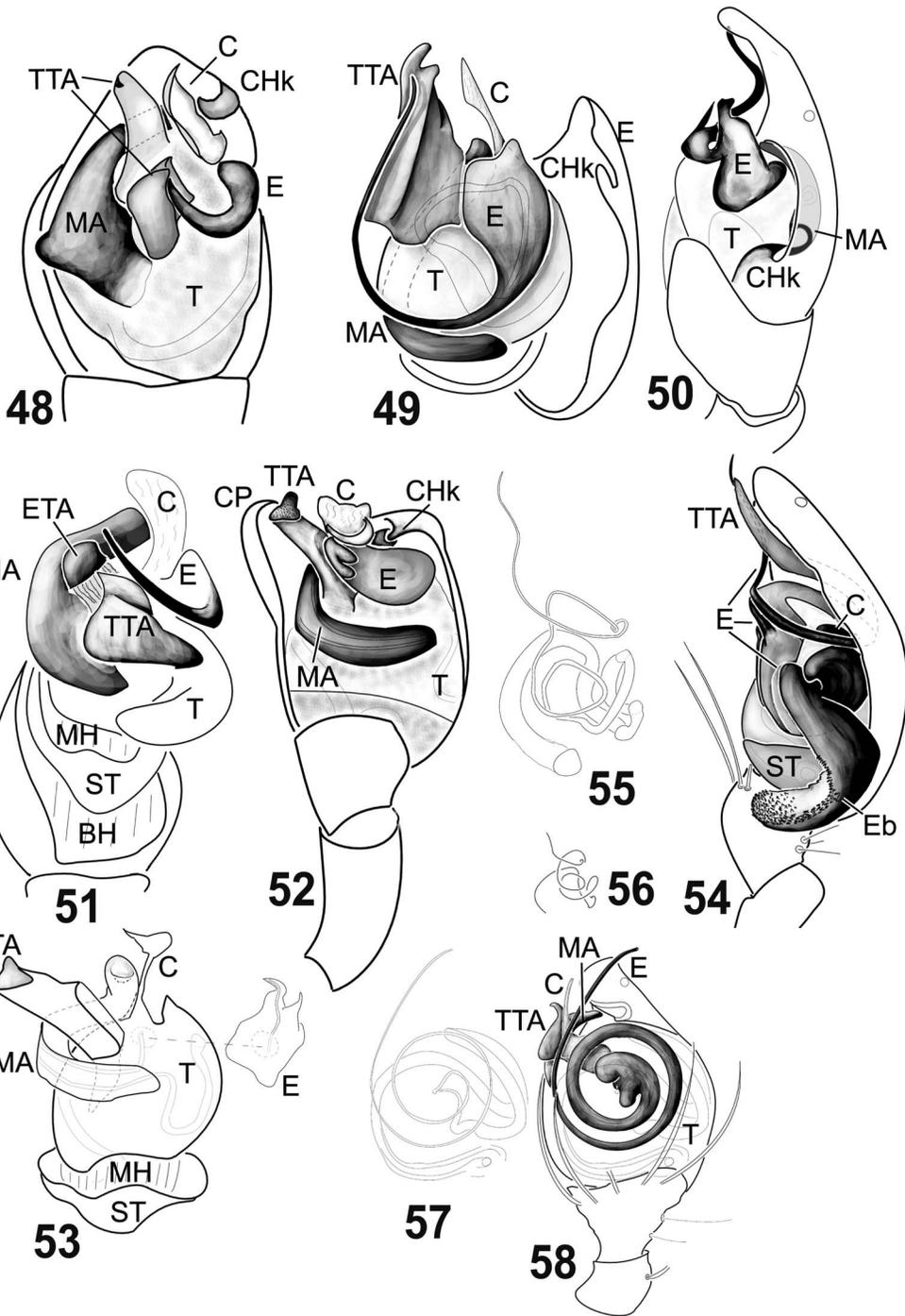
is phylogenetically informative. A distal cymbial process is present in *Argyrodes* (Figs. 52, 60), *Crustulina* (Fig. 31), *Theonoe minutissima* (O.Pickard-Cambridge 1879) (Figs. 96, 97), and some *Achaearanea* species (Fig. 118). The cymbium extends well beyond the alveolus in some taxa (Figs. 14, 20, 50, 58, 96, 100, 105, 118, 193, 194), and a pronounced incision of the mesal margin of the cymbium characterizes most *Anelosimus* species (Fig. 62) (see Agnarsson 2005, 2006b; Agnarsson & Kuntner 2005; Agnarsson & Zhang 2006).

Paracymbium: The araneoid paracymbium is an "apophysis arising from the base of the cymbium" (Comstock 1910, p. 175). This retrolateral, proximal process on the cymbium (Figs. 190–192, 195–198) has long been recognized as an araneoid synapomorphy (Coddington 1986, 1990; Hormiga et al. 1995; Griswold et al. 1998). In some taxa, the paracymbium articulates to the cymbium (Linyphiidae, e.g., *Linyphia triangularis* (Clerck 1757), Fig. 196), whereas in others it is rigidly fixed (e.g., Araneidae, *Araneus diadematus* Clerck 1757).

Theridiid cymbia usually lack a basal apophysis (Figs. 3, 4, but see 50), but have a distal apophysis that forms one half of the cymbium-bulb locking mechanism (Figs. 3, 13, 14, 17, 31, 37, 38, 47, 52, 59, 63, 68, 79, 80, 84, 88, 92, 97, 173–182), or a functionally identical cymbial pocket in the same place (Figs. 65, 105, 106, 113, 117, 124, 129, 142, 183–188).

Some authors regarded this process as the transformed homolog of the araneoid paracymbium (e.g., Levi & Levi 1962; Shear 1967; Wunderlich 1978; Heimer 1982, 1986; Heimer & Nentwig 1982; Coddington 1990; Forster et al. 1990; Knoflach 1996b; Levy 1998). Coddington (1990), for example, argued that "transformation" of one structure into another (one step) was, in general, a more parsimonious and efficient explanation than complete loss of a plesiomorphic feature and gain of an apomorphy (two steps). The theridiid locking mechanism between a tegular sclerite and the cymbium is an unusual example of a morphological function being assessable even in preserved material. Influenced by Heimer's work on the interaction between the araneoid paracymbium and tegular sclerites, and Bhatnagar & Remple's (1962) demonstration of profound morphological displacements of apophyses during palpal ontogeny, he proposed homology of the theridiid distal cymbial apophysis or notch with the araneoid paracymbium via transformation, rather than loss of the plesiomorphic paracymbium and gain of the novel locking mechanism. This view presumes both topological and detailed morphological change. It argues that both are cymbial apophyses that never co-occur (Agnarsson 2004), and that both may interact with palpal tegular sclerites of the palpal bulb during natural expansion of the palp (Heimer & Nentwig 1982; Huber 1993; Knoflach 1998, 2004; Agnarsson 2004; Knoflach & Pfaller 2004).

Others regard the araneoid paracymbium as lost and the theridiid feature as a novelty (Saaristo 1978; Griswold et al. 1998). Heimer (1982, 1986) and Heimer & Nentwig (1982, p. 289) envisioned the transformation of the paracymbium from the nesticid type: "In plesiomorphic Theridiidae (e.g., *Robertus* O.P.-C., 1879) the paracymbium is distally transferred but maintains its function. It conducts the median apophysis which glides at its ventral side and fixes it. A further reduction of paracymbium and median apophysis shortens the distance the median apophysis must be moved. Finally, the paracymbium is modified

←

Figures 48–58.—48, *Enoplognatha gemina* Bosmans & van Keer 1999, palp ventral (redrawn from Levy 1998; sub *E. mandibularis* (Lucas 1846)); 49, *Phoroncidia americana* (Emerton 1882), palp loosened from cymbium, ectal (redrawn from Levi & Levi 1962); 50, *Carniella schwendingeri* Knoflach 1996, palp ectal (redrawn from Knoflach 1996b); 51, *Enoplognatha* sp. expanded; 52, 53, *Argyrodes argyrodes* (Walckenaer 1842) (redrawn from Saaristo 1978). 52, ventral; 53, schematic of bulb removed from cymbium and E removed from T; G-I, *Anelosimus vittatus* (C.L. Koch 1836). 54, palp ectal; 55, sperm duct trajectory, see Agnarsson (2004) for nomenclature and discussion; 56, schematic look at duct loops; 57, 58, *Anelosimus* sp. 57, palp ventral; 58, sperm duct trajectory. 50, 57, 58 reproduced from Agnarsson (2004) with permission from Blackwell Publishing.
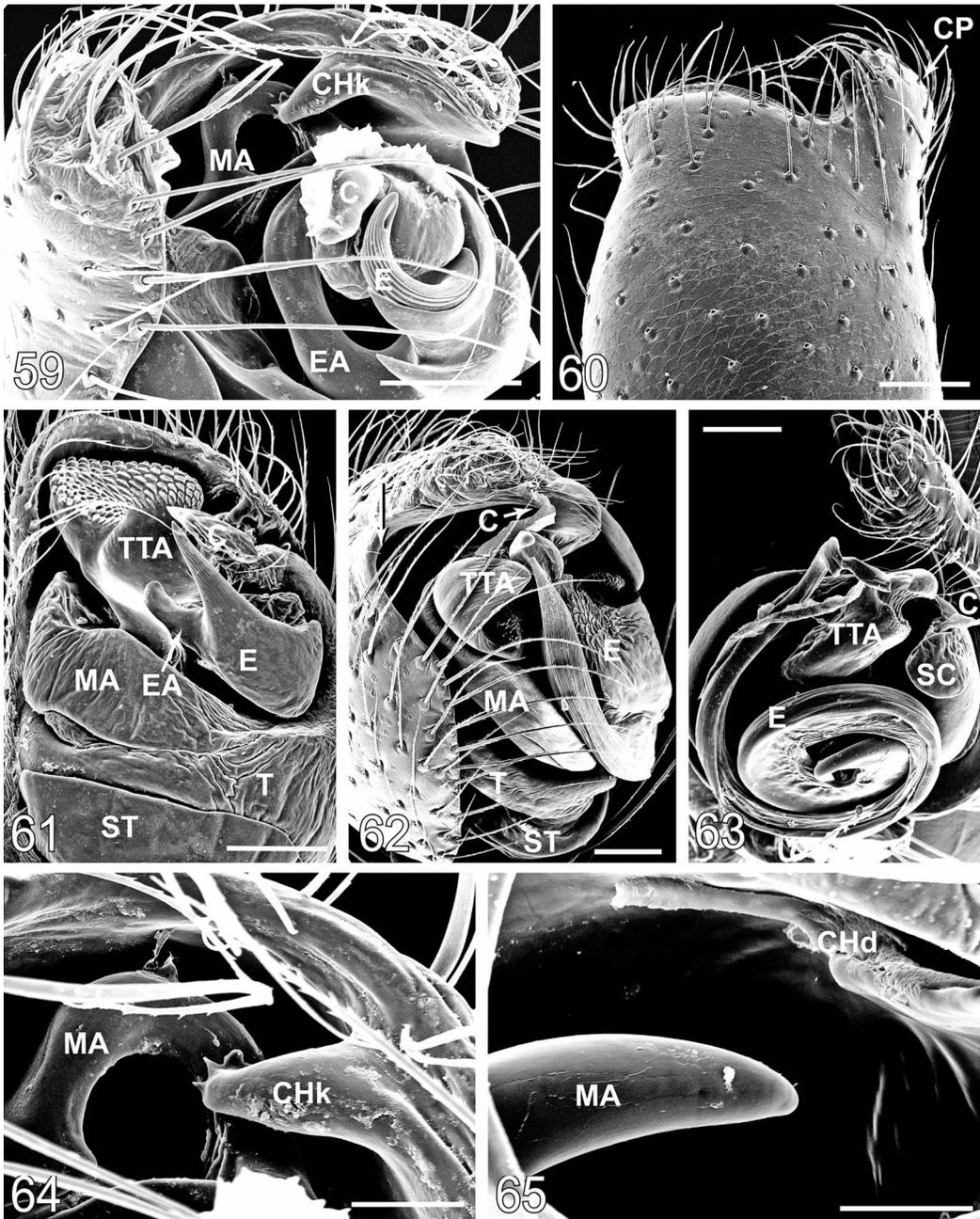
Figures 59–65.—59, 60, 64 *Argyrodes elevatus* Taczanowski 1873 male palp. 59, apical; 60, dorsal; 61, *Neosphintharus trigonum* (Hentz 1850), palp ventral; 62, 63, *Anelosimus eximius*. 62, apical view of mesal side, note strong cymbial incision, an *Anelosimus* synapomorphy; 63, apical view of ventral side, showing clearly the C coming out of the base of the SC; 64, hooked bulb to cymbium lock system; 65, *Anelosimus* sp. hooded BC-lock system. Rather than representing independent lines of evolution the hooded system is derived from the hooked one (see Fig. 201). Scale bars: 59–63 = 100 μm; 64, 65 = 50 μm.
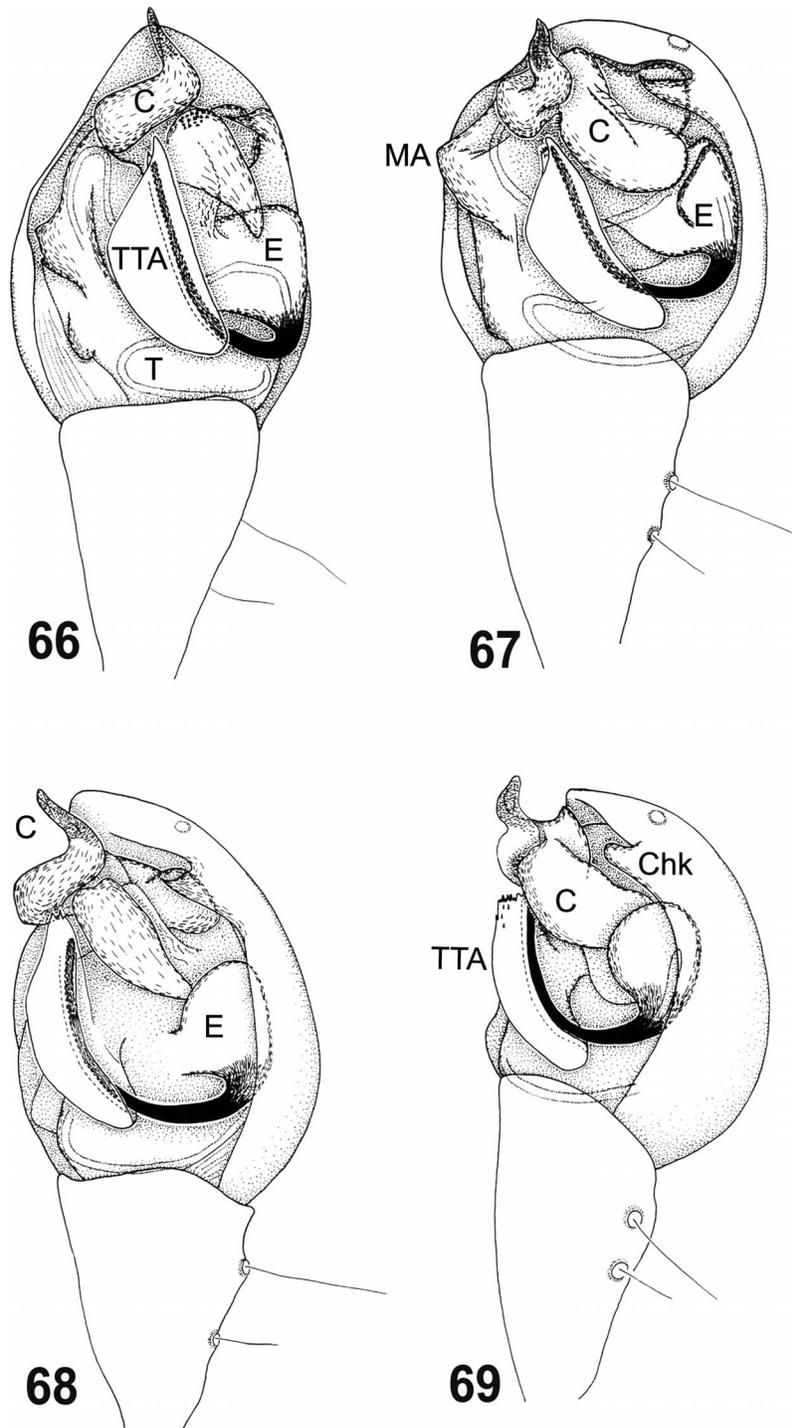
Figures 66–69.—66, 68, *Enoplognatha ovata*. 66, ventral; 68, ectal; 67, 69, *E. latimana*. 67, ventral; 69 ectal; note TTA conducting E in the unexpanded palp.
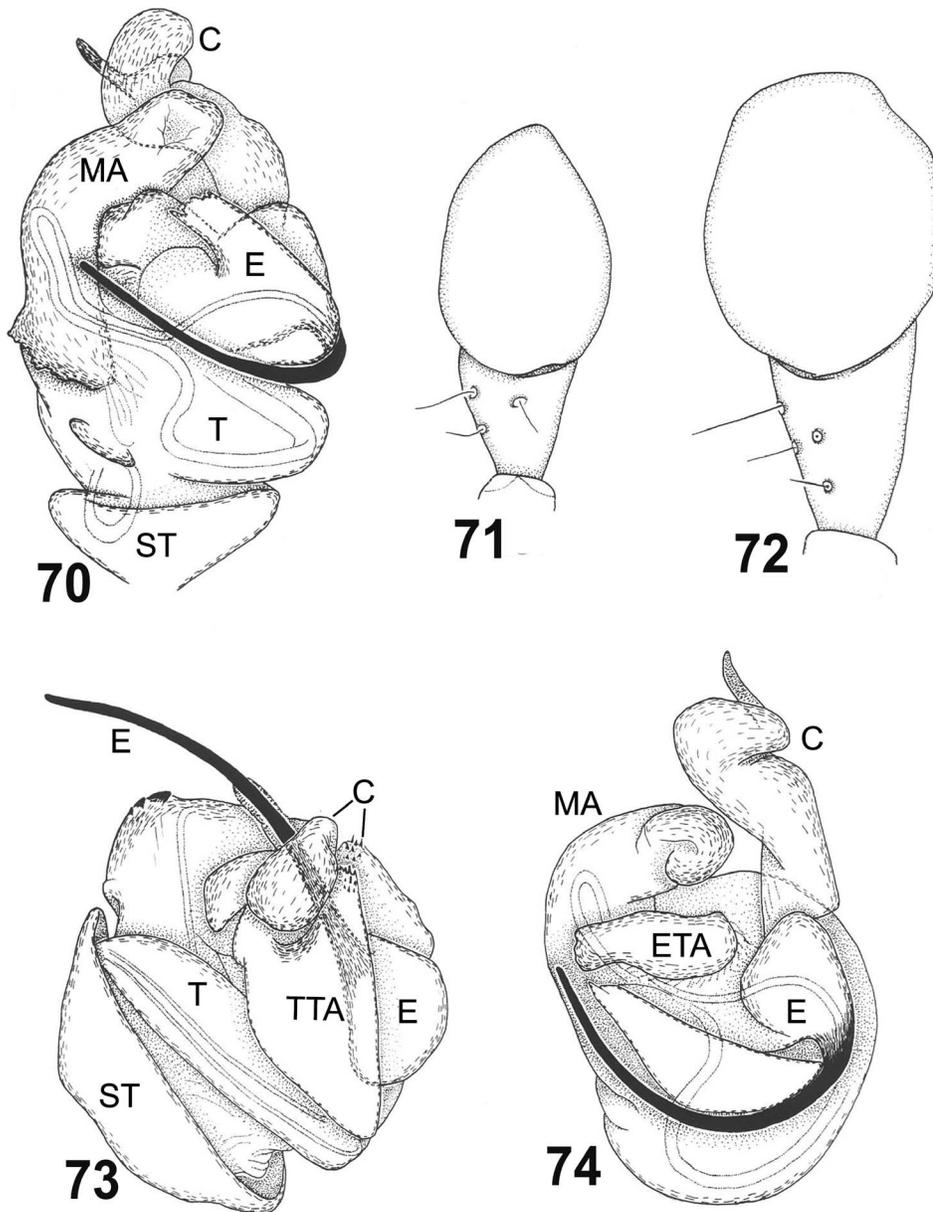
Figures 70–74.—70, 71, 73, 74, *Enoplognatha ovata*. 70, 73, 74, bulb slightly expanded and removed from cymbium; 70, ventral; 71, cymbium and tibia, dorsal; 72, *Enoplognatha latimana*, cymbium and tibia dorsal; 73, ''naturally'' expanded, ventral-mesal, note embolus shifted into furrow of conductor; 74, apical, note third tegular sclerite.

up to a degree in which no free sclerite of the cymbium can be found. Now the median apophysis is fastened in pocket-like deepenings at the inside of the cymbium during the fixation of the palp. . . . Genera with this modified palpal mechanism are e.g. *Episinus* Latreille, 1809, *Theridion* Walckenaer, 1805,

and *Dipoena* Thorell, 1869.'' The view that the theridiid cymbial hook is not homologous to the paracymbium, on the other hand, is based on difference in position, shape, and function. Saaristo (1978, p. 112) criticized the hypothesis on topological grounds: ''This [homology of the theridiid cymbial process with
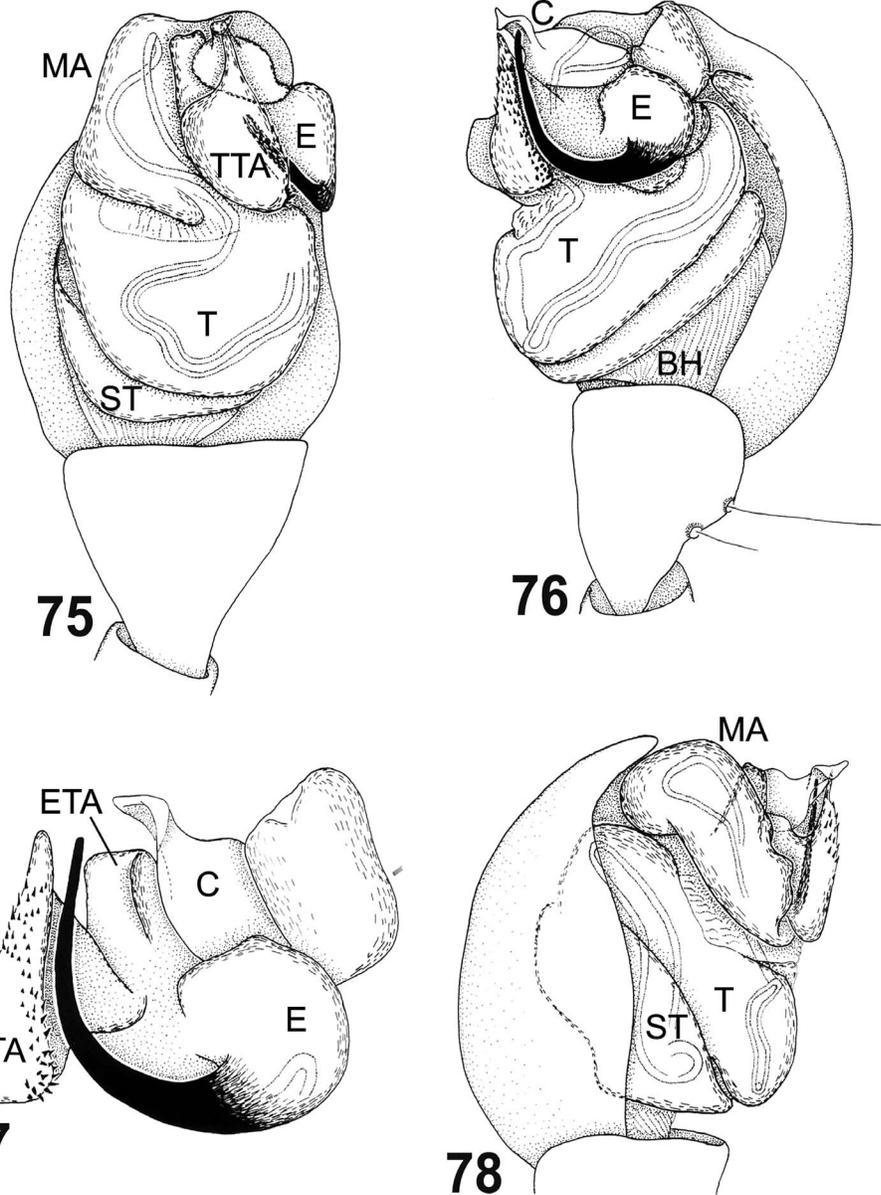
Figures 75–78.—*Enoplognatha thoracica*. 75, 76, 78, male palp slightly expanded, ventral, ectal, mesal. 77, distal palpal sclerites, ectal.

the paracymbium] must be an error, because the cymbial hook lies near the tarsal organ and distally to it, whereas in araneids and liny-phiids the paracymbium is far from the tarsal organ and proximal to it.'' Although the theridiid process is usually very different from araneoid paracymbia, in others its position and shape are somewhat similar (compare *Carniella* (Fig. 50) to the synotaxid *Synotaxus* *waiwai* Agnarsson 2003 (Fig. 191)). Saaristo's (1978) criterion of topological relation to the tarsal organ does not, furthermore, apply to all taxa. The paracymbial hook of *Carniella*, for example, is proximal to the tarsal organ and far away from it (Fig. 50).

Phylogenetic analysis treating the theridiid hook as a transformed araneoid paracymbium or as different, independent characters both re-
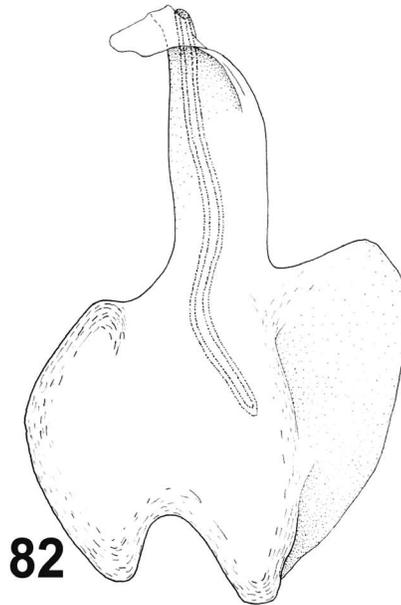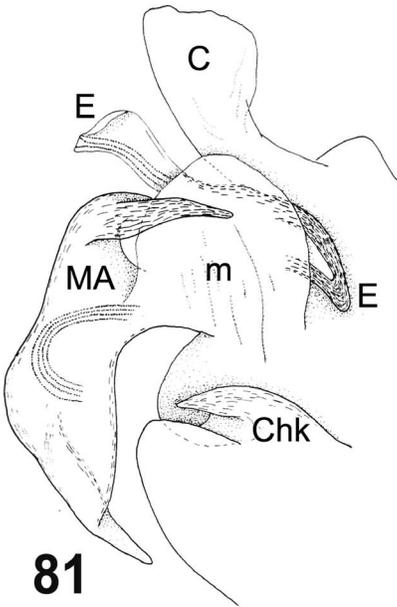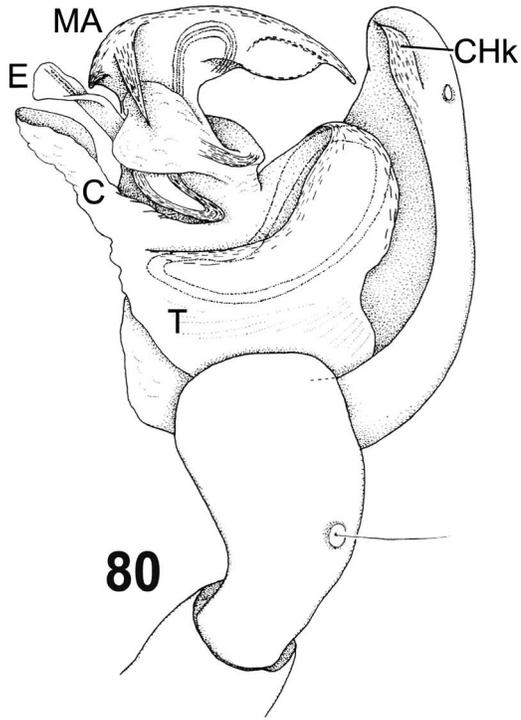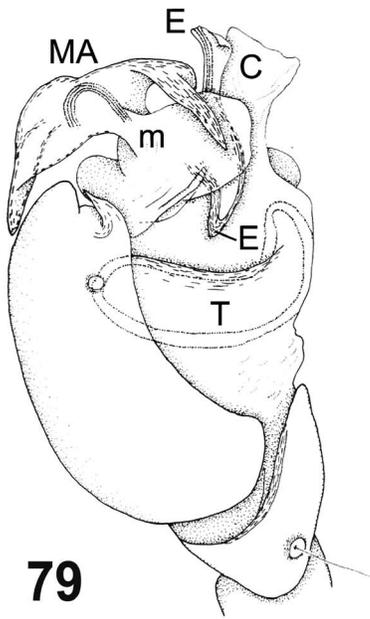
Figures 79–82.—*Robertus neglectus*. 79, 80, male palp expanded, ectal-apical, ectal; 81, distal sclerites, ectal; only one tegular apophysis present; 82, embolus.
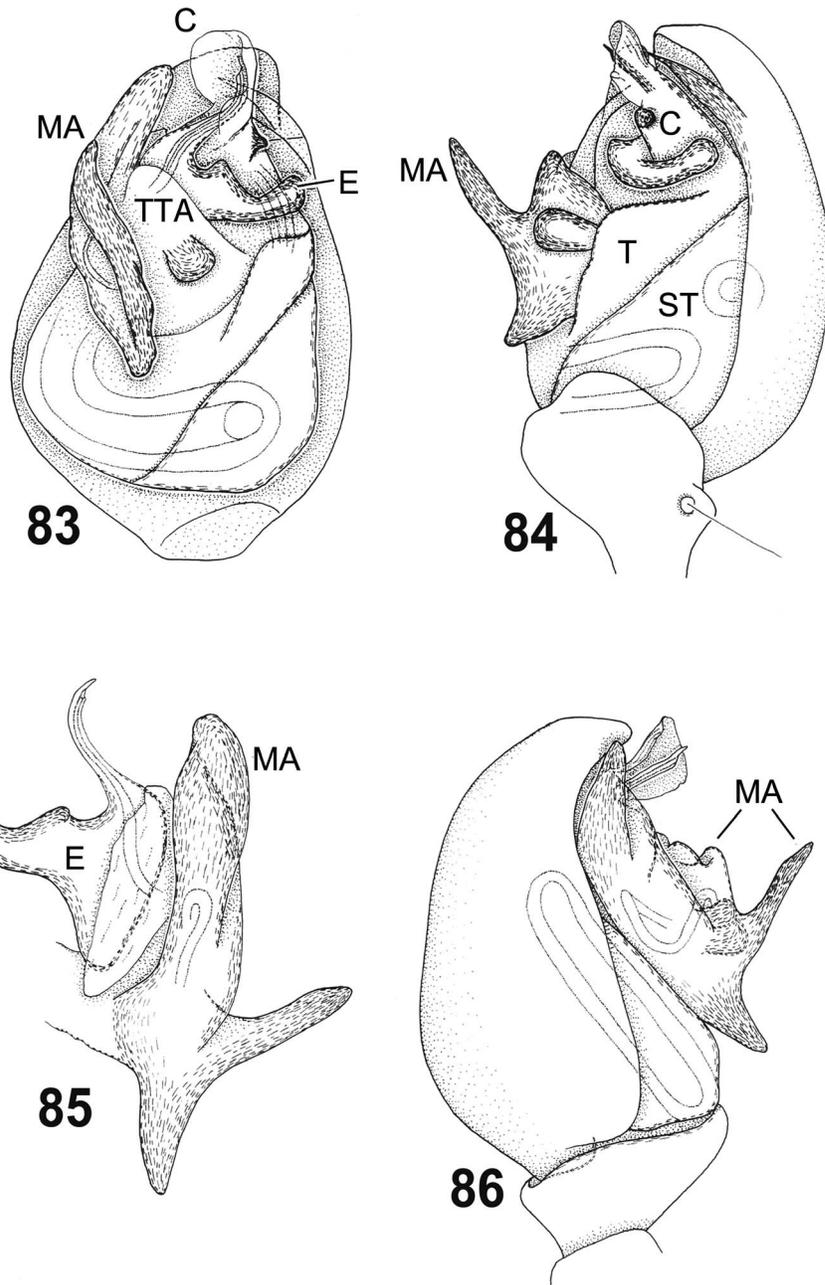
Figures 83–86.—*Robertus scoticus*. 83–85, male palp, ventral, ectal, mesal; 86, distal palpal sclerites.

sult in same topology (Figs. 2, 201; Agnarsson 2004), which refutes Heimer & Nentwig's speculation about the primitive theridiid condition (as well as the basal position of *Robertus*). Instead, the primitive condition is a knob distally inside the cymbium locking the MA ''securely'' (e.g., *Dipoena*, Fig. 176). The

more paracymbium-like hook on the cymbial margin (e.g., in *Carniella*, Fig. 50) and *Robertus* (Fig. 182) is derived. *Robertus* is a pholcommatine, for which the rather loose connection between the cymbial hook and the MA is synapomorphic. The pronounced basal paracymbium in the outgroups (e.g., *Pimoa*,
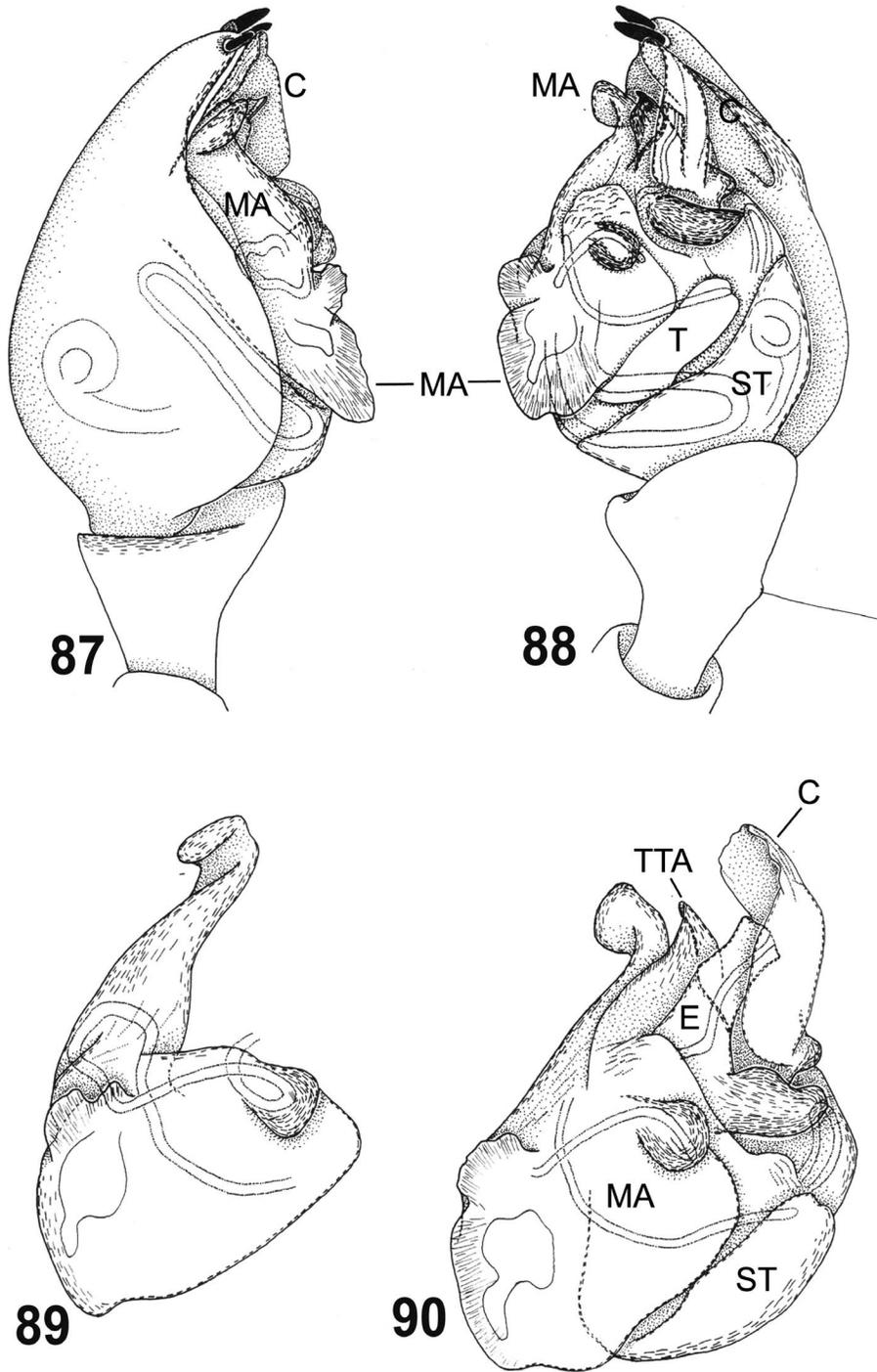
Figures 87–90.—*Robertus ungulatus*. 87, 88, male palp, mesal, ventral; 89, median apophysis; 90, distal palpal sclerites; two tegular apophyses present.
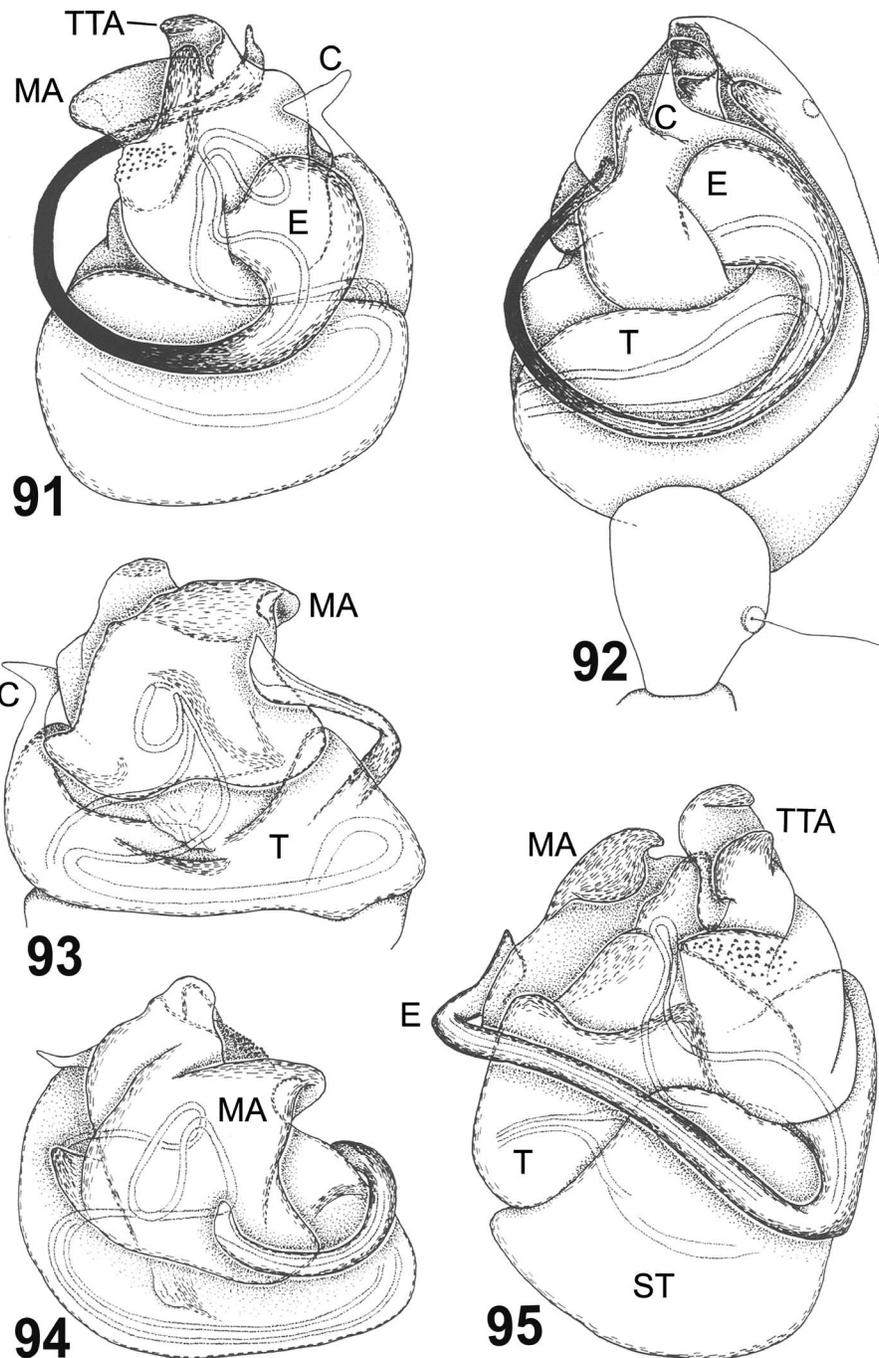
Figures 91–95.—*Pholcomma gibbum*. 91, bulb slightly expanded and removed from cymbium, ectal; 92, ventral; conductor hyaline, slender and apparently without guiding function, whereas MA and TTA show a broad groove, which presumably supports the embolus; 93–95, distal bulb, removed from cymbium, 93, mesal-dorsal; 94, apical-dorsal; 95, caudal-ventral; note loop of sperm duct within MA.
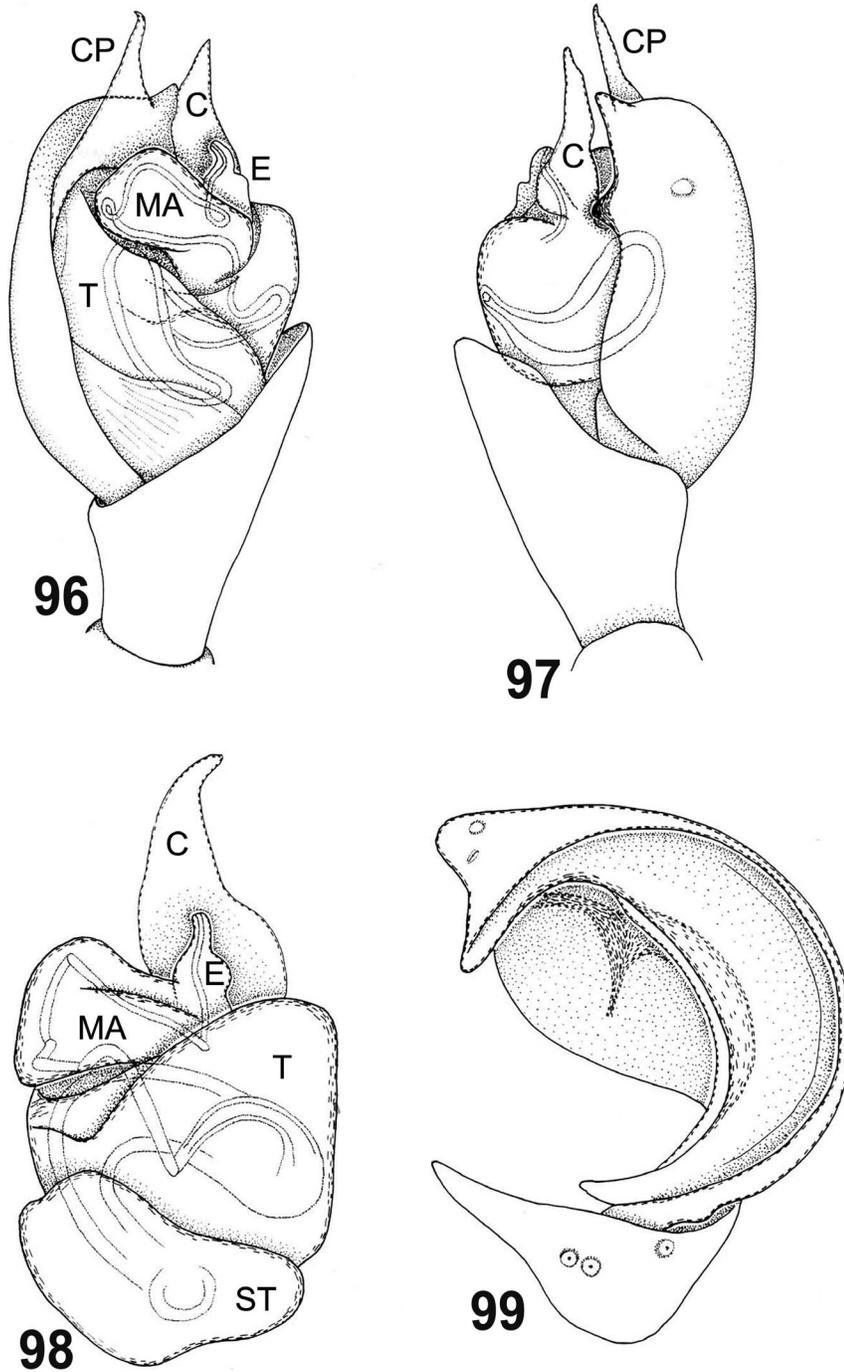
Figures 96–99.—*Theonoe minutissima*. 96, 97 male palp, ventral-mesal, ectal; 98, bulb, ventral; note distal process of cymbium and distinct constriction of sperm duct within T; embolus and median apophysis probably fused; 99, *Kochiura aulica*, cymbium ectal, largely excavated.

Fig. 195; *Linyphia*, Fig. 196; *Synotaxus*, Fig. 197; and *Nesticus*, Fig. 198) and the plesiomorphic distal cymbial knob in hadrotarsids and basal theridiids, such as latrodectines (Fig. 17), have little in common beyond being parts of the cymbium. Because the homology hypothesis fails the criteria of position, special similarity, and function, the gain-loss interpretation receives support using our method, and is preferred on the phylogeny (Fig. 201). The theridiid cymbial hook is unique to theridiids, and the araneoid PC has been lost in hadrotarsids and theridiids (Saaristo 1978; Griswold et al. 1998; Agnarsson 2004). Of course, transformation is currently an "elastic" concept; any amount of change can be packed into a single cladistic step.

Griswold et al. (1998) and Agnarsson (2004) used the terms "theridiid cymbial hook" and "theridiid cymbial hood," which we follow. Other names (apart from PC) applied to this structure include "cymbial tooth" (Bhatnagar & Rempel 1962), "cymbial pit" (Saaristo 1978), and "distal hook" (Griswold et al. 1998).

Theridiid bulb-cymbium lock mechanism: The theridiid BC-lock mechanism is unique to and universal among theridiids (highly modified in *Paratheridula* and *Theridula*). In it the median apophysis (usually the sclerite most flexibly attached to the tegulum) interacts with the theridiid cymbial process to lock the bulb in the palp (Levi 1961) as it expands (Knoflach 1998; Knoflach & van Harten 2000), or even in the unexpanded palp (Coddington 1990). It takes two forms: (1) Theridiid "cymbial hook"; and (2) "Theridiid cymbial hood." The hook (Fig. 3) is the primitive condition, and it engages a distal pit on the median apophysis (Figs. 3, 59, 64). Alternatively, the median apophysis may simply lodge under the process and the MA distal pit is sometimes indistinct or absent. In the theridiid cymbial hood condition, the cymbial hook has apparently been submerged into the cymbium (Figs. 65, 129). Saaristo (1978, p. 112) considered the cymbial hook and hood to be unrelated and independent, making a clear distinction between the two: "Levi (1961) did not realize that this coupling of bulbus and cymbium is accomplished in two entirely different ways, which possibly represent two main evolutionary lines in Theridiidae. They are here referred to as locking systems A and B." Phylogenetic analysis, in addition to topology, rejects Saaristo's distinction (Fig. 201); the hook is plesiomorphic with respect to the hood. The same conclusion has been reached by Heimer (1982), Forster et al. (1990), and most recently, by Saaristo (2006) himself. In contrast to the situation with the araneoid paracymbium, the hook and hood are topologically, morphologically, and functionally similar. The transformation required is plausible, in part due to extant intermediates, such as *Anelosimus*, where the hood is formed on the cymbial margin by thin cuticle. In other cladistically distal theridiids this hood is further away from the margin, but of the same form. A gain-loss scenario requires the simultaneous loss of the hook and gain of the hood while they are topologically identical and serve the same function.

Some hadrotarsids, latrodectines, and spintharines have a "hood-like" groove beneath the cymbial hook (see also discussion of Forster et al. 1990 about *Thwaitesia*). The presence of a hook and hood simultaneously might seem to fail Patterson's (1982) test of conjunction. However, the phylogeny rejects the homology of this groove to the hood because it is absent in the "hood lock clade" sister taxon. The conjunction test, as pointed out by de Pinna (1991), actually indicates homoplasy rather than decisively refuting homology. That homoplasy is here more parsimoniously attributed to the "sub hook groove" being a unique feature, not homologous to the hood found in the hood lock clade (Agnarsson 2004).

When present, the MA interacts with the cymbium via the locking mechanism. In a few taxa the MA has either been lost or has fused with the embolus (Figs. 96–98, 109, 119, 121–123, 125–128). In this case the basal portion of the embolus (or the fused embolus-median apophysis complex) assumes this function.

Alveolus: The alveolus is the cymbial cavity in which the genital bulb rests (Figs. 3, 17). Plesiomorphically the alveolus is usually central or ectal in the cymbium. Its placement flush on the mesal side of the cymbium is synapomorphic for theridiids (Fig. 1; see also Agnarsson 2004, fig. 92).

Basal haematodocha: The membranous basal haematodocha connects the alveolus to the subtegulum (Figs. 3, 17, 29, 51, 76, 120).
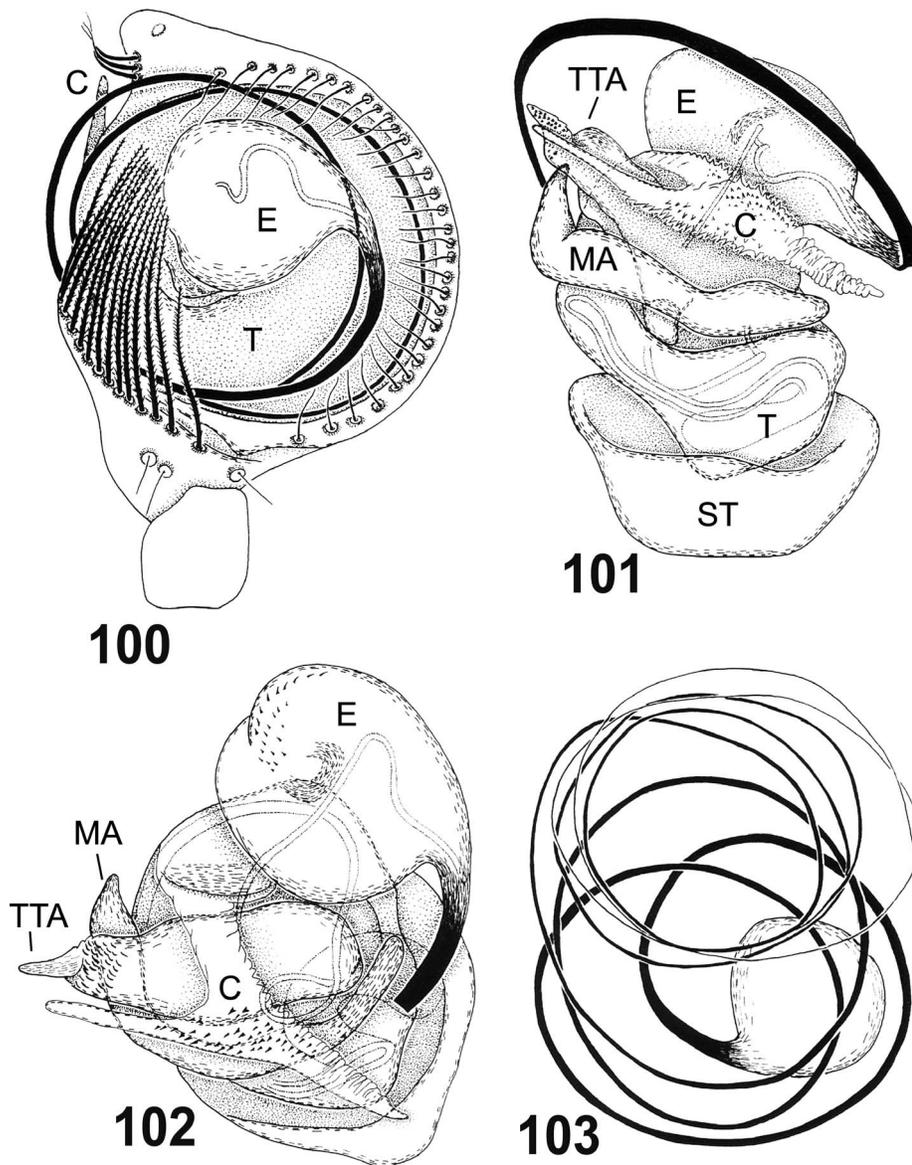
Figures 100–103.—*Kochiura aulica*. 100, male palp, ectal; 101, 102, bulb expanded, dorsal, apical; modified tibial and cymbial setae support the embolus, whereas conductor is comparatively inconspicuous; 103, embolus separated from palp, coiling up in spirals; its remarkable length measures three times the male's total body length.

It inflates during copulation and artificial expansion of the palp.

Petiole: In distant outgroups, the petiole is a large and prominent sclerite in the wall of the basal hematodocha (e.g., lycosoids, Sierwald 1990). In araneoids, it is usually small or even absent. Bhatnagar & Rempel (1962, p. 476) described a petiole in *Latrodectus* as

''A distinct sclerite lodged within the hematodocha on the ectal side of the genital-bulb . . . this sclerite has no articulation with the subtegulum. . . . In the expanded bulb, the petiole appears as an extended, flat, heavy sclerite.'' According to our observations, theridiids generally lack a petiole, although a small, indistinct, and lightly sclerotized region
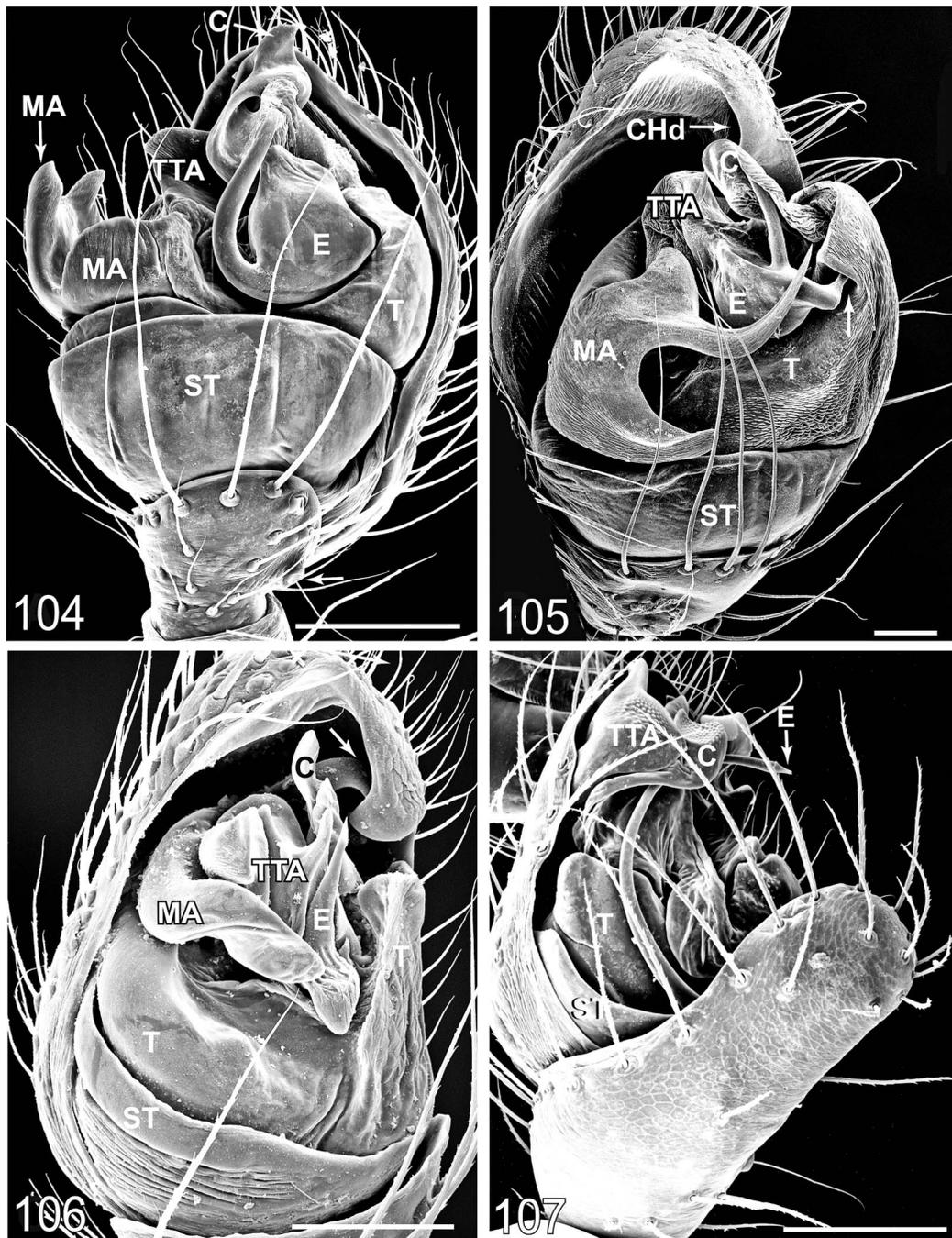
Figures 104–107.—Male palps ventral; 104, *Theridion varians* Hahn 1833, note furcated MA, typical of *Theridion* and relatives; 105, *Theridion frondeum* Hentz 1850, note also tegular pit (arrow) involved in a lock mechanism with E via a embolic apophysis (see also Avilés et al. (2006, fig. 4) for SEM photographs of the closely related *T. nigroannulatum*); 106, *Ameridion* sp. like all theridiines with a hooded BC-lock system (arrow); 107, *Thymoites* nr. *prolatus* (Levi 1959), the grossly enlarged tibial rim is shared with some other *Thymoites*. All scale bars = 100 µm.
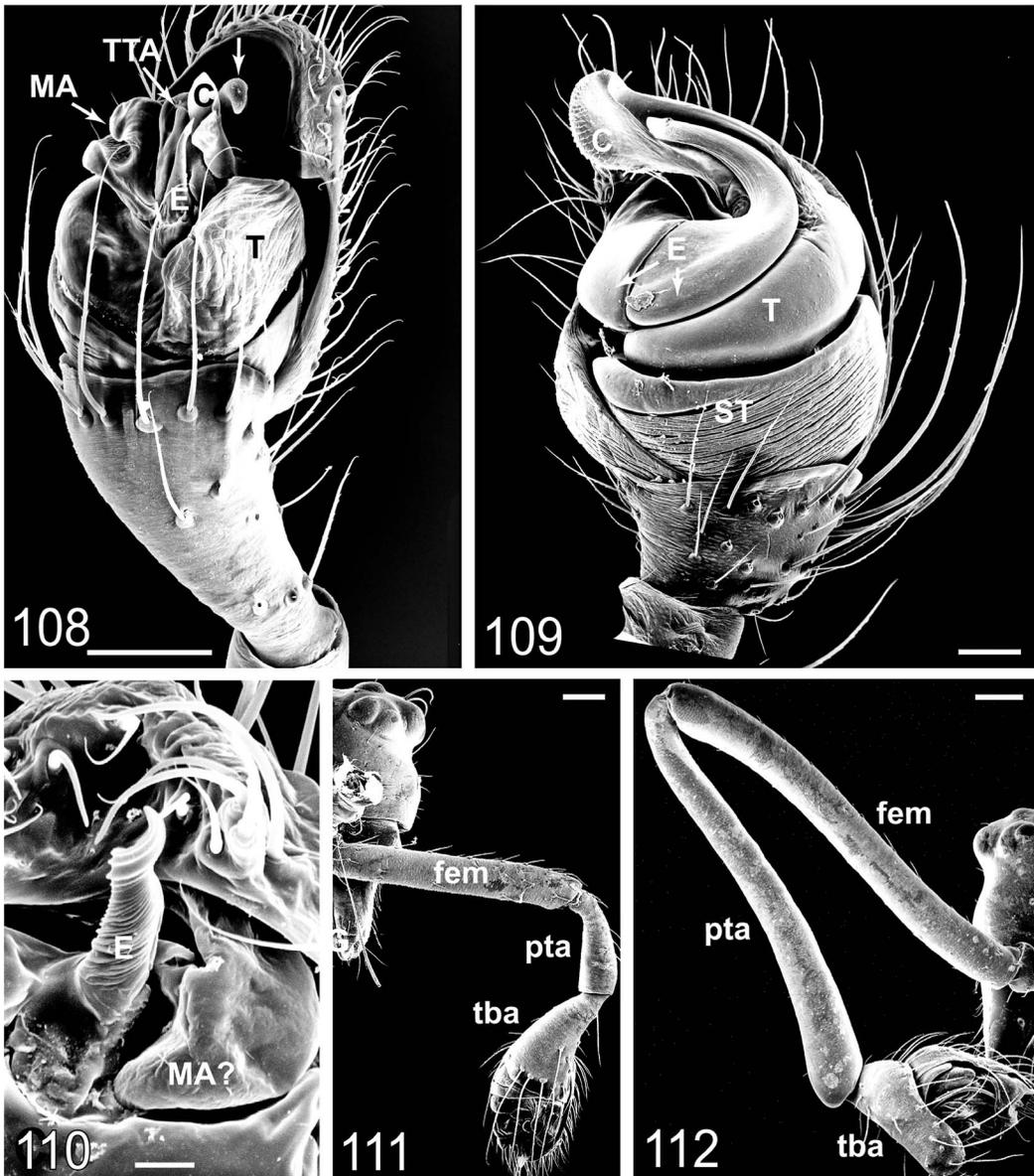
Figures 108–112.—108, *Ameridion* sp., arrow indicates tip of MA; 109, *Achaearanea tepidariorum*, like most other *Achaearanea* the TTA has been lost. Note the seam in the embolus (or possibly the fusing point between the E and MA, see discussion); 110, *Theridula opulenta* (Walckenaer 1842), among the simplest palps of theridiids, the TTA has been lost (independently from the loss in *Achaearanea*, see Fig. 201), the C is also absent, while a membranous connection exists between the T distally and cymbium. This membrane is possibly a homolog of the MA; 111, *Ameridion* sp., note elongated palpal femur; 112, *Thymoites* nr. *prolatus*, here not only the femur, but also the palpal patella is grossly elongated. Scale bars: 108, 109, 111, 112 =100 μm; 110 = 10 μm.

within the basal haematodocha in some taxa may be homologous to the petiole. At the very least, the sclerite is difficult to see and rarely mentioned or drawn in species descriptions of theridiids and other araneoids. Its distribution remains little known.

Subtegulum: The subtegulum is the ring-like sclerite that forms the base of the bulb, and connects to the alveolus via the basal haematodocha and to the tegulum via the middle haematodocha. It contains the fundus of the sperm duct (Fig. 3).

Sperm duct: Comstock labels the sperm duct "receptaculum seminis," a term more usually reserved for the female sperm storage organ; we prefer the term sperm duct or spermophore. The sperm duct consists of three distinct parts: first, the proximal end of it, the fundus, is enlarged so as to form a pouch; second, the intermediate portion, the reservoir, is a large coiled tube occupying the middle division of the genital-bulb; third, the terminal portion constitutes the ejaculatory duct; this is the slender tube traversing the apical division of the bulb (Comstock 1910, p. 163). In theridiids, the fundus is normally adjacent or fused to the subtegular wall. The so-called reservoir (a functional term that may not be appropriate since the fundus may be the main reservoir) spirals and sometimes switchbacks through the tegulum. The ejaculatory duct occupies the length of the embolus and opens at its tip.

Sperm duct trajectory: Primitively the sperm duct spirals simply in the tegulum (Comstock 1910; Coddington 1990). In many araneoids, however, the sperm duct trajectory (hereafter referred to as SDT) is moderately complex to very complex with numerous loops and switchbacks (Figs. 55–58; also 4–11, 24–27, 29, 33, 34, 36, 39–46, 96, 101, 102, 121, 123, 125–128, 134–138, 145–148, 165–168, 169). Coddington (1986) homologized individual loops and switchbacks in theridiosomatids and suggested the SDT could be an important new character system in spider systematics. This system was used by Agnarsson (2004); however, most other recent phylogenetic analyses of spiders have not looked at STD in detail. Hormiga et al. (1995), for example, identified the presence of switchbacks as a synapomorphy of higher araneoids, but did not attempt to make further specific homology statements. Griswold

(2001) describes the variation found within cyatholipids, but does not include it in his phylogenetic analysis.

The SDT varies greatly between theridiid genera, but within genera and species is often quite constant. At least some switchbacks and loops are consistent enough to homologize across theridiid genera (Agnarsson 2004). In some cases, differences in the sperm duct trajectory even define species groups within a genus (Agnarsson & Kuntner 2005).

Tegulum: The tegulum forms the middle part of the bulb, contains most, or all, of the sperm duct reservoir, and bears all remaining palpal sclerites. Some sclerites are fused to the tegulum and some articulate to it via a membrane. In some species, a tegular pit (Fig. 3) is present into which the base of the embolus, or an embolic apophysis, fits. This constitutes another locking mechanism that presumably also affects palpal expansion.

Embolus-tegulum membrane: The theridiid embolus typically articulates to the tegulum via a narrow membrane, which is traversed by the sperm duct on its way to the embolus tip. This membrane has been called the distal haematodocha, but that term was originally applied to one between the embolus and the radix and/or stipes in some araneids (Comstock 1910, p. 177; Hormiga et al. 1995, character 36; Scharff & Coddington 1997). The embolus-tegulum membrane is apparently homologous in tetragnathids, nephilids, and araneids, but is independently derived in linyphiids. There it is quite different because the "column" separates the entire embolic division from the tegulum (Hormiga et al. 1995; Griswold et al. 1998). Despite the discovery of an embolus-tegulum membrane in theridiids (previously coded as absent [Hormiga et al. 1995; Griswold et al. 1998]), these three similar features apparently all arose independently. The name theridioid embolus-tegulum membrane therefore seems appropriate. Apparently the same membrane usually connects to the MA and TTA (Fig. 17). However, the distal membranes are hard to interpret and apparently the MA and TTA are either connected to the tegulum via their own membranes, or they are closely associated and share a membrane, which then broadly attaches to the tegulum (Figs. 163, 164).
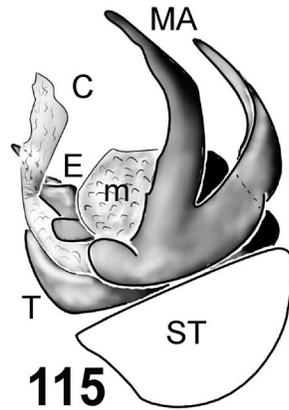
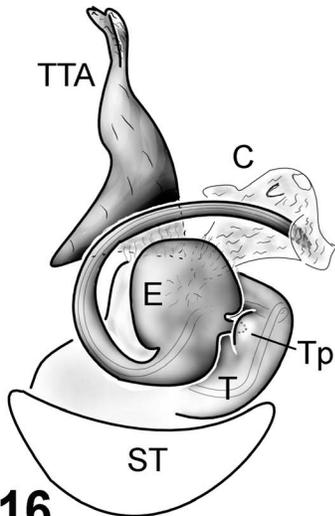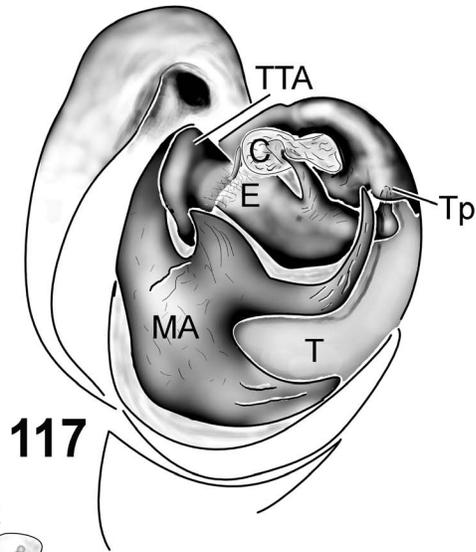*Median apophysis:* Comstock (1910, p. 172) described and named the MA: "arising
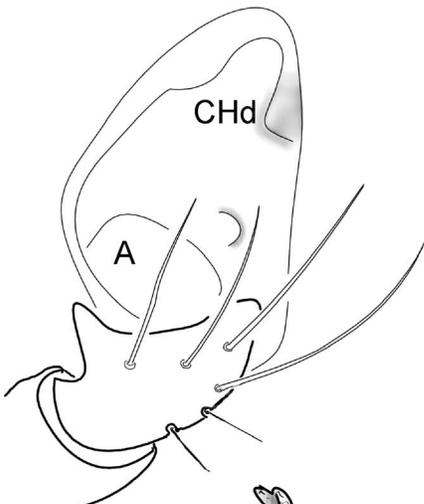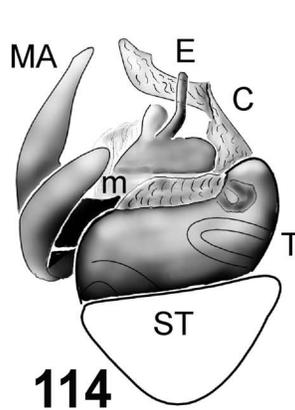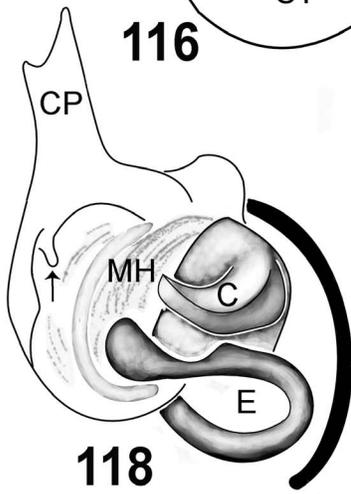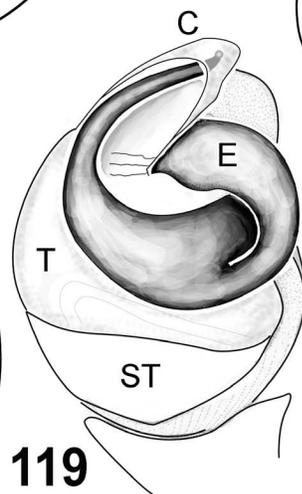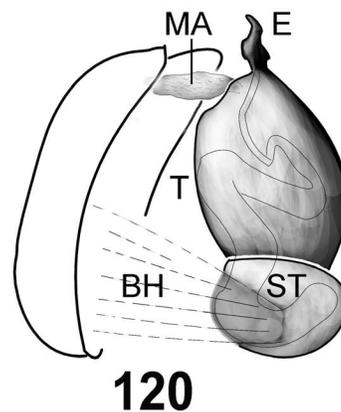
within the distal margin of the tegulum there is an appendage. . . . this is the *median apophysis.* In many spiders this appendage is very conspicuous and to it have been applied several names. In fact in several instances a writer has applied different names to this part in his description of different genera.'' The situation in theridiids has been no less confused than Comstock described for spiders in general. Being an ''appendage of the tegulum'' does not set it clearly aside from other sclerites that arise from the tegulum, and theridiids usually have three besides the embolus. Other definitions of the MA broadly agree that it is a distinct mesal process of the tegulum, typically, but not invariably, connected flexibly to the tegulum via a membrane (Lehtinen 1967; Shear 1967; Coddington 1986; Sierwald 1990; Griswold 1993). It is generally true in spiders that if a bulb has two apophyses, the ''conductor'' is usually close to the E, and if it has only one tegular apophysis, it is also usually close to the E. For that reason, Griswold et al. (1998) made the heuristic decision to consider the MA as ''the second tegular process in araneoids, once the conductor has been accounted for.'' Of course, if taxa lose the C rather than the MA, such an approach will fail. Hormiga (1994a) considered a small tegular knob of pimoids (see Fig. 195) the homolog of the araneid MA, based on similarity criteria, but a similar knob in cyatholipids has been interpreted as being the C (Griswold 2001), where the MA is presumed absent (following the ''conductor first'' rule). Linyphiids are considered to lack both MA and C, yet many linyphiid tegula bear various lobes (Fig. 196) that have received new names (Hormiga 2000). Examples include the ''mynoglenine tegular process'' found in the mynoglenine linyphiid genera *Haplinis* and *Novafroneta* (Hormiga 1994b, fig. 5B) and the suprategu-

lum present in most linyphiids. An effort to deflate linyphiid sclerite names has been made by Miller (2007, and Miller & Hormiga 2004).

Correctly identifying non-embolic tegular apophyses is daunting, especially the MA versus conductor if only one is present. The MA and C seem to be intimately associated in their ontogeny (Bhatnagar & Rempel 1962; Coddington 1990). Its topology is fairly consistent: the MA is usually positioned on the mesal side of the tegulum (often retrolaterally) towards the center or the base in the tegulum, further away from the embolus than is the conductor. The MA is generally the sclerite that interacts with the araneoid paracymbium. This description conforms closely to most of Comstock's (1910) use of MA. Secondly, our emphasis here is to provide internally consistent terminology (across theridiids), so that if what we call a MA in theridiids turns out to be something else, at least that nomenclatural change should apply to all sclerites so labeled here; the homology of this tegular apophysis among theridiids themselves is strongly corroborated.

The MA of theridiids has been a particularly great source of confusion. Myriad names have been applied to the structure we now term the MA in theridiids; examples include: ''locking apophysis A'' (Saaristo 1978, p. 113, fig. 126), ''locking apophysis B'' (Saaristo 1978, p. 119, fig. 193), ''theridiid tegular apophysis'' (Coddington 1990, p. 41, fig. 76), ''tegular apophysis I'' (Knoflach 1997, p. 134, fig. 4), and ''radix'' (Levy 1998, p. 33, fig. 47), to name a few. In addition, most of the sclerites of the theridiid palp have at one time or another been labeled MA. Griswold et al. (1998), for example, studying *Steatoda grossa* (C. L. Koch, 1838), labeled an apophysis of the embolus as MA (their figure 16C), while the large and conspicuous MA is itself miss-

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Figures 113–120.—113–115, *Theridion cochise* Levi 1963 dissected palp. 113, cymbium; 114, bulb ventral, absence of TTA and flat based E are shared with some other *Theridion*, e.g.,*T. grallator* Simon 1900; 115, bulb dorsal; 116, *Coleosoma floridanum* Banks 1900, schematic drawing of a dissected palp, MA is present, but not shown; 117, *Theridion frondeum*, palp ventral; 118, *Achaearanea trapezoidalis* (Taczanowski 1873), the type species of *Achaearanea*, uniquely among theridiines, has a hooked BC-lock system (arrow); 119, *Achaearanea tabulata* Levi 1980 (redrawn from Knoflach 1991), like most *Achaearanea* lacks TTA; the MA is either lost as well or fused with the embolus; 120, *Theridula emertoni* Berland 1920 (redrawn from Levi & Levi 1962), lacks a conductor, TTA is also absent. The tegulum is distally attached to the cymbium via a membranous sclerite, most likely the MA.
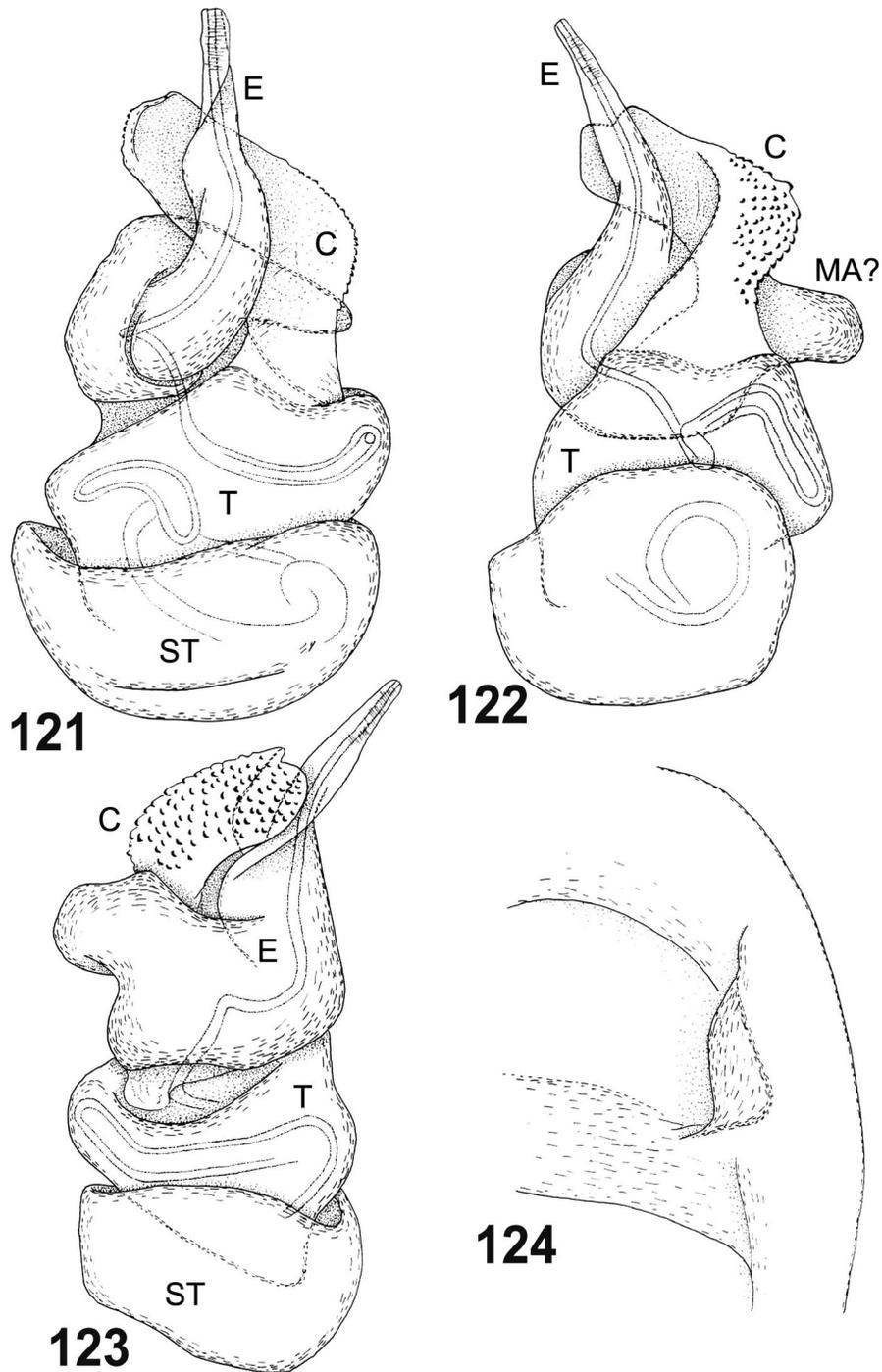
Figures 121–124.—*Achaearanea lunata*. 121–123, bulb slightly expanded and removed from cymbium, ventral, ectal, mesal; the TTA has been lost; it is uncertain whether the MA has been fused with the embolus, or lost, in which case the embolus base interacts with the BC-lock system; 124, distal ectal margin of cymbium in ventral view with cymbial hood.
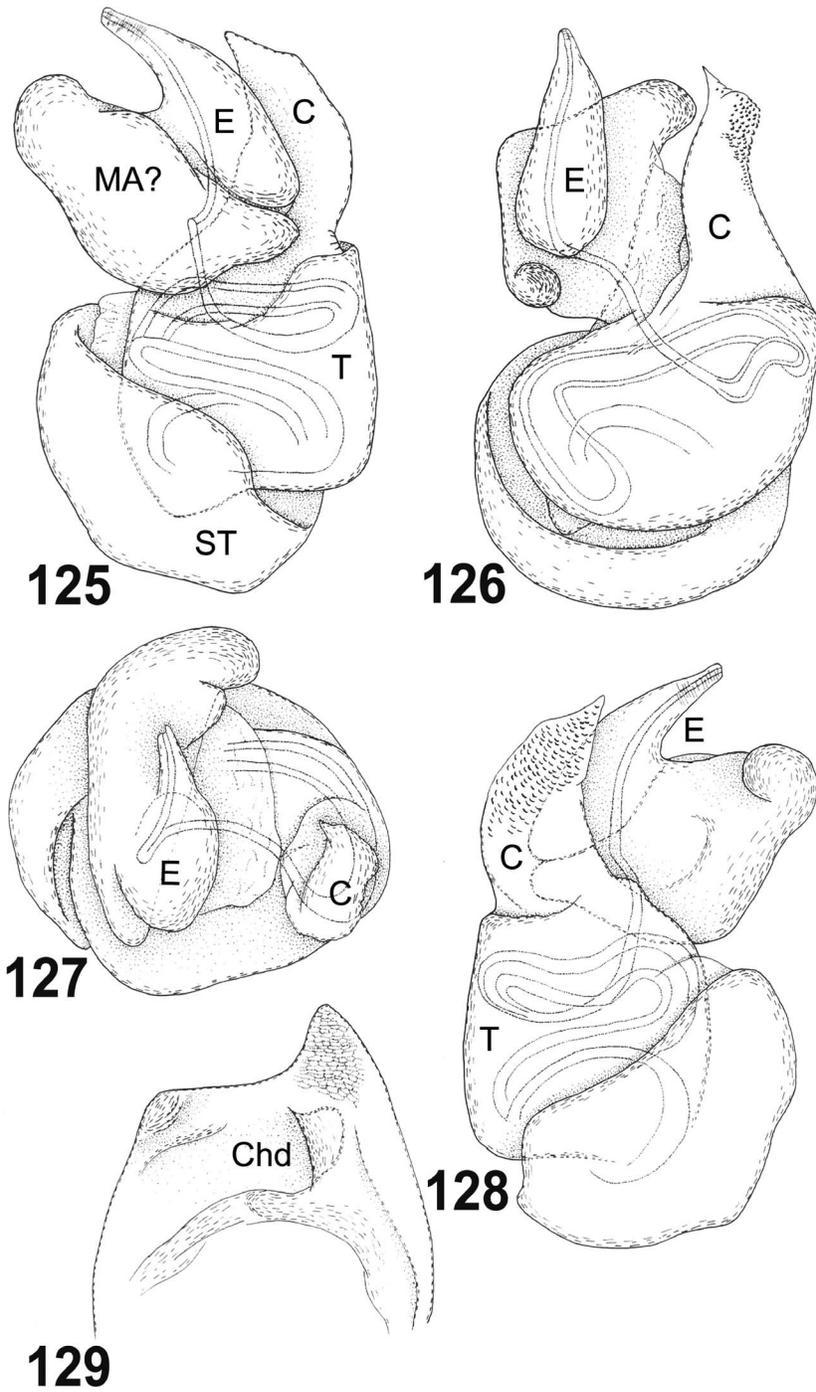
Figures 125–129.—*Achaearanea riparia*. 125–127, bulb slightly expanded, ventral, mesal, ectal-dorsal; 128, apical; conductor with scaly surface as present in many *Achaearanea* species. 129, distal cymbium in ventral view, with protruding tip.
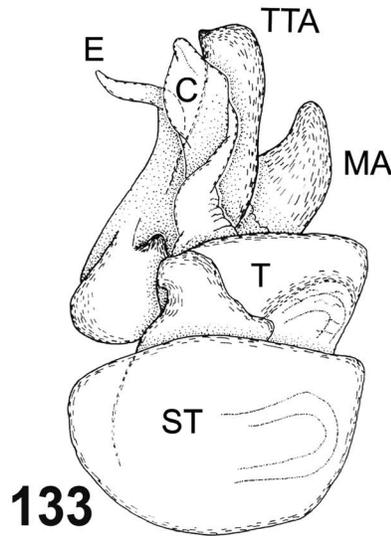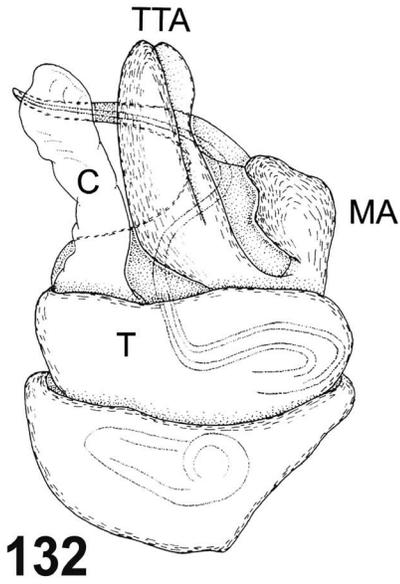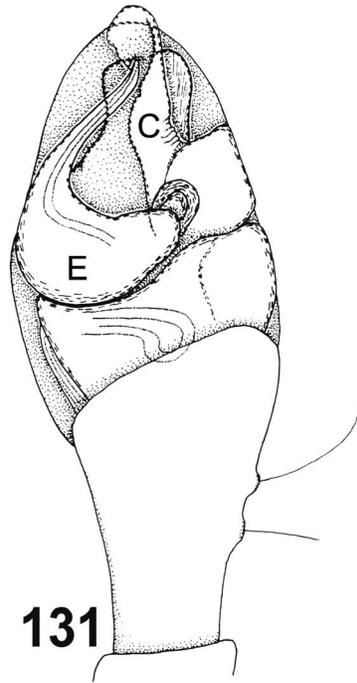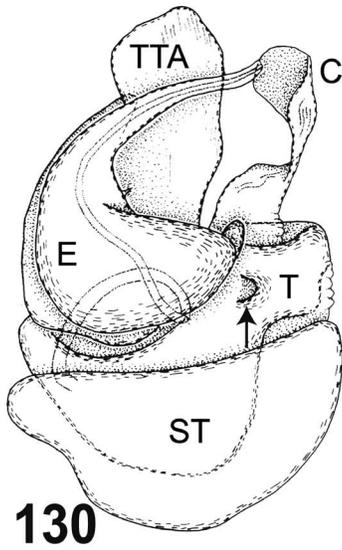
Figures 130–133.—*Keijia tincta*. 130, 132, 133, bulb slightly expanded, ventral, ectal, dorsal; 131, male palp, ventral; both tegular apophyses present; note tegular pit and corresponding embolar process (arrow).
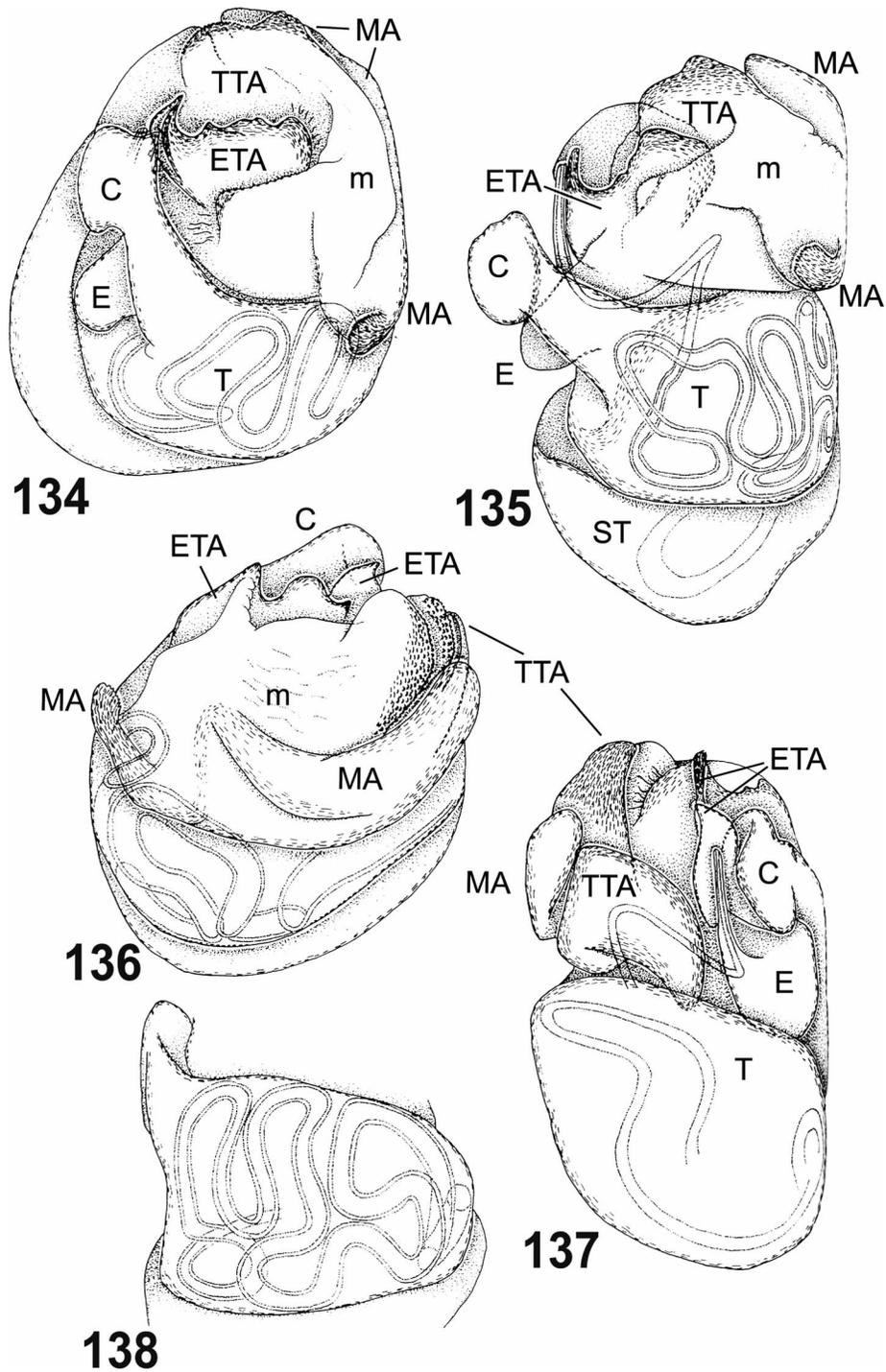
Figures 134–138.—*Neottiura bimaculata*. 134–137, bulb removed from cymbium and slightly expanded, apical-ectal, ectal, apical-dorsal, ventral; three tegular apophyses present, which are complexly folded and connected by a large membrane; 138, tegulum, dorsal; note convoluted course of sperm duct within T.
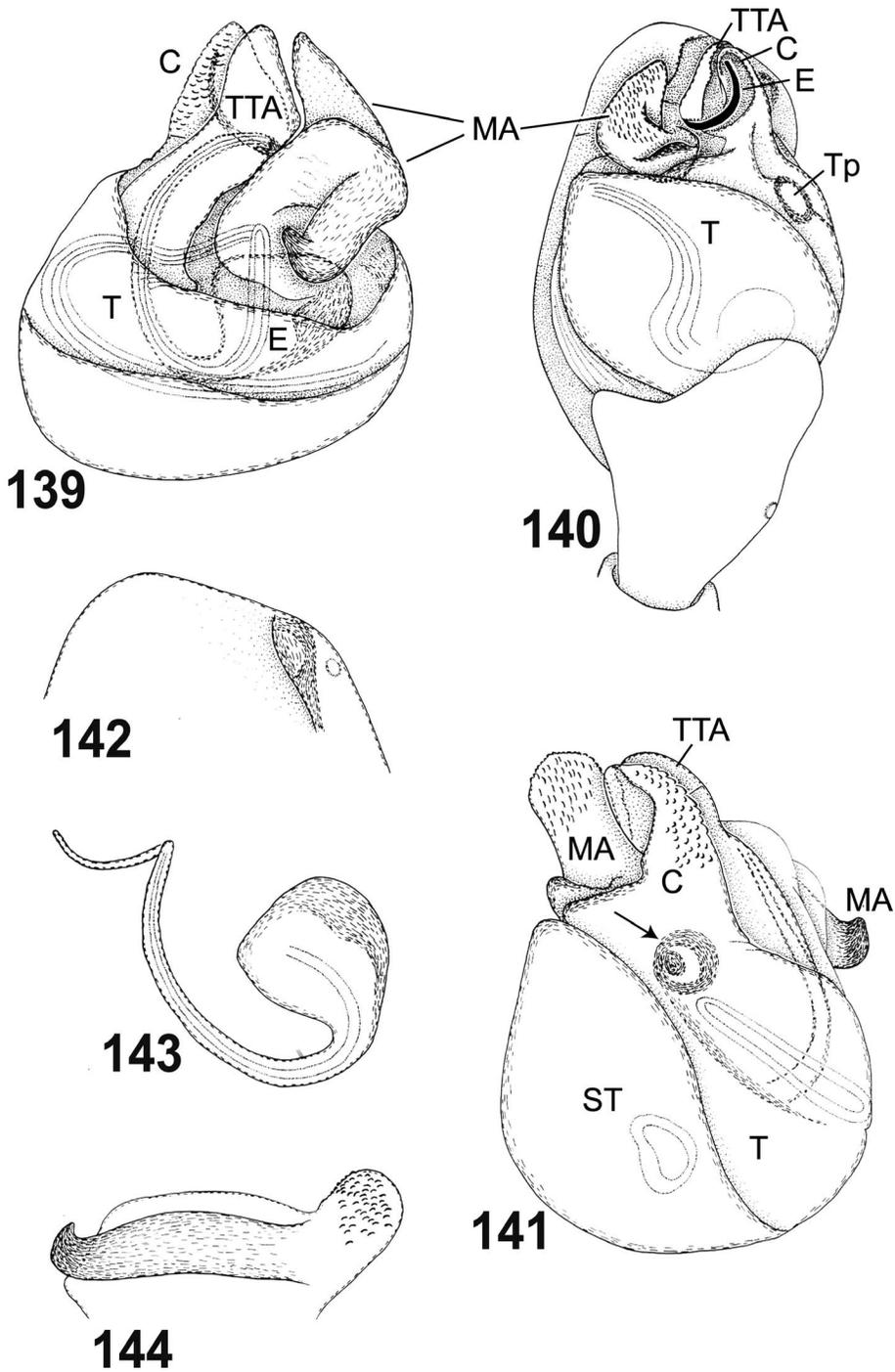
Figures 139–144.—*Rugathodes bellicosus*. 139, 141, bulb removed from cymbium and slightly expanded, dorsal, ectal; both tegular apophyses present; 140, male palp in ventral view; 142, distal cymbium in ventral view with cymbial hood; 143 embolus removed from bulb. 144, median apophysis, mesal. Embolus submerged deeply into tegulum, only its tip being free, accompanied by the conductor; its articulation into the tegular pit also inside but visible through tegulum (arrow).
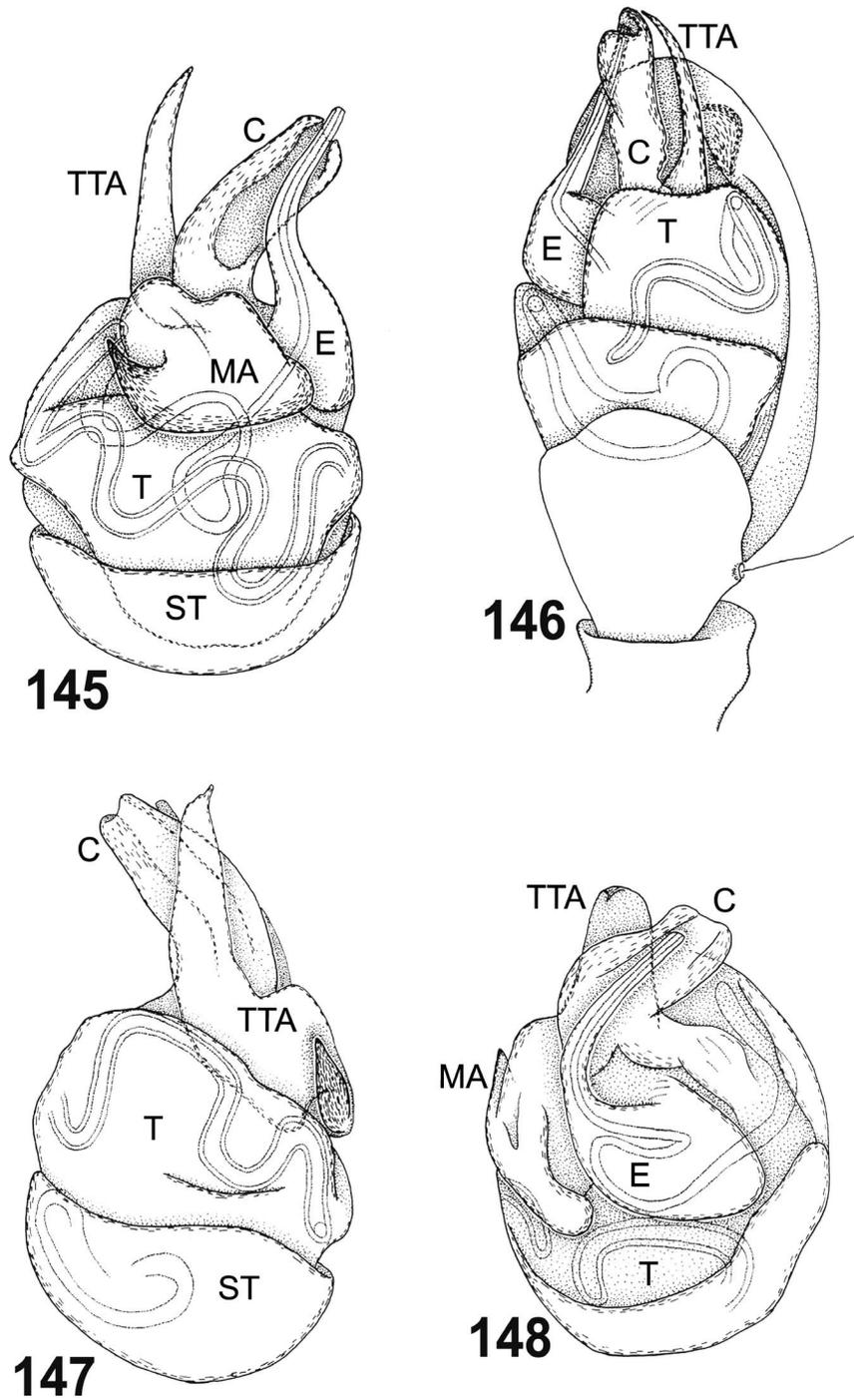
Figures 145–148.—*Simitidion simile*. 145, 147, 148, bulb removed from cymbium and slightly expanded, mesal, dorsal, apical-ventral; sperm duct forms numerous coils within tegulum; 146, male palp, ectal; both tegular apophyses present, connected by a membrane.
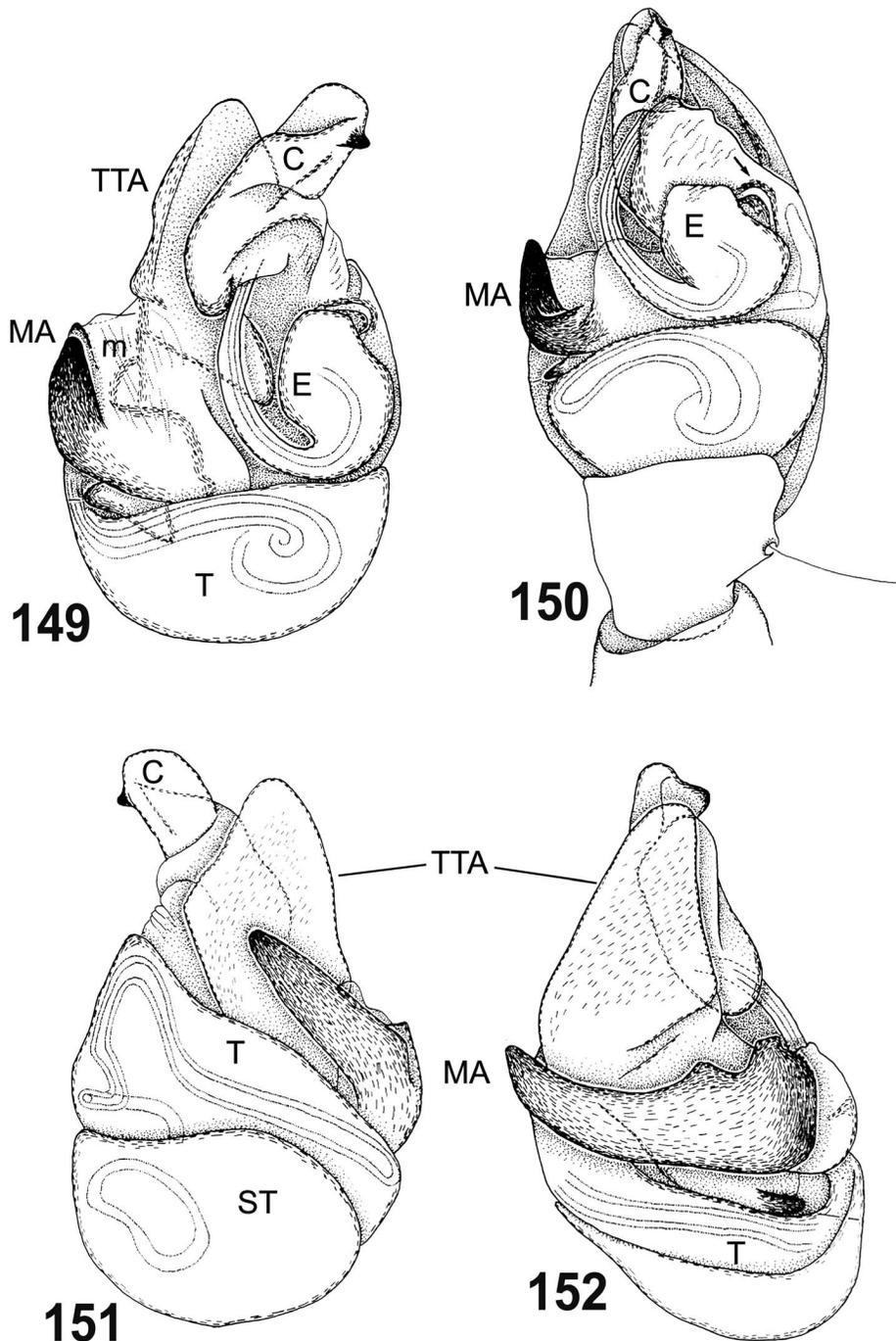
Figures 149–152.—*Theridion pictum.* 149, 151, 152, bulb removed from cymbium and slightly expanded, ventral, dorsal, mesal; both tegular apophyses present, both without sperm duct; conductor with broad, short channel supporting the embolus; scales on TTA indicate contact to the female epigynum; 150, male palp, ventral; arrow points to tegular pit.
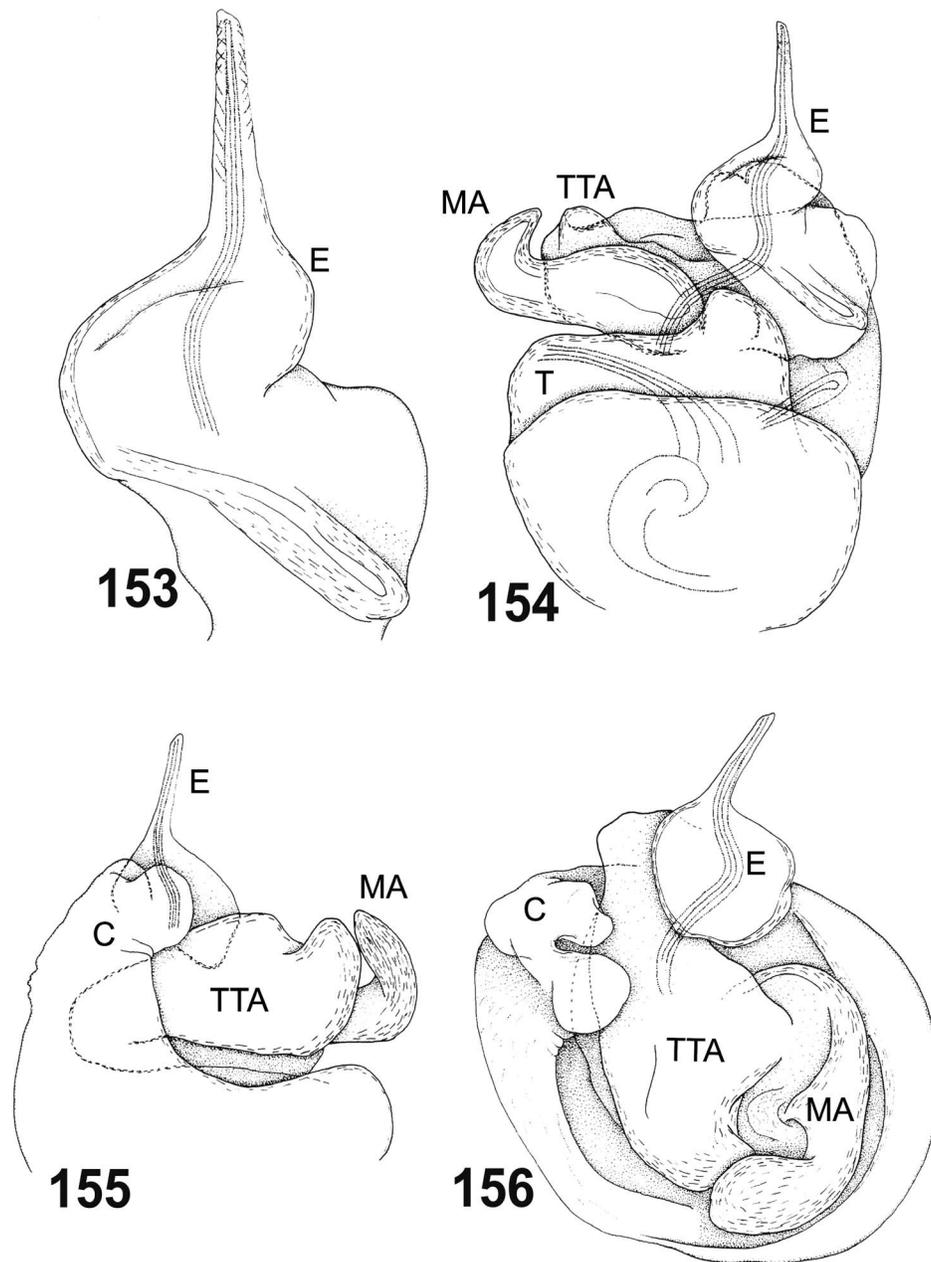
Figures 153–156.—*Theridion conigerum.* 153, embolus, ventral; distal part corrugated; 154, 156, bulb removed from cymbium and slightly expanded, ventral, apical-mesal; 155, distal bulb, dorsal; conductor lobe-like, forming a fold.

ing from the drawing. Saaristo (1978, 2006) maintained that MA was not present in theridiids at all and furthermore that the apophysis interacting in the lock mechanism was not homologous across theridiids (his locking apophysis A and B). Coddington (1990) agreed with Saaristo's second point, but not his first, using the terms TTA for his laA and MA for his laB.

Coddington (1990) and Sierwald (1990) paid particular attention to the theoretical basis for homology in their consideration of pal-
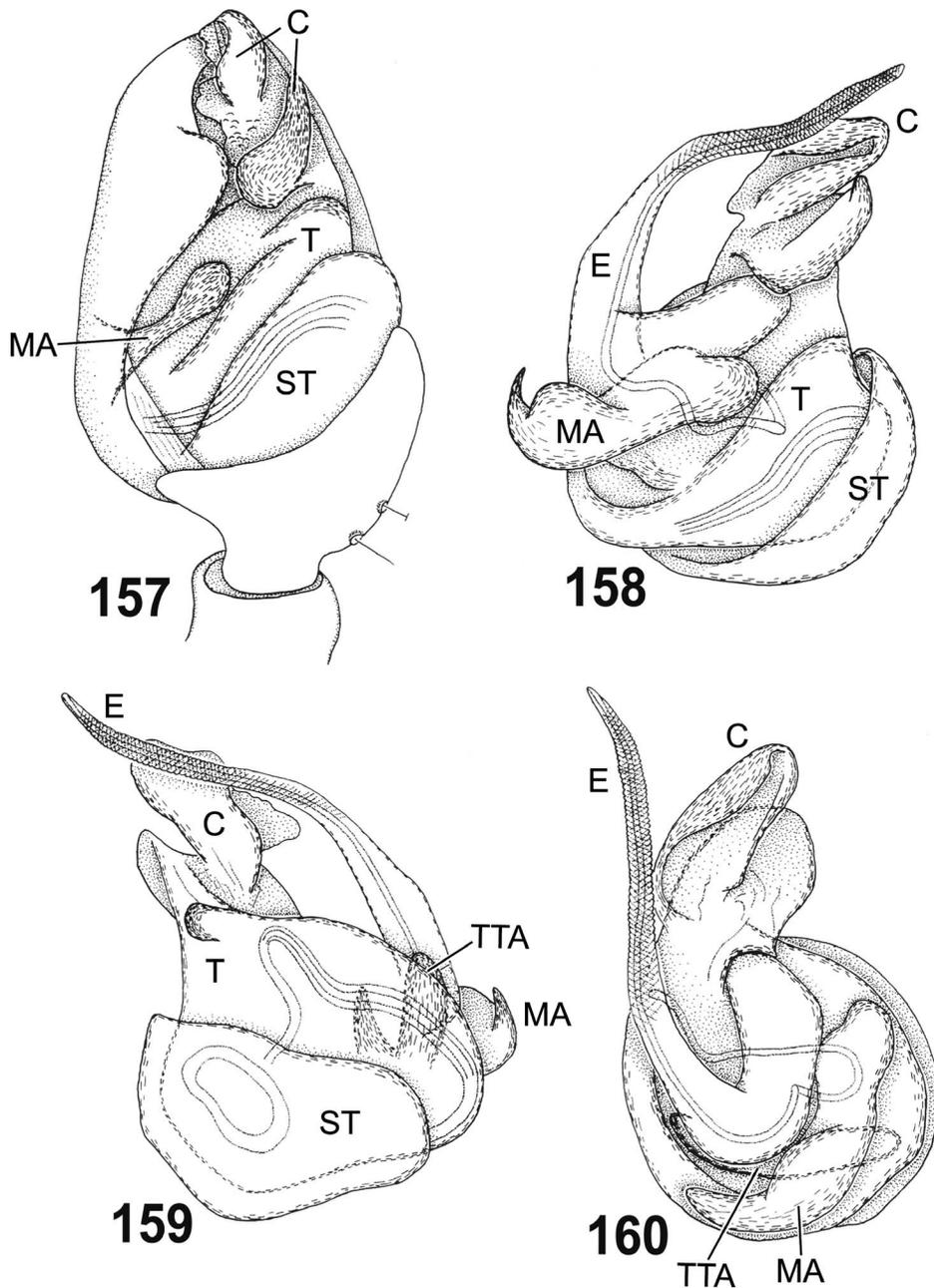
Figures 157–160.—*Theridion ohlerti*. 157, male palp, ventral; embolus hidden by cymbium; 158–160, bulb removed from cymbium and slightly expanded, ventral, dorsal, apical-mesal; TTA small and submerged into tegulum; distal embolus corrugated; tegulum with distinct lobe close to conductor.

pal sclerites in spiders. Influenced by the theoretical debates of the times (e.g., Nelson 1978; Patterson 1982), Coddington chose ontogeny and the potential for transformation during ontogeny over topology or function as homology criteria for two controversial sclerites. Unusually, ontogeny applied to Theridiidae because of the study of *Latrodectus* "*curacaviensis*" (may have been *hesperus*, see below) by Bhatnagar & Remple (1962). First,

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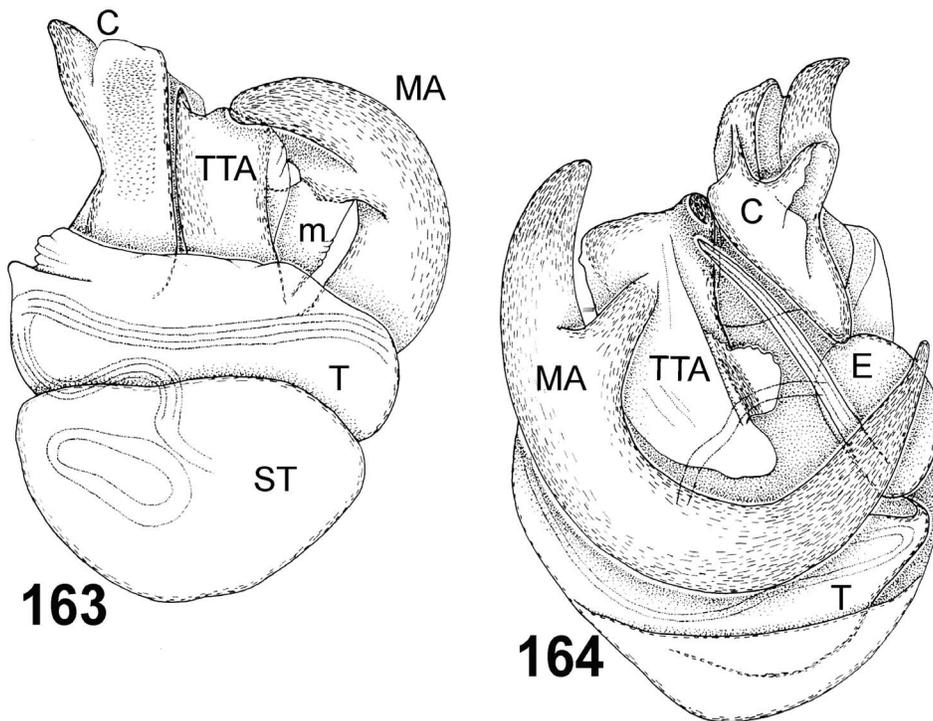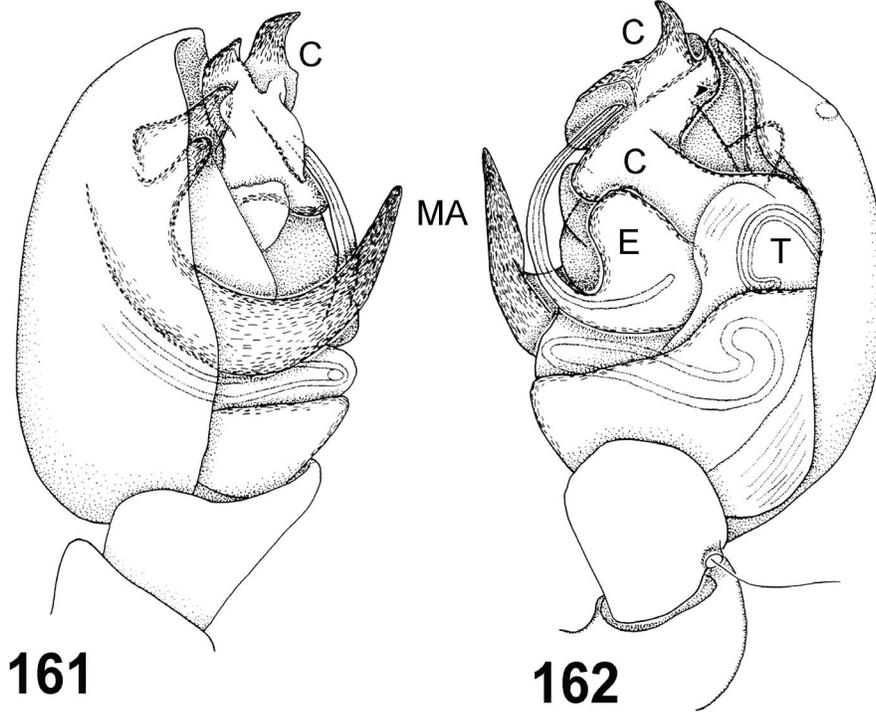
Figures 161–164.—*Theridion petraeum.* 161, 162, male palp, mesal, ectal; 163, 164, bulb removed from cymbium and slightly expanded, dorsal, apical-mesal; conductor bifid, containing a groove and channel for embolus; ventral end of MA typically sickle-shaped.
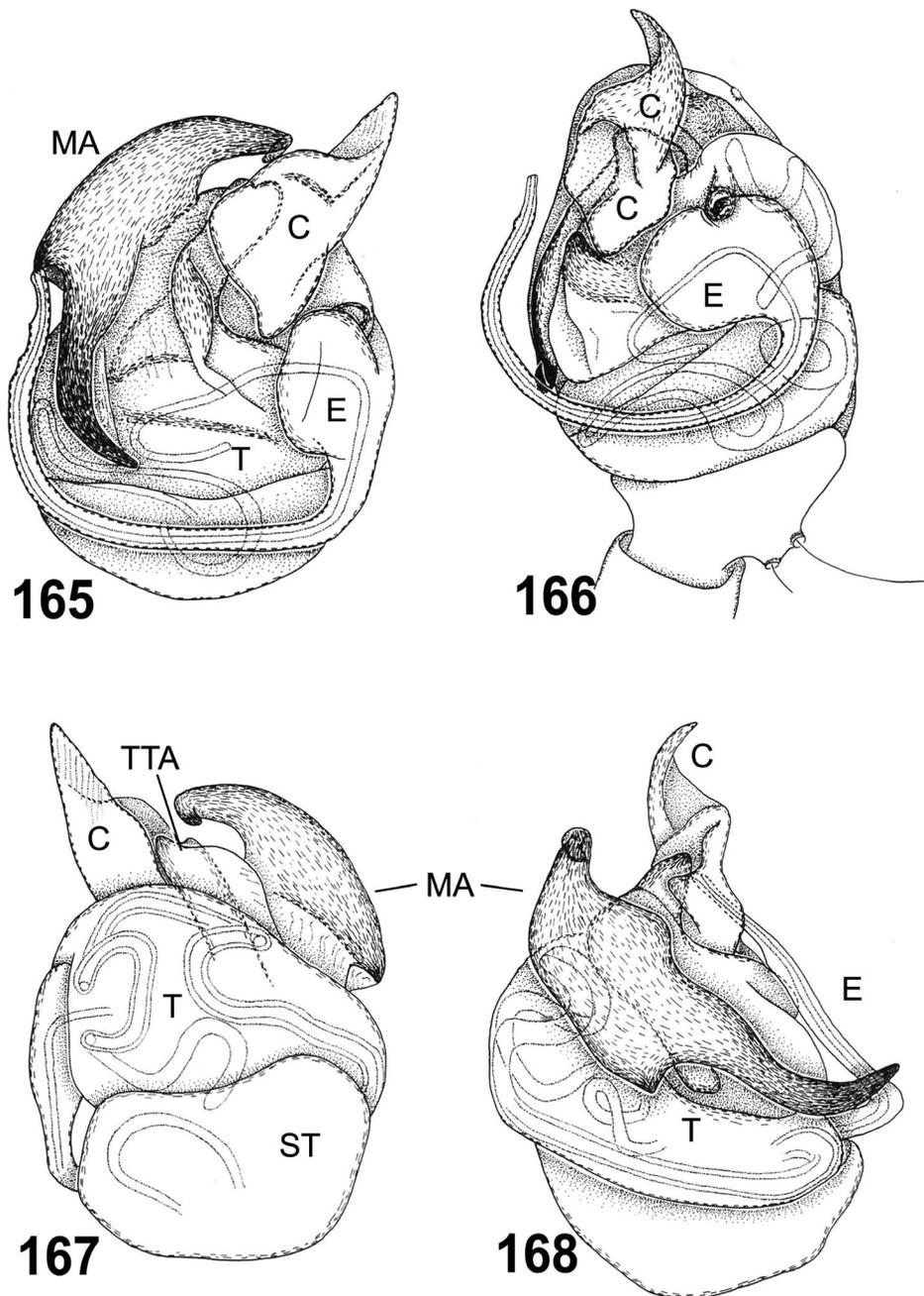
Figures 165–168.—*Theridion pinastri*. 165, 167, 168, bulb removed from cymbium and slightly expanded, apical-ventral, mesal, dorsal; the TTA is relatively small; 166 male palp, ventral; note articulation between embolus and tegulum.

theridiids clearly have an ''extra'' tegular sclerite beyond those normally present (median apophysis and conductor). One clue was that one of the three theridiid tegular sclerites

had a loop of the ejaculatory duct running through it. Outgroup comparison to other spider groups implied that the sperm duct never traverses either the MA or C. Bhatnagar &
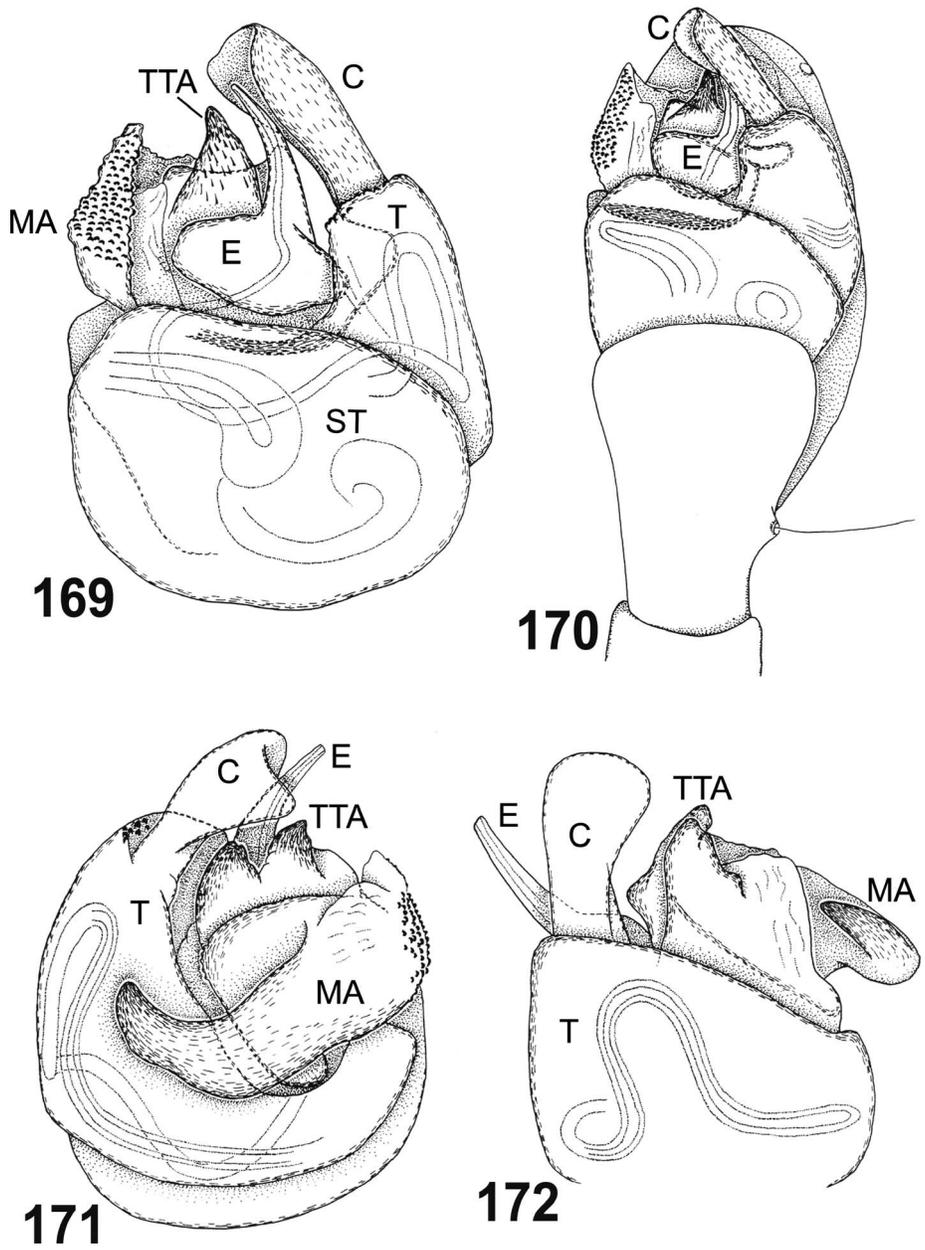
Figures 169–172.—*Theridion sisyphium*. 169, 171, 172, bulb removed from cymbium and slightly expanded, ventral, apical-mesal, dorsal; TTA small and bifid; 170, male palp, ventral.

Remple also showed that the MA and C were closely linked ontogenetically, differentiated early from the rest of the palp, and before the invagination of the ejaculatory duct. Coddington therefore concluded that the theridiid sclerite containing a loop of sperm duct was neither MA nor C but something new, which

he called the ''theridiid tegular apophysis.'' In our reassessment here, we reach a different conclusion in light of new and more detailed data and analyses (contra Saaristo 2006).

We agree with Levi (see Levi 1961 and Levi's numerous other publications on theridiids (1953–1972)) in considering MA in ther-
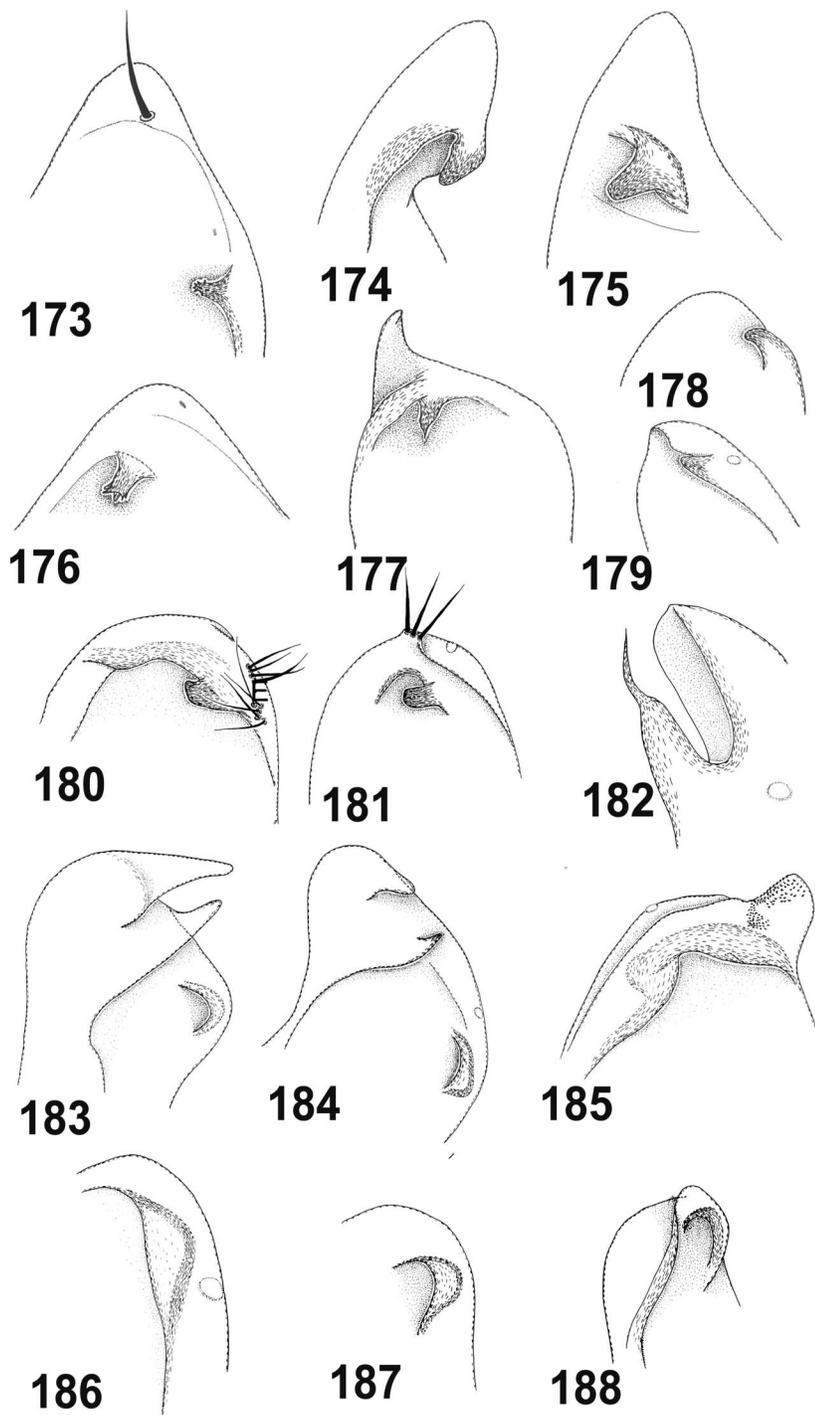
Figures 173–188.—Distal cymbium with cymbial hook, 173–182, and hood, 183–188. 173, *Lasaeola tristis*; 174, 175, *Steatoda phalerata*; 176, *Dipoena melanogaster*; 177, *Euryopis flavomaculata*; 178, 179, *Pholcomma gibbum*; 180, *Episinus truncatus*; 181, *E. theridioides*; 182, *Robertus neglectus*; 183, 184, *Neottiura bimaculata*; 185, *Theridion nigrovariegatum*; 186, *Keijia tincta*; 187, *Simitidion simile*; 188, *Theridion sisyphium*.

idiids as a sclerite positioned retrolaterally on the mesal side of the tegulum (Figs. 4–11, 18, 20–24, 27, 30, 32–34, 36, 42–44, 46, 48–54, 58, 59, 61, 62, 67, 70, 74, 75, 78–81, 83–91, 93–96, 98, 101, 102, 104–106, 108, 114, 115, 117, 132–137, 139–141, 145, 148–152, 154–165, 167–172). It is closely associated with the tegulum, and contains a loop of the sperm duct in the more basal theridiids (Figs. 4–11, 23, 24, 27, 30, 32–34, 36, 42–44, 46, 58, 74, 75, 78–81, 83–91, 93–96, 98). The MA in theridiids is always attached by a membrane to the tegulum (Fig. 3, in some cases the membrane is very narrow, so that the MA appears fused to the tegulum), often sharing a membrane with the TTA and E. The MA is present in most theridiids, it is topologically very consistent across genera, and if present always functions as the sclerite that interacts with the cymbium in the cymbial lock system (Figs. 64, 65). The link to MA in the outgroups is supported by topological similarity (araneid and nesticid MA's are a retrolateral process of the tegulum, Fig. 198), similarity in structure and association with other palpal elements (nesticid MA resemble theridiid MA in shape, and often contains a loop of the sperm duct, as do basal theridiids Fig. 198) and similarity in function (nesticid MA interacts with the cymbium during palpal expansion) (Huber 1993). This outgroup comparison contrasts with Saaristo's (1978, 2006) view that his laA and laB (our MA) are confined to theridiids. Furthermore, contrary to Saaristo (1978, 2006) and Coddington (1990) it is simpler, according to our method, to hypothesize a transformation of the MA structure (loss of sperm duct and MA hood, both of which seem to take place gradually if optimized on a cladogram) than a sudden and drastic topological, structural, and functional shift in this sclerite. In either case, the loss of the sperm duct loop must be accounted for anyway.

As noted, Levi (1961) consistently used the term MA as we suggest here. Knoflach (1991–2002; Knoflach & Thaler 2000; Knoflach & van Harten 2000, 2001; Knoflach & Pfaller 2004) also viewed the structure involved in the lock mechanism as homologous across theridiids, although she hitherto used a neutral term for it (tegular apophysis I).

Conductor: Like the MA, the term "conductor" has not been consistently applied across araneoid palpal sclerites (Griswold et al. 1998), although its usage in theridiids has been fairly consistent. Comstock's definition of the C was, rather atypically and unfortunately, functional: "the conductor . . . [is] easily recognized by its relation to the embolus, which rests upon it . . . " (Comstock 1910, p. 172), but it now seems clear that there is more than one sclerite that can serve as conducting the embolus tip in araneoid spiders (see Lehtinen 1967; Coddington 1990). However, Comstock (1910, p. 176) gave other criteria as well: "The conductor arises at the base of the apical division and is closely connected with the tegulum" and "[it] is easily recognized by its . . . membranous texture" (Comstock 1910, p. 172). Other authors have followed in treating the C as the sclerite most closely associated with the tegulum. Bhatnagar & Rempel (1962, p. 478) showed that in *Latrodectus*: "Histological study indicates its [the conductor's] origin from the median wall of the tegulum". Sierwald (1990, p. 21) described the pisaurid C: "The conductor inserts directly on the tegulum and appears to be a mere extension of the tegular wall . . . immovably attached to and continuous with the tegular wall" and the lycosid C is a "tegular outgrowth of the same texture and color as tegulum" Griswold (1993, p. 10).

In theridiids, at least two sclerites, the C and the TTA, may perform the act of conducting the E. Many theridiids have a relatively small C, sometimes only vestigial, in which case the TTA serves to "conduct" (or support) the E (Figs. 8, 49, 77, 91–94). This seems also to be the case in nesticids and synotaxids (Figs. 189, 190, 197, 198). The theridiid C is always a direct and immovable outgrowth of the tegulum, lying close to (but behind) the E, centrally or slightly ectally in the palp (Figs. 3, 6, 7, 12, 17, 18, 20–23, 28–30, 33, 34, 36, 39–41, 44, 45, 74, 79–81, 83, 84, 88, 90, 91–93, 97, 101, 102, 105, 107, 109, 114, 115, 121, 122, 125–128, 130–135, 141, 146, 148, 149, 155, 156, 158–160, 162, 163, 165, 166, 169–172). The C is often membranous or of the same texture as the tegulum, but sometimes heavily sclerotized and rugose (e.g., *Achaearanea lunata* (Clerck 1757) and *A. tepidariorum* (C. L. Koch 1841), Figs. 109, 122, 123). In *Anelosimus* the tegulum has a sclerotized area, or a separate outgrowth at the base of the C, the subconductor (see below).
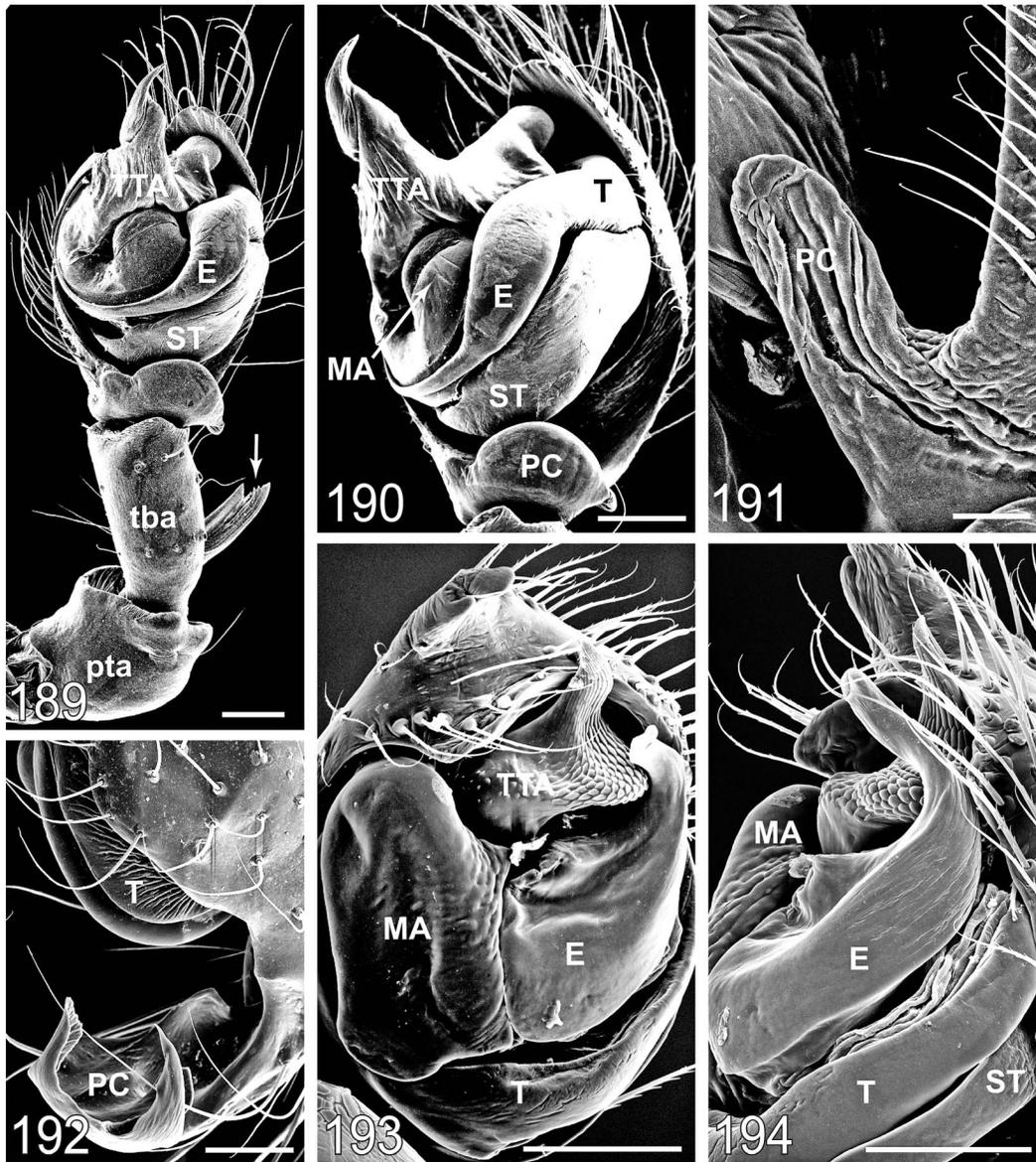
Figures 189–194.—189, 190 *Synotaxus monoceros* (Caporiacco 1947) (Synotaxidae). 189, ventral, note patellar spur (arrow), a rather uniform tibia, and a large excavate TTA; 190, ectal, the E is a direct outgrowth of the tegulum, note also a distinct, cup shaped PC; 191, *S. waiwai* paracymbium; 192, *Nesticus silvestrii* Fage 1929, huge and rigid PC; 193, 194, *Euryopis gertschi* Levi 1951. 193, ventral, conductor absent; 194, ectal, note small membrane between T and E. Scale bars: 189, 190, 192–194 = 100 μm; 191 = 20 μm.

In *Theridula* (Fig. 120), *Euryopis* (Figs. 8–11), and perhaps *Carniella* (Fig. 50; see Agnarsson 2004) the C is absent.

The nomenclature of the theridiid C has been remarkably stable, considering its variability and that it does not always function to conduct the E. Saaristo (1978) generally referred to the C as ''conductor A'' calling the TTA or an appendage of it ''conductor B.'' Only in a few cases, have the TTA and the C been confused, for example Levi (1963, p. 43, fig. 44) in *Selkirkiella*, where the TTA is
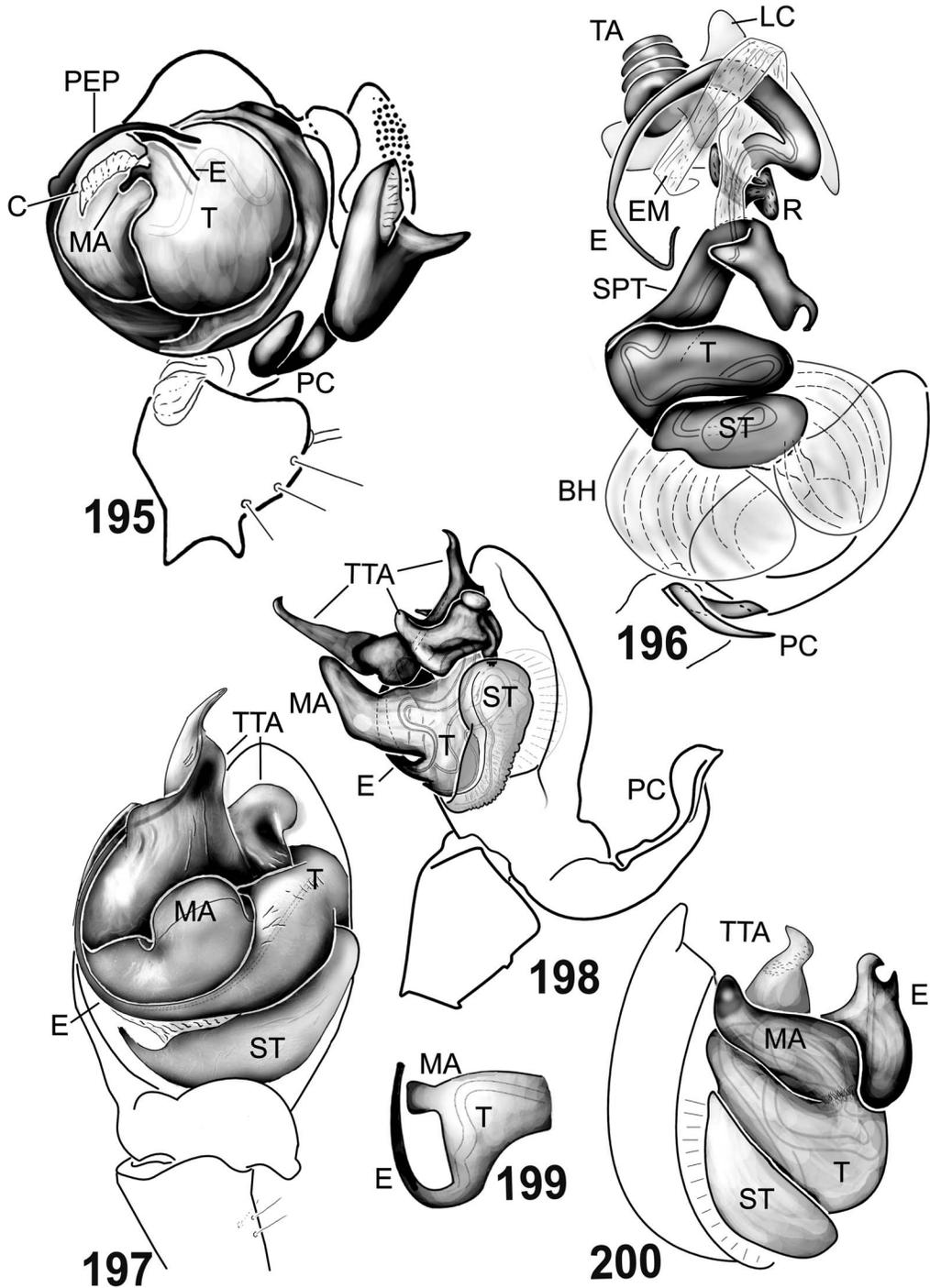
Figures 195–200.—195, *Pimoa rupicola* (Simon 1884) (PEP = pimoid embolic process); 196, *Linyphia triangularis* (EM = embolic membrane, LC = lamella characteristica, R = radix, SPT = suprategulum, TA = terminal apophysis); 197, *Synotaxus monoceros*; 198, *Nesticus cellulanus* (Clerck 1757); 199, *Eidmanella pallida*, part of tegulum showing MA and E; 200, *Euryopis flavomaculata* (redrawn from Levi & Levi 1962). 195–199 reproduced from Agnarsson (2004) with permission from Blackwell Publishing.
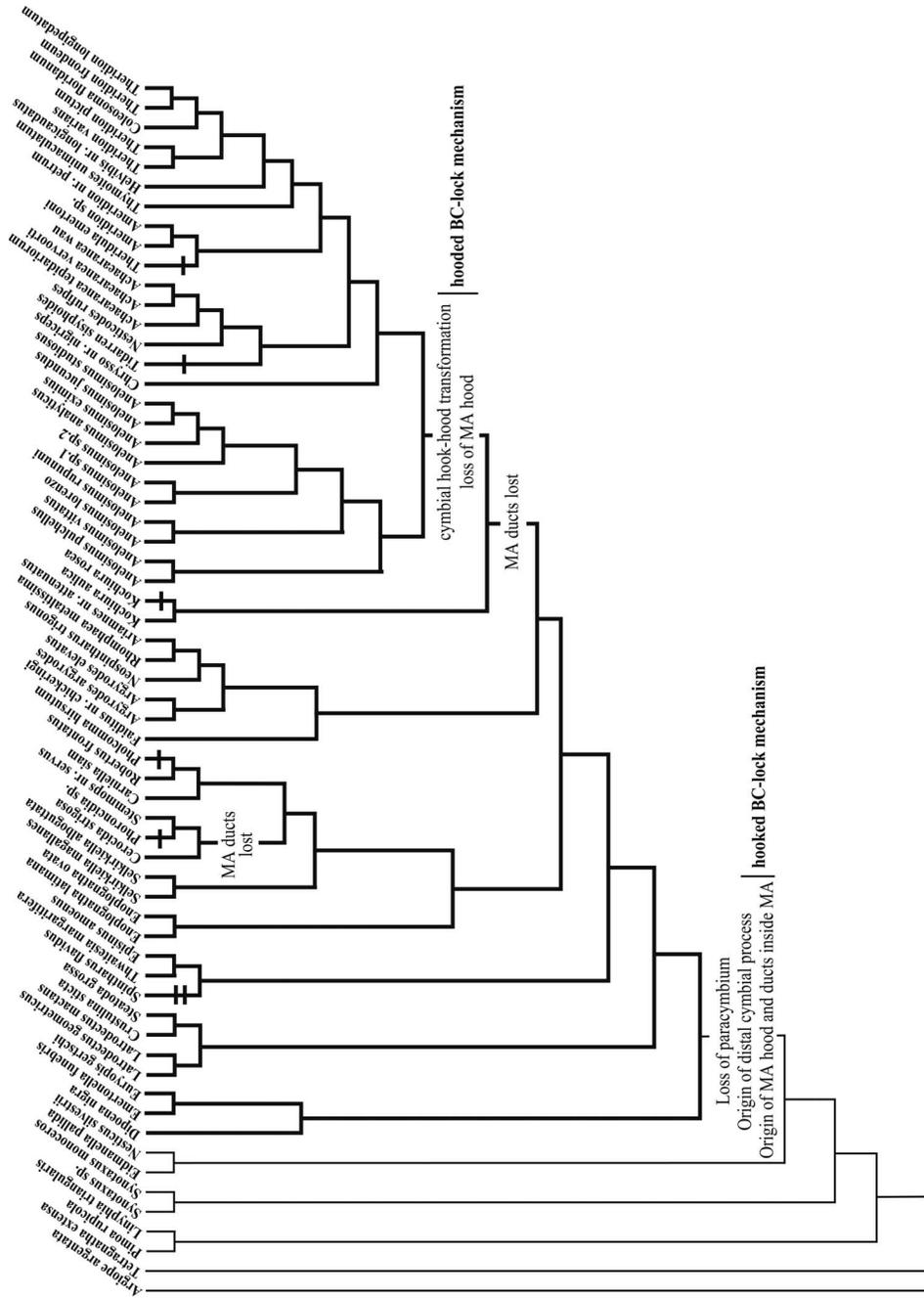
Figure 201.—Evolutionary changes in the unique theridiid BC-lock system. The cladogram is taken from Agnarsson (2004), see Figure 2 for clade names. Theridiidae is indicated with bold lines. Black horizontal bars each indicate one instance of homoplasy: *Spintharus* independently evolved a hooded lock system and lacks the hood on the MA; *Phoroncidia* lacks the MA hood; the MA of *Pholcomma hirsutum* Emerton 1882 does not contain a loop of the sperm duct (but in *P. gibbum* does, see Figs. 91–95; *Kochiura rosea* (Nicolet 1849) lacks the MA hood, *Tidarren* has a hook BC lock system (uniquely among Theridiinae); the lock system of *Theridula* is unique (see text).

strongly modified and forms a long sheath around the E.

Subconductor: In *Anelosimus* (Fig. 63) an outgrowth of the C base overhangs the E. We here name this structure "subconductor" following Agnarsson (2004) and Agnarsson & Kuntner (2005). The only clear reference to the subconductor we are aware of is in Levi (1956, p. 411, fig. 17), and following him, Coddington (1990, p. 42, fig. 94) where in *Anelosimus eximius* (Keyserling 1884), it is labeled as the C. The tiny membranous "true" C, arising from the back of the subconductor (Fig. 63), is missing from their drawings.

Theridiid (theridioid) tegular apophysis: Most theridiids have a tegular apophysis in addition to the ones already accounted for. This apophysis is always a "free" sclerite, connected to the tegulum via a membrane (or sometimes partially imbedded within the tegulum, although never fused to it). Levi generally used the term "radix" for this tegular apophysis but it now seems not to be homologous to any sclerites present in araneids, linyphiids, pimoids, or symphytognathids. Hence Coddington (1990) introduced the term theridiid tegular apophysis (TTA) for this structure. However, because the TTA seems to be present in nesticids (which Coddington (1990) acknowledged) and perhaps in synotaxids, it should be henceforth named the theridioid tegular apophysis (with the same abbreviation, TTA).

Based on the present results, Coddington (1990) did not apply the term TTA consistently in his treatment of theridiid palps. He applied it to the MA whenever the MA had sperm ducts going through it (e.g., figs. 76, 77, 79, 81, p. 41), but to the "true" TTA when the MA was without ducts (e.g., figs. 90, 92, 94, p. 42).

The TTA is a tegular apophysis normally lying in between the E, C, and MA somewhat centrally in the palp (Figs. 4, 5, 8, 9, 11, 17, 18, 23, 24, 27, 30, 32, 33, 36, 39-43, 45, 46, 48, 49, 51, 52, 61, 62, 66, 67, 73, 74, 75–77, 95, 102, 106, 117, 132, 134, 135, 139, 145–148, 151, 152, 155, 156, 163, 164, 171, 172). It is connected to the tegulum via a membrane, usually the same membrane that connects the MA and the E to the tegulum. The TTA commonly terminates in a hook (Figs. 5, 8, 9, 17, 18, 20, 21, 24, 26, 27, 30, 32, 33, 34, 36, 39–42, 46, 48, 52, 54, 95, 102, 145–148) and frequently functions to support the embolus. Based on detailed studies of nesticids (Huber 1993), it is likely that the TTA in theridiids interacts closely with the epigynum during copulation. Usually the TTA has a rugose surface at or near its tip, which may help to stabilize its interaction with the epigynum.

Many names have been applied to the TTA in theridiids; "radix" (e.g., Levi & Levi 1962, figs. 185, 197, 303), "conductor" (Levi 1963d, p. 43, fig. 44), "tegular apophysis" and "conductor B" (Saaristo 1978, p. 119, fig. 194), "median apophysis" (e.g., Coddington 1990, p. 41, fig. 76), "tegular apophysis II" (e.g., Knoflach 1996a, p. 143, fig. 13), and "accessory apophysis" (Levy 1998, p. 33, fig. 48) to name a few.

Despite this confusing nomenclature, in some cases reflecting mistaken homologies, some previous authors have arrived at the same concept that we present here as the TTA. Levi applied the term "radix" very consistently to this sclerite (with exceptions mentioned above) in his many treatments on theridiids, and Knoflach (1991–2002; Knoflach & van Harten 2000, 2001; Knoflach & Thaler 2000; Knoflach & Pfaller 2004) and coauthors have consistently used the term "tegular apophysis II" for it.

Extra tegular apophysis: The spintharines *Episinus* and *Thwaitesia* have palps that are considerably more complex than those of most other theridiids. The C in these taxa is a huge and complex sclerite (note in *Spintharus* the C is also huge and of similar shape; both resemble the C in *Selkirkiella*), and near its distal tip there is an additional tegular apophysis (Figs. 22–25), absent in most other theridiids (but see below). This small, but strongly sclerotized, pointed sclerite, connects to the tegulum via a membrane, and is Knoflach's (1993b, p. 362, fig. 10) "TA3" or tegular apophysis III. This sclerite appears not to be labeled in any of Levi's treatments of these genera.

Similarly, some species of the genera *Enoplognatha* and many other pholcommatines, and of *Neottiura*, have a tegular apophysis, in addition to the MA, TTA, C and E. This apophysis is closely associated with the TTA and is connected to the tegulum in the same manner (Figs. 74, 77, 134–137). Although topologically similar, it seems that the additional tegular apophysis has arisen more than once

across theridiid taxa, and is not homologous. However, this optimization may change as further taxa are added; meanwhile we here label it neutrally as the ''extra tegular apophysis.''

Embolus: The E is simply ''the organ through which the ejaculatory duct opens'' (Comstock 1910, p. 173). The E of different groups of spiders can be quite different; for example, it is an outgrowth of the tegulum in *Nesticus* (Fig. 198) and *Synotaxus* (Figs. 189–190, 197), but a free sclerite connected to the tegulum via a membrane in theridiids. (In this case, the sperm duct travels through the membrane between the tegulum and the embolus). Even within theridiids, the E is extremely variable (Figs. 4, 5, 9–12, 15, 17, 20, 22, 25, 26, 29, 30, 32, 33, 34, 39–41, 44–46, 49, 50, 52, 54, 58, 59, 61, 63, 66–69, 76, 77, 82, 83, 85, 89–92, 95, 96, 98, 100, 101, 103–110, 114–123, 125–128, 130, 131, 137, 143, 148–150, 153, 154, 156, 158–160, 165, 166, 169, 193, 194, 200). The E may be split along some or most of its length, as is the case in many *Anelosimus*, (Fig. 54), or it may be split transversally (or fuse to the MA) as in *Achaearanea tepidariorum* (Figs. 109, 119, 121–123, 125–128). In *Achaearanea* spp., the actual extent of the E is problematic. Two alternative interpretations are possible: 1) MA is absent in some species, and the E contains a suture, or 2), the MA has fused to the E. The former is an attractive interpretation in some closely related species, such as *A. wau*, where there is no trace of a MA and the E (which is not split in any way) interacts in the CB-lock. The alternative interpretation would be fusion of the MA to the E in those taxa; both hypotheses could be tested with ontogenetic and phylogenetic data. *Theonoe* is somewhat similar (Figs. 96–98), although apparently the embolus and median apophysis are simply closely associated because the MA clearly contains a loop of the sperm duct, as in related taxa. A remarkable type of E is found in *Stemmops* sp. where the extremely long coiling tip does not contain the sperm duct. Rather it exits through an apophysis that shares a membranous base with the more typical embolus (Agnarsson 2004).

Embolic division b: The E in some *Anelosimus*, is distinctly bipartite and divided into the E spiral and embolic division b (Fig. 54), or Eb (terminology from Levi 1956). The Eb often closely follows and may support, the E. The embolic division b is variable in size, degree of sclerotization, orientation, and rugosity. It is here not considered a potential homolog of other embolic apophyses (following Agnarsson 2006b, and Agnarsson & Kuntner 2005), because it is dissimilar and distinct in topology (branching off the embolus spiral, rather than off the embolus base), and presumably in function.

Embolic sclerite: In several species of *Steatoda*, a unique sclerite is attached by membrane to the E base (Fig. 17). We have not seen this sclerite in any other theridiids, but suggest the name embolic sclerite for it.

Embolic apophysis: The E of several theridiids bears a small apophysis (Figs. 28, 29, 59, 60, 105, 116, 117) here labeled embolic apophysis (see also Agnarsson 2004).

CONCLUSIONS

We have reviewed the morphology of the male palpal organ in theridiid spiders and relatives through extensive illustrations and literature review. Using a recently proposed method to evaluate primary homology hypotheses we arrive at a scheme of palpal homology hypotheses for theridiid spiders that is more coherent and congruent than prior attempts. In theridiids, topology—that is to say the relative position of sclerites—seems to be the most reliable criterion to recognize homologous sclerites that differ in various ways such as function, shape, texture, etc., across taxa.

Under this homology scheme, the three most problematic sclerites in the theridiid palp, the median apophysis, the conductor and the theridioid tegular apophysis, can be characterized as follows (left palp, ventral view). The median apophysis is positioned retrolaterally on the mesal side of the tegulum, to which it attaches via a membrane. When present, the MA interacts with the cymbium in the cymbial lock system, and, remarkably, it contains a loop of the sperm duct in basal theridiids. The conductor is positioned close to, but slightly ectal to, the embolus. It is a direct and immovable outgrowth of the tegulum, but can be either membranous or sclerotized and may or may not function to conduct the embolus. The theridiid tegular apophysis is positioned in between the embolus and the median apophysis, caudal to both the embolus and

conductor. It is connected to the tegulum by a membrane, and may or may not conduct the embolus.

All the tegular sclerites provide a number of important characters for phylogenetic analyses, as do various other palpal features such as alveolus position, the cymbial lock system, cymbial and tibial shapes, the sperm duct trajectory, and tibial trichobothrial number and distributions (Fig. 3; see also Agnarsson 2004).

We test a number of hypotheses regarding both homology and evolution of theridiid palpal elements. Two of the more detailed hypotheses are refuted. First, both phylogenetic evidence and the novel homology method refute homology of the basal araneoid paracymbium with the distal theridiid cymbial process (hook or hood). Phylogenetically a hypothesized ''transformation'' between the two structures is contradicted by the placement of supposedly ''intermediate'' state taxa (e.g., *Robertus* and *Carniella*) well within Theridiidae, leaving the condition in basal theridiids very dissimilar to that of the outgroups. Putative homology is also refuted by every similarity criterion as the theridiid cymbial process differs from the paracymbium in topology, detailed similarity, and function. Second, Saaristo's (1978) hypothesis that theridiids comprise two main ''evolutionary lines'' defined by the type of cymbial lock present (his non-homologous locking systems A or B) is also refuted. The two locking mechanisms are instead homologs because the hooked cymbium is primitive, and the hooded cymbium is derived. Thus at least one (and perhaps both) of Saaristo's lineages must be paraphyletic; phylogenetically it is more parsimonious to presume that locking system B is locking system A transformed. Homology criteria also support this transformation view as the cymbial hook and hood share topological and functional similarities.

Our results also show that broad homology hypotheses are especially problematic in the absence of a phylogeny. On the other hand, phylogenetic analysis requires primary homologies, which, if incorrect, cannot be corrected by phylogenetic analysis. We address this ''chicken and egg'' problem by proposing a procedure that critically compares primary homology hypotheses prior to analysis in order to minimize conflict between classical homology criteria such as topology, function, and special similarity. The method, of course, is not completely independent of phylogeny but rather embedded in the larger context of phylogenetically-based comparative morphology, but in this case it did clarify errors in homology and homoplasy at the ''local'' phylogenetic level that conventional analysis would have missed. Homology can be effectively tested, not only during phylogenetic analysis, but also prior to it. Both kinds of tests may be helpful whenever character identity (i.e., primary homology) is in doubt.

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Appendix A – Abbreviations

BC	bulb-cymbium lock mechanism
BH	basal haematodocha
C	conductor
CA	cymbial apophysis
Cb	conductor base
CHd	theridiid cymbial hood
CHk	theridiid cymbial hook
Cy	cymbium
E	embolus
EA	embolic apophysis
Eb	embolic division b
ES	embolic sclerite
ETS	extra tegular sclerite
MA	median apophysis
MH	median haematodocha
PC	paracymbium
SC	subconductor
ST	subtegulum
T	tegulum
Tp	tegular pit
TTA	theridiid tegular apophysis

Appendix B – Material Examined (deposited in the CTh Collection Thaler & Knoflach)

For additional material examined, see Agnarsson (2004).

Achaearanea lunata (Clerck 1757). Austria, Northern Tyrol, Innsbruck, Hötting, 15 May 1992, leg. Knoflach.

Achaearanea riparia (Blackwall 1834). Italy, Treviso, Quartier del Piave, Palu, pitfall trap, 1989/1990, leg. Targa.

Crustulina guttata (Wider 1834). Austria, Northern Tyrol, Ötztal, Längenfeld, 14 April 1992, leg. Knoflach.

Dipoena melanogaster (C.L. Koch 1837). Austria, Northern Tyrol, Innsbruck, Hötting, 15 May 1992, leg. Knoflach.

Enoplognatha latimana Hippa and Oksala 1982. Austria, Burgenland, Parndorf, 1988, leg. Thaler, Meyer, Steinberger.

Enoplognatha ovata (Clerck 1757). Austria, Northern Tyrol, Innsbruck, Martinswand, 3 August 1991, leg. Knoflach. Telfs, Zimmerberg, 17 July 1991, leg. Bertrandi. Ötztal Bahnhof, Forchet, 16 May 1992, leg. Knoflach. Kufstein, Langkampfen, tree eclector, 28 June–23 July 1988, leg. Thaler, Meyer, Steinberger.

Enoplognatha thoracica (Hahn 1833). Italy, Veneto, Treviso, pitfall trap, 1990–1991, leg. Schiroto, Paletti.

Episinus angulatus (Blackwall 1836). Austria, Northern Tyrol, Innsbruck, Kranebitten, 12 July 1991, leg. Knoflach.

Episinus theridioides Simon 1873. France, Corsica, Col de Vizzavona, 1100–1400 m, 1 October 1974, leg. Thaler.

Episinus truncatus Latreille 1809. Austria, Northern Tyrol, Innsbruck, Kranebitten, 20 July 1991, leg. Knoflach.

Euryopis flavomaculata (C.L. Koch 1836). Austria, Vienna, Lobau, 19 May–2 June 1972, leg. Steiner.

Keijia tincta (Walckenaer 1802). Austria, Northern Tyrol, Innsbruck, Kranebitten, 10 May 1991, leg. Knoflach.

Kochiura aulica (C.L. Koch 1838). Croatia, Rovinj, 29 July–26 August 1965, leg. Thaler.

Lasaeola tristis (Hahn 1833). Austria, Northern Tyrol, Ötztal, Sautener Forchet, 26 June 1992, leg. Bertrandi.

Neottiura bimaculata (Linné 1767). Austria, Northern Tyrol, Innsbruck, Kranebitten, 23 June 1991, leg. Knoflach.

Pholcomma gibbum (Westring 1851). Austria, Northern Tyrol, Innsbruck surroundings, Halltal, 13 June 1992, leg. Thaler.

Robertus neglectus (O. Pickard-Cambridge 1871). Italy, Veneto, Treviso, Riese, pitfall trap 1990–1991, leg. Schiroto, Paoletti. Germany, near Immendingen, Zimmern, leg. Wunderlich 1973.

Robertus scoticus Jackson 1914. Austria, Carinthia, Großglockner 1700 m, pitfall trap, 1978, leg. Thaler.

Robertus ungulatus Vogelsanger 1944. Austria, Northern Tyrol, Innsbruck surroundings, Lanser Moor, fen, pitfall trap, 14 May–18 September 1963, leg. Thaler.

Rugathodes bellicosus (Simon 1873). Austria, Northern Tyrol, Obergurgl, 2600 m, 26 June 1992, leg. Thaler.

Simitidion simile (C.L. Koch 1836). Italy, Trentino, Civezzano, 30 April 1990, leg. Foddai.

Steatoda bipunctata (Linné 1758). Austria, Northern Tyrol, Innsbruck, Hötting, November 1992, leg. Knoflach.

Steatoda triangulosa (Walckenaer 1802). Italy, Toscana, Grosseto, Castiglione, 8 June 1987, leg. Thaler.

Theonoe minutissima (O. Pickard-Cambridge 1879). Germany, Kempten, Schorenmoos, 15 December 1974–17 May 1975, leg. Mendl.

Theridion conigerum Simon 1914. Germany, Oberharz, Ilsenhütte, June 1972, Staatliches Museum für Tierkunde Dresden, leg. Heimer.

Theridion nigrovariegatum Simon 1873. Switzerland, Unterengadin, Ramosch, 12 July 1987, leg. Thaler.

Theridion ohlerti (Thorell 1870). Austria, Northern Tyrol, Kühtai, 2200 m, 18 June 1992, leg. Bertrandi.

Theridion petraeum L. Koch 1872. Austria, Northern Tyrol, Innsbruck surroundings, Patscher-kofel, 2200 m, 7 July 1991, leg. Knoflach.

Theridion pictum (Walckenaer 1802). Austria, Northern Tyrol, Innsbruck West, university surroundings, 14 May 1992, leg. Knoflach.

Theridion pinastri L. Koch 1872. Austria, Northern Tyrol, Ötztal, Sautener Forchet, 26 June 1992, leg. Bertrandi.

Theridion sisyphium (Clerck 1757). Austria, Northern Tyrol, Innsbruck surroundings, Gnadenwald, 11 June 1991, leg. Bertrandi.

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